

GR Letter

Microbially induced sedimentary structures in Archean sandstones: A new window into early life

Nora Noffke*

Old Dominion University; Department of Ocean, Earth and Atmospheric Sciences; Norfolk, VA 23529, USA

Received 14 June 2006; received in revised form 30 September 2006; accepted 4 October 2006

Available online 5 December 2006

Abstract

Until now, the most valuable information on the early life on the Archean Earth derived from bacterial fossils and stromatolites preserved in precipitated lithologies such as chert or carbonates. Also, shales contain complex biomarker molecules, and specific isotopes constitute an important evidence for biogenicity.

In contrast, because of their low potential of fossil preservation, sandstones have been less investigated. But recent studies revealed a variety of ‘microbially induced sedimentary structures — MISS’ that differ greatly from any other fossils or sedimentary structures. ‘Wrinkle structures’, ‘multidirected ripple marks’, ‘biolaminites’, and other macrostructures indicate the former presence of photoautotrophic microbial mats in shallow-marine to tidal paleoenvironments. The MISS form by the mechanical interaction of microbial mats with physical sediment dynamics that is the erosion and deposition by water agitation. The structures occur not only in Archean tidal flats, but in equivalent settings throughout Earth history until today.

MISS are not identified alone by their macroscopic morphologies. In thin-sections, the structures display the carpet-like fabrics of intertwined filaments of the ancient mat-constructing microorganisms. Geochemical analyses of the filaments proof their composition of iron minerals associated with organic carbon.

In conclusion, microbial mats colonize sandy tidal settings at least for 3.2 Ga years. Therefore, Archean sandstones constitute an important archive for the exploration of early life.

© 2006 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.

Keywords: Microbial mat; Archean; Tidal flats; MISS; Early life

1. Introduction

It is an intriguing task to reconstruct life in the Archean, the oldest time period of Earth recorded in rocks. One reason is that during the past 3.8–2.5 billion years and beyond, a multitude of diagenetic and tectonic processes may have altered any primary lithological features. Despite the great loss of information due to taphonomic processes, some geological windows remained that permit insight into Earth’s earliest worlds.

In carbonate and cherts, rapid syndimentary mineral precipitation and early cementation preserved tiny fossils of filigrane bacteria, or lead to the formation of sturdy, stromatolitic build-ups (e.g., Walter, 1976; Lowe, 1980; Awramik, 1984;

Buick, 1992; Hofmann et al., 1999; Grotzinger and Knoll, 1999; Schopf et al., 2002; Brasier et al., 2002; Tice and Lowe, 2004; Allwood et al., 2006). In black shales, complex biomolecules are finely distributed, where they have been protected against degradation by heterotrophic microorganisms or by oxygenation (e.g., Brocks et al., 1999). Isotope signals support the evidence of ancient organic matter in the Archean material (e.g., Shen et al., 2001; Knoll, 2003; Strauss, 2003; Faure and Mensing, 2004).

In contrast to precipitated or fine-grained lithologies, siliciclastic deposits are rarely sites of good fossil preservation. Therefore, the expectation to find fossils of tiny bacteria in siliciclastic rock successions especially of very old ages has been low, and such deposits have been far less examined. Now, studies detected biosignatures of Archean ages in sandy deposits as well (Noffke et al., 2003b, 2006a,b). The studies document biogene sedimentary structures that strongly suggest the occurrence of photoautotrophic microbial mats in tidal

* Fax: +1 757 683 5303.

E-mail address: nnoffke@odu.edu.

habitats from the Archean to today. Therefore, also sandstones provide a valuable window for the understanding of early life on Earth.

This review gives a brief summary about the biogenic sedimentary structures in siliciclastic deposits, and discusses their significance for the reconstruction of the Archean Earth.

2. Microbially induced sedimentary structures — MISS

In contrast to cherts, carbonates and shales, sandstones display biogenic sedimentary structures that resemble neither body fossils, nor stromatolites. Those unusual sedimentary structures in sandy deposits show a great variety of geometries and morphologies, and size ranges of meter to millimeter scales. Characteristic examples include ‘petees’ (Gehling, 1982), ‘Arumberia’ (Bland, 1984), ‘old elephant skin structures’ (e.g., Runnegar and Fedonkin, 1992; Gehling, 1999, 2000), ‘sand chips’ (Pflueger and Gresse, 1996); ‘wrinkle structures’ (Hagadorn and Bottjer, 1997); ‘multidirected ripple marks’ (Noffke, 1998), ‘erosional remnants and pockets’ (Noffke, 1999); ‘roll-up structures’ (Schieber, 1999; Simonson and Carney, 1999), ‘mat cracks’ (Parizot et al., 2005), compare also the overviews in Noffke et al., 2001b, 2003a, or Schieber, 2004. Those ‘microbially induced sedimentary structures — MISS’ do not arise from chemical processes, but from the biotic-physical interaction of microbial mats with the sedimentary dynamics of aquatic environments (overview in Noffke et al., 2003a). Because of their unique biotic-physical modes of formations and their so different appearances, MISS were placed as own category in the Classification of Primary Sedimentary Structures *sensu* Pettijohn and Potter 1964 (Noffke et al., 2001b, 2003a).

Especially valuable are MISS for the analyses of early Archean (and extraterrestrial) deposits (Noffke et al., 2003b; 2006a,b). The reason is that whereas the chemical conditions of marine and atmospheric environments might have changed in course of the past billions of years, the physical laws of nature must have remained the same. Therefore, actualistic studies on the biotic-physical interactions of microbial mats with the sediment dynamics are key also for the understanding of the strange Archean (or extraterrestrial) worlds. Oversimplified, modern microbial mats in tidal settings serve as an analogue to ancient (or extraterrestrial) micro-epibenthos.

3. Modern MISS and their formations

The first examples of MISS have been described in modern tidal flats of Mellum, an island situated at the North Sea coast of Germany (e.g., Gerdes and Krumbein, 1987; Gerdes et al., 1993; Noffke et al., 1996; Gerdes et al., 2000). Here, microbial mats composed of cyanobacteria overgrow quartz-rich sands of fine sand sizes (Stal et al., 1985; Gerdes and Krumbein, 1987; Noffke and Krumbein, 1999; Stal, 2000). The dominant microbial mat builder is *Microcoleus chthonoplastes*, which prefers to colonize the lower supratidal zone. This tidal zone is typically inundated by sea water only during the spring high tides or during strong landward winds. *M. chthonoplastes* is

well adapted to the long lasting periods of subaerial exposure of the tidal surface. Its ubiquitous ‘extracellular polymeric substances — EPS’ protect the filaments of this cyanobacterium against desiccation or osmotic pressure. EPS are polysaccharides that, simply put, form a slimy mass which the bacterial cells are embedded (Decho, 1990). Towards the intertidal zone, another cyanobacterial species becomes abundant: *Oscillatoria limosa*. The trichomes (single filaments) of *O. limosa* are highly mobile thus being able to move quickly through the sediments. Because the intertidal zone is reworked with every flood current, this high motility is of great advantage for this cyanobacterium (Villbrandt, 1992).

A tidal flat is an extreme environment, because strong flood currents or storm waves rework the sediments significantly. The microbial mats are well adapted to those conditions. They stabilize their substrata by forming a dense and coherent network of entangled filaments that interweave the mineral grains of the depositional surface. In addition, their EPS smoothens the mat surface thus reducing the frictional forces of a current passing the sea floor. This microbial sediment fixation has been termed ‘biostabilization’ (Paterson, 1994). Measurements on the erosion stability of microbial mat-overgrown tidal flats document biostabilization values of 3 (*O. limosa*) –12

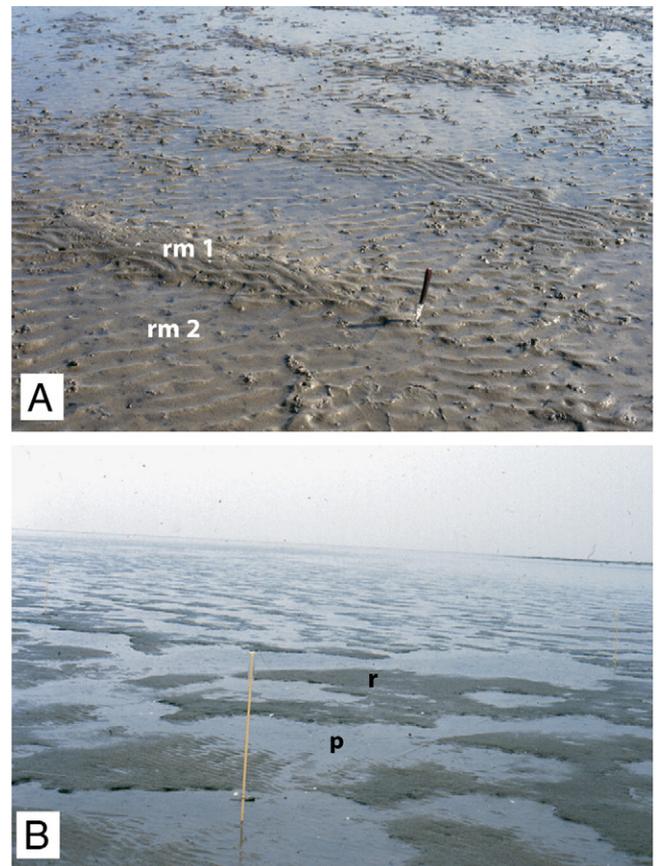


Fig. 1. Modern microbially induced sedimentary structures (MISS) from sandy tidal flats, island of Mellum, North Sea. A: Multidirected ripple marks; rm 1 indicates the first generation of ripple marks, rm 2 is the second one; scale: 20 cm (after: Noffke, 2003a); Erosional remnants and pockets; r indicates an erosional remnant, p indicates an erosional pocket; scale 1 m.

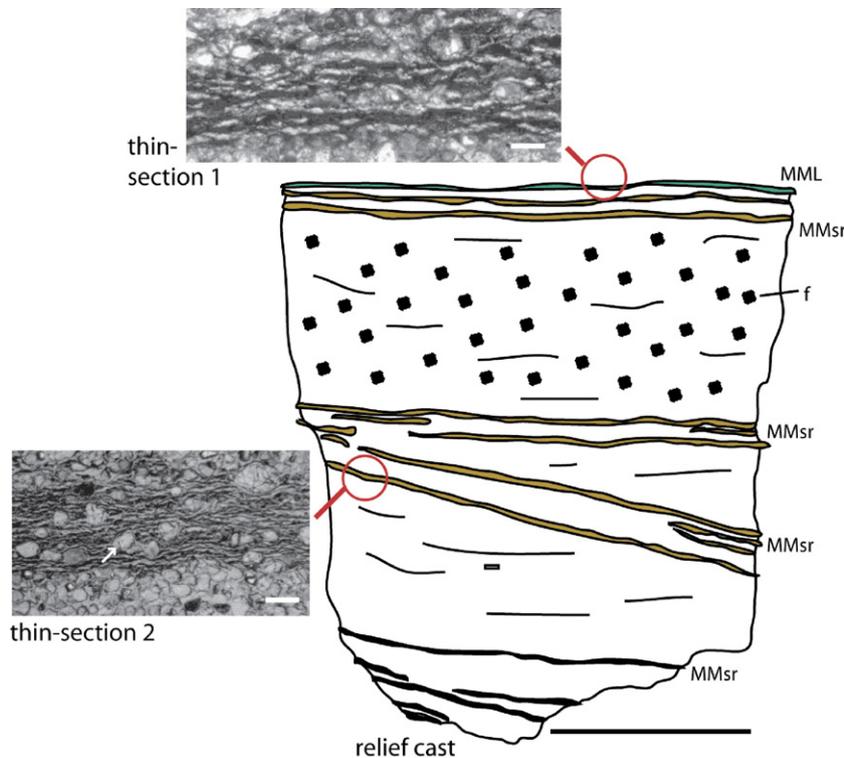


Fig. 2. Intra-sedimentary MISS visible in a relief cast from sandy tidal flats of the island of Mellum, North Sea. Relief casts are artificially resin-hardened sediment cores that display internal structures in three dimensions. MML=living microbial mat atop the deposits; MMsr=subrecent, now buried and decaying microbial mat layers; f=pores (fenestrae) in the sandy interlayers; scale: 5 cm. The close-ups show the filaments of cyanobacteria constructing a carpet-like mat fabrics (1), and a texture of oriented grains (arrow) within a mat layer (2); scales: 0.2 mm.

times higher (*M. chthonoplastes*) compared to the values of loose sands (Villbrandt, 1992; Yallop et al., 1994). If buried by sand, the cyanobacteria quickly migrate upward towards the new sedimentary surface, where they establish a new mat fabrics. This ‘baffling, trapping and binding’ has also been well studied in the formation of modern carbonate stromatolites (e.g., Reid et al., 2000). The different reactions of the microbial mats to erosion or deposition of sediment causes ‘traces’ in or on the sediments, the MISS. This will be elucidated with two examples of MISS, ‘multidirected ripple marks’, and ‘erosional remnants and pockets’.

Multidirected ripple marks (Noffke, 1998) are patterns of ripple marks of various directions that cover large areas of the upper intertidal to lower supratidal zones, Fig. 1A. This ripple pattern arises from a set of subsequent storms that each forms a generation of ripple marks. During the periods in between the storm events, the newly formed ripple marks are overgrown and biostabilized by microbial mats, and thus cannot be reworked by the later events. Multidirected ripple marks form during the growth season during the summer, and are typical feature of tidal flats in fall (Noffke, 1998).

‘Erosional remnants and pockets’ is another example of MISS (Fig. 1B). It is a tidal surface morphology composed in patches of two elements: (i) elevated, mat-covered surface portions, and, (ii) deeper, ripple-marked and non-colonized surface areas. This morphology evolves, if a microbial mat cover is locally destroyed so that the bare sand is exposed. At

those spots, the bottom currents remove the sands, and undermine the microbial mats. Over time, the spots widen, and ‘erosional pockets’ of up to several meters extension form (Gerdes et al., 1993; Noffke, 1999).

Also internal sedimentary structures belong to the group of MISS. They are visible in sediment cores which have been artificially hardened by resin. In such a ‘relief cast’ displaying vertical sections of tidal deposits, mm-thick, microbial mat laminae are visible that alternate with sandy interlayers, Fig. 2. Such laminated patterns are termed ‘biolaminites’ (Gerdes et al., 1991). The sandy interlayers often include pores, secondarily formed by the pressure of gas entrapped underneath the sediment-forming mat layers. In carbonate rocks, such pores are known as fenestrae structures. Sometimes, the gas pressure lifts up the microbial mat, and local upheavals form, cm-high dome-shaped elevations. Those are located mainly along the mean high water line, and are termed ‘gasdomes’ (e.g., Gerdes et al., 1993).

In close view with high magnification, the mat laminae display their carpet-like fabrics composed of intertwined filaments and trichomes of cyanobacteria. A very characteristic microscopic texture within microbial mat layers are also ‘oriented grains’. This texture provides in fossil deposits a clear signal on ancient microbial presence (Noffke et al., 1997a, 2006b). Oriented grains are single particles that originally derived from the substrate underneath a microbial mat. The initial biofilm that in microscopic scale covered the sand grains of a sedimentary surface grows over time. By this development

of a thicker and thicker organic envelope, the grains become pushed upward until they are embedded in an organic matrix without contact to each other. Sometimes, their long-axes are oriented parallel to the sedimentary surface that is the particles rotate due to loading pressure.

4. Examples for MISS of Archean age, and their interpretation

MISS have been detected in sandstones of nearly all Earth ages, and independently of silicified microfossils and stromatolites provide a different perspective for the interpretation of Archean or extraterrestrial deposits. MISS-bearing sandstones occur in the 3.2 Ga Moodies Group (Noffke et al., 2006a), and the 2.9 Ga old Pongola and Witwatersrand Supergroups, South Africa (Noffke et al., 2003b, 2006b).

The most common fossil MISS are ‘wrinkle structures’ (Fig. 3A). These are upper bedding planes covered by wrinkles of mm to sub-mm heights and distances. Wrinkle structures represent ancient microbial mats that are preserved *in situ* (Hagadorn and Bottjer, 1997; Noffke, 2000; taphonomy in Noffke et al., 2002).

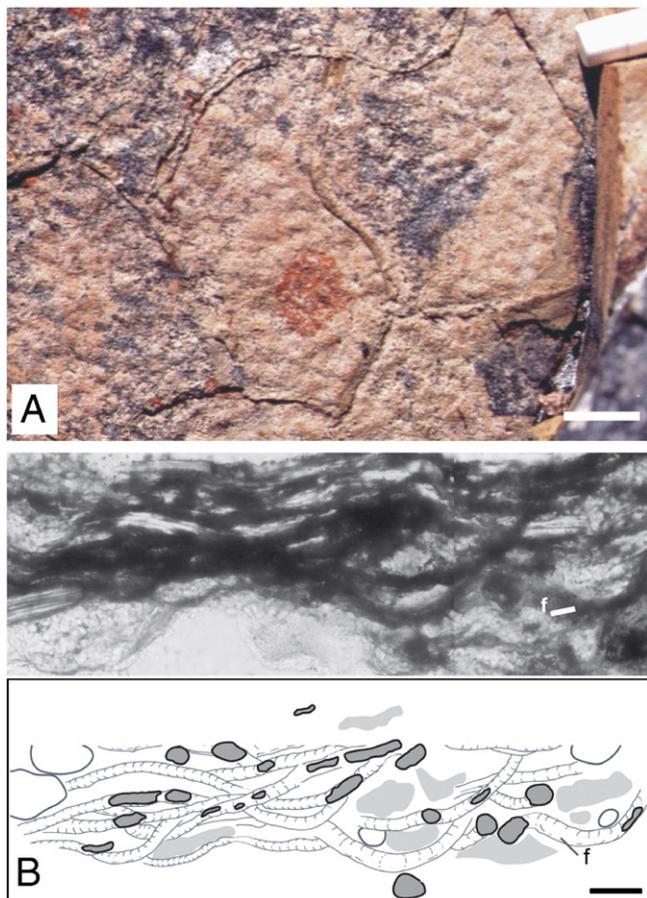


Fig. 3. Fossil MISS: Wrinkle structure from the 3.2 Ga Moodies Group, South Africa; scale 2 cm (from: Noffke et al., 2006b). The structure is covered by syaeresis cracks. B: Filamentous textures preserved in sandstones of the 2.9 Ga old Mozaan Group, Pongola Supergroup, South Africa; above a photo of a thin-section perpendicular through an ancient mat layer (f=fossil filament); below a sketch of the filaments visible in this thin-section; scale 100 μ m (after: Noffke et al., 2003b).

In close view on vertical thin-sections, wrinkle structures contain microbial mat laminae (Fig. 3B). Such fossil mat laminae are an important diagnostic tool to differentiate biogenic wrinkle structures from similar, but abiogenic features. The mat laminae are wavy crinkled, and dark brown coloured. Mostly, the laminae are undisturbed (Fig. 2). That is during the placement of sediment on top of the microbial mats, syndepositional erosion could not destroy the coherent mat layer, and cannibalism of the sediment underneath the microbial mat did not occur. In consequence, MISS-bearing sandstone beds are rarely amalgamated (Noffke et al., 1997a; Noffke, 2003c). The microstructures are almost identical to that of the trichomes and filaments of modern cyanobacteria.

Wrinkle structures result from the burial of microbial mats by freshly deposited sand. The load pressure squeezes water out of the organic layers, and early diagenetic processes induce the preservation of the microbial mat layers. In the lithification of the mat layers, heterotrophic bacteria play a major role (e.g., Krumbein, 1979a; Schulze-Lam et al., 1996; Beveridge, 1989). They decompose and mineralize the organic matter of the filaments and trichomes. The resulting chemical compounds eventually react with ions from the surrounding seawater, and initial, amorphous gels are formed. Later those gels crystallize to form e.g., aragonite, tenorite (the precursor of pyrite), or other minerals such as iron oxides and iron hydroxides. That is those minerals replaced the organic matter of the filaments and trichomes.

Such as in similar lithologies of younger Earth ages, the wrinkle structures of the Moodies Group, and the Pongola and Witwatersrand Supergroups, correlate with shallow shelf and tidal areas. The structures are especially frequent in regression–transgression cycles (Noffke et al., 2006a), Fig. 4. That is that as soon as the ancient sea level rose, large shallow-marine areas developed, shelves widened, and tidal flats formed. Those shallow areas with warm and only moderately agitated water obviously provided excellent ecological conditions for thriving microbial mats. This correlation between a rising sea level and in increased microbial mat development we can observe today along the coasts of the North Atlantic. The Holocene transgression lead to wide tidal flats that nowadays are widely overgrown by extensive microbial mats.

The distribution of fossil MISS in ancient shallow water areas suggests that the former microbial mats most probably have been constructed by photoautotrophic bacteria, maybe cyanobacteria (Noffke et al., 2003, 2006b). The bacteria or cyanobacteria enriched oxygen in the Archean atmosphere until today. In consequence, the atmosphere of early Earth might have been less reducing than sometimes assumed (Ohmoto, 2004). If the filament-like textures indeed represent ancient cyanobacteria or not, is debated (discussion Brasier et al., 2002; Schopf et al., 2002; Tice and Lowe, 2004). Clearly, the final proof of the presence of cyanobacteria in the Archean must still be made.

In conclusion, the large volume of sandstones in Archean lithologies constitute a valuable archive for the exploration of ancient life, and for the life detection on other planets such as Mars. Future research will continue to study this new chapter of Earth’s oldest fossil record.

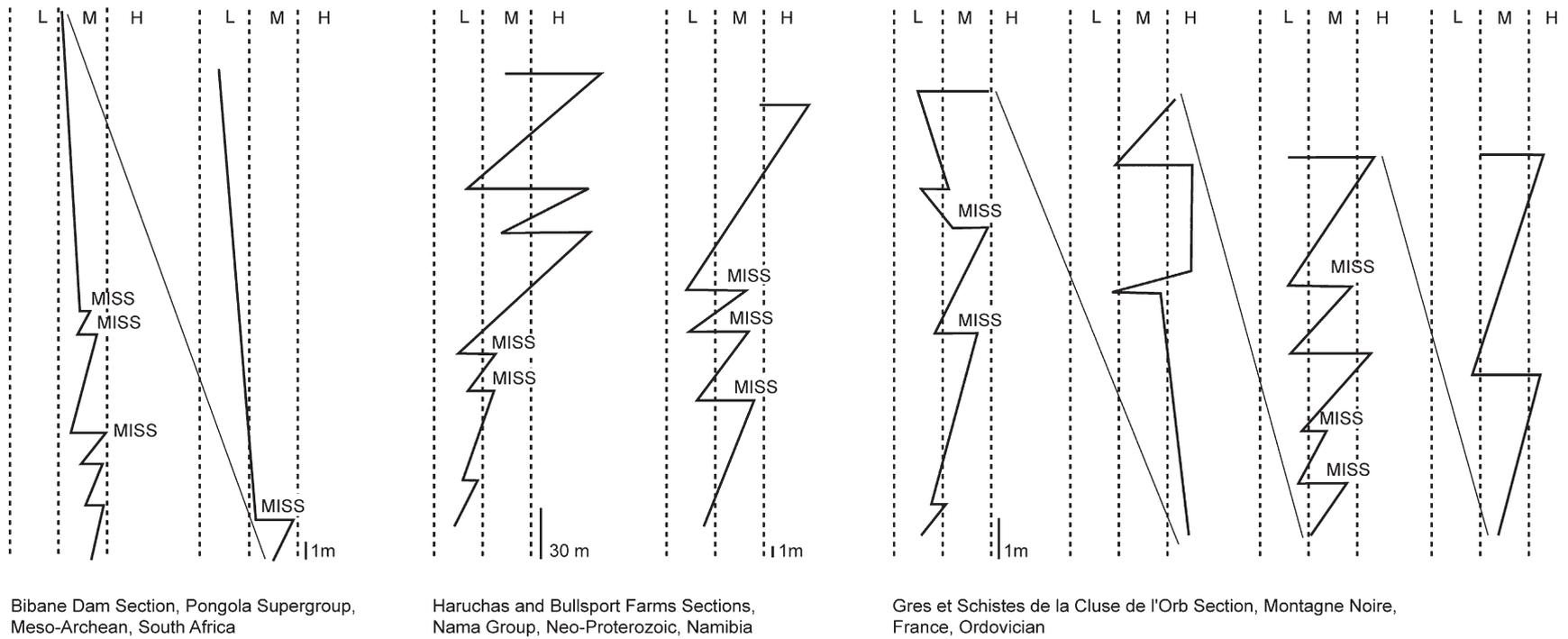


Fig. 4. Stratigraphic sections of various Earth ages show that fossil MISS occur especially at turning points between regression and transgression (from: Noffke et al., 2006b). Today, we can observe extensive microbial mats along the coast of the North Atlantic. Here, tidal flats did form in course of the Holocene transgression, and now provide favourable conditions for thriving microbial mats.

Acknowledgements

The studies on modern and ancient microbial mats have been funded by the NASA Mars Fundamental Research and Exobiology Programs, the NSF Geology–Paleontology Program, and an Old Dominion University Summer Research Grant.

References

- Allwood, A., Walter, M.R., Kamber, B.S., Marshall, C.P., Burch, I.W., 2006. Stromatolite reef from the early Archean are of Australia. *Nature* 441, 714.
- Awramik, S.M., 1984. Ancient stromatolites and microbial mats. In: Cohen, Y., Castenholz, R.W., Halvorson, H.O. (Eds.), *Microbial mats: stromatolites*. Alan R. Liss, New York, pp. 1–22.
- Beveridge, T.J., 1989. Role of cellular design in bacterial metal accumulation and mineralization. *Annual Reviews Microbiology* 43, 147–171.
- Bland, B.H., 1984. *Arumberia* Glaessner and Walter, a review of its potential for correlation in the region of the Precambrian Cambrian boundary. *Geological Magazine* 121, 625–633.
- Brasier, M.D., Green, O.R., Jephcoat, A.P., Kleppe, A.K., Van Kranendonk, M.J., Lindsay, J.F., Steele, A., Grasslmeau, M.V., 2002. Questioning the evidence for Earth's oldest fossils. *Nature* 416, 76–91.
- Brocks, J.J., Logan, G.A., Buick, R., Summons, E.E., 1999. Archean molecular fossils and the early rise of eukaryotes. *Science* 285, 1033–1036.
- Buick, R., 1992. The antiquity of oxygenic photosynthesis: evidence from stromatolites in sulfate-deficient Archean lakes. *Science* 255, 74–77.
- Decho, A.W., 1990. Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. *Oceanographic and Marine Biology. Annual Review* 28, 73–154.
- Faure, G., Mensing, T.A., 2004. *Isotopes: Principles and Applications*, 3rd ed. John Wiley, New York. 897 p.
- Gehling, J.G., 1982. The sedimentology and stratigraphy of the Precambrian Pound Subgroup, Central Flinders Ranges, South Australia. MSc Dissertation, University of Adelaide, 112p.
- Gehling, J.G., 1999. Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. In: Hagadorn, J.W., Pflueger, F., Bottjer, D.J. (Eds.), *Unexplored microbial worlds*, *Palaios*, vol. 14, pp. 40–57.
- Gehling, J.G., 2000. Environmental interpretation and a sequence stratigraphic framework for the terminal Proterozoic Ediacara member within the Rawnsley Quartzite, South Australia. *Precambrian Research* 100, 65–95.
- Gerdes, G., Krumbein, W.E., 1987. *Biolaminated Deposits*. Springer–Verlag, Berlin. 183 p.
- Gerdes, G., Krumbein, W.E., Reineck, H.E., 1991. Biolaminations — ecological versus depositional dynamics. In: Einsele, G., Ricken, W., Seilacher, A. (Eds.), *Cycles and events in stratigraphy*. Springer, Berlin, pp. 592–607.
- Gerdes, G., Claes, M., Dunajtschik-Piewak, K., Riege, H., Krumbein, W.E., Reineck, H.E., 1993. Contribution of microbial mats to sedimentary surface structures. *Facies* 29, 61–74.
- Gerdes, G., Noffke, N., Klenke, Th., Krumbein, W.E., 2000. Microbial signatures in peritidal sediments — a catalogue. *Sedimentology* 47, 279–308.
- Grotzinger, J.P., Knoll, A.H., 1999. Stromatolites in Precambrian carbonates: evolutionary mileposts or environmental dipsticks? *Annual Review of Earth and Planetary Science* 27, 313–358.
- Hagadorn, J.W., Bottjer, D.J., 1997. Wrinkle structures: microbially mediated sedimentary structures in siliciclastic settings at the Proterozoic–Phanerozoic transition. *Geology* 25, 1047–1050.
- Hofmann, H.J., Grey, K., Hickman, A.H., Thorpe, R.I., 1999. Origin of 3.45 Ga coniform stromatolites in the Warawoona Group, Western Australia. *Geological Society of America Bulletin* 111, 1256–1262.
- Knoll, A.H., 2003. *Life on a Young Planet*. Princeton University Press, Princeton. 378p.
- Krumbein, W.E., 1979a. Photolithotrophic and chemoorganotrophic activity of bacteria and algae as related to beachrock formation and degradation (Gulf of Aquaba, Sinai). *Geomicrobiology Journal* 1, 156–202.
- Lowe, D., 1980. Stromatolites 3400 Myr old from the Archean of Western Australia. *Nature* 284, 239–283.
- Noffke, N., 1998. Multidirected ripple marks rising from biological and sedimentological processes in modern lower supratidal deposits (Mellum Island, southern North Sea). *Geology* 26, 879.
- Noffke, N., 1999. Erosional remnants and pockets evolving from biotic-physical interactions in a Recent lower supratidal environment. *Sedimentary Geology* 123, 175–181.
- Noffke, N., 2000. Extensive microbial mats and their influences on the erosional and depositional dynamics of a siliciclastic cold water environment (lower Arenigian, Montagne Noire, France). *Sedimentary Geology* 136, 207–215.
- Noffke, N., 2003a. Microbially induced sedimentary structures: formation and application to sedimentology. In: Middleton, C. (Ed.), *Encyclopedia of sediments and sedimentary rocks*. Kluwer, Dordrecht, pp. 439–441.
- Noffke, N., 2003c. Epibenthic cyanobacterial communities counteracting sedimentary processes within siliciclastic depositional systems (present and past). In: Paterson, D., Zavarzin, G., Krumbein, W.E. (Eds.), *Biofilms through space and time*, Congress Proceedings. Kluwer, Dordrecht, pp. 265–280.
- Noffke, N., Krumbein, W.E., 1999. A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics. *Sedimentology* 46, 417–426.
- Noffke, N., Gerdes, G., Klenke, Th., Krumbein, W.E., 1996. Microbially induced sedimentary structures — examples from modern sediments of siliciclastic tidal flats. *Zbl. Geol. Paläont., Teil I*, 1995, H.1/2, 307–316.
- Noffke, N., Gerdes, G., Klenke, Th., Krumbein, W.E., 1997a. A microscopic sedimentary succession indicating the presence of microbial mats in siliciclastic tidal flats. *Sedimentary Geology* 110, 1–6.
- Noffke, N., Gerdes, G., Klenke, Th., Krumbein, W.E., 2001b. Microbially induced sedimentary structures — a new category within the classification of primary sedimentary structures. *Journal of Sedimentary Research* 71, 649–656.
- Noffke, N., Knoll, A.H., Grotzinger, J., 2002. Sedimentary controls on the formation and preservation of microbial mats in siliciclastic deposits: a case study from the upper Neoproterozoic Nama Group, Namibia. *Palaios* 17, 1–14.
- Noffke, N., Gerdes, G., Klenke, Th., 2003a. Benthic cyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty and evaporitic carbonatic). *Earth-Science Reviews* 12, 1–14.
- Noffke, N., Hazen, R., Nhlenko, N., 2003b. Earth's earliest microbial mats in a siliciclastic marine environment (Mozaan Group, 2.9 Ga, South Africa). *Geology* 31, 673–676.
- Noffke, N., Beukes, N., Hazen, R., 2006a. Spatial and temporal distribution of microbially induced sedimentary structures: a case study from siliciclastic storm deposits of the 2.9 Ga old Witwatersrand Supergroup, South Africa. *Precambrian Research* 146, 35–44.
- Noffke, N., Hazen, R., Eriksson, K., Simpson, E., 2006b. A new window into early life: microbial mats in a siliciclastic early Archean tidal flat (3.2 Ga Moodies Group, South Africa). *Geology* 34, 253–256.
- Ohmoto, H., 2004. The Archean atmosphere, hydrosphere, and biosphere. In: Eriksson, P.G., et al. (Ed.), *The Precambrian Earth: tempos and events*. Developments in Precambrian geology. Elsevier, Amsterdam, pp. 361–388.
- Paterson, D., 1994. Siliciclastic intertidal microbial sediments. In: Stal, L.J., Caumette, P. (Eds.), *Microbial mats*. Springer, Berlin, pp. 97–109.
- Parizot, M., Eriksson, P.G., Aifa, T., Sarkar, S., Banerjee, S., Catuneanu, O., Altermann, W., Bumby, A.J., Bordy, E.M., vanRooy, J.L., Boshoff, A.J., 2005. Suspected microbial mat-related crack-like sedimentary structures in the Palaeoproterozoic Magaliesberg Formation sandstones, South Africa. *Precambrian Research* 138, 274–296.
- Pflueger, F., 1996. Microbial sand chips — a non-actualistic sedimentary structure. *Sedimentary Geology* 102, 263–274.
- Reid, R.P., Visscher, P.T., Decho, A.W., Stolz, J.F., Bebout, B.M., Dupraz, C., MacIntyre, I.G., Pearl, H.W., Pinckney, J.L., Prufert-Bebout, L., Steppe, T.F., DesMarais, D.J., 2000. The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. *Nature* 406, 989–991.

- Runnegar, B.N., Fedonkin, M.A., 1992. Proterozoic metazoan body fossils. In: Schopf, J.W., Klein, C. (Eds.), *The Proterozoic biosphere, a multidisciplinary study*. Cambridge University Press, New York, pp. 369–387.
- Schopf, J.W., Kudryvtsev, A.B., Agrestl, D.E., Wdowlak, Th.J., Czaja, A.D., 2002. Laser-Raman imagery of Earth's earliest fossils. *Nature* 416, 73–76.
- Schieber, J., 1999. Microbial mats in terrigenous clastics: the challenge of identification in the rock record. In: Hagadorn, J.W., Pflueger, F., Bottjer, D.J. (Eds.), *Unexplored microbial worlds*. *Palaios*, vol. 14, pp. 3–13.
- Schieber, J., 2004. Microbial mats in the siliciclastic rock record: a summary of diagnostic features. In: Eriksson, P.G., Altermann, D.R., Nelson, D.R., Mueller, W.E., Catuneanu, O. (Eds.), *The Precambrian Earth: tempos and events*. Elsevier, Amsterdam, pp. 663–673.
- Schulze-Lam, S., Fortin, D., Davis, B.S., Beveridge, T.J., 1996. Mineralization of bacterial surfaces. *Chemical Geology* 132, 171–181.
- Simonson, B.M., Carney, K.E., 1999. Roll-up structures: evidence of *in situ* microbial mats in Late Archean deep shelf environments. In: Hagadorn, J.W., Pflueger, F., Bottjer, D.J. (Eds.), *Unexplored microbial worlds*. *Palaios*, vol. 14, pp. 13–24.
- Shen, Y., Buick, R., Canfield, D.E., 2001. Isotopic evidence for microbial sulphate reduction in the early Archean era. *Nature* 410, 77–81.
- Stal, L.J., 2000. Cyanobacterial mats and stromatolites. In: Whitton, B.A., Potts, M. (Eds.), *The Ecology of Cyanobacteria*. Kluwer Academic Publishers, Dordrecht, pp. 62–120.
- Stal, L.J., van Gemerden, H., Krumbein, W.E., 1985. Structure and development of a benthic marine microbial mat. *FEMS Microbial Ecology* 31, 111–125.
- Strauss, H., 2003. Sulphur isotopes and the early Archean sulphur cycle. *Precambrian Research* 126, 349–361.
- Tice, M.M., Lowe, D.R., 2004. Photosynthetic microbial mats in the 3.5 Ga old Ocean. *Nature* 431, 549–550.
- Villbrandt, M., 1992. Interactions of nitrogen fixation and photosynthesis in marine cyanobacterial mats (Mellum, southern North Sea), PhD Thesis University of Oldenburg, 153 p.
- Walter, M.R. (Ed.), 1976. *Stromatolites*. *Developments in Sedimentology*, vol. 20. Elsevier, Amsterdam, Oxford, New York. 790 p.
- Yallop, M.L., De Winder, B., Paterson, D.M., Stal, L.J., 1994. Comparative study on primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. *Estuarine, Coastal and Shelf Sciences* 39, 565–582.