Chapter 17

EPIBENTHIC CYANOBACTERIAL COMMUNITIES INTERACTING WITH SEDIMENTARY PROCESSES IN SILICICLASTIC DEPOSITIONAL SYSTEMS (PRESENT AND PAST)

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1. INTRODUCTION

Siliciclastic depositional systems like sandy tidal flats or shelf environments are predominantly governed by erosion, deposition and deformation (Pettijohn & Potter 1964). But also microbiological parameters influence the sedimentary dynamics, because the sediments are widely colonized by a variety of epibenthic microorganisms like cyanobacteria. Epibenthic microbes attach to the surfaces of depositional grains by adhesive mucous secretions that are known as 'extracellular polymeric substances (EPS)' (Decho 2000 and literature therein). Such organic coatings around grains are termed 'biofilms' (see Charaklis and Wilderer 1989, Decho 2000; Stolz 2000; also Paterson and Black 2000). At sites of favorable ecological conditions, biofilms continue to grow to form thick and significant organic layers that are known as 'microbial mats' (compare Krumbein 1983, also Gerdes & Krumbein 1987, Cohen et al. 1984, or Cohen & Rosenberg 1989, Neu 1994, Stolz 2000, Noffke in press b). Microbial mats can cover large areas of a sedimentary surface. Within shallow-marine depositional environments, the sedimentary dynamics controlls abundance and distribution of epibenthic microorganisms, and also the formation of biofilms and mats (Noffke et al. 2001a, b, Noffke et al. 2002).

From the geological point of view, cyanobacteria are an important goup (Cameron et al. 1985, Gerdes & Krumbein 1987, Knoll & Bauld 1989, Golubic & Knoll 1993, and literature therein, Gerdes et al. 2000b). Epibenthic species construct 'stromatolites', laminated sedimentary structures, that are known since the earliest Earth history until today (e.g. Walter 1976, Reid et al. 2000, see Krumbein 1983 for general terminology). Significant, reef-like stromatolites are characteristic for carbonate environments, where early mineral precipitation during degradation of organic matter by heterotrophs fascilitates early diagenetic cementation (Krumbein 1979b, Reid et al. 2000). In siliciclastic environments, which are focus of this paper, such updomed 'chemical' stromatolites do not occur. In such physically governed environments, the epibenthic cyanobacterial assemblages interact syndepositionally with the sedimentary dynamics like e.g. erosion. This biotic-physical interaction forms characteristic 'Microbially Induced Sedimentary Structures (MISS)' that can be observed microbial both in Recent and fossil (for overview see Gerdes et al. 1993, 1994, 2000b, Noffke et al. 2001a,b, 2003, Noffke in press a). MISS differ significantly from common stromatolites. Very common are 'wrinkle structures', fossilized microbial mats, that are widely distributed in consolidated rocks (Noffke 2000, 2002, Noffke et al. 2002, ~~definition of~~ wrinkle structures by Hagadorn & Bottjer 1997).

The purpose of this paper is to give an overview on strategies of epibenthic cyanobacterial communities in interacting with physical sedimentary dynamics, and on the significance of the biotic influence for the sedimentology of modern and ancient siliciclastics.

2. STUDY AREAS

2.1 Tidal flats of Mellum Island (southern North Sea)

Mellum Island is located in the southern North Sea (Fig. 1A). The sandy tidal flats are overgrown by epibenthic cyanobacteria forming thin biofilms in the lower intertidal zone, and thick microbial mats in the upper intertidal and lower supratidal zones (Stal 1985; Gerdes and Krumbein 1987; Gerdes et al. 1987, Villbrandt 1992; Noffke and Krumbein 1999b).

2.2 Lower arenigian siliciclastics, Montagne Noire, France

Siliciclastic shallow-marine rocks of Lower Arenigian age crop out in the Montagne Noire, southern France (Fig. 1 B). The succession includes mud- and siltstones, as well as fine to coarse-grained sandstones and record a depositional area that was located within a cool paleoclimate zone. The paleoenvironment resembles sedimentologically and geomorphologically the modern southern North Sea coast (compare Noffke 1992, Noffke & Nitsch 1994, Noffke 2000). A stratigraphic section comprising the Schistes et Gres de la Cluse de l'Orb – Formation (GCO-Fm.) was measured.

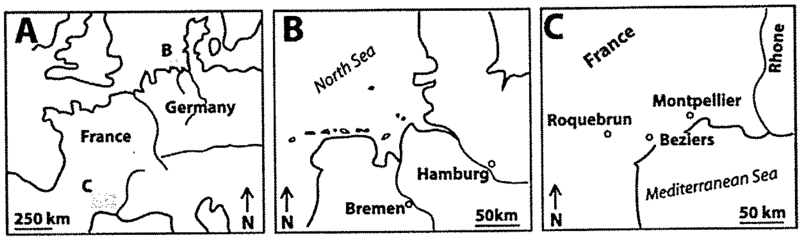

Figure 1. Location of study areas.
Tidal flats of Mellum Island, North Sea; B- Lower Arenigian siliciclastics, Montagne Noire, France

3. THE BIOFILM-CATENA OF THE TIDAL FLATS OF MELLUM ISLAND

The siliciclastic tidal flats of Mellum Island are colonized by different cyanobacterial populations of which each is dominated by one of the three species *Merismopedia punctata, Oscillatoria limosa,* or *Microcoleus chthonoplastes* (Stal 1985, Gerdes et al. 1987, Gerdes & Krumbein 1987, Noffke 1997, Noffke & Krumbein 1999). The dominance of the species within the cyanobacterial populations changes with the topographical height of the tidal flats. The reason for this is that from the mean low to the spring high water line the sedimentary conditions change and as a response to this, a lateral succession of distinct cyanobacterial populations establishes (Fig. 2). Within the lower intertidal zone, we can find *Merismopedia punctata*-dominated populations, whereas the upper intertidal area is overgrown by mats constructed mainly by *Oscillatoria limosa.* The bacterial community of the lower supratidal zone is dominated by *Microcoleus chthonoplastes.*

The lower intertidal zone is characterized by steady rework of the sediments by waves or tidal currents. How do photoautotroph cyanobacteria escape lethal burial in such an hydrodynamically active environment? *Merismopedia punctata*, a coccoid species that forms pillow-like clusters of spheroidal cells, attaches as biofilms on single mineral grains of the depositional surface. In experiment is shown, that if the bacterially overgrown sediment is disturbed by water agitation, the biofilm-coated grains float up more easily than 'sterile' quartz sand particles. As long as the water moves, the biofilm-coated grains stay in suspension, whereas the non-colonized sand grains mainly just roll back and forth on the sedimentary surface. Only after the water movement calmes down, the biofilm-coated grains sink to the floor and are thus deposited always ontop the sedimentary surface. This reaction of a biofilm-coated grain on water agitation is result of its small relative specific weight related to its larger diameter compared to the relatively high specific weight related to the smaller diameter of 'sterile' quartz grains. By this mechanism, *Merismopedia punctata*-overgrown grains stay atop the depositional surface. Its influence on the sedimentary dynamics is less important, e.g. no biostabilization effect (see paragraph 4) was measured (Noffke & Krumbein 1999).

The upper intertidal zone of Mellum Island is overgrown by *Oscillatoria limosa*. This organism forms single trichomes of high mobility, and constructs very thin, temporary mat layers (Villbrandt 1992). The upper intertidal area is characterized by diurnal, periodical rework by the flood current. *O. limosa* reacts on each of the regular burial events by rapid migration towards the new sedimentary surface, where it re-establishes a mat layer within a few hours (Villbrandt 1992, Noffke & Krumbein 1999). Because of the periodical inundation of the tidal surface, salinity values show moderate ranges compared to those of higher tidal areas, and desiccation events are rare. Therefore, *O. limosa* does not produce great amounts of EPS to protect itself against osmotic pressure or desiccation. In experiment in a flume chamber was shown that biostabilization effects on the sediments are about 3-5 times greater than that of non-colonized sands (compare paragraph 4). A specific surface morphology of the tidal flats document this effect (Noffke & Krumbein 1999).

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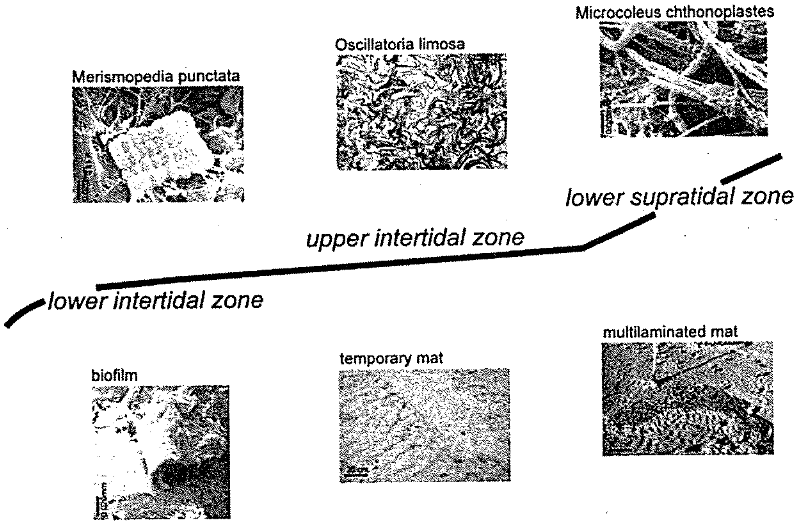

Figure 2. The biofilm-catena of the tidal flats of Mellum Island. Three species dominate cyanobacterial populations that colonize the main tidal zones. They form biofilms or mats in response to prevailing hydrodynamic conditions.

The lower supratidal zone of Mellum Island is covered by microbial mats of significant appearance (see figures in Gerdes & Krumbein 1987, Krumbein 1987, and older literature therein). The uppermost layer of these mats is predominantly constructed by *Microcoleus chthonoplastes* (e.g., Gerdes & Krumbein 1987, Krumbein 1987, Noffke & Krumbein 1999). This cyanobacterial species forms 'spaghetti-like' bundles of trichomes that are surrounded by an EPS-rich glycocalix. Together with heterotrophic bacteria, *M. chthonoplastes* generates a complex multilaminated and versicoloured mat system, that was termed 'Farbstreifen-Sandwatt - versicoloured tidal sand' by Schulz (1936). With its long lasting subaerial exposure in between the spring high tides the lower supratidal zone implies special ecological conditions the cyanobacteria have to respond to. During hot summer days, evaporation produces high values of salinity (Riege, 1994) and the mat-covered deposits may even dry out. After few hours of rain fall, the values decrease rapidly (Riege, 1994) and the mat surface is re-wetted. To protect itself against these extremely varying conditions, *M. chthonoplastes* secrets lots amounts of EPS and surrounds its trichomes by a robust sheath. The mucilages buffer salinity and provide a constant degree of moisture within the mat system, so a mat surface feels always wet. Because of reworking of the substrate take place only during spring high tides, it is sufficient for survival of the cyanobacterial population that only the hormogonia (pieces of trichomes falling apart) of *M. chthonoplastes* can move through sediments to escape lethal burial (Gerdes & Krumbein, 1987, see experiments by Gerdes et al. 1991). The thick mats contribute greatly to stabilization of the deposits, and the characteristic surface relief composed of erosional remenants and pockets evolves (Noffke & Krumbein 1999, Noffke 1999).

The example of the tidal flats of Mellum Island shows, how cyanobacterial species adapt to particular sedimentary conditions prevailing within each of the tidal zones. As a response to the different sedimentary dynamics, the species compositions of the epibenthic cyanobacterial populations changes from the low water to the high water line. Thus a lateral succession of different cyanobacterial populations establishes on the tidal flats. To describe such a succession, the term 'biofilm-catena' was proposed (Noffke 1997). 'Biofilm-catenae' can be observed also at other coastal environments (Noffke et al. 2001a).

4. CYANOBACTERIAL ACTIVITIES INTERACTING WITH SEDIMENTARY PROCESSES IN MODERN TIDAL FLATS AND THE FORMATION OF 'MICROBIALLY INDUCED SEDIMENTARY STRUCTURES'

Microbial assemblages interact with erosion or deposition, and this interference is recorded by particular 'Microbially Induced Sedimentary Structures' (Fig. 3). The main cyanobacterial activities processing the formation of the structures are leveling, biostabilization, imprinting, grain-separation, and baffling, trapping, and binding (Gerdes et al. 2000, Noffke et al. 2001b, Noffke in press a).

4.1 Leveling

Thick mats ovregrow a preceedingly rippled tidal surface and smoothens out the original surface relief, e.g. ripple marks. A mature microbial mat has a planar surface and the original tidal surface morphology of its substrate below is not longer visible (compare Noffke & Krumbein 1999a).

4.2 Biostabilization

The term biostabilization was first defined by Paterson (1994), and it describes the fixation of sediment by microorganisms such as diatoms, cyanobacteria, fungi, and others (compare also Neumann et al. 1970, De Boer 1981, Grant and Gust 1987, Dade et al. 1990, Gerdes et al. 2000, the volume on 'biostabilization of sediments' by Krumbein et al. 1994, or, Paterson 1997 for review, Noffke et al. 2001b, 2003). Biostabilization increases the resistance of microbial-interwoven sedimentary surfaces to erosion, but it reduces also the exchange of gases between sediment and water or sediment and atmosphere (Gerdes et al. 2000b, Noffke et al. 2001b). The reason for the immense stabilization effect of such filamantous cyanobacteria is threefold: (i) the copious and soft EPS fill in the original gruff tidal surface, so the frictional forces between the bottom water current and the depositional surface are reduced; (ii), additionally, the sedimentary grains are glued together and fixed by the adhesive bacterial mucilages, and (iii), the filaments themselves construct a dense network around the mineral particles (Noffke 1998, 1999, Noffke et al. 2001b). One can compare the construction of filaments (composed of several trichomes surrounded by a sheath) with the ropes of a suspension bridge. Bundled ropes (or trichomes) can react more flexible to tensile forces than single ropes (trichomes). Indeed, it was shown by Yallop et al. (1994) that a microbial mat of *Microcoleus chthonoplastes* reacts on drag forces by oscillation. It is assumable that this flexible reaction result from the specific construction of the filaments.

4.3 Imprinting

Biofilms grow over physically shaped surface structures, like ripple marks, without altering the original sedimentary relief. We can detect buried depositional surfaces in vertical sections through the sediment with the aid of their former biofilms. The biofilms line (=imprint) the surfaces (Noffke et al. 1996).

4.4 Grain separation

Grain separation is a process of upward transportation of sedimentary grains by a growing microbial mat. Over time, the biofilms around mineral grains grow and become thicker. The thickening biomass elevates the mineral grains and separates them from each other, and the grains 'float' without contact with each other within the organic mass (Noffke et al. 1997a,b).

4.5 Baffling, trapping and binding

Filamentous cyanobacteria like *Microcoleus chthonoplastes* accumulate actively sediment by baffling, trapping and binding (Black 1933, for tidal flats of Mellum Island: Gerdes & Krumbein 1987, Krumbein 1987, Noffke et al. 1997a, b, 2003, Noffke & Krumbein 1999). The cyanobacteria orient themselves perpendicularly to the mat surface and reach into the supernatant water, where they generate microzones of reduced flow velocity (,baffling‘). The lowered current velocity triggers fall-out and settling of suspended mineral grains, a process which is termed 'trapping' (Black 1933). The baffled and trapped grains are incorporated into the mat fabrics during growth of the microbial layer ('binding' sensu Black 1933).

4.6 Primary sedimentary structures rising from cyanobactrial activities: ‘microbially induced sedimentary structures’

The term ‘primary sedimentary structures’ comprises all structures that are formed syndepositionally. This term includes on the one hand physical sedimentary structures that originate from erosion, deposition or deformation of sediments like e.g. ripple marks, parting lineation or dish structures. On the other hand, the term includes biogene structures like burrows and traces that originate from activities of macroorganisms like polychaets. Stromatolites are grouped therein (compare Pettijohn & Potter 1964). We proposed to introduce an additional group 'Microbially Induced Sedimentary Structures (MISS)' (Noffke et al. 2001b, 2003, Noffke in press a), which comprises phenomena that rise from interaction of bacterial communities with physical parameters (Fig. 3). microbial

Biotic-physical structures are ‘leveled surfaces’, in the fossil record to be recognized as 'wrinkle structures', crinkled bedding planes (Hagadorn & Bottjer 1997, Noffke 2000, Noffke et al. 2003). 'Microbial mat chips' were torn from their parent mat during storms by water agitation (Logan 1961; Neumann et al. 1970; Gerdes and Krumbein 1987, Noffke et al. 1996, fossil examples reported by Pflüger and Gresse (1996). Characteristic tidal surface morphologies that document interactions of biostabilization and erosion are 'erosional remnants and pockets' (Reineck 1979; Gerdes et al. 1993; Noffke 1999), or 'multidirected ripple marks' (Noffke et al. 1995, 1996; Noffke 1998). Intrasedimentary gas entrapped underneath sealing microbial mat layers produce a characteristic 'sponge pore fabrics' (Noffke et al. 1996; Noffke et al. 1997a, b; Gerdes et al. 2000b). Preceeding ripple mark valleys can be traced as 'sinoidal laminae' in vertically cut sediment cores (Noffke et al. 1997b, Gerdes et al. 2000b). Grains incorporated into the mat fabrics often show an orientation with their long-axes parallel to the depositional surface. This texture in thin-sections are described as 'mat layer-bound oriented grains' (Noffke et al., 1997a,b). Baffling, trapping and binding is reflected by 'biolaminites' in the tidal sands of Mellum Island (Gerdes and

Krumbein 1987, or Gerdes et al. 1991, Gerdes et al. 2000b; compare also Grotzinger & Knoll 1999, and Reid et al. 2000).

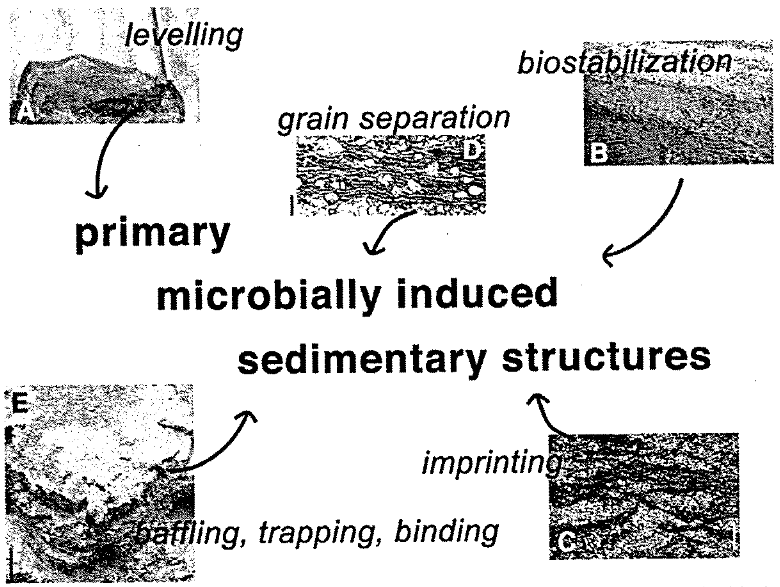

Figure 3. Cyanobacteria interact with physical sedimentary dynamics. This biotic-physical interference produces 'Primary Microbially Induced Sedimentary Structures', which are placed as own category into the Classification of Primary Sedimentary Structures.

5. THE SIGNIFICANCE OF BIOTIC-PHYSICAL INTERFERENCE IN THE FORMATION OF BEDDING PLANES

A bedding plane separates a single bed from adjoining beds. It represents either a period of non-deposition during sediment formation, or a sudden change of depositional conditions (e.g., Fuechtbauer 1988).

Within sediment that is composed of loose grains, e.g. tidal sands, one presupposition for the formation of a bedding plane is that the depositional surface was immobilized before a subsequent sediment layer was deposited. That is, the sedimentary surface was sheltered against primary destruction by erosion during placement of a fresh sand layer. Thus the preservation potential of a surface becomes higher. Loose surface sands of tidal flats can become fixed by different physical parameters. A thin salt crust can develop during ebb tides, but also wetting of a previously dry sandy surface by fog or rime can fasten the mineral particles (Reineck et al. 1995). Aside grain fixation, also a physically derived intra-sedimentary texture that imprints a former depositional surface may induce a bedding plane within an otherwise homogeneously composed sediment. Specific uni-directional grain orientation in a tidal surface is produced by particular current flow patterns during ascending flood (Allen 1964, compare Reineck et al. 1995). Drapes of grains of smaller (or coarser) grain sizes deposited during ebb tides (or during storms) onto the depositional surface may trigger the formation of bedding planes (Reineck et al. 1995).

The question is, if aside these physical effects, also microbial mats, by colonizing the interface between sediment and water, induce the formation of bedding planes in siliciclastics (Fig. 4).

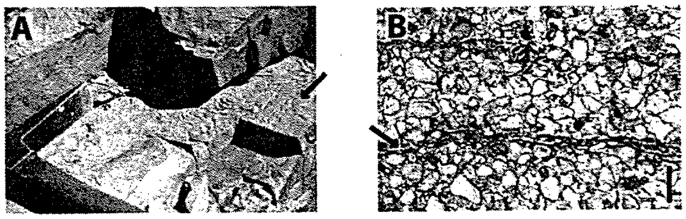

Figure 4. Do microbial mats contribute to the formation of bedding planes ? A- Bedding plane in consolidated rocks, Lower Arenigian, Montagne Noire, France; Note crinkled appearance of rock surface. B- Microbial mat ~~covering ripple marks~~. Vertical section through sediment core from tidal deposits, Mellum Island. Lining ~~former~~ buried sedimentary surfaces

5.1 Mat-related effects producing bedding planes in tidal sediments of Mellum Island

In relief casts of core samples and in thin-sections of artificially hardened tidal deposits, mat layer-bound oriented grains or enrichments of fine-grained particles can be observed. The layers separate the sandy deposits. As documented by field observations and measurements, such textures are first result of cyanobacterial leveling and stabilization of the sedimentary surface. Microbial leveling reduces the frictional forces between the sediment surface and moving bottom water, whereas the network of cyanobacterial filaments entangles the depositional grains and protects them from being ripped off by erosion (compare 4.1. and 4.2.). Grain separation and orientation originates during microbial mat growth and EPS-enrichment (compare 4.4.). This bacterial effect, as well as baffling, trapping and binding (active accumulation of fine sediment by microbial mats, compare 4.5.) leads to specific textures. The biogene textures line former depositional surfaces the same way like the physically induced ones. After consolidation of the sediment and rock formation, weathering may later hammer out ancient surfaces along these planes of differing, both biologically or physically derived textures.

5.2 Microbial mat-induced bedding planes in lower arenigian siliciclastics, Montagne Noire, France

We can find bedding planes that were formed not only by physical but also by biological factors in a stratigraphic section of the Lower Arenigian, Montagne Noire, in France (Noffke 2000). Within the stratigraphic section of the GCO-Fm., we can distinguish 4 groups of physically derived bedding planes, and 2 groups of bacterially induced ~~ones~~ (Fig. 5).

microbial

Nine bedding planes show wrinkle structures (~~= lithificated microbial mats, Hagadorn & Bottjer 1997~~) atop. In vertical sections through the wrinkle structures, we can see its internal biolaminated pattern, and a few single mineral grains floating within the ancient mat fabrics. The fossil mats contain also small-sized grains (silt) that lack in the sandy interlayers. The bedding planes show no original surface morphology, therefore it is concluded that the former mats were thick enough to level completely the relief of its substrate below. Because of the planar appearance of the bedding planes, they were termed 'non-transparent wrinkle structures' (Noffke 2000, Noffke et al., 2002).

Five wavy upper bedding planes show similar internal textures like the wrinkled surfaces, and 4 rippled rock bed surfaces are covered by crinkles that resemble a skin. Wavy upper bedding planes and skin-like crinkled bedding planes record former, very thin microbial mats that did not level the preceeding depositional surface and the surface structures. Because the original surface relief is still visible underneath the ancient mat, such bedding planes were termed 'tranparent wrinkle structures' (Noffke 2000, Noffke et al. 2002). In thin sections, they contain silt-size particles and a great amount of mica flakes.

Thirty-two of the bedding planes studied are covered by fine-grained sediments, but show none of the microbial mat-induced structures or textures. Therefore the fines were probably deposited during periods of lower hydrodynamic energies. Nineteen bedding planes are amalgamated, that is they record severe storms that eroded parts of the former depositional surface before fresh sediment was placed. Finally, we distinguish mud- and siltstone beds that contain no distinct bedding planes.

Biogenic bedding planes make 12.6 % of all bedding planes studied, and they thus represent a significant category within the total amount of bedding planes. Conversely, physically derived bedding planes make the greatest portion within the GCO-Fm., and record tidal areas of unfavourable hydrodynamic conditions that are avoided by cyanobacteria (compare Noffke et al., 2002).

The results show that bacterial activities contribute to the formation of bedding planes in siliciclastic tidal flats. Depositional surfaces are protected against erosion by biostabilization, and the bacterial communities produce distinct textures within the otherwise homogeneous sediments. Along these textures, weathering may later hammer out the depositional surfaces in the consolidated rock.

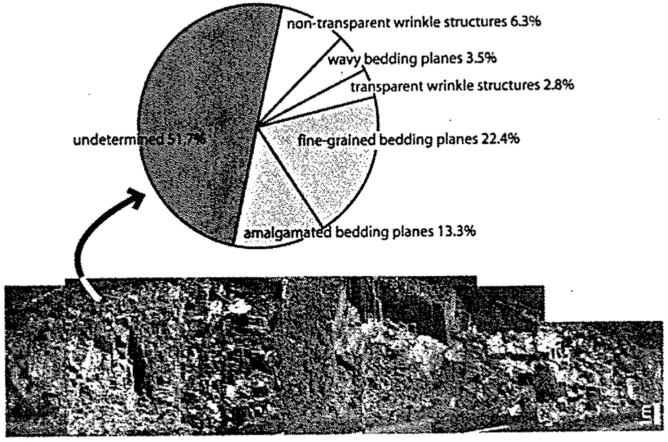

Figure 5. Types of bedding planes in the stratigraphic section of the Gres et Schistes de la Cluse de l'Orb, Lower Arenigian, Montagne Noire, France. We distinguish physically derived and bacterially induced bedding planes.

6. CONCLUSIONS

Shallow-marine siliciclastic deposits are colonized by various populations of benthic microorganisms, of those cyanobacteria are important parameters in sedimentary processes. The tidal flats of Mellum Island, southern North Sea, show how in correspondence with the tidal zones and the changing characteristic sedimentary dynamics, a lateral succession of different cyanobacterial populations establishes. We term such a succession 'biofilm-catena'. Biofilm-catenae interfere the physical parameters (erosion, deposition, deformation) that govern siliciclastic sedimentary systems. Such biotic-physical interaction produces 'Microbially Induced Sedimentary Structures (MISS)'. MISS are grouped as own category into the existing classification scheme of primary sedimentary structures. Another important aspect is the contribution of benthic cyanobacteria to the formation of bedding planes. Bedding planes in tidal sands or consolidated sandstones may not only result from physical factors affecting the former sedimentary surface, but could also be formed by cyanobacterial activities. Biogene and physical bedding planes are shown with the example of the Lower Arenigian, Montagne Noire, France. The knowledge of microbial activities in erosional and depositional processes within physical sedimentary systems should give rise to new perspectives in sedimentological investigations of siliciclastic environments of Earth, but also other planetary bodies.

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REFERENCES

Allen, J. R. L., 1964, Primary current lineation in the lower Old Red Sandtsone (Devonian), Anglo Welsh Basin: Sedimentology, v. 3, p. 98-108.

Black, M., 1933, The algal sediments of Andros Islands, Bahamas: Royal Society of London Philosophical Transactions, Ser. B, v. 222, p. 165-192.

Cameron, B., Cameron, D., and Jones, J.R., 1985, Modern algal mats in intertidal and supratidal quartz sands, northeastern Massachussetts, USA: Society of Economic Paleontologists and Mineralogists, p. 211-223.

Charaklis, W. G., and Wilderer, P. A., 1989, Structure and function of biofilms: Dahlem Workshop Reports, Life Sciences Research Report 46, Chichester, 386p.

Cohen, Y., Castenholz, R.W., and Halvorson, H. O., 1984, Microbial mats: Stromatolites: Alan R. Liss Press, New York, 498 p.

Cohen, Y. and Rosenberg, E., 1989, Microbial mats. Physiological ecology of benthic microbial communities: American Society of Microbiologists, Washington, D.C., 494p.

Dade, W.B., Davis, J. D., Nichols, P. D., Nowell, A. R. M., Thistle, D., Trexler, M. B. and White, D. C., 1990, Effects of bacterial exopolymer adhesion on the entrainment of sand. Geomicrobiological Journal, 8, 1-16.

De Boer, P.L., 1981, Mechanical effects of microorganisms on intertidal bedform migration: Sedimentology, v. 28, p. 129-132.

Decho, A.W., 2000, Exopolymer microdomains as a structuring agent for heterogeneity within microbial biofilms, *in* Riding, R. and Awramik, S., eds., Microbial Sediments: Berlin, Springer-Verlag, p. 9-15.

Gerdes, G. and Krumbein, W. E., 1987, Biolaminated deposits: Berlin, 183p.: Gerdes, G., Krumbein, W. E. & Reineck, H. E. (Eds.): Mellum – Portrait einer Insel. p. 62-76, 5 Figs., Kramer, Frankfurt/Main.

Gerdes, G., Krumbein, W.E., and Reineck, H.E., 1991, Biolaminations – ecological versus depositional dynamics, *in* Einsele, G., Ricken, W. and Seilacher, A., eds., Cycles and events in stratigraphy: Springer, Berlin, p. 592-607.

Gerdes, G., Claes, M., Dunajtschik-Piewak, K., Riege, H., Krumbein, W. E., and Reineck, H. E., 1993, Contribution of microbial mats to sedimentary surface structures. Facies, 29, 61-74.

Gerdes, G., Krumbein, W.E. and Reineck, H.E., 1994a, Microbial mats as architects of sedimentary surface structures, *in* Krumbein, W.E., Paterson, D.M., and Stal, L., eds., Biostabilization of sediments: Oldenburg, Bibliotheks und Informationssystem der Universität Oldenburg, 526 p .

Gerdes, G., Noffke, N, and Klenke, Th. 2000b, Microbial signatures in peritidal siliciclastic sediments: A catalogue: Sedimentology, v. 47, p. 279-308.

Golubic, S. and Knoll, A.H., 1993: Prokaryotes, *in* Lipps, J., ed., Fossil prokaryotes and protists: Blackwell, Boston, p. 51-76.

Grant, J. and Gust, G., 1987, Prediction of coastal sediment stability from photopigment content of mats of purple sulfur bacteria: Nature, 330, p. 244-246.

Grotzinger, J.P. and Knoll, A.H., 1999, Stromatolites in Precambrian Carbonates: Evolutionary Mileposts or Environmental Dipsticks?: Annual Review of Earth and Planetary Science, v. 27, p. 313-358.

Hagadorn, J.W. and Bottjer, D., 1997, Wrinkle structures: microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition: Geology, v. 25, p. 1047-1050.

Knoll, A.H. & Bauld, J., 1989, The evolution of ecological tolerance in prokaryotes: Transactions of the Royal Society of Edinburgh: Earth Sciences, v. 80, p. 209-223.

Krumbein, W.E., 1979, Photolithotrophic and chemoorganotrophic activity of bacteria and algae as related to beach rock formation and degradation (Gulf of Acaba (Sinai)). - Geomicrobiol. J., 1, 139-203

Krumbein, W.E., 1983, Stromatolites – The challenge of a term in space and time: Precambrian Research, v. 20, p. 493-531.

Krumbein, W.E., Paterson, D.M., and Stal, L.J., eds., 1994, Biostabilization of Sediments: BIS, University of Oldenburg, 526p.

Logan, B.W.,1961, *Cryptozoon* and associated stromatolites from the Recent, Shark Bay, Western Australia. *Journ. Geol.*, 69, no.5, 517-533.

Neu, T.R., 1994, Biofilms and microbial mats. In: *Biostabilization* (Ed. by W.E. Krumbein, D.M. Paterson and L.J. Stal), 9-16, Oldenburg.

Neumann, A.C., Gebelein, C.D., and Scoffin, T.P., 1970, The composition, structure and erodiability of subtidal mats, Abaco, Bahamas: Journal of Sedimentary Petrology, v. 40, p. 274-297.

Noffke, N. & Nitsch, E., 1994, Sedimentology of Lower Ordovician clastic shelf deposits, Montagne Noire, France: Geologie de France, v. 4, p. 3-19.

Noffke, N., Gerdes, G., Klenke, Th., and Krumbein, W.E 1995, Microbially induced sedimentary structures: Tagung Sediment 95 Freiberg, Abstract, p. 141.

Noffke, N., Gerdes, G., Klenke, Th., and Krumbein, W.E. 1996, Microbially induced sedimentary structures – examples from modern sediments of siliciclastic tidal flats: Zentralblatt für Geologie und Paläontologie Teil I, v. 1995, p. 307-316.

Noffke, N., 1997, Mikrobiell induzierte Sedimentstrukturen in siliziklastischen Wattablagerungen: PhD Thesis, University of Oldenburg, 127p.

Noffke, N., 1998, Multidirected ripple marks rising from biological and sedimentological processes in modern lower supratidal deposits (Mellum Island, southern North Sea): Geology, v. 26, 10, p. 879-992.

Noffke, N., 1999, Erosional remnants and pockets evolving from biotic-physical interactions in a Recent lower supratidal environment: Sedimentary Geology, v. 123, p. 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, v. 136, p. 207-215.

Noffke, N., in press a, Microbially induced sedimentary structures: formation and application to sedimentology. - Middleton, C. (Ed.): Encyclopedia of sediments.

Noffke, N., in press b, Bacteria in sediments. - Middleton, C. (Ed.): Encyclopedia of sediments.

Noffke, N., 2002, ONLINE: The concept of geobiological studies: the example of microbially induced sedimentary structures in physical depositional systems: Palaios, v. 17, i-iii.

Noffke, N., Gerdes, G., Klenke, Th., and Krumbein, W.E., 1997a, A microscopic sedimentary succession of graded sand and microbial mats in modern siliciclastic tidal flats: Sedimentary Geology, v. 110, p. 1-6.

Noffke, N., Gerdes, G., Klenke, Th., and Krumbein, W.E., 1997b, The impact of sediment-stabilizing biofilms on the architecture of sedimentary structures (Mellum Island, southern North Sea): Courir Forschungs-Institut Senckenberg, v. 201, p. 297-305.

Noffke, N., Gerdes, G., Klenke, Th. & Krumbein, W.E., 2001a, Microbially induced sedimentary structures indicating small-scale facies zones within coastal environments of southern Tunisia (Recent and Pleistocene): Facies, v. 44, p. 23-30.

Noffke, N., Gerdes, G., Klenke, Th. & Krumbein, W.E., 2001b, Classification of primary microbially induced sedimentary structures: Journal of Sedimentary Research, v. 71, 5, 649-656.

Noffke, N., Gerdes, G., and Klenke, Th., 2003, Benthic cyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty and evaporitic carbonatic).- *Earth Science Review,* 12, 1-14.

Noffke, N., Knoll, A.H. & Grotzinger, J., 2002, Sedimentary parameters controlling occurrence and preservation of microbial mats in siliciclastic depositional systems: Palaois, v. 17, 1-12.

Noffke, N. and Krumbein, W.E., 1999, A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics: Sedimentology, v. 46, p. 417-426.

Paterson, D. M., 1994, Microbiological mediation of sediment structure and behaviour, in Stal, L.J. and Caumette, P., eds., Microbial Mats, Berlin, Springer-Verlag, p. 97 – 109.

Paterson, D. M., 1997, Biological mediation of sediment erodiability: ecological and physical dynamics, *in* Burt, N., Parker, R. and Watts, J., eds., Cohesive sediments: Wiley, London, p. 215-229.

Paterson, D. M., and BLACK, K. S., 2000, Siliciclastic intertidal microbial sediments, *in* Riding, R., and Awramik, S., eds., Microbial sediments, Berlin, Springer, p. 217 – 225.

Pettijohn, F.J., & Potter, P.E., 1964, Atlas and glossary of primary sedimentary structures: Berlin, Springer-Verlag, 370 p..

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. and DesMarais, D.J., 2000, The role of microbes in accretion, lamination and early lithification of modern marine stromatolites: Nature, v. 406, p. 989-991.

Reineck, H.E., 1979, Rezente und fossile Algenmatten und Wurzelhorizonte: Natur und Museum, v. 109, p. 290-296.

Reineck, H. E., Gerdes, G. and Noffke, N., 1995, Physikalische Kraefte, die Rippelfelder erhalten, ehe sie versteinern: Natur und Museum, v. 125, p. 163-172.

Riege, H., 1994, *Untersuchungen zur Karbonatfällung in Mikrobenmatten.* PhD Thesis, University of Oldenburg, pp. 139.

Schulz, E., 1936, Das Farbstreifen-Sandwatt und seine Fauna, eine ökologisch-biozönotische Untersuchung an der Nordsee. *Kieler Meeresforsch.*, 1, 359-378.

Stolz, J. F., 2000, Structure of microbial mats and biofilms, *in* Riding, R., and Awramik, S., eds., Microbial sediments, Berlin, Springer-Verlag, p. 1-8.

Stal, L.J., 1985, Ökologie der Bakterien des Farbstreifen-Sandwattes. In: Gerdes, G., Krumbein, W. E., Reineck, H. E. (Eds.), *Mellum - Porträit einer Insel.* (Ed. by G. Gerdes, W.E. Krumbein, and H.E. Reineck), 188-202, Frankfurt am Main.

Yallop, M.L., De Winder, B., Paterson, D.M. and 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, v. 39, p. 565-582.

Villbrandt, M., 1992, Interactions of nitrogen fixation and photosynthesis in marine cyanobacterial mats (Mellum, southern North Sea): PhD Thesis University of Oldenburg, 153p.

Walter, M.R., ed., 1976, Stromatolites: Developments in Sedimentology, v. 20, Elsevier, Amsterdam, Oxford, New York, 790p.