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Microbial Mats in Sandy Deposits from the Archean Era to Today

Springer

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ISBN 978-3-642-12771-7 e-ISBN 978-3-642-12772-4
DOI 10.1007/978-3-642-12772-4
Springer Heidelberg Dordrecht London New York

Library of Congress Control Number: 2010929104

Cover design: deblik, Berlin

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Foreword

A murmur is heard from the depths of time. Life and Earth are engaged in a dialog that has lasted for four billion years. Sometimes it's a whisper, sometimes a roar. One part sometimes gets the upper hand, dominates the discussion and sets the agenda. But mostly the two have some kind of mutual understanding, and the murmur goes on. Most of us don't listen.

Nora does. She listens, and she tries to understand.

Nora Noffke has focused her scientific career on the interaction between the living and the non-living. This is no mean task in an academic world where you are usually either this or that, such as either a biologist or a geologist. The amount of stuff you need to grasp is so large that it usually feels better to sit comfortably on one chair, rather than to risk falling between them. Geobiology is not for the faint of heart.

Nora's focus is on that all-important biological substance mucus, or EPS (extracellular polymeric substance). EPS is the oil in the machinery, the freeway to travel for many small animals and protists, the coat of armour for others, the mortar in the brick wall for yet others. For microbes such as cyanobacteria it may be the world they built, the world they live, eat, fight, multiply, and die in.

In siliciclastic sediments, EPS and the organisms that made it are hardly ever fossilized. Yet while there they interacted with the sediment, trapping grains, binding them together, forming sheets that could wrinkle, fold, tear and crack. Thus their whispering conversation with the physical environment leaves an echo in the rock. Nora listens to the whispers and the echos, learns, and teaches us to do the same.

It's no surprise that Nora spent formative years learning from scientists who themselves are astute observers of life in sediments of today and in rocks of yore. Her mentor in Tübingen was Dolf Seilacher, the man whose astute mind, and eye taught us to appreciate biological shapes both for the insights they give us and for their sheer beauty, and who laid the foundation for modern trace fossil studies. She has worked intensively with Gisela Gerdes and Wolfgang Krumbein, biologists who share her enthusiasm for microbial life and its interactions with Earth. And teaming up with Andy Knoll gave her the perspective of the full four billions. Nora listened to them, as she listens to the murmurs from deep time.

Listen and learn. Here's a book to teach you how.

Stefan Bengtson
Stockholm, 14 April 2010

Preface

Sand is everywhere, and sandy deposits belong to the oldest sediments preserved in Earth's geological record. With the formation of the first continental crust, the first shorelines were created, tidal currents had the first opportunity to rework loose grains, and shallow shelves were the result of first transgressions. It is here, in sands, where life found one of its earliest habitats. And despite all evolutionary changes that took place in the worlds of Earth during its travel through time – the shorelines and the moving waters remained the same for at least 3 billion years.

Benthic prokaryotes, sea floor inhabiting bacterial microbes, are known as the constructors of the famous stromatolites, reef-like boulder heads that constitute the most valuable witnesses of the dawn of life. In recent years, research has wrenched opened a new window that allows hopeful glances back in time. Stromatolites are beautiful geological features, laminated, branched, and full of preserved energy. It seemed therefore an odd idea that Robert Riding and I had in spring of 1993, when discussing in the stair well of the Geological-Paleontological Institute of the University of Tuebingen in Germany: to focus my future work on sandy deposits and prokaryotic build-ups therein. As student of Dolf Seilacher it was logical consequence to search for traces and trace fossils in sand and sandstones. Traces made by microorganisms.

Following Robert Riding's advice, I scratched my last savings together and participated the "Mini Mat Meeting MMM" in Oldenburg 1993. This meeting was organized by Wolfie Krumbein, and a short introduction by Robert opened the doors to a new approach. Working with Gisela Gerdes, pioneer in sandy microbial mat structures, I learned to understand modern shorelines and the study of cyanobacteria. The following two years were devoted to gather information for the ultimate goal: to have handy modern models that serve to explore Earth's most antique worlds. I investigated the famous tidal flats of the North Sea, detected MISS in Tunisia, and worked in Egypt.

My first postdoctoral research at the University in Frankfurt/Main let me back to my master thesis study area, the 480 Ma Ordovician of the Montagne Noire, France. After 4 days of looking for something I did not know what it would look like, the late afternoon sun illuminated wrinkled sandstone beds of a fossil tidal flat and shelf in the Gres et Schistes de la Cluse de l'Orb. Suddenly the structures seemed to pop out everywhere in the outcrop recording ancient microbial mats.

Like for so many successful young scientists in Germany, the doors for a continuing career in academia remained closed also for me. My note to Andy Knoll, however, was answered warmly. With Andy Knoll and John Grotzinger I had the opportunity to study 550 Ma Neoproterozoic tidal and shelf successions in Namibia. Containing the same paleoenvironments like the Ordovician tidal flats and shelves, the Neoproterozoic Nama Group allowed the continuation of my walk into older Earth's history.

A year later, in 2001, as starting professor at Old Dominion University, I had funds for a ten day field trip to South Africa, the desperate task ahead of me to detect something as tiny as a bacterial fossil in an area as big as half of the country. In the afternoon of the last day (it was a very hot and dusty day) my already discouraged colleagues RC Kidd and Noah Nhleko and myself stumbled along a last road cut, when the light of the already sinking sun shone on a characteristically crinkled sandstone surface – a fossil microbial mat. Like the much younger sandstone successions I studied before, also the 2.9 Ga Mesoarchean Pongola and Witwatersrand Supergroups contained tidal flats and shelves, and showed the same facies-related distribution of photoautotrophic microbial mats. It was not a surprise to find the same situation two years later in the 3.2 Ga Paleoarchean Moodies Group, likewise in South Africa. The star of all study sites, however, was the Nhlazatse Section, a close to 3 Ga old tidal flat spotted with the most beautifully preserved MISS in Earth's record known so far.

It is this journey of mine through the career of a scientist, the migration from one continent to another, and from present times to most antique ones, which inspired me to summarize this book. This first text on MISS cannot be perfect and many issues will be resolved only in the future. I encourage the reader to contact me with suggestions, corrections and comments that may serve to improve this text for the future editions.

I am deeply grateful to my families on both sides of the Atlantic Ocean for their endurance to cope with my long absences, to my friends in Boston, Washington, and Norfolk for their warm welcome in the States, my colleagues all over the world for their support through my metamorphosis from a fossil-collecting kid to a scholar. I owe major thanks to Kurt Risser, who in long and persistent hours transformed the one or other Germanism in the manuscript into proper English. In stratigraphic order, most of the research on which this text is based has been supported by the Deutsche Forschungsgemeinschaft DFG, the Leopoldina Deutsche Akademie der Wissenschaften, the Sedimentary Geology and Paleobiology Program of the National Science Foundation NSF, and NASA's Exobiology and Mars Exploration Programs.

Nora Noffke
April 2010

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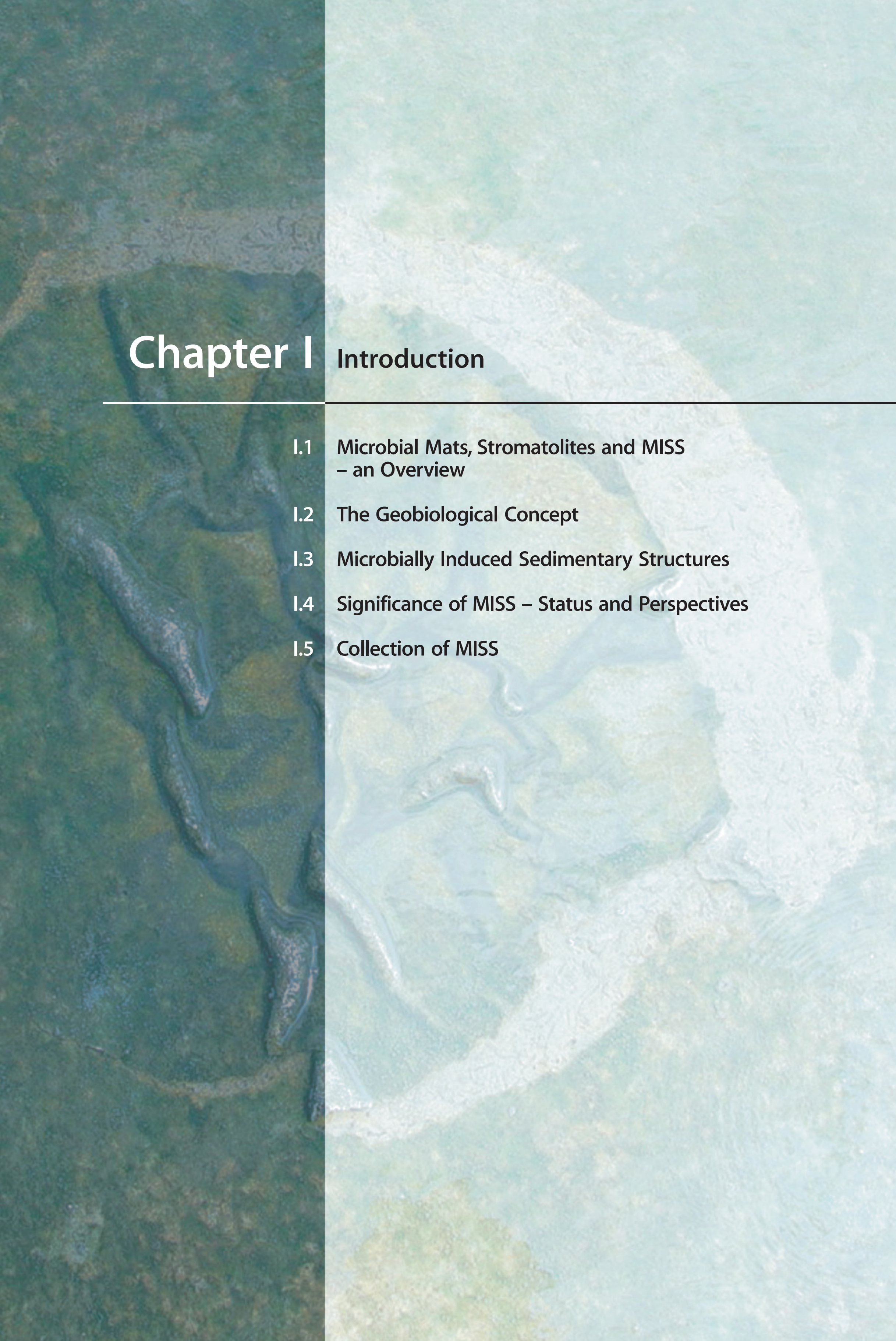


Chapter I Introduction

Chapter I

Introduction

I.1

Microbial Mats, Stromatolites and MISS – an Overview

Sediments on the ocean floor are not merely accumulations of mineral grains. In close-up the grains are densely populated by a world of benthic microorganisms – an integral, highly complex cosmos of which is known little to nothing.

The microbes form biofilms, thin organic coatings, around individual sediment grains, or they grow to thick, carpet-like layers (microbial mats) that cover many kilometers of tidal, lagoonal and continental shelf sediments. Both biofilms and microbial mats contain ubiquitous amounts of extrapolymeric substances (EPS). EPS are highly adhesive mucilages in which the bacteria are embedded. Microbial mats are indeed 'mats'. These coherent, organic layers can be lifted from the sediment, rolled up and carried away like a carpet (Fig. I.1).

Under the microscope, microbial mats are composed by countless individual microorganisms that form a dense and coherent network. The main mat-constructing microbial group is photoautotrophic cyanobacteria. Because of the large sizes of their filaments, and their blue-green colour, cyanobacteria were formerly termed 'blue algae' or 'blue green algae'. However, Stanier et al. 1977 detected that the algae in fact are prokaryotes, not eukaryotes. Prokaryotes include *Bacteria* and *Archaea*, microbes without a nucleus and generally without cell organelles. Eukaryotes include protista such as algae, fungi, and all multicellular plants and animals. Eukaryotes have a nucleus and various cell organellae. Older literature refers to 'algal mats', but more recently the term 'microbial mat' is used.

Microbial mats and biofilms have a significant influence on how sediments respond to the hydraulic dynamics of waves and currents. For a long time microbial influences on marine sediments were generally understood only as biogeochemical processes that cause stromatolites. These rigid, reef-like build-ups are composed of a stack of layers which become visible in vertical section through the stromatolite. In the present and past, these layers derive from *in situ* precipitation (fall-out) of carbonate or silica minerals. This precipitation is triggered by the metabolism of biofilm and mat-forming microbiota. It is characteristic of chemical marine environments. Stromatolites, like sturdy coral reefs, are important for geologists and biologists. They constitute solid rock units that can become preserved easily. Stromatolites can be found abundantly in the fossil record, and they allow insight into Earth's earliest life.

However, biofilms and microbial mats do not always form stromatolites. Indeed, in modern times most do not. Stromatolites can be observed mainly in the tropics, where carbonate minerals precipitate from seawater. Cementation takes place. But benthic

N. Noffke, *Geobiology*, DOI 10.1007/978-3-642-12772-4_1,

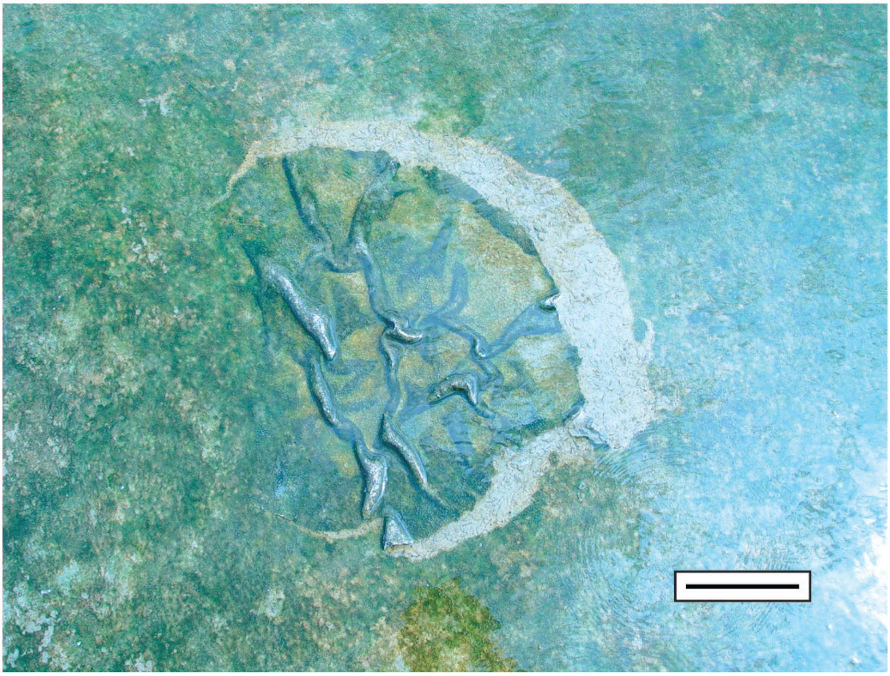


Fig. I.1. Microbial mats like this modern example from Portsmouth Island, USA, are coherent organic layers composed of countless microorganisms. This mat is constructed by photoautotrophic cyanobacteria, hence its blue-green colour. Note how the mat crinkles like a table cloth. The grayish sandy sediment is visible underneath the ruptured mat, where the halfmoon-shaped crack opens; (scale: 10 cm)

microbiota also colonize cold-water oceans, where the sea floor is composed of siliciclastic (sandy) deposits. Sand is reworked by waves and currents. This interaction between moving water and sediment is termed 'physical sediment dynamics'. In such physical environments, chemical precipitation of minerals does not take place, and stromatolites do not build up. However, microbenthos still leaves traces in the mud and sand.

Typically, traces are made by macroorganisms such as worms, clams and polychaetes that inhabit marine sediments. The animals burrow through the sand, graze on the seafloor surface, or tunnel vertically downward in search of a good place to live. Burrows, grazing traces and tunnels can become preserved, and are found as trace fossils in consolidated sedimentary rock (Seilacher 2007). However, traces are left not only by worms and clams, but are also left by benthic microorganisms. Like macroorganisms, microbes respond actively to the hydraulic displacement of their muddy or sandy substrate. Prokaryotes react to physical erosion, and to deposition of sand, and their active migration leaves traces behind. This microbial-physical interaction contrasts with biogeochemical processes (Noffke and Paterson 2008).

Microbial traces in sandy deposits are termed 'microbially induced sedimentary structures', and are known by its acronym 'MISS' (Noffke et al. 1996). The structures form counterparts to stromatolites that occur in carbonate settings, Fig. I.2. The structures, like traces and trace fossils, occur in modern sediments as well as in fossil sedi-

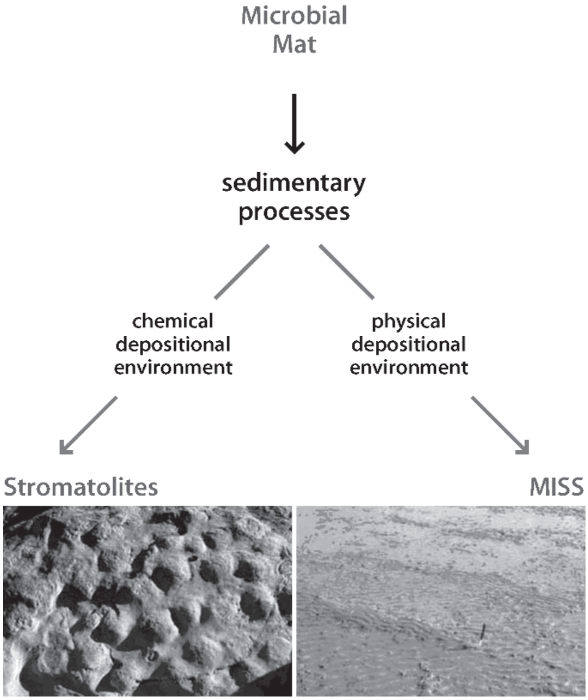


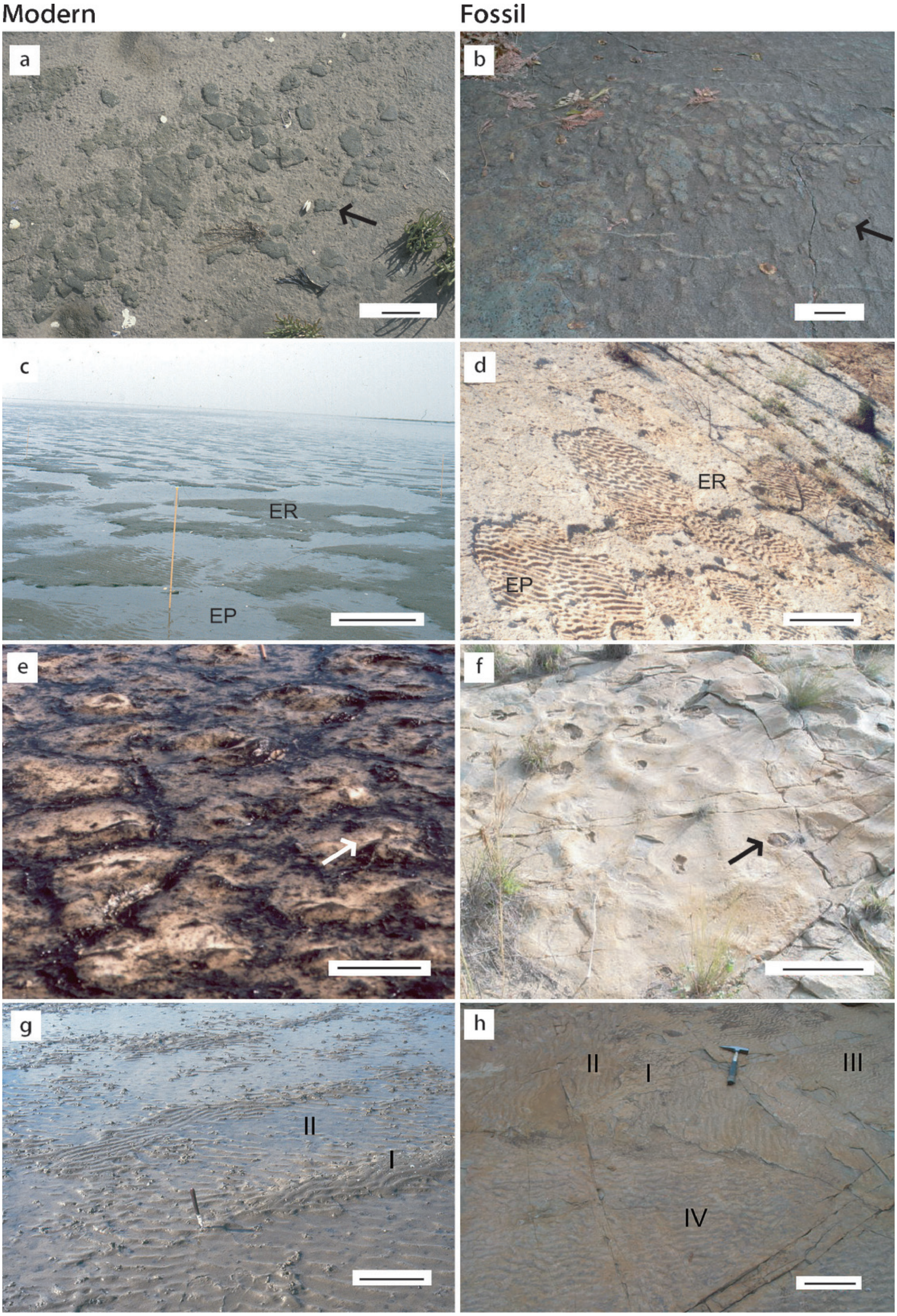
Fig. I.2.
Microbial mats (and biofilms) are constructed by benthic cyanobacteria and other microorganisms. In carbonate ('chemical') depositional environments, microbial mats induce the formation of stromatolites. In siliciclastic ('physical') environments, where mineral precipitation or cementation play no role, microbial mats form 'microbially induced sedimentary structures – MISS'. MISS do not resemble stromatolites, but display a great variety of morphologies. The photo on the left shows typical, domal stromatolites; (scale: 10 cm; photo by Brian Pratt). The photo on the right shows multidirected ripple marks; (scale: knife 25 cm)

mentary rocks (Fig. I.3). Most important, MISS do not resemble stromatolites. They come in 17 different types.

Recent research documented that the structures have the same significance for the interpretation of Earth history as stromatolites. Stromatolites occur since early Archean times, and witness the existence of biofilms and microbial mats for at least 3.4 Ga years. MISS show the same distribution through time, and record that microbial mats were present in tidal flats, lagoons, and continental shelves throughout Earth history. The oldest examples are reported from the 3.2 Ga old Moodies Group, South Africa. Both stromatolites and MISS occur until today. However, modern stromatolites are restricted to rare and very small scaled habitats, such as the famous Shark Bay in Australia. In contrast, modern microbial mats that form MISS are distributed worldwide. They fringe the oceans like a blue-green seam and constitute one of modern Earth's largest ecosystems. Conveniently, microbial mats can be monitored everywhere along sandy beaches. The microbial-physical processes that form the MISS can be measured and quantified.

The study of microbial mats and MISS in the present environment enables geobiologists to draw conclusions about fossil microorganisms in ancient oceans. This comparison of modern with ancient environments is termed the 'actualistic principle'. Geoscientists say "The present is the key to the past". This actualistic principle is the fundamental approach in geobiological studies (Noffke 2003a, 2005).

Geobiological research inherently calls for the comparison of modern with ancient life and environment. The study of MISS therefore is setting the direction for this developing discipline.


Modern
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◀ **Fig. I.3.** Microbially induced sedimentary structures (MISS) in sandy tidal flats – modern examples on the left and fossil analogues on the right. **a** Microbial mat chips (Fishermans Island, USA; scale: 5 cm). **b** Fossil mat fragments (2.9 billion years (Ga) Pongola Supergroup, South Africa; scale: 5 cm). **c** Erosional remnants (*ER*) and pockets (*EP*) (Mellum Island, North Sea; scale: 1 m). **d** Fossil erosional pockets (*EP*) situated in a mat-stabilized sedimentary surface (*ER*) (Cretaceous Dakota Sandstone, Colorado, USA; scale: 1 m). **e** Oscillation cracks define a polygonal pattern in the surface of a microbial mat. The center of each polygon shows an erupted gas dome, one example marked with an *arrow* (southern Tunisia; scale: about 30 cm). **f** Same polygonal structure. *Arrow* indicates a hole where a gas dome erupted (2.9 Ga Pongola Supergroup, South Africa; scale: 25 cm). **g** Multidirected ripple marks. Two generations of ripples (I and II) are displayed on this tidal surface (Mellum Island; scale: 50 cm). **h** Multidirected ripple marks with 4 generations of ripple marks (I–IV) (2.9 Ga Pongola Supergroup, South Africa; scale: 30 cm)

I.2
The Geobiological Concept

Understanding Earth as a system calls for new concepts in modern sciences. About 150 years ago, science diversified into a wide spectrum of individual and special disciplines. The recent trend is to fuse many discrete disciplines, constituting an overarching, inclusive scientific concept. One example of such fusion is the discipline of geobiology. This rapidly evolving field opens new and exciting perspectives for the understanding of environmental problems of global scale, the history of life on our planet, and the exploration of extraterrestrial worlds. By definition, geobiology is the study of life in the context of its environment, modern and past.

The goal of geobiology is to close the traditional gap between the two parent disciplines geology and biology (Fig. I.4). What is the traditional gap between the parent disciplines? Biology and geology are basic research disciplines that investigate the Earth and its life. Biologists mainly focus on the present, whereas geologists commonly study the past. Biological investigations first differentiate individual environmental and biological parameters, and then quantify their interaction in coupled processes. An example of a parameter could be solar radiation. An example of a process could be how solar radiation affects flowering plants. Parameters and processes can be studied by direct methods of investigation. Direct methods are measurements and experiments in the modern environment and in the laboratory. The drawback of direct methods is

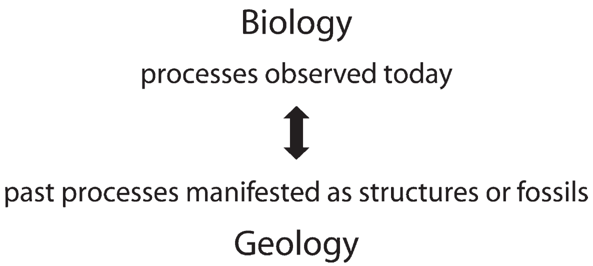


Fig. I.4. The traditional gap between the two scientific disciplines biology and geology. Biology observes and measures processes of life interacting with its environment today. Geology reconstructs past worlds by describing and interpreting sedimentary structures and fossils. Structures and fossils are manifested processes that took place in Earth's past that parameters and processes can only be determined in their present state. Long-term changes can neither be detected nor quantified.

Geological investigation must follow another approach, because it cannot measure parameters and processes directly. Why? Because parameters and processes that existed in the past are now manifested in rocks as sedimentary structures or fossils. Ancient life and paleoenvironmental conditions can only be determined indirectly by description and interpretation. This is because the study of the rock record faces one fundamental problem: the fossil record is incomplete. Not only a bit. Most of Earth history is unknown, and the sobering perspective is that it will remain unknown. By nature, geological studies are highly subjective. They frequently provide topics for hot (and entertaining) debates amongst scientists with strong personalities.

The enormous time that Earth has existed is barely recorded in the rocks of Earth. For example, all Archean rocks if taken together might be several kilometers thick, but constitute less than 1% of the Archean Era. The Archean Era comprises the massive amount of time of 2 000 million years (Ma).

Another reason for the incomplete rock record is taphonomic selection. The majority of organisms do not become fossils. During fossilization many details are lost. In modern populations of living clams, older clams have thicker shells than young clams. If such a clam population becomes fossilized, thicker shelled clams are more likely to become preserved than thinly shelled clams. A fossil rock bed would only include thick shelled clams. Only the senior members of the original clam population are known of, whereas the juniors left no fossil.

Diagenetic alteration is the change of a sedimentary rock by a geological process. In an original limestone, fossils may have been beautifully preserved. A long time after the beautiful fossils were formed, they might become altered thoroughly by dolomitization. Dolomitization is the chemical replacement of aragonite by dolomite, a Mg-rich carbonate mineral. Consequently, some details that were originally preserved become lost.

Taphonomic selection does not only affect populations. It also affects the record of ancient environments, which provide context for fossils. A thick unit of sandstone will record an ancient sandy beach. However, in the absence of any other indications, there are no means to determine the paleotemperature.

Weathering contributes to the distortion of the original information on life and habitat. Oxygenation of sulfide minerals destroys many fossils.

How can the traditional gap be closed between the parent disciplines of geology, which focuses on the past, and biology, which focuses on the present? Here the geobiological concept is helpful. The parent disciplines formulate a biological or geological hypothesis. In order to test the hypothesis, geobiologists combine direct and indirect methods of investigation. They combine measurements or experiments conducted in the laboratory or modern environment with the indirect study of rocks. The biological exploration of the present world helps to reconstruct Earth's past, particularly if the rock record is incomplete. Conversely, knowledge of Earth's past provides context for understanding the present. This provides a basis for predictions about the future, which hopefully will result in intelligent precautions. This dual methodological approach is the core of geobiology, mirroring its parentage (Fig. I.5).

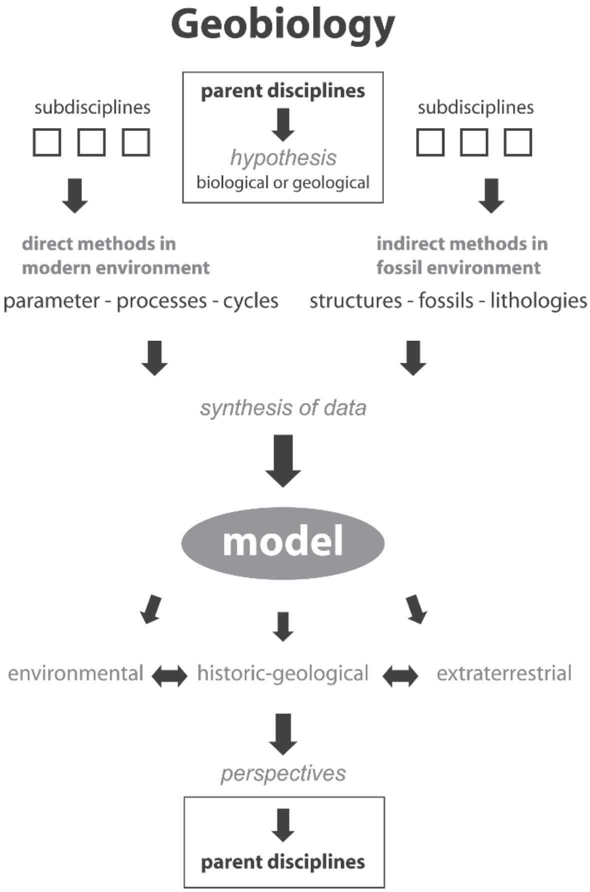


Fig. I.5.
Structure of the scientific discipline geobiology. The parent disciplines biology and geology provide methods that explore both modern and ancient life and environment. The combination of the actualistic observations in the present world with analyses of the fossil record results in a model of Earth and her past. The model feeds back into the parent disciplines offering new perspectives for basic research

The ultimate goal of geobiology is to create a model of Earth as a system. The model is not a static snap shot of present day Earth, but a dynamic, self-moderating system. This system reflects its ancient origin. It accommodates countless reiterative triggering and feedback effects associated with global change over time. Past mass extinctions warn of the dangers of a rapidly warming global temperature, or sudden drops of atmospheric oxygen. A detailed model of Earth as a system provides a basis for modeling extraterrestrial environments. The sister discipline of geobiology, astrobiology, draws heavily upon our knowledge of Earth's system when considering the best ways to detect life.

What is the relation of geobiology to its parent disciplines? Biology and geology are not replaced by geobiology, but continue to exist as archives of basic knowledge and lively sources of hypotheses. Geobiology supports the original research disciplines by a interdisciplinary methodological approach. This opens new perspectives in environmental, historic-geological, and extraterrestrial research. Geobiology is an applied science, providing momentum for the basic research discipline.

The geobiological concept enables the study of benthic microorganisms and their interaction with their environment through Earth history. Fifteen years ago, research on biofilms and microbial mats in modern and ancient sandy tidal flats established this approach (Noffke et al. 1996). Because individual microbes are very small, this early research did not focus on the effect of individual cells on the sediment, but on the effect of the whole microbial population. The actualistic studies in modern coastal sites revealed where biofilms and microbial mats grow, how they interact with sediment dynamics, and which sedimentary structures arise. Because the microbiota, predomiantly photoautotrophic cyanobacteria, respond as a whole entity to environmental parameters, the structures they form are exquisite indicators of the prevailing environment. The structures record the average hydrodynamic pattern, temperatures, salinities, solar radiation, and other conditions. The structures reflect the long-term environmental situation for a given study area.

There have been two rewarding paths to access information on ancient microbiota: the study of fossil bacterial cells, and the study of stromatolites. The search for individual fossils of microorganisms faces the challenge that microbes are very small. The likelihood that they are visibly preserved as tiny body fossils in a rock is minor. Unique exceptions are cherts in Precambrian cratons, where not only bacterial cells, but even whole bacterial populations are preserved. Stromatolites, on the other hand, are sturdy build-ups of considerable size, and their preservation potential is high. They constitute the second cornerstone for paleontological research.

For a long time, paleontologists did not even consider sandstone as a possible host rock for fossils. The reason is that sands and sandstones are highly porous and easily penetrated by circulating water or air. Organic material therefore is quickly dissolved – even in Earth's earliest time, when oxygen levels perhaps were low. Because earlier studies showed that microbial mats form sedimentary structures in modern sandy deposits, the occurrence of fossil structures in equivalent ancient environments was expected. A systematic study by the author explored fossil marine environments starting from young to increasingly old sandstones (Noffke 2000; Noffke et al. 2002, 2003b, 2006a,b, 2008). This work detected fossil MISS in Phanerozoic, Proterozoic, and Archean rocks, revealing that biofilms and microbial mats occurred on Earth's sandy beaches for 3.2 Ga (billion years). Data gained earlier from actualistic measurements in modern settings proved to be highly valuable, because they serve to substitute information not provided by the rock record. Because the fossil MISS reflect the ancient environmental conditions, insight is gained not only into the microbes themselves, but also into their paleoenvironment.

One vital aspect in the search for life on other planets is to determine whether a structure or a fossil in an extraterrestrial deposit is of biological origin. Is a structure or fossil indeed the remains of an ancient organism, or is it something else? Is it an artifact, a mineral assemblage, a thing that appears to be of biological origin, but is not? For example, layered rock units that resemble stromatolites can be caused by abiotic (non-biological) processes as well (Buick et al. 1981; Grotzinger and Rothman 1996; Grotzinger and Knoll 1999). Microfossils must be carefully analyzed to understand their true nature (e.g., Brasier et al. 2006; Schopf et al. 2007). Following these discussions for the biogenicity of stromatolites and microfossils, a set of criteria for the biogenicity of MISS was developed (Noffke 2009).

I.3
Microbially Induced Sedimentary Structures

I.3.1
The Scholarly Definition

The scholarly correct and therefore terribly dry definition of MISS is: Microbially Induced Sedimentary Structures (MISS) are primary sedimentary structures that arise syndepositionally from the interaction of biofilms and microbial mats with the physical sediment dynamics in siliciclastic aquatic environments. Biostabilization counteracts erosion; baffling and trapping responds to deposition of sediment; and binding and growth take place during latencies (the time periods of no or low sediment reworking). Nearly all biotic-physical interactions overlap in the formation of MISS. Whereas primary mineral precipitation does not play any role in the formation of the MISS, secondary mineral accretion induced by the decay of the microorganisms assists in the preservation of these structures. In thin-section, the macroscopic MISS must include microscopic textures that are related to, have been caused by, or represent ancient biofilms or microbial mats. MISS occur from the early Archean to the present, and allow conclusions about the continental shelf and tidal flat environments. MISS are significant indicators for narrow facies zones in marine settings (Noffke 2003b, 2009).

I.3.2
Taxonomic Relation of MISS to Stromatolites

It is important to understand why MISS are not stromatolites. In their classical essay, Buick et al. (1981) describe that the term stromatolite means 'layered rock' (Kalkowsky 1908), and that the term was introduced first for structures of specific morphology and of specific microbial origin (mainly the biologically induced precipitation of carbonate minerals). Later contributions, so Buick et al., either reduced the term for the description of any updomed sedimentary structure with a layered internal texture independent from the origin of this structure; or the term was used exclusively for laminated structures of definitively biological origin (organo-sedimentary structures). The biological influence is mostly understood as microbial baffling, trapping and binding of sedimentary particles plus the *in situ* precipitation of mineral substance. Stromatolites occur only in chemical sedimentary systems, where mineral substance precipitates.

In the description of MISS in siliciclastic settings, Noffke et al. 1996 and 2001b, distinguished sedimentary structures that differ greatly in morphologies from stromatolites. In the formation of the structures, mineral precipitation plays no role. Whereas stromatolites include planar to updomed features, MISS constitute a group of sedimentary structures of currently 17 individual morphologies, from meter to millimeter scale (Noffke 2009).

Because the morphologies of the MISS do not resemble the morphologies of stromatolites at all, MISS are separated as specific types from Buick et al.'s stromatolites.

Five categories of MISS are distinguished: structures induced by growth, by biostabilization, by baffling, trapping and binding, as well as structures that are induced by the interference of all these parameters.

I.3.3
Etymology of the Term

The term arose from a discussion with my fellow student Edgar Nitsch, University of Tuebingen in Germany. He suggested 'microbially induced sedimentary structures'. He found that 'MISS' would be – in his words – 'a sweet abbreviation'. The term was eventually introduced 1996 by Noffke et al. in the journal 'Zentralblatt fuer Geologie und Palaeontologie'.

I.3.4
History of MISS Research

The classical publications on microbial structures in siliciclastic deposits describe 'stromatolites' (Kalkowsky 1908), 'spongiostromata' (Pia 1927), 'algal sediments' (Black 1933), 'growth bedding' (Pettijohn and Potter 1964), 'cryptalgal fabrics' (Aitken 1976), 'algal mats' (Golubic 1976), or 'bluegreen algal bioherms' (Richter et al. 1979). The terms 'microbial mats' and 'potential stromatolites' are used in Brock 1976, and Krumbein 1986, and 'biolaminated deposits' by Gerdes and Krumbein 1987. Researchers interested in Late Proterozoic Ediacaran fossils suggested in the 1980s that 'elephant skin textures', crinkled upper bedding planes, might record ancient microbial mats (e.g., Runnegar and Fedonkin 1992; Gehling 1999). Similar conclusions have been made by Seilacher et al. (1985) in lagoonal sediments of Solnhofen, Germany, by Schieber (1989) in Mesoproterozoic shales of Montana, and Hagadorn and Bottjer 1997. Those early observations on microbial mat-related structures were summarized in the classical volume by Hagadorn et al. (1999), and by Bottjer et al. 2000. This was followed later by a beautiful photo atlas (Schieber et al. 2007). Physical sedimentary systems such as sandy coastal areas are governed by erosion, deposition, and deformation of sediment (Pettijohn and Potter 1964). Typical for such areas are physical sedimentary structures, such as ripple marks, current laminations, dish structures, ball and pillow structures, and convolute bedding, flute marks, bubble sand, and many others (Reineck and Singh 1986). In his classical study on the Bahamas, Black (1933) describes microbial baffling, trapping, and binding, and in 1970, Neumann et al. published their groundbreaking paper on the erodability of subtidal 'algal mats'. The scientific community became aware of the possible influence of microorganisms on non-stromatolitic sediments. Later, the term 'biostabilization' was introduced (Paterson 1994), and the fixation of sediment by microorganisms more closely investigated. All these bacterial activities accumulate sediment, protect the seafloor deposits against erosion, and enhance the preservation potential of fossils (Gehling 1999). About the same time, when elephant skin textures were first discussed as possible fossil microbial mats in sandstones, researchers started to work on modern microbial mats and the sedimentary structures they form (e.g., Cameron et al. 1985; Gerdes and Krumbein 1987; Gerdes et al. 1991, 1993, 1994).

The term 'microbially induced sedimentary structures (MISS)' was coined in 1996, based on quantitative analyses on modern microbial mat-related structures in sandy tidal flats (Noffke et al. 1996). It was shown that 17 main types of MISS arise exclusively from the interaction of biofilms and microbial mats with the physical sediment dynamics, whereas – as in case of stromatolites – chemical precipitation does not play any role (e.g., Noffke et al. 1996, 1997a; Noffke 1998, 1999).

Because of their mixed biotic-physical genesis, MISS differ in morphologies significantly from stromatolites (Fig. I.2), and therefore are regarded as specific types of stromatolites. In 2001 the first classification of MISS was published. The MISS were placed as a separate category into the classification of primary sedimentary structures *sensu* Pettijohn and Potter 1964 (Noffke et al. 2001b).

I.3.5
Distribution of MISS in Space and through Time

I.3.5.1
Temporal Distribution

During the past decade, a set of subsequent studies revealed that fossil MISS occur in tidal flat and continental shelf sandstones of Phanerozoic, Proterozoic, and Archean ages. This systematic exploration showed that the structures seem unchanged for at least 3.2 billion years (Noffke 2000; Noffke et al. 2002, 2003b, 2006a,b, 2008).

The first step has been to investigate modern microbially induced sedimentary structures. Careful observations have described their appearance, and where they occur with respect to their marine environment. Based on this work on modern material, fossil structures in equivalent paleosettings were studied, starting with younger and proceeding towards older rock successions. In the Ordovician rocks of the Montagne Noire, a mountain belt in France, wrinkle structures were interpreted as *in situ* preserved photoautotrophic microbial mats. Detailed mapping of the Ordovician sandstones showed that different types of wrinkle structures occur at different ancient water depths. The structures occur on the ancient continental shelf, in a lagoon, and on a tidal flat. The microbial mats indeed covered the ancient seafloor like a coherent and thick carpet, even affecting the net erosion of the sedimentary basin.

The next step was to visit the Neo-Proterozoic Nama Group in Namibia, a sandstone succession beautifully exposed on the farm Haruchas. Various types of wrinkle structures were discovered. Surprisingly, the fossil photoautotrophic microbial mats occur exclusively in a special environmental setting narrowly characterized by a specific substrate (quartz rich sand) and moderate hydraulic energy. This same relation between microbial mats, type of sediment, and average hydraulic reworking is typical, even today. The study in the Nama Group revealed for the first time that the occurrence of microbial mats coincides with transgression phases.

Subsequent studies focused on much older sandstones of Archean ages. The studies investigated wrinkle structures in the 2.9 Ga old Pongola and Witwatersrand Supergroups, South Africa, and confirmed the occurrence of microbial mats in tidal flats, lagoons, and continental shelves of this old age. Also in the Paleo-Archean, 3.2 Ga Moodies Group, South Africa, ancient microbial mats are recorded as wrinkle structures that indicate extensive carpeting of the sandy seafloor by benthic microbiota, possibly photoautotrophic.

A highlight of this systematic exploration of MISS was the detection of exceptionally preserved structures in the Wit Mfolozi River, South Africa. Here, a 2.9 Ga old sandy tidal flat is exposed with a unique array of 600 individual MISS that correspond in appearance and location exactly with the modern MISS in equivalent tidal flats today.

Since then, MISS were found in sandstones of all Earth ages (Fig. I.6).

Despite the many findings of MISS in the past years, the fossil record of microbial mats in siliciclastic deposits is still spotty as compared to that of stromatolites.

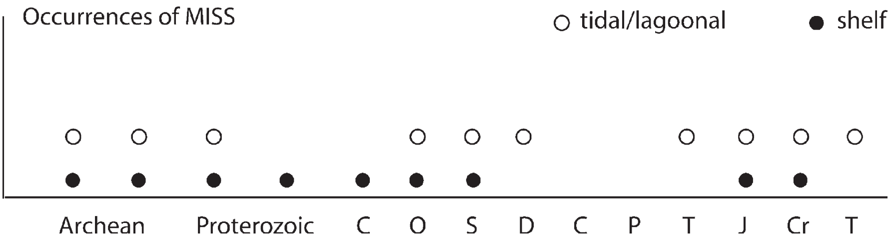


Fig. I.6. Microbially induced sedimentary structures occur from the early Archean Era to today. The structures record that photoautotrophic microbial communities colonized continental shelves, lagoons and tidal flats. They grew at sites where the average hydraulic conditions and the composition of the sediments allowed favourable exposure to light. (The gap for the Carboniferous and Permian is related to the lack of data for MISS occurrences in rocks of this age)

I.3.5.2
Spatial Distribution

In modern and ancient shallow-marine areas, microbially induced sedimentary structures show that biofilms and microbial mats are not distributed at random. The microorganisms grow preferentially in specific habitats, where the average hydraulic dynamic and the composition of the sediments allows the establishment of a biofilm or microbial mat. At all sites described above, ancient photoutotrophic microbes preferentially colonize fine sand substrata composed of clear (translucent) quartz grains. Moderate waves and currents prohibit the deposition of fine mud. Mud blocks sun light, which is essential for photoautotrophic microorganisms. However, the water motion is not so strong that it would erode the benthic microbial assemblages.

The formation of a biofilm or mat includes communication between individual microbes, their migration to form a dense, carpet-like meshwork, and the secretion of EPS (the adhesive mucilages in which the microbes are embedded). All these processes take some time, and can best be accomplished during calm water conditions. As a rule of thumb, microbial mats are thick at marine sites of long-lasting calm water, whereas thin microbial mats indicate less favorable conditions in frequently and strongly reworked coastal areas. For example, on a continental shelf, storms regulate the development of microbial mats. Microbial mats grow more thinly where storms frequently rework seafloor sediments. Another example are tidal flats. In tidal flats, storms are not as significant for the growth of microbial mats as is the duration of subaerial exposure of the tidal surface. In general, the longer the period of exposure, the thicker the microbial mats.

Of interest is that the long-term pattern of storms and of tidal cyclicities creates at all sites a lateral succession of microbial mats from the deepest water towards the land. In over 20 modern study sites, this characteristic change of microbial mat types with the water depth was observed. This same distribution can be seen in the fossil record as well. A beautiful example is the 2.9 Ga tidal flat exposed in the river Wit Mfolozi in South Africa. Here, the same microbial mats are found at the same locations in the fossil tidal flat just as in modern tidal flats (Noffke et al. 2008). The term 'biofilm-catena' was introduced for this pattern of occurrence of specific mat types related to water depth and average dynamic conditions (Noffke 2003c).

I.4
Significance of MISS – Status and Perspectives

I.4.1
Sedimentology

The term ‘sediment’ must no longer be understood merely to describe an accumulation of mineral particles. This is especially the case for sandy sediments often regarded as accumulations of loose quartz grains. In nature, sediments are the habitat for benthic microorganisms, and therefore many sedimentological principles must be reconsidered. In 2010, the first international field conference on MISS was organized by the Society of Sedimentary Geologists (SEPM). The results of this meeting will be published in a SEPM Special Publication.

I.4.1.1
Biotic-Physical Sediment Dynamics Versus Physical Sediment Dynamics

The reworking and transport of sediment by water motion is termed ‘physical sediment dynamics’. However, now sedimentologists are aware that benthic microorganisms colonize the sediments. The microbes affect the primary physical sedimentary processes. This book explains microbial biostabilization, binding, or baffling and trapping. This spectrum of microbiotic-physical sediment dynamics is added to the spectrum of physical sediment dynamics.

I.4.1.2
A New Group of Primary Sedimentary Structures

Primary sedimentary structures comprise both physical sedimentary structures such as ripple marks, and biological sedimentary structures such as trace fossils and stromatolites. Primary structures are formed as sediment is deposited. For example, as sand is deposited, it is rippled by water currents. If the same water currents cross sand which is overgrown by biofilms or a microbial mat, differently shaped ripple marks are formed. Because these differently shaped ripple marks are a consequence of microbial modification, they are termed biotic-physical sedimentary structures. Biotic-physical structures are a new group with equal significance to physical and biological sedimentary structures.

I.4.1.3
Indicators for Sequence Stratigraphy and Basin Analysis

Microbial mats develop on tidal flats, lagoons, and on continental shelves. Analyses of fossil sandstone successions of various Earth ages show that microbial mats thrive especially well during transgressions. A transgression is a rise in sea level. Large areas of continental margins are submerged and constitute new sunlight-flooded habitats for photoautotrophic microbial mats. If the rock successions are composed of monotonous sand-, silt-, and mudstones, the biogenic structures serve to detect and to quantify the sea level oscillations of past ocean systems.

I.4.2
Paleontology and Microbiology

The significance of MISS for understanding the biological record of Earth was the focus of two special issues edited by Noffke and Paterson 2008, and Noffke 2009.

I.4.2.1
First Cyanobacteria

One of the most intriguing paleontological questions is, when did cyanobacteria evolve? Why is this question so important? Because cyanobacteria are photoautotrophic, and they produce oxygen similarly to green plants. It is assumed that the early atmosphere of Earth was free of oxygen. In the course of time, evolving cyanobacteria may have contributed to the first accumulation of oxygen in the atmosphere. The spectacularly preserved MISS in the Wit Mfolozi River of the Pongola Supergroup, South Africa, record that already 2.9 Ga ago, cyanobacteria may have evolved to a high diversity (Noffke et al. 2008). This suggests that cyanobacteria originated much earlier. The formation of such complex microbial cells that include chloroplasts might have taken millions of years.

I.4.2.2
First Photoautotrophic Microbiota

Photoautotrophy does not necessarily go with oxygen production, because there is oxygenic photoautotrophy and anoxygenic photoautotrophy. The oldest photoautotrophic microbiota are found in the 3.2 Ga old Moodies Group, Barberton Greenstone Belt, South Africa (Noffke etal. 2006b). As in younger, equivalent paleoenvironments, these microbial mats clearly were distributed exclusively in the photic zone. The photic zone is the water depth in an ocean which is penetrated by sun light. However, it is not clear if these Moodies microbial mats were constructed by cyanobacteria, or by other photoautotrophic microorganisms.

I.4.3
Astrobiology

I.4.3.1
Earthly Analogues

Earthly analogues are both life forms and environments present on Earth that are similar to life and environments expected on other planets. For example, a microbial mat in an Antarctic lake on Earth represents an ecosystem that potentially might occur in the polar regions of Mars.

Water is life everywhere, not only here on Earth. NASA's missions to other planets use remote sensing equipment to gather information about the presence of water. On Mars, sandy sediments originally deposited under water are much more frequent than any other type of Martian deposit. If life was, or is present on Mars, sandy deposits are likely to contain MISS (Fig. I.7). Indeed, the successful rover missions to Mars have found sandy, aquatic deposits. Biogenic sedimentary structures such as MISS can be expected.

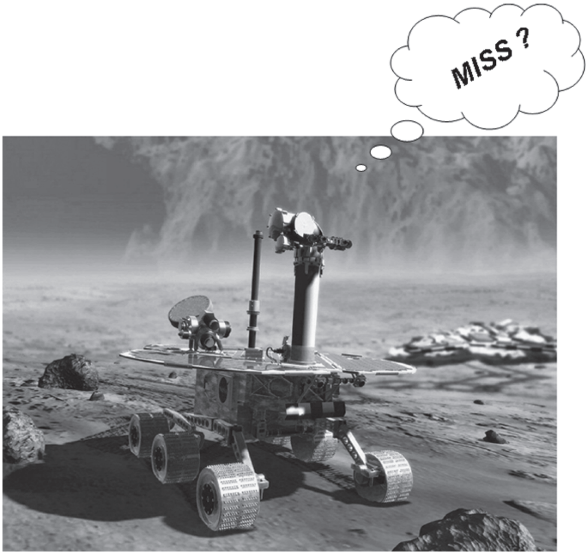


Fig. I.7.
A remotely controlled rover moves across the surface of Mars. Its camera systems scan the surface of Mars for possibly biogenic structures such as MISS

I.4.3.2
Biosignatures

Biosignatures is a term commonly used for signs of life on other planets. In their definition of universal life, Nealson and Berelson (2003) correctly state that the form of life on other planets is unknown. The problem therefore is to detect life even without knowing specifically what to look for. Astrobiologists solve this dilemma by first investigating the 'background noise' of a planet. What is the common signature of the atmosphere, hydrosphere, and lithosphere? As soon as this background noise is mapped, any local deviation could be a sign that life exists. Life must employ a physical structure that enables it to maintain a chemical gradient different from its immediate environment. This structure and gradient may cause a deviation that stands out from the background noise. This deviation is the biosignature.

MISS are biosignatures formed by microorganisms in sandy deposits (special issue edited by Noffke and Bottjer 2009). NASA needs information to know what biosignatures to look for – if life is out there.

I.4.4
Oceanography and Climatology

Shallow-marine areas along the coasts are interfaces, where various hydraulic, sedimentary, and meterological parameters interact, shaping and sculpturing the depositional surface into a multitude of sedimentary structures. In a tidal flat, the ascending flood currents generate ripple marks of various sizes and forms. During the ebb tide the same tidal surface is exposed to sunshine, rain, and even frost. All these environmental factors together give rise to desiccation cracks, evaporitic minerals, wind ripples, and many other structures. Biofilms and microbial mats overgrow and shelter

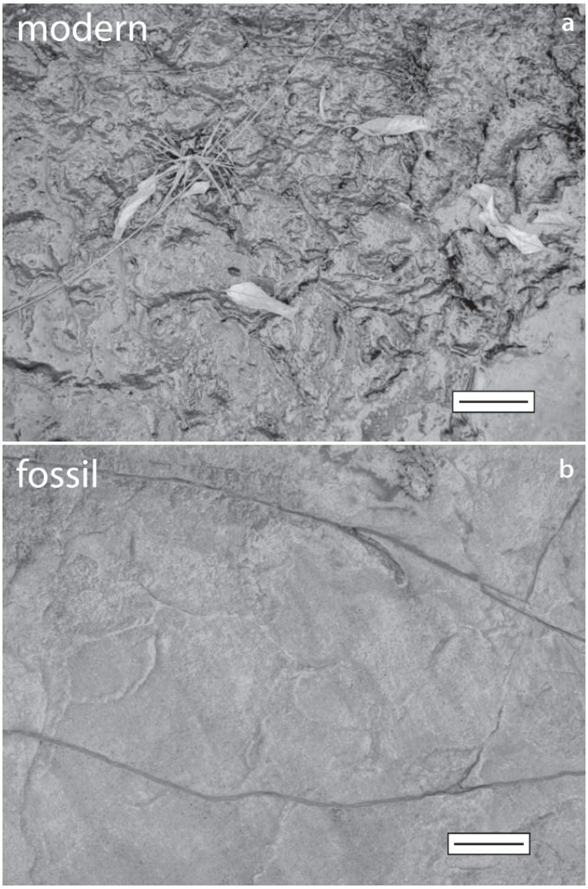
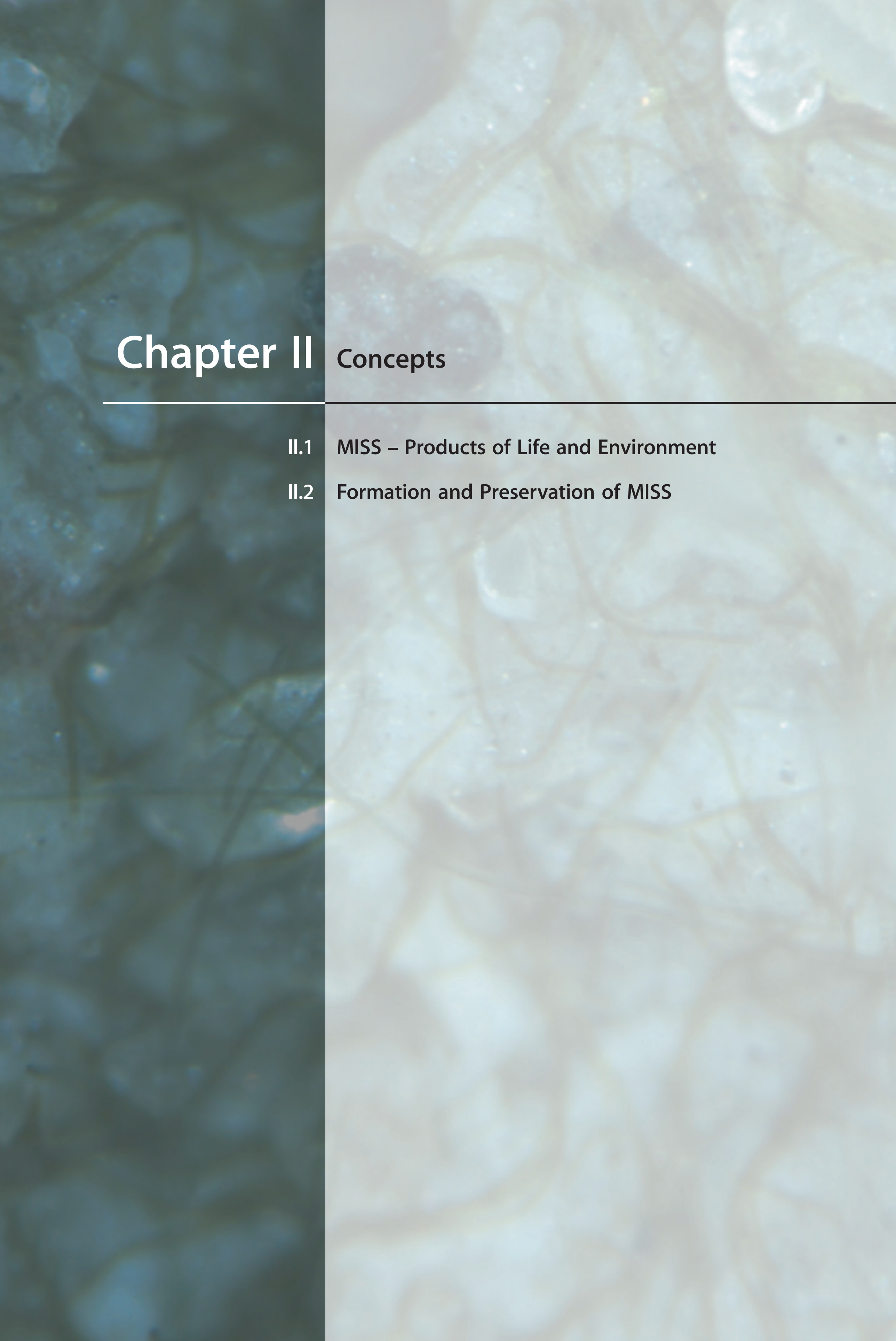


Fig. I.8.
Microbial mats seal information on weather conditions at the time of deposition of sediments. **a** A microbial mat grows in a shallow pool on a modern beach. Because the weather was dry and hot for several days, desiccation cracks have started to form in the mat (Fishermans Island, Virginia, USA). **b** The same situation, but 2.9 Ga ago: a fossil microbial mat in an ancient tidal flat shows desiccation cracks and records dry and hot summer days (Pongola Supergroup, South Africa)

sediments, and preserve the moment when surface structures were just formed. An ancient tidal surface constitutes a snap shot, a picture, of a long past world. Biofilms and mats seal, conserve and archive the information written by the elements into the sedimentary surface billions of years ago (Fig. I.8). The study of MISS gives insight into past oceans and climates. MISS play a dominant role in understanding microbiota in cold and moderate climate zones, both modern and ancient.

I.5
Collection of MISS

A systematic collection of modern and ancient MISS is stored by the Smithsonian Museum for Natural History, Washington, DC. The collection is updated regularly by the author. It includes rock samples, relief casts, thin-sections and fixed modern microbial mats. The MISS in the 3.2 Ga old Moodies Group belong to the proposed UNESCO world heritage site Barberton Makhonjwa Mountain Lands, South Africa.



Chapter II Concepts

II.1 MISS – Products of Life and Environment

II.2 Formation and Preservation of MISS

Chapter II

Concepts

II.1

MISS – Products of Life and Environment

The first part of this chapter (Sect. II.1) illustrates the complex interaction between benthic microbiota and their sedimentological environment. Although the sedimentological environment directs distribution and growth of benthic microbiota, the microbiota also influence their depositional habitat. These interactive processes produce MISS.

In the second part of this chapter (Sect. II.2), the preservation of MISS is elucidated. It will also be shown, how to differentiate biogenic MISS from similar structures of abiotic origin. This evaluation of biogenicity of MISS is important for the reconstruction of prokaryotic evolution on Earth, and the search for extraterrestrial life.

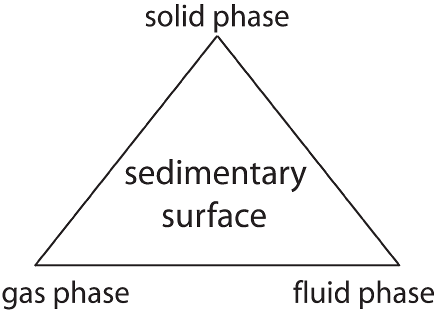
Regarding the complexity of microbe-sediment interactions and their manifestation as MISS, the best place to start is where all connect: the sedimentary surface.

II.1.1

The Sedimentary Surface – an Interface

Much oversimplified, the sedimentary surface is the interface between a solid, a fluid and a gas phase (Fig. II.1). At this interface, sedimentary structures arise, manifestations of the exchange of thermodynamic energies of the different phases. What does this mean? Here are two examples: In nature, water currents (fluid phase) affect the seafloor and form ripple marks in the sand (solid phase). The kinetic energy of a fluid phase is transformed into deformation energy, when affecting a solid phase. A second example is: During the ebb tide, a tidal flat is exposed to hot and dry weather. Consequently, water evaporates from the tidal sediments. The sediment dries out. The fluid phase (water) turns into a gas phase (vapor) and leaves the solid phase (sediment).

Fig. II.1. The sedimentary surface is the interface, where the three phases 'gas', 'fluid', and 'solid' meet



N. Noffke, *Geobiology*, DOI 10.1007/978-3-642-12772-4_2,

This transformation of thermodynamic energy of one phase into another may cause desiccation cracks in the sediment.

This simple model of interfering phases becomes very complex in the study of natural marine environments. In continental shelves, lagoons and tidal flats, three main types of sedimentary systems can be distinguished. Each sedimentary system is characterized by specific sediment-dynamic processes, basically highly interwoven interferences of the three phases.

II.1.1.1

The Three Main Types of Sedimentary Systems

The three main types of sedimentary systems comprise the physical, the chemical I, and the chemical II systems, Noffke et al. 2003a, (Fig. II.2).

II.1.1.1.1

Physical Sedimentary System

Physical sedimentary systems are governed by 'physical sediment dynamics'. Physical sedimentary dynamics comprise erosion, deposition and deformation of loose mineral grains by hydraulic reworking. Resulting from this reworking are physical sedimentary structures such as ripple marks. Good examples of physical sedimentary systems are siliciclastic (sandy) depositional areas, such as the tidal flats of the North Sea in Germany. Sand consists of loose particles, and no secondary mineral precipitation takes place that would cement the grains.

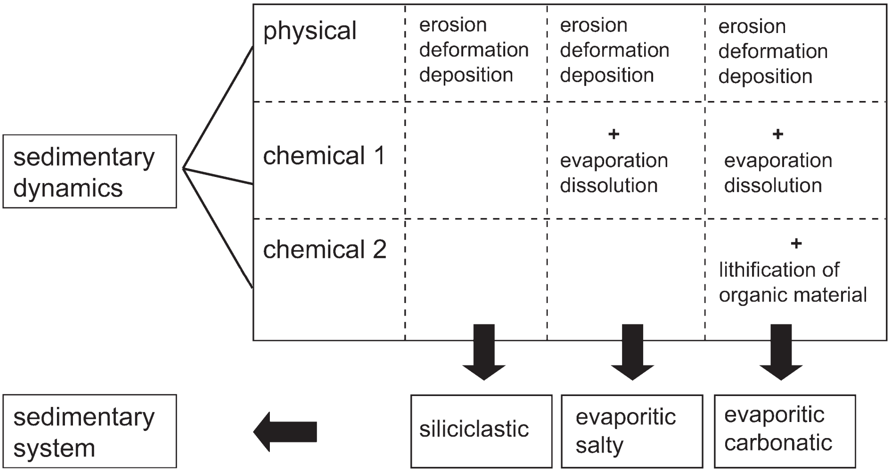


Fig. II.2. Sedimentary systems such as tidal flats can be divided into three main groups: physical, chemical I and chemical II. Each group is characterized by specific sedimentary dynamics. Erosion, deformation or deposition of sediment is caused by water motion. Evaporation of minerals might take place when the tidal flat surface is subaerially exposed, and the weather is hot and dry. As soon as rain sets in, or the flood current inundates the tidal flats, these minerals dissolve again. Lithification of organic matter is the *in situ* mineralization of biomolecules by heterotrophic microbes

II.1.1.1.2
Chemical I Sedimentary System

In chemical I sedimentary systems, the physical sediment dynamics play also a role. Evaporation and dissolution of minerals occurs as well. During ebb tide, a tidal flat surface is subaerially exposed. In the sediment, salt-rich capillary water migrates upward until it reaches the depositional surface. Here, the water evaporates and releases ions. The ions immediately react with each other and form salt crystals. The freshly crystallized salt minerals accumulate in pore spaces between the sedimentary grains close to the surface. The precipitation of salt minerals such as anhydrite, gypsum, or halite is typical for evaporitic-salty depositional areas (Warren 1999). Evaporitic-salty sedimentary systems characterize climate zones that are hot and arid. Examples include sabkha-like settings along the coast of the Red Sea, and the Persian Gulf (Friedman et al. 1985; Purser 1973; Gerdes and Krumbein 1987; Gerdes et al. 2000a,b).

II.1.1.1.3
Chemical II Sedimentary System

In chemical II sedimentary systems, erosion, deposition, and deformation take place. Evaporation and dissolution of salt minerals may also be observed. The special characteristic of chemical II systems, however, is the *in situ* degradation of organic matter that produces carbonate minerals (Krumbein 1979; Friedman et al. 1992; Warren 1999). The transformation of biomass into mineral substance is termed 'destructive biomineralization'. This *in situ* mineralization will be explained in detail later in this chapter. In contrast to chemical I settings, evaporitic-carbonatic depositional areas indicate a hot-humid climate. A good example of such an environment is the tidal area of the Bahamas, where modern stromatolites occur (e.g., Dill et al. 1986; Reid et al. 2000, 2003).

The division of sedimentary systems into the three groups is not strict. Many intermediate systems exist. For example, in the North Sea tidal flats, which represent a siliciclastic sedimentary system, carbonate minerals form as a result of bacterial decay. Requirements for this process are extreme high temperature and high humidity during summer months. Carbonate formation in the North Sea tidal flats is exceptional and temporary. Only very small carbonate particles of microscopic sizes are formed (Kropp et al. 1997; v. Knorre and Krumbein 2000).

II.1.2
Life at the Interface

Interfaces are not only communication areas for the solid, fluid and gas phases. The phases can be biologically controlled in cells or biofilms that colonize the interface. Many believe that life is a consequence of communication of different phases along interfaces. This concept is discussed later in the section on biofilms. If physical or chemical parameters affect the sedimentary surface, then organisms that colonize this interface can also affect sediments. A close look at a tidal sedimentary surface reveals that the sand grains are overgrown by countless microbial cells (Fig. II.3). The huge

Fig. II.3.
A modern tidal flat appears to be composed of sterile sand. However, viewed in close-up, the sands are widely colonized by a great variety of benthic microbiota (Mellum Island, North Sea, 1995)

numbers of single cells modify the interaction of phases, the formation of structures, and eventually the writing of Earth's lithological script.

Of high geological significance are benthic cyanobacteria, because they form biofilms and coherent, leathery microbial mats. These biofilms and mats affect sedimentary processes significantly thus generating MISS. The following section describes biofilms and microbial mats.

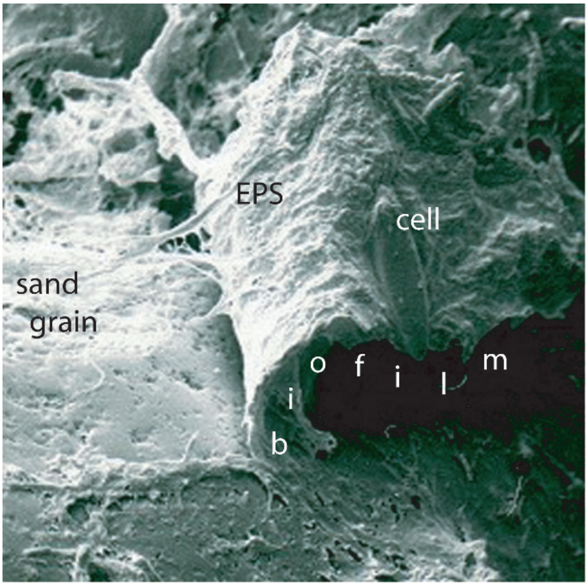
II.1.2.1
Biofilm

A close look at the sedimentary surface reveals an exotic, complex world. It is here where all phases connect. The science on biofilms points to the very beginning of existence. It gives insight into the surprising abilities of prokaryotes, which earlier generations of scientists termed 'simple life'.

For a long time, the general concept on bacteria was that of blobs of plasma surrounded by a membrane that gives the cell a round or an elongated shape. The blob would drift randomly gaining energy and building organic material from nutrients or sun light. However, this picture has changed by new research (e.g., Marshall 1976; Characklis and Marshall 1990; Decho 1990, 2000; Sutherland 2001; Harrison et al. 2005; Stoodley et al. 2002; Flemming et al. 2007). In the past twenty years, microbiologists have detected stunning facts about prokaryotes and the world they live in. Nothing happens without their consensus. In natural environments, the majority of prokaryotes occur as 'biofilms' (Costerton et al. 1995). A biofilm can be regarded as a microscopic lump of gel dumped flat onto a substrate. Everywhere in nature, where a solid surface is covered by a few layers of water molecules a biofilm may form. It is noteworthy that most scientific work has been conducted on planktonic prokaryotes, though the first observations on biofilms were made in the late 1600s by Antonie van Leeuwenhoek (Harrison et al. 2005).

Analyses of the microscopic blobs revealed that the biofilms are highly complex assemblages of single celled organisms. The assemblages are often composed of different species. The biofilm is held together by a mucous matrix, the so-called extracellular polymeric substances (EPS), (Decho 1990, 2000). Water constitutes up to 97% of the biofilm mass (Cookey 1992; Krumbein 1994; Zhang et al. 1998). The outer shape of a

Fig. II.4.
Under scanning electron microscope (SEM), a biofilm composed of microbes and EPS envelopes a quartz grain. The surface of the quartz grain is exposed on the left



biofilm can be a layer, a lump, a stalk, or a mushroom-like morphology (Harrison et al. 2005), Fig. II.4. The production of EPS by microbes is dynamic and can follow cyclic patterns (Decho et al. 2005).

In a biofilm, cells form microcolonies distributed in a controlled pattern in the translucent EPS (e.g., Moeller et al. 1998). Microbes in a biofilm are optimally organized so that their nutritional, temperature, salinity, and other needs are met. A community that serves the well being of its constituent members requires cooperation and communication. The microbes have to interact, to compromise, and to compete for niches in the biofilm community. Biofilms are controlled by the microbial genes (intrinsic factors) and by the environment (extrinsic factors) (e.g., Wimpenny 2000; Sutherland 2001; Stoodley et al. 2002).

EPS formerly thought to be just 'slime' turned out to be well structured gels. These mucilages contain channels and voids often filled by water. The EPS immediately respond to changes in the environment of the biofilm. Their structure is also a function of the constituent microbial species. In a biofilm, the microbes are in equilibrium with their environment, because the EPS buffer external stress factors (Sutherland 2001). EPS are mechanically stable mucilages composed of complex polysaccharides. Enzymes, proteins, lipids, extracellular DNA, as well as detritus from the environment are also present (Decho 1990, 2000; Sutherland 1990; Flemming et al. 2007). It is very interesting to note that EPS are secreted by Archea, Bacteria and also many Eukaryotae. EPS must have been repeatedly invented via convergent evolution as a useful mechanism in these different groups.

EPS are adhesive, and their sorption properties enable the microorganisms to attach to solid surfaces, and to transport necessary nutrients. Flemming et al. 2007 term the EPS 'house of cells', which provides a stable, structural frame. Flemming and Wingender 2001, and Klausen et al. 2004 describe the molecular structure of EPS, where hydrophobic interactions, links by cations, and the entangled arrangement of the polymeric chains form a viscous-elastic, firm build-up. The mechanical stability of EPS ensures the specific spatial arrangements for cells in order to facilitate interaction. Microbes are not confined to their sites of colonization. They can move around. However, their mobility depends on viscosity of surrounding EPS. When EPS have low viscosity, microbes can move about freely. When EPS have higher viscosities, microbes are immobile (Sutherland 2001).

Channels that penetrate the biofilm are like a system of pipes that flush the microbial community. The channels are arranged in a fashion that allows nutrients and gases to reach all members of the biofilm (Lawrence et al. 1998).

EPS also serve to filter UV light. This ability may provide insight into the evolutionary challenges of the early prokaryotic environment. Early life might have developed in shallow water, which was flooded by the UV-rich radiation of the young Sun (Kieber et al. 1990; Mopper et al. 1991).

EPS are electrostatically charged so that food particles, clays and other minerals are trapped. EPS include pyrovate ketals, uronic acids, sulfate and phosphate groups that provide chemical bonding sites (Decho 2000). The trapped matter contributes to the formation of microniches, which serve as habitats for different microbiota. This structuring in habitats increases diversity in the microbial community.

EPS also might serve as a food source in times of nutritional scarcity. They can be hydrolyzed and digested by the microbes (Kolenbrander et al. 1999).

EPS are an 'activated matrix' that can transport vesicles filled with enzymes around like parcels. These parcels provide nutrients for every microbe in the biofilm (Schooling and Beveridge 2006). The vesicles may also serve to exchange genetic material. This is termed horizontal gene transfer from one microbe to another – even between different species! The parcels also may include less friendly gifts such as antibiotic substances that attack another group of microbiota in the biofilm (Joubert et al. 2006). Tait and Sutherland 2002, describe such microbial warfare in the beginning stages of a biofilm, when various microorganisms come together and compete for the most suitable space and access to nutrients. Sadly, their behaviour resembles all too well that of their primate descendants. After the initial competition during the early stages of a biofilm, the community becomes an orderly, smoothly functioning system. The microorganisms profit from the exchange of genetic material (information), and they can share metabolic by-products thus effectively exploiting all available sources of energy at low cost for every member. Different microbes that act in concert have a multitude of abilities and can provide shelter against external stresses including invading pathogenic (disease-causing) microbes.

New research shows that planktonic and biofilm life styles are nothing more than two different phenotypes of the same genome (Stoodley et al. 2002). That means that single microbes most frequently give up their planktonic life style in order to join other microorganisms in a biofilm. Intercellular communication by cell-cell signaling is prerequisite to organize a biofilm.

When is a biofilm formed? An answer could be found at the beginning, the origin of life. In 1983, Cairns-Smith wrote that clay platelets served as an assembly surface for enzyme molecules. Biofilms, like ancient clay templates, provide infrastructure to enable stable positioning of microbes with respect to a gradient of any kind. The reason for the assembling of microbes along a surface could be to effectively process nutrients. In their planktonic state, prokaryotes form a 'roiling mass in constant Brownian molecular movement' (Stoodley et al. 2002). Once the position of a microbe is secured, the cell can adapt its metabolism to the available resources.

Indeed, this can be observed in nature (Stoodley et al. 2002). In the ocean, prokaryotes form plankton as soon as nutrients become scarce. The plankton constitutes the 'planktonic pattern of gene expression' that responds to a temporary nutrient-poor environment (Fig. II.5).

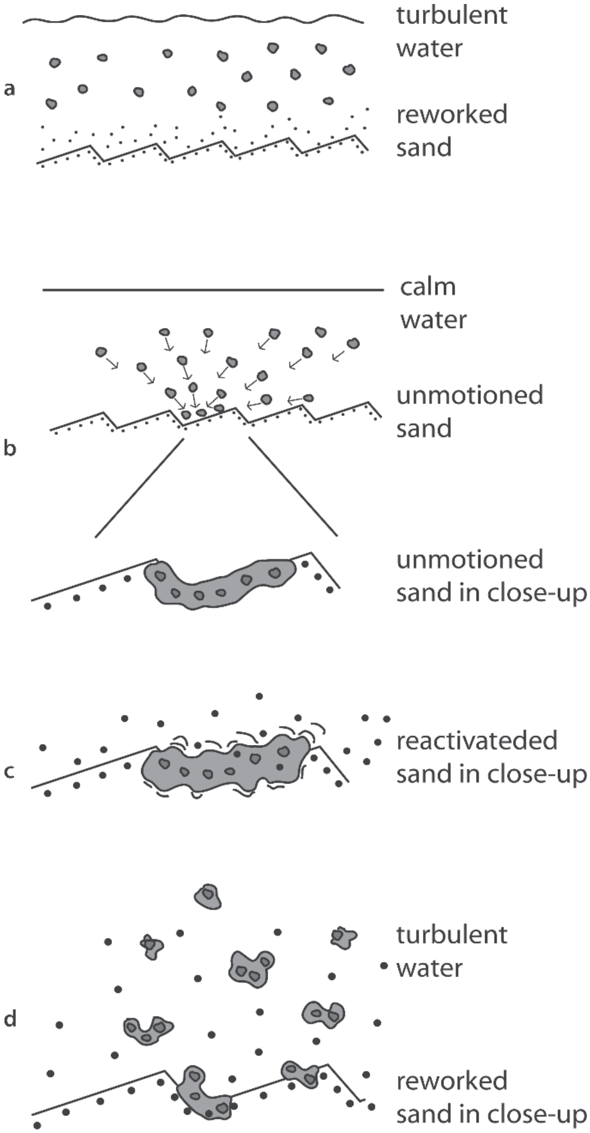


Fig. II.5. Formation and disintegration of a cyanobacterial biofilm in response to sediment-dynamic conditions. *Stage a:* The planktonic stage of microorganisms. The cells are distributed at random in water, because turbulence does not allow formation of a biofilm on strongly reworked sea floor deposits. *Stage b:* The hydraulic reworking ceases. In order to establish themselves into a favorable position with respect to a gradient, the microbes start to settle on the sandy substrate. They form a well-organized biofilm. *Stage c:* If the sandy substrate is affected by waves or currents, the biofilm keeps up with the moving surface. The biofilm does so by baffling, trapping and binding. Following Stoodley et al. 2002, this could be termed 'active redistribution'. *Stage d:* The biofilm disintegrates, and fragments of biofilm are transported away from the original site. This could be termed 'passive redistribution' of microorganisms

A sudden input of nutrients can change the situation immediately. Stoodley et al. 2002, give the example of gas exhalations along an oceanic rift system. As soon as gases escape from the seafloor, prokaryotes very quickly establish a biofilm. The prokaryotes have switched from their planktonic to a benthic life style. The biofilm is formed so that the prokaryotes can use all nutrients supplied by the gases more effectively. The biofilm is the 'biofilm pattern of gene expression' of the prokaryotes (Stoodley et al. 2002). The microorganisms gather around this spot of food supply, a gathering like a party, stationary, but temporary. As soon as the food source is exploited, the biofilm disintegrates.

Stoodley et al 2002, summarize the formation and disintegration of a biofilm in 4 main steps. First, the planktonic cells form a film attached to a surface. The cells are mobile, and only a little amount of EPS can be found. The prokaryotes even can leave to resume their planktonic lifestyle. When colonizing a nutrient-poor surface, biofilms have simple structures, and often are populated only by a single species. Laboratory studies with the confocal microscope show that microbes accumulate especially at the margins of the biofilm near the nutrient-rich water. Because microorganisms can give up their membership to this initial consortium and leave in planktonic form, the term 'reversible adhesion' is used for this first phase. The section on microbial mats and biofilm-catenae will explain that biofilm-type colonization corresponds to this phase of biofilm-formation.

The second phase is characterized by quick EPS production. The microbes are now irreversibly adhered to the substrate. In laboratory experiments this second phase can be as short as 15 minutes. In this stage, intercellular cell-cell communication becomes a dominant controlling factor. The prokaryotes have quorum-sensing inducer genes that become active as soon as the density of cells in an area becomes sufficiently high (Fuqua et al. 1996; Ruby 1996; Dunlap 1997; Davies et al. 1998). The microbes communicate by sending enzymes. This complex system includes different levels of exchange of information, even between different species. The intercellular signal triggers the formation of EPS, and coordinates the placement of microbes in the biofilm matrix. This may lead to the third phase, biofilm-maturation. In nutrient-poor environments, biofilms may not attain the third phase. They remain a simple layer of cells with no complex structure. The section on microbial mats will describe such simple layers as endobenthic microbial mats.

Highly complex biofilms can develop in environments that offer sufficient nutrients. The prokaryotes in the biofilm rearrange their positions in the EPS to make space for channels to be built. These channels flush the biofilm, transport nutrients, and remove waste. Newly arriving prokaryotes use the channels to migrate into the biofilm. The established microbes are now mostly fixed in place. The microbial community is composed of physiologically fully integrated members. This level of organization might be compared with the organization of a macroorganism, composed of organs. If the nutrient can only be cracked by a multistage digestive process, then many microbes organize to form stable, metabolically coupled layers. Each layer is composed of a species that is physiologically integrated by its metabolism to the microbial layer beneath or above. The microbes form a 'digestive cooperative'. This ability is prerequisite for the functionality of multilayered microbial mats. In the next section, epibenthic microbial mats belong to this group. Once the nutrients are exploited, the biofilm disintegrates.

The fourth phase is the disintegration of the biofilm, defined by the detachment of microbes, or even of portions of the biofilm. A current can rip off pieces of the biofilm that can be transported downstream until they are redeposited again. It is assumed that biofilms can multiply by this mechanism. The prokaryotes that detach return to their planktonic stage (planktonic revertants, Stoodley et al. 2002). The termination of a biofilm could be triggered by nutrient scarcity, or simply overpopulation. The circumstances that induce the disintegration are not always obvious. The microbes might simply 'decide' that it is time to move on, and to leave the community. Disintegration of microbial mats with the seasons is explained in the next section.

II.1.2.2
Microbial Mat

There are many excellent definitions of microbial mats (e.g., Krumbein 1983; Gerdes and Krumbein 1987; Stolz 2000; Konhauser 2007). In general, the term is understood as replacing the term 'algal mats'. Especially in carbonate sedimentology, the significance of algal mats was always recognized. Mileposts in research on microbial mats in marine settings are studies by Black 1933, Hardie and Garrett 1977, Davis 1983, Cohen and Rosenberg 1989, Ginsburg 1991, Des Marais et al. 1992, Friedman et al. 1992, Krumbein et al. 1994, Stal and Caumette 1994, Reid et al. 1995, Stal 2000, as well as outstanding research of many others.

Algal mats are constructed predominantly by benthic cyanobacteria. Cyanobacteria are large, photoautotrophic microbes. Many benthic groups are able to move through the sediment (e.g., Golubic and Knoll 1999).

Thomas Neu (1994) applies the concept of biofilms to microbial mats that occur in sandy tidal flats of the North Sea. He understands microbial mats as advanced biofilms. Indeed, the development of microbial mats and their disintegration corresponds to the four stages of biofilm formation of Stoodley et al.'s 2002.

Early stages of a microbial mat are simple biofilms (Fig. II.4). Cyanobacteria attach to the surfaces of sand grains and start to secrete EPS. This biofilm-type of colonization is reversible. The cells easily can be washed off the grains and water samples often include a great amount of individual cells, trichomes or filaments. This initial consortium corresponds to Stoodley et al.'s first phase. This following section of Chap. II will explain that these early stages of colonization are typical end stages for marine environments constantly reworked by water motion.

In favourable environments biofilms form around individual sand grains. These initial biofilms of adjacent grains grow until they form a laterally continuous, organic layer. This layer is visible macroscopially. It is a microbial mat. These primary microbial mats are extremely well adapted benthic consortia that immediately respond to changes in their environment. In sandy tidal flats along the North Sea, such pioneering microbial mats are formed by *Oscillatoria limosa*. The following sections will describe how this microbe constructs endobenthic microbial mats within just a few hours. Such pioneer mats correspond to stage 2 of Stoodley et al.'s system.

In some tidal flat areas, microbial life flourishes. Nutrient sources are abundant and a sandy substrate favours mat formation. At such sites, multicoloured sand flats can be found (Gerdes and Krumbein 1987). Multicoloured sand flats are thick, epibenthic microbial mats composed of three main bacterial groups (Fig. II.6). These mature microbial mats represent Stoodley et al.'s stage 3. Figure I.1 is a fine example.

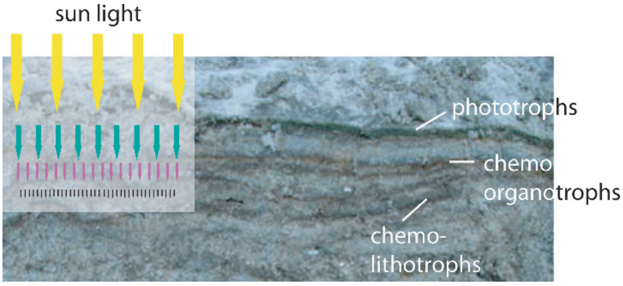


Fig. II.6. Digestion of sun light by a microbial mat. A vertical cut through microbial mat-overgrown tidal sediment reveals a stack of layers of each different colour. Each layer is composed by a different group of bacteria. The metabolisms of the bacteria interact with each other forming a digestive cooperative in the sense of a biofilm. The energy of sun light is transformed by photosynthesis into organic substance. The organic substance then is decomposed by various chemoautotroph bacteria

Microbial mats are living systems and as such only temporary. In its final stage, a microbial mat is fragmented into mat chips that are transported away by water currents. These mat fragments can dissolve completely releasing individual cells into the water. If redeposited at another site, they also can serve as nucleus for the reestablishment of a new microbial mat. This disintegration of a microbial mat corresponds to Stoodley et al.'s stage 4.

In sandy tidal flats, microbiologists focus on algal mats especially of stage 3, multicoloured sand flats. These epibenthic mats are composed of three main microbial groups: cyanobacteria, colourless and purple sulphur bacteria, and sulfate-reducing bacteria. Each group of bacteria forms a discrete layer in the sediment. The metabolic cycles of each vertically adjacent bacterial layer are coupled, thus forming a stack. This stack of layers is visible in vertical cross-sections through tidal flat sediments (Fig. II.6).

The top layer of this stack is formed by cyanobacteria. They are primary producers assembling organic material using sun light by photosynthesis. Organic substance of deceased primary producers is gradually decomposed by heterotrophic microbes. These heterotrophic prokaryotes establish directly beneath the cyanobacteria layer. Chemoorganotrophic bacteria deconstruct large biomolecules deriving from deceased cyanobacteria and EPS into simpler chemical compounds. By cracking large biomolecules, the prokaryotes release the energy of the binding forces that hold the biomolecules together. This energy drives their metabolism. The bacteria are 'organotroph', meaning that they live on organic chemical compounds.

Below the chemoorganotrophic bacteria, another group of prokaryotes establishes. This group of prokaryotes decomposes the simple chemical compounds discarded by the chemoorganotrophic bacteria above. These prokaryotes manage to use even the little energy provided by smallest chemical compounds and therefore are 'chemolithotrophic'.

Some compare a microbial mat with a bioreactor (Noffke 2003c). The original energy provided by sunlight is incrementally consumed by benthic microbiota. The microbes form a biofilm-like digestive coorperative. The utilization of sun light functions like an assembly line.

II.1.2.3
Cyanobacteria for Beginners

Because microbial mats are coherent surfaces, they affect sedimentary processes. It is the top layer of microbial mats that is of primary geological significance. This layer is exposed to moving water, thus subject to sediment erosion or deposition. In this way, the study of cyanobacteria assists geobiologists working on microbe-sediment interaction. Examples of cyanobacteria are shown in Fig. II.7.

In microscopic close-up a microbial mat includes a carpet-like network of filaments. A 'mat lamina' is a single layer of microbial mat, independent of its species composition. A 'trichome' is one individual filamentous cyanobacterium. A 'filament' is one bundle of trichomes. A 'coccoid' cell is round shaped. Coccoid cells are often arranged in clusters. EPS are extracellular polymeric substances. Mineral components in a microbial mat include *in situ* mineralized particles such as carbonate pellets (Gerdes et al. 2000), or detrital grains that were transported into the mat, trapped or bound.

The name 'cyanobacteria' derives from the Greek word 'cyanos' for a blue-green colour. Botanists prefer to call this microbial group 'blue-green algae'. Cyanobacteria are not algae, but gram-negative, photosynthetic bacteria (e.g., Staley et al. 1989; Whitton and Potts 2000). Filaments of considerable sizes such as of *Microcoleus chthonoplastes* indeed look like algae. Advanced analyses revealed the bacterial nature of cyanobacteria (e.g., Stanier et al. 1976).

Cyanobacteria are complex microorganisms that include pigments such as chlorophyll *a* to facilitate photosynthesis. They employ two photosystems, I and II. In general, the two photosystems work together. In this case, H_2O is used as an electron donor. The microbes crack water molecules in order to gain the binding energy between hydrogen and oxygen. Because this binding energy is relatively high, energy-rich short-waved light triggers this photoreaction. This type of photosynthesis, oxygenic photosynthesis releases $O_{2.}$

Some cyanobacteria are able to employ only photosystem I. This is especially helpful, when only long-wave, low-energy light and an alternative electron donor (e.g., H_2S, Fe(II), As(III)) is available. This light is not sufficient to crack the high chemical binding energy between hydrogen and oxygen. As this photoreaction does not involve the release of oxygen, it is anoxygenic photosynthesis.

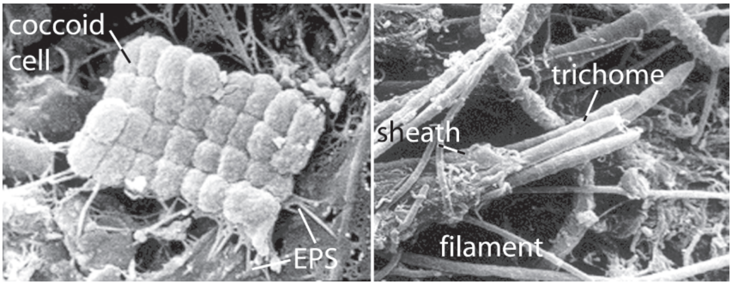


Fig. II.7. Cyanobacteria in SEM. The left photo shows *Merismopedia punctata.* It forms pillow-like clusters of cells that are attached to sand grains. Attachment is facilitated by extracellular polymeric substances (EPS). The right photo shows *Microcoleus chthonoplastes*. It is a filamentous species. Both cyanobacteria are cosmopolitan that is they occur worldwide in sandy tidal flats. It is for the large filaments of *M. chthonoplastes* for which microbial mats for a long time have been termed algal mats

II.2
Formation and Preservation of MISS

The previous section explains how phases define and affect the sedimentary surface. Now this theoretical concept is applied to the study of microbial mats. The following section elucidates the formation of MISS, and the primary and secondary processes that result in their preservation.

II.2.1
Development and Preservation of Microbial Mats: the Ecological and the Taphonomic Window

By definition, MISS are primary biotic-physical sedimentary structures that form syndepositionally by the interaction of benthic microbiota with the physical sediment dynamics. It is of significance to understand that the distribution of MISS in the fossil record is a function of the ecological and the taphonomic windows (Fig. II.8). The ecological window is the establishment and growth of biofilms and microbial mats at ecologically suitable sites. The taphonomic window is the preservation of the microbenthos by primary, syndepositional and secondary, post-depositional events. MISS only occur where these two windows overlap. The following section describes the ecological and taphonomic windows in detail.

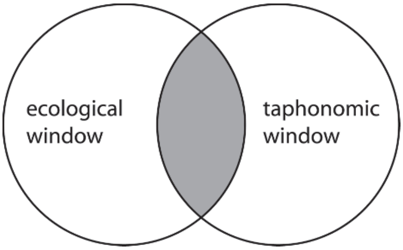
II.2.1.1
The Ecological Window: Primary Processes of MISS-Formation

The ecological window is the sum of all ecological parameters that control the development of biofilms and microbial mats in tidal flats, lagoons, and continental shelves. In practice, a geobiological study does not consider all parameters that characterize an ecosystem. It is more pragmatic to focus on those parameters that affect the sediment. Only those ecological parameters that influence sediments are recorded. Ultimately, sediment constitutes the medium on which ancient worlds have left their traces.

II.2.1.1.1
The Sedimentary Ecology of Benthic Cyanobacteria

Of interest is the sedimentary environment, where biofilms and microbial mats thrive. The classical study sites for MISS have been the cool-temperate coasts of the North Sea, and the semi-arid, hot coast of southern Tunisia.

Fig. II.8.
The ecological window defines the habitat where microbial mats develop. The taphonomic window defines the parameters that lead to preservation of MISS. MISS occur, where the two windows overlap



II.2.1.1.1.1
Tidal Flats

Tidal flats are coastal zones with a flat morphology that are affected by periodic flood and ebb currents, and by episodic storm events (Eisma et al. 1998). The word ‘tide’ derives from an old English term, which meant ‘time’. This term is related to the fact that the ‘tides’ (that is the coming and going of the sea water) occur in a regular pattern. Among the oldest descriptions of tides is that of Roman historian Pliny the Elder, who in AD 47 visited the German North Sea coast (Flemming 2003). He writes that at this coast the sea would inundate and drain an area close to the shore two times a day. Therefore, Pliny the Elder was doubtful whether this area close to the shore would be part of the land, or part of the ocean (Flemming 2003). This question is still debated!

The two main types of tidal systems are the diurnal type, where the coast is flooded once per day, and the semidiurnal type, where the coast is flooded twice per day (Allen 1997). What causes tidal currents?

Kvale (2003) explains that tides are the periodic rise and fall of the ocean surface caused by the gravitational attraction of the Moon and Sun on Earth. If Earth were completely covered by an ocean of equal water depth all around the globe, the gravitational attraction of the Moon in combination with centrifugal forces produced by the spin of Earth would produce two mountains of water in the oceans located on opposite sides of the globe. Because the Earth is rotating beneath each of the water mountains twice a day, two tides are formed. If a given point on the surface of this theoretical Earth enters a water mountain, the tide rises (flood tide), and if the same point exits the mountain, the tide falls (ebb tide). In reality, Earth consists not only of water, but also of continents with complex coast lines. As soon as the tidal bulge approaches the land (or, as soon as the land approaches the tidal bulge), the water rises. Depending upon the morphology of the coast, tides of different heights (tidal ranges) develop. Davies (1964) differentiates microtidal shores that are affected by very minor tidal ranges of only up to 2 m, mesotidal shores of between 2–4 m range, and macrotidal shores of higher than 4 m. Tidal ranges can be significant, such as along the North Atlantic coast of France. The island of Noirmoutier experiences immense tidal currents of more than 2 m s^{-1} velocity, and a tidal range of 14 m.

Neap-spring tidal cycles are related to the phases of the Moon and occur every fortnight (14 days). At the new and full Moon phases, Earth, Sun and Moon align, and their combined gravitational forces cause spring tides. Spring tides are very high flood currents. In contrast, very low tides, neap tides, are related to the first and fourth phases of the Moon, when the Sun and the Moon are aligned at right angles to Earth. The tidal pattern is even more complicated, but for this discussion knowledge of daily, spring and neap tides is sufficient.

The tidal rhythm of inundation and drainage defines the tidal flat. As the name implies, most tidal flats have a flat morphology. A tidal flat is divided into zones. Each zone is defined by different time periods of inundation and subaerial exposure. From the low water line to the high water line, the subtidal zone, the intertidal zone, and the supratidal zone are distinguished (Fig. II.9).

The term ‘subtidal’ indicates a tidal flat zone not affected by ebb tide. This tidal zone is below the neap water line.

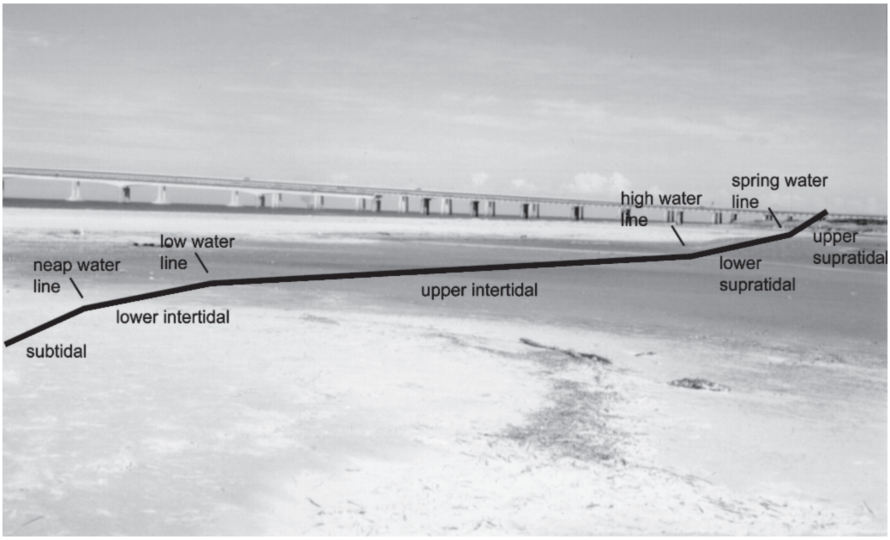


Fig. II.9. The tidal zones along a transect from the low to the high water lines (Fishermans Island, USA)

The intertidal zone is located in between the neap and the high water lines. This area is flooded and drained once or twice daily. The area located between the neap and the normal low water lines is termed 'lower intertidal zone'. Accordingly, some authors term the area between the low and the high water lines 'upper intertidal zone'.

The supratidal zone is the highest area of a tidal flat. This zone is located above the normal high water line and therefore is not affected by the daily tidal currents. The supratidal zone is divided into two areas: *(i)* the lower supratidal zone is located between the normal water line and the spring water line. This means that the lower supratidal zone is flooded every fortnight. *(ii)* The upper supratidal zone is located above the spring water line. This area is not usually affected by the fortnightly tides. However, spring water tides reinforced by strong landward storms may push sea water far onto this area.

In general, the size of sand grains composing tidal flats decreases from the low to high water lines (Flemming 2000). Close to the low water line, the average size of sand grains is bigger than those close to the high water lines. The reason is that the hydraulic energy of the ascending flood current weakens over the distance from the low to the high water lines. Increasingly smaller grains are released from the suspension load of the water. In other words, the grain size of particles that still can be transported by the constantly weakening flood current decreases.

Typical sedimentary structures that occur in a tidal flat are wave and current ripple marks (Reineck and Singh 1989). Current ripples are made by the ascending flood current. In vertical cross-section through a ripple mark, their cross-bedding is visible. In a high energy setting, water currents that pass the sandy surface of a tidal flat with high velocities do not cause ripple marks, but plane lamination, a stack of even laminas. 'Flaser bedding' is a set of sedimentary layers, each composed of a sand layer topped by a mud layer. Flaser bedding records the flood current (sandy layer) and the weak ebb current (muddy layer). Desiccation cracks form during subaerial exposure of the tidal surface, especially in the lower supratidal zone. Various traces also are characteristic of a tidal flat. Indeed, the scientific discipline ichnology, the science of traces and trace fossils, originated from tidal flat sedimentology (Seilacher 2007).

II.2.1.1.1.2

Sabkhas and Salt Marshes

Specific types of tidal flats are tidal sabkhas and salt marshes. Both are usually affected by tides of only microtidal range. Typically, the flat land along the coast is subaerially exposed. Only once or twice a month, or even every few years does water inundate the area (Kelley et al. 1988; Warren 1989, Demicco and Hardie 1994). Both sabkhas and salt marshes are lower and upper supratidal zones (Fig. II.10).

Sabkhas are typical for the arid hot climate zones on Earth. The sabkhas are flat coastal areas that are usually exposed to the hot Sun. Sabkhas (the Arabian word for ‘salt flat’) are encrusted with evaporite minerals such as gypsum or halite. The min-

Fig. II.10.
Sabkhas and marshes are flat coastal areas. They belong to mostly subaerially exposed lower supratidal zones. Sabkhas are typical for hot-arid climates such as the coast of Tunisia. Marshes are typical for humid climate zones such as the east coast of the USA

erals form either on top of the sedimentary surface, or within the sediment in the capillary zone. While sabkhas are not affected directly by the tides, the daily tidal pressure raises the groundwater level within the sediment. This groundwater nourishes the capillary water that ascends upward towards the tidal surface. About every month, or perhaps even every few years, sea water floods the sabkha. Even then, the water is never more than 1 or 2 m deep. Shortly thereafter the water drains back to the sea, leaving behind shallow ponds on the sabkha surface.

Many MISS are described from the sabkha Bahar Alouane in southern Tunisia (Noffke et al. 2001a, 2008). The structures show that microbial mats respond to local hydraulic and climatological parameters (Noffke et al. 2001a). The mat surface typically shows a polygonal pattern of fractures. These fractures open or close with the changing moisture in the sediment. In the mats, evaporitic minerals such as aragonite, gypsum and halite occur.

Salt marshes are typical in humid climate zones. They are characterized by the dominant occurrence of salt tolerant (halophytic) grasses and bushes. Other vegetation cannot colonize these areas. Tidal salt marshes form behind barrier islands, in sheltered estuaries and deltas. Often they occur in low angle sloped portions of the meso- and microtidal North American coast (Kelley et al. 1988). Tidal currents move in clearly defined tidal channels. Salt marshes are often overgrown by thick microbial mats that share the space with halophytic plants (Fig. II.10).

II.2.1.1.1.3

Geomorphological Characteristics of Microbial Mat Habitats

Over the past 15 years, the author studied microbial mats at more than 30 sites along the coasts of the North Sea, the Red Sea, the Mediterranean, and the North Atlantic Ocean. At all sites, microbial mats are located behind barriers that protect them against relatively strong currents (Fig. II.11). A barrier can be a huge dune field such as on Portsmouth Island, North Carolina, that allows only little water to flood the plain behind. A barrier also can be just a few cm high, such as on the little island Al-Dahira in the Red Sea. All sites are flooded in a characteristic pattern: during the spring tides (or occasional storm events), water rapidly floods the plain areas behind the barrier. The water does not recede quickly, but drains very slowly. The mats are often covered for a few days by shallow, lukewarm water. In the following, the hydrodynamics that govern the habitats of cyanobacteria are explained in more detail.

II.2.1.1.1.4

Hydrodynamic Pattern in Microbial Mat Habitats

Microbial mats develop in response to the prevailing hydrodynamic pattern at their growth site. In order to explore this mechanism, first the sediment-dynamics along a tidal surface must be understood. If the tidal surface were just a horizontal plane, the passing tidal currents would erode the sand grains. With decreasing current velocities, many sand particles would be released from the water and settle back onto the sedimentary surface.

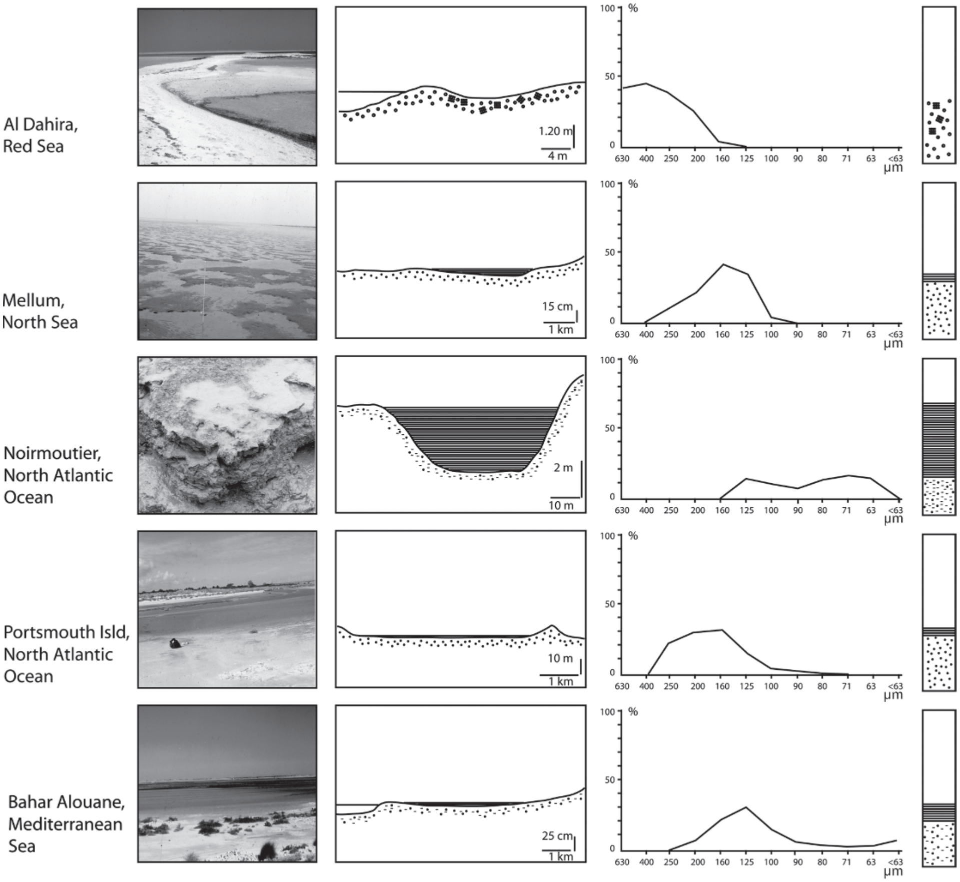


Fig. II.11. Geomorphological and sedimentological characteristics of different growth sites of microbial mats. The photos on the left provide a view into the field for each growth site. The geomorphological profiles next to the photos show that microbial mats preferentially develop behind barriers. Such barriers can be just a few centimeters high as in the case of Mellum, but also several meters such as on Portsmouth Island. The grain size distributions document the sediment compositions for each location. Note that microbial mats seem to grow especially well on fine sand composed of translucent quartz. Noirmoutier shows a higher percentage of mud. In contrast, Al Dahira's sediment is coarse sand, so that only biofilms develop. On the far left, sediment cores taken from each growth site show the thickness of the microbial mats. Study period 1995–2001

However, tidal flats are not a completely horizontal plane, but always dip in an angle towards the sea water surface. Consequently, the sediment dynamic pattern is altered (Fig. II.12). The kinetic energy of the ascending flood current drives the deformation of the sand as expressed by ripple marks. The formerly flat sedimentary surface is now deformed. Because the flood current moves upward, it experiences friction along the sedimentary surface. This friction reduces the velocity of the flood current, because some kinetic energy is used to move sand grains and to build up ripple marks.

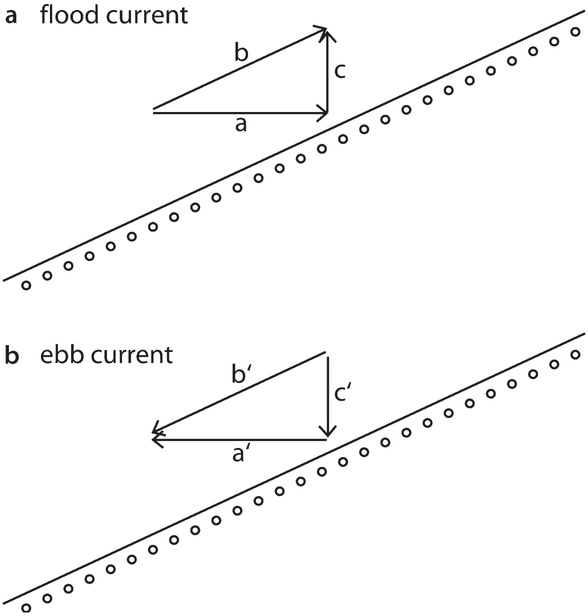


Fig. II.12. Formation of sedimentary surface structures by flood and ebb currents in a sandy tidal flat. A tidal flat is always inclined towards the ocean. **a** Over a given distance *a*, the ascending flood current *b* moves 'up hill'. The moving water has to overcome the height *c* caused by the inclination. The kinetic energy of the water is transferred into deformation of the sediment. Ripple marks form. **b** The descending ebb current *b*' runs off the depositional surface over the same distance *a*'. The water moves now 'down hill' *c*'. Because the water has lost all its kinetic energy during the ascent, it now has no energy left to deform the sediment. Only faint sedimentary surface structures are caused by ebb currents

In contrast, the ebb current is much weaker. The water has lost all its motion energy during its ascent and now runs back to the ocean. The water just runs 'downhill' – and running downhill is easier than running uphill (as long as one has healthy knees). The deformation energy is considerably low. Consequently, sedimentary surface structures such as ripple marks are rarely formed, and when they do, only faintly. The flood current is the dominant factor forming sedimentary structures in a tidal system.

In detail, the effects of a flood current on a tidal surface can be divided into three dynamic conditions (Noffke et al. 2003a): *(i)* erosion of sediment; *(ii)* deposition of sediment, defined here as suspended mineral particles no longer retained in the water flow; and, *(iii)* latencies, which represent periods of calm (low energy) conditions. During latencies very little erosion or deposition takes place. Benthic cyanobacteria respond to erosion by biostabilization, to deposition of sediment by baffling and trapping, and to latencies by binding, and to some degree, growth.

Interactions between moving water and microbenthos take place at the sedimentary surface. Sea water is also perculating through the sediment, pushing air and other gases through sedimentary pores. Even if air migration does not affect the biofilms or microbial mats *per se*, it may induce the formation of specific MISS such as gas domes.

Tidal flats are 'extreme environments'. Upon close examination, they provide rather harsh conditions for any benthic life. The rhythmic change between inundation and subaerial exposure of tidal flats causes rapid fluctuations of temperatures, salinities, light infall, and sediment reworking. In addition, these conditions may change quickly, sometimes within minutes. All benthic life has to adjust to these extreme conditions. The long-term dynamic pattern along transects from the low to the high water lines is characterized by cycles of erosion, deposition and latencies. The dynamic pattern is reflected by a characteristic distribution of microbial mat types that establish lateral

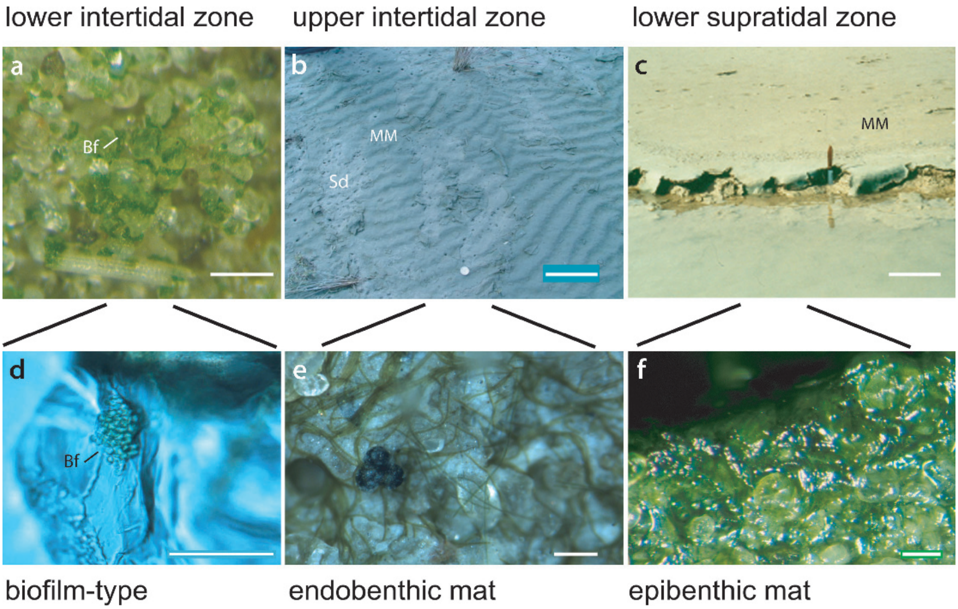


Fig. II.13. Biofilm-catena of temperate siliciclastic tidal flats. A suite of different biofilms, endobenthic microbial mats and epibenthic microbial mats develop along transects from low to high water lines. **a** In the lower intertidal zone, microbial mats do not occur. In close up, the single grains of the sedimentary surface are overgrown by biofilms (*Bf*); (scale: 0.7 cm). **d** Under high magnification, the pillow-shaped colonies of *Merismopedia punctata* are attached to the surfaces of the quartz grains; (scale: 0.02 mm). **b** The upper intertidal zone is overgrown by microbial mats that do not project from the mineral tidal surface. These mats are termed endobenthic. Ripple marks remain visible under the mat cover; *MM* = microbial mat, *Sd* = non-colonized, 'sterile' sand; (scale: 25 cm). **e** In microscopic view, the single trichomes of *Oscillatoria limosa* (the main builder of endobenthic mats) interweave the sand particles of the uppermost few millimeters of the sedimentary surface; (scale: 1.2 mm). **c** The lower supratidal zone is colonized by planar microbial mats that project from the mineral sedimentary surface (epibenthic microbial mat). *MM* = microbial mat, *Sd* = non-colonized, sterile sand; (scale: 10 cm). **f** Under the microscope, *Microcoleus chthonoplastes* (the main constructor of epibenthic mats) forms a coherent microbial mat network, and covers the sand particle by its ubiquitous, shimmering EPS (extracellular polymeric substances); (scale: 2 mm)

successions from the low to the high water lines (Noffke and Krumbein 1999). Each biofilm or microbial mat type of these successions is dominated by one or two cyanobacterial species that are best adapted to the local dynamic conditions at their colonization sites. Such a lateral succession of benthic microbiota is called 'biofilm-catena' (Noffke 1997, 2003a,c, Noffke and Krumbein 1999). The term derives from soil sciences, where 'catena' describes a lateral succession of soils that form in dependence to the water content in different geomorphological heights. At all 30 sites studied, the biofilm-catenae are composed of 3 main mat types (Fig. II.13):

i) lower intertidal zone: biofilm-type
ii) upper intertidal zone: endobenthic microbial mat
iii) lower supratidal zone: epibenthic microbial mat

The following sections describe each type of microbial community of a typical biofilm-catena. The microbiota develop during quiet dynamic conditions ('latencies'). In a dynamic environment, water motion is not always gentle. Cyanobacteria have to withstand erosive forces of jet-like currents. If the erosion exceeds a certain threshold, the mat is disrupted. If covered by sediment, cyanobacteria move upward towards the new sedimentary surface. By this movement, the microorganisms escape burial. However, if the sediments accumulate too quickly, the microbes cannot keep up. Overall, these biotic-sedimentary interactions define a dynamic window in which mat development is possible (Noffke et al. 2002). The following section elucidates the interaction of biota with water motion in greater detail, and explains the lower and upper boundary of the dynamic window.

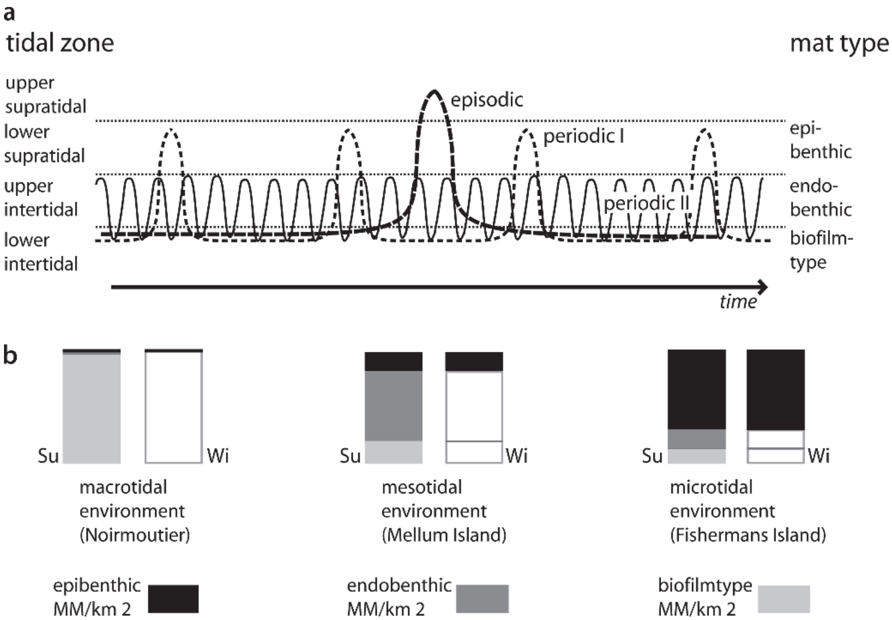


Fig. II.14. Generalized scheme of the tidal zones, and the hydraulic dynamics controlling the development and extension of different types of microbial mats. **a** The tidal current and storm dynamics defines the three main zones of a tidal flat: lower supratidal, upper intertidal, and lower intertidal zone. Those tidal zones are overgrown by specific microbial mat types: epibenthic, endobenthic, and biofilm-type. The lower supratidal zone is affected by episodic storm events (*thick, stippled line*), and the periodic spring high tidal currents (*thin, stippled line*). Here, epibenthic microbial mats thrive. The upper intertidal zone is reworked by the diurnal tidal currents (*non-stippled line*), and is colonized by endobenthic microbial mats. The lower intertidal zone is constantly inundated by seawater, and therefore only biofilms can develop. Such lateral successions of different mat types that establish from low to high water lines in response to the average hydraulic pattern are termed biofilm-catenae (compare Fig. II.13). **b** The *rectangles* document the extent of the three different microbial mat types in a macro-, a meso-, and a microtidal flat. Seasonal changes of the colonization pattern of microbial mats are typical. Summer (*Su*): The macrotidal environment (Noirmoutier) was dominated by biofilm-forming cyanobacteria; at the mesotidal environment (Mellum Island), the endobenthic microbial mats were most abundant; at microtidal settings (Fishermans Island), the epibenthic microbial mats were most common. Winter (*Wi*): At all three study sites, the epibenthic microbial mats remained clearly visible even during the winter, whereas endobenthic microbial mats and biofilms were very rare or absent. Studies conducted 1994–2007

II.2.1.1.1.4.1

Microbial Mat Development during Latencies: the Optimal Dynamic Window

During latencies, when erosion and deposition of sediment are minor, benthic cyanobacteria are able to build up biofilms and microbial mats. Three main types of microbial populations form in response to the change in dynamic conditions from the low to high water lines. A biofilm-catena is established. The distribution of a specific population depends upon the tidal range, and the seasons (Fig. II.14).

II.2.1.1.1.4.1.1

Biofilm-Type

At a glance, the bare sands of a lower intertidal area do not appear overgrown by microorganisms. However, magnification reveals that the sand is not sterile, but covered by numerous microbial cells. Of these microorganisms, cyanobacteria are the most abundant. In the lower intertidal zone, microbes do not form microbial mats, because sediments are almost constantly reworked. Occasionally in summer, a faint bluegreen coloring of the sandy surface may be noticed. Viewed microscopically, clusters of coccoid cells of *Merismopedia punctata* are firmly attached to quartz sand grains (Fig. II.13a,d). This type of colonization is called 'biofilm-type colonization'. When calm conditions persist for at least 12 hours, *Merismopedia punctata* can develop a microbial mat. Indeed, this cyanobacterium forms mats in supratidal pools of Mellum Island (Villbrandt 1992).

Biofilms do not affect sedimentary processes significantly enough to form sedimentary structures. Quantitative analyses of the morphology of an intertidal surface show that the influence of biofilms is insignificant (Noffke and Krumbein 1999). Sediment cores from the lower intertidal zone predominantly show cross-stratification and planar lamination. Together with broken shells of millimeter sizes, these sedimentary structures record turbulent dynamic conditions (Fig. II.15). Laminas caused by microbial mats do not occur.

II.2.1.1.1.4.1.2

Endobenthic Microbial Mats

The term 'endobenthic' was introduced to imply that this mat type develops in the sediment, not on top of it. Microbial mats are situated within the uppermost millimeters of tidal deposits, and do not project above the sandy surface. Therefore, sedimentary surface structures such as ripple marks remain clearly visible (Fig. II.13a). In the field, the only indication of the presence of endobenthic microbial mats is a shimmer of blue-green colour.

On Mellum Island, endobenthic microbial mats are dominated by the filamentous cyanobacteria *Lyngbya aestuarii* and *Oscillatoria limosa*. *M. chthonoplastes* and coccoid groups occur in low numbers as well.

In microscopic close-up, the single trichomes of filamentous cyanobacteria such as *Oscillatoria limosa* form a network that interweaves the quartz grains similar to an organic carpet (Fig. II.13e). In contrast to the epibenthic mats that will be described in the next section, the sand particles of this mat-interwoven surface do have grain-to-grain contact. They are not dislodged from their original position during the growth of the mat. In epoxy-hardened thin-sections of this type of mat, all trichomes together comprise <5% of the total sediment volume.

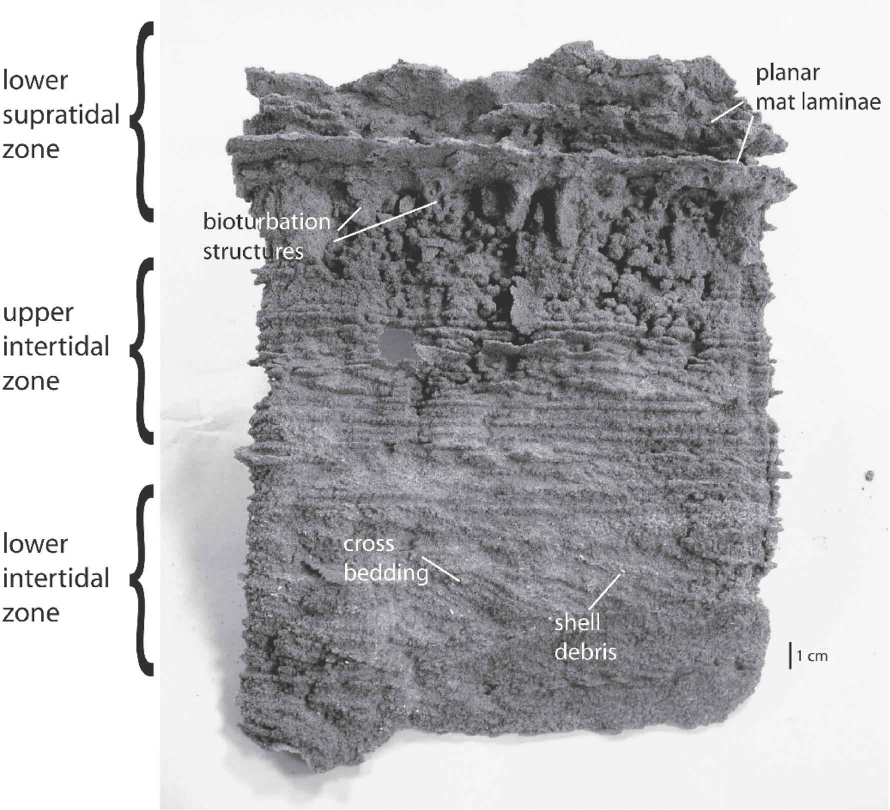


Fig. II.15. Relief cast of a tidal sediment core. Relief casts show internal sedimentary structures in three dimensions. From the base towards the top of the core, the sediments become younger. The base of the core documents a lower intertidal zone: ripple cross bedding and shell debris record strong reworking of the sands by currents. The middle portion of the core records an upper intertidal zone: planar laminated sand records gently ascending and descending tidal currents. The top of the core represents the present, lower supratidal zone. Note the thick, planar mat layers. Overall, the sediment core records a regressive shoreline. Over time the sea level was falling. The core shows an area once situated in a lower intertidal zone. Over time, this area shifted into the lower supratidal zone

Endobenthic mats are characteristically found in the upper intertidal zone (Noffke and Krumbein 1999), Fig. II.14. This tidal zone is periodically reworked once or twice a day. The microbes have the ability to form mat fabrics quickly within the few hours of latency between two daily flood currents (Villbrandt 1992). The rapid establishment of microbial mat fabrics by trichome migration is called 'binding'.

In sediment cores collected from an upper intertidal zone, sinoidal structures are typical. Sinoidal structures are curved, organic lines that indicate buried ripple marks that have been covered by a thin mat layer (Noffke et al. 1996, 1997b).

Field studies show that the endobenthic microbial mats are seasonal (Fig. II.14). They develop in spring, flourish in summer, then decompose towards autumn, when storm frequency increases (Noffke and Krumbein 1999).

II.2.1.1.1.4.1.3

Epibenthic Microbial Mats

The term 'epibenthic' is used for microbial mats which develop on top of sediment. This mat type, up to 1.5 cm thick, resembles a blue-green, organic carpet. The biomass smoothes out the original morphology of the sedimentary surface (Fig. II.13c). In the field, the mat-covered tidal flat areas appear planar. No sedimentary surface structures, such as ripple marks, can be seen. It is this epibenthic type of microbial mat that is commonly shown in photos. These mats are typically found in the supratidal zone (Fig. II.14). As described above, this tidal zone is subdivided into two areas: *(i)* a lower supratidal area, periodically inundated by spring tides; and *(ii)* an upper supratidal area, inundated only during storm floods. The latencies in these supratidal zone areas vary from 2 weeks in the lower, to several months in the upper zone.

On Mellum Island, the epibenthic microbial mats are dominated by the cyanobaterium *Microcoleus chthonoplastes*. Associated filamentous species are *Oscillatoria limosa*, *Lyngbya aestuarii*, and *Phormidium* spp., with minor occurrences of *Spirulina* sp. Coccoid cyanobacteria are less frequent, but *Pleurocapsa*, *Merismopedia*, *Gloethece*, *Synechnocystis*, and *Gloecoccales* are common. The formation of this mat type takes a full year. The development of planar tidal surfaces by the growth of epibenthic mats is described as 'leveling' (Noffke 1998; Noffke and Krumbein 1999; Noffke et al. 2001b).

In microscopic close-up, the fabrics of microbial mats are characterized by thick filament bundles of *M. chthonoplastes.* This cyanobacterial species forms a very coherent, carpet-like network embedded in EPS. In epoxy-hardened thin-sections, this microorganism and its EPS occupies 37% of the total sediment volume. The values range from 5–88% of total sediment volume, (Fig. II.13f).

It is characteristic for *M. chthonoplastes* to secrete large amounts of EPS. EPS protect microbes against rapid changes in osmotic pressure caused by the highly variable salinities in the supratidal zone. For example, after a week of intense sunshine the salinity of the sediment is high. However, the value drops significantly within minutes, if a thunderstorm with heavy rain introduces fresh water.

In vertical cuts through epibenthic microbial mats, 'oriented grains' are visible (Noffke et al. 1997a). These grains are quartz particles embedded in the mucilage-rich network of the mat. The grains have no grain-to-grain contact, but float independently from each other in the organic matrix (Noffke et al. 1997a, 2001b; Noffke 2003b; fossil example in Noffke et al. 2006a). Similar to lenses or glass fiber cables, the quartz grains serve to conduct light into deeper portions of the microbial mat. This light channeling system of quartz grains results in much thicker microbial mats. In vertical cross-section, even microorganisms situated several mm deep in sand are able to conduct photosynthesis. They are driven by light that is transferred by the quartz lenses into deeper layers.

On Mellum Island, the long-lasting latencies of the lower supratidal zone favours the development of epibenthic microbial mats, which develop especially in course of the warmer spring and summer months. Relief casts display nicely the thick laminae of microbial mats (Fig. II.15) The epibenthic microbial mats are perennial and do not decompose in the autumn.

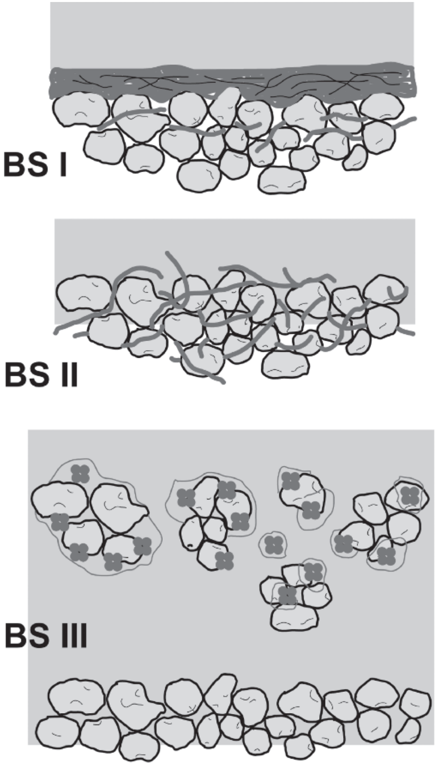


Fig. II.16.
Biostabilization of sand by benthic cyanobacteria. Biostabilization type I (*BS I*) is function of the sediment-fixing effect of extracellular polymeric substances (*EPS*) and the coherent network of the thick filament bundles of the epibenthic microbial mats. Biostabilization type II (*BS II*) is function of the sediment-fixing effect of single trichomes that interweave the particles of the uppermost sedimentary surface layer (endobenthic microbial mats). *BS III* is function of biofilms that coat grains and form biotic-mineral aggregates. These aggregates float easily and remain in suspension before they are deposited on the tidal surface

II.2.1.1.1.4.2
The Responsive Behavior of Benthic Cyanobacteria to Erosion – the Upper Limit of the Dynamic Window

The erosion of quartz sand is generally described as an increase in bed shear stress (‘traction’) until the first grains begin to move (the point of incipient erosion). The level of stress at the point of incipient erosion is described as the critical shear stress (e.g., Miller et al. 1977; Middleton and Southard 1985; Bridge 2003, and references therein). Any increase in the critical threshold that is caused by a microbial mat entangling the sand grains can be described as biostabilization (Paterson 1994).

How do the biofilms and microbial mats react to erosion? For each of the three main populations of the biofilm-catena a different type of biostabilization (BS I–III) can be distinguished (Fig. II.16). In the following, the biostabilization of epibenthic microbial mats is described first, then the biostabilization by endobenthic microbial mats, and then of biofilms.

II.2.1.1.1.4.2.1
Epibenthic Microbial Mat, Biostabilization Type I

In field experiments using a portable MANZENRIEDER flume chamber (Fig. II.17), the initial erosion of epibenthic mats begins at current velocities between 0.90 m s^{-1} to 1.60 m s^{-1} (3–5 cm water depths). These values are up to 9 times higher than comparable critical velocities for the initial erosion of sterile sands of similar grain size. Earlier studies even report values up to 12 times higher (Fuehrboeter and Manzenrieder 1986; Manzenrieder pers. comm. 2002; Yallop et al. 1994; Paterson 1997; Noffke 1998). The effective biostabilization by epibenthic microbial mats is probably a result of the EPS-rich, smooth and 'slippery' surfaces of the mats. These smooth surfaces significantly reduce the frictional forces of the overlying flow (Paterson 1994), Fig. II.16.

In microscopic close-up, the EPS-embedded microbial mat surface is smooth. No obstacles (sand grains etc.) project into the flow field and cause turbulent disturbances. The viscous (laminar) sub-layer of the boundary layer is retained even at high current velocities. Only laminar flow, not the more intensive turbulence, affects the mat surface. The relationship between the thickness of the viscous sub-layer and the shear velocity can be expressed by:

$$\delta_{\mathrm{VL}} = \upsilon / u_*$$

where δ_{VL} is thickness of the viscous sub-layer of the boundary layer (in m); υ is kinematic viscosity (in $\mathrm{m}^2\,\mathrm{s}^{-1}$); u_* is critical shear velocity (in $\mathrm{cm\,s}^{-1}$). The equation indicates that the thickness of the viscous sub-layer is function of the average current velocity (e.g., Middleton and Southard 1984; Dyer 1986). Since the grains do not protrude through the viscous sublayer, the flow across a microbial mat is hydrodynamically smooth. Consequently, epibenthic microbial mats are not rippled, but display a planar surface (Fig. II.13c). If the sediment were not overgrown by the microbial mat, it would have a rough surface. This rough surface would induce turbulent flow, and ripple marks would form in the sediment.

It appears from those experiments that in a natural tidal environment, the epibenthic microbial mats protect their own sandy substrata against erosion by spring tidal currents. Only strong storms can mechanically destroy microbial mats.

The nature of microbial mat erosion has been studied in detail. An epibenthic microbial mat is not just sitting on the sand, like an immobile carpet. When a current crosses its surface, the millions of filaments in concert respond to the tensile forces like the rope of a suspension bridge. They react in flexible modes, and the mat layer is oscillating up and down (Yallop et al. 1994). However, there is a limit, and at some point the mat cover ruptures and a hole forms – surrounded by a fringed mat margin. From this moment on, the water current reaches the loose sand below the mat. Sand grains are lifted up and carried away by the turbulence, and the gaping hole in the microbial mat widens more and more. These processes are manifested by the sedimentary structures of 'erosional remnants and pockets' (detail study in Noffke 1999). The flat-topped, elevated surface portions (erosional remnants) are overgrown and stabilized by a microbial mat. The holes (erosional pockets) are not overgrown by microbes, and the loose sandy surface is generally rippled. Over time, the erosional pockets enlarge, mat chips are released from the fringed mat margin, and scattered at random across the tidal flats (Noffke et al. 1996; Noffke 1999).

The effect of biostabilization type I can be visualized by plotting erosion threshold data on a Shield's relationship (compare also Fuehrboeter and Manzenrieder 1986; Cady and Noffke 2009). The measurements from biostabilized sediment fall outside of the normal Shield's curve, well above the predicted line for the actual grain size (*D*) (Fig. II.7). The

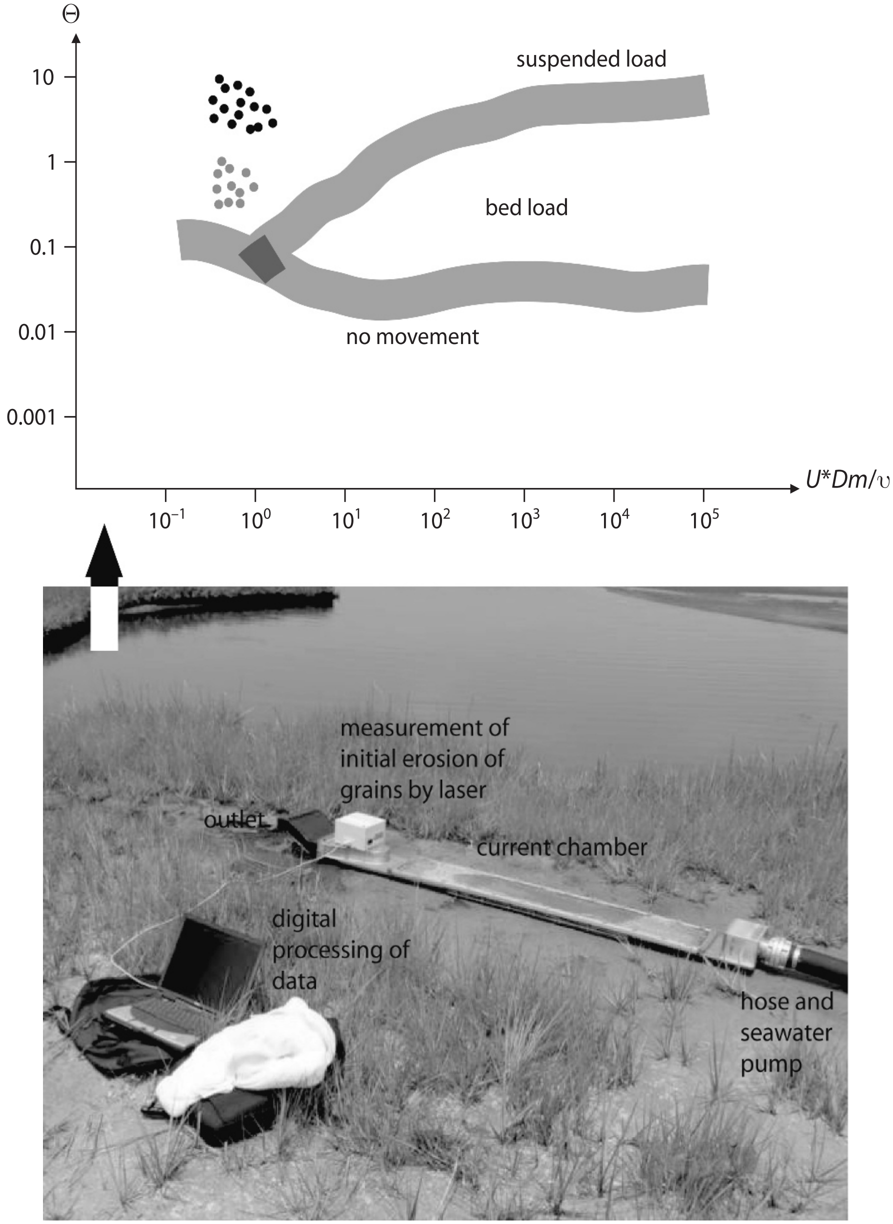


Fig. II.17. Measurement of erosion stability of microbial mats, and expression in Shield's diagram. For our field study (2002–2005), Dr. Manzenrieder rebuilt his portable erosion meter (see pioneer study by Fuehrboeter and Manzenrieder 1987). The field experiments show that endobenthic microbial mats stabilize sandy sediments by magnitudes of 3–5 (*gray dots* in Shield's diagram), whereas epibenthic microbial mats stabilize sediments by magnitudes of up to 12 (*black dots* in Shield's diagram) data can be moved horizontally back on to the predicted curve, which gives a value for the 'effective' grain size of the sediment (D^b). Thus one way of quantifying the stabilization effect is to report the increase in effective grain size ($Db - Dl$) as expressed by interpretation of the Shield's relationship, or as an exponent (n) by which D is raised to give D^b (this is discussed in more detail for the endobenthic microbial mats in the following section).

II.2.1.1.1.4.2.2

Endobenthic Microbial Mats, Biostabilization Type II

The erosion threshold of sediments stabilized by endobenthic mats can be 3 to 5 times higher than sterile sands (biostabilization type II, Fig. II.16). Comparable values were determined by Fuehboeter and Manzenrieder 1986; Noffke 1998; Noffke and Krumbein 1999; Mellum Island. The flume experiments on endobenthic microbial mats, demonstrate initial erosion at current velocities of 0.30 cm s^{-1} to 60 cm s^{-1} (3–5 cm water depths). These values are far higher than those for loose sand not overgrown by microorganisms, however not as high as for epibenthic microbial mats (Fig. II.17). How does the biostabilization mechanism by endobenthic microbial mats differ from that of epibenthic ones?

The cyanobacteria *Oscillatoria limosa* or *Lyngbya aestuarii* form an organic network that interweave and fix the quartz grains in their positions. This network increases the stability of the sand bed relative to the shear velocity of bottom currents however not as effectively as the smooth surface of mat type I (Paterson 1997; Noffke 2003a). This is, because epibenthic microbial mats have a smooth, slippery surface, whereas endobenthic microbial mats are rough like sandpaper (Fig. II.16). The surface of an endobenthic microbial mat feels much gruffier than the surface of an epibenthic mat. In close up view, the sand grains project from the mat fabrics into the water. This abrasive surface affects the viscous sub-layer to become unstable. The smooth laminar flow turns into a rough turbulent flow (e.g., Dyer 1986).

This biotic-physical process is reflected by the morphology of the mat surface. Ripple marks record turbulent flow (Fig. II.13b). It is noteworthy that the ripple marks of endobenthic microbial mats are smaller than those of non-colonized tidal surfaces (Fig. II.18). What does this mean? Smaller ripple marks show that the sediment reacts as if the bottom current were slower than it actually is, or as if the grain sizes were bigger than they actually are. In other words, in presence of an endobenthic microbial mat, the nominal diameter of the sedimentary grains is increased. This has been observed with type I biostablization as well. This microbial effect can be expressed by a simple modification of the Shield's relation for sediment movement, such that

$$\Theta = \rho u_*^2 / (\rho_s - \rho_f)\, g D^n$$

where u_* is the shear velocity (in cm s^{-1}); ρ_f is the density of fluid (in kg m^3); ρ_s is the density of sediment; g is the gravity constant; D is the actual grain diameter (in m) under the influence of biostabilization; and n is the exponent to which D is raised for the data to comply to the Shield's relationship (compare with Fuehrboeter and Manzenrieder 1987).

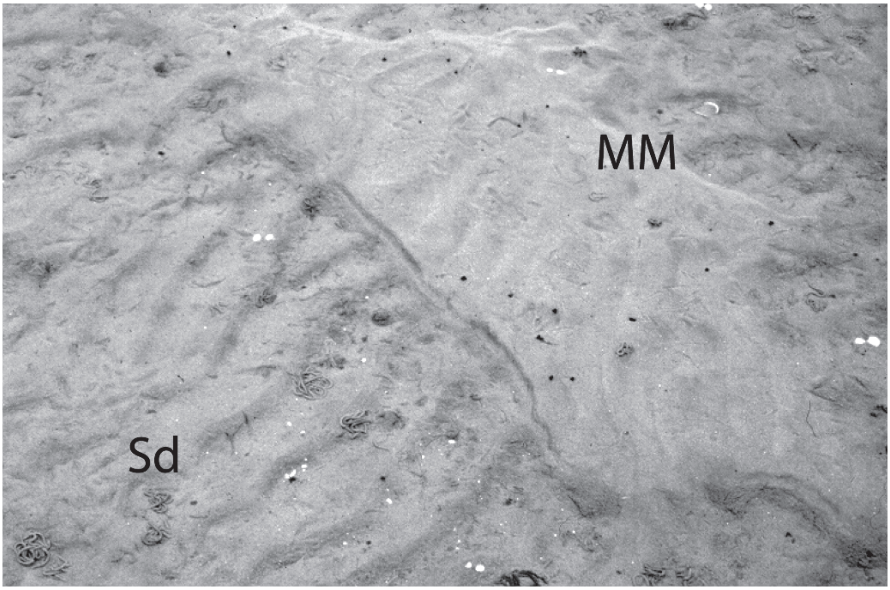


Fig. II.18. View onto a tidal flat surface with ripple marks. Note the island-like elevation in the right half of the photo. This elevated area is overgrown by an endobenthic microbial mat (*MM*). On this elevated surface, the ripple marks are smaller than the ripple marks of the deeper lying tidal surface area (left half of photo). This deeper lying surface area (*Sd*) is not overgrown by microorganisms. Therefore its ripple marks are not modified by microbial activities and are of their original, larger size. *MM* = microbial mat; *Sd* = sand

II.2.1.1.1.4.2.3

Biofilms, Biostabilization Type III

Biostabilization type III means the formation of microbiotic-physical aggregates composed of one or more grains surrounded by biofilms (Fig. II.16). These aggregates react differently in response to hydraulic influence than grains that have no biofilm coating.

At sites of constant current and wave action close to the low water line of tidal flats, benthic cyanobacteria cannot form dense microbial mats. Instead, the single cells attach to individual sand grains by their cohesive EPS, and become stirred up by each wave. As long as the water is moving, most microbially coated grains stay in suspension, but sink down as soon as calm conditions set in. Such coated grains stay longer in suspension, thus are always deposited on top of the sedimentary surface (Fig. II.16). By this mechanism, the photoautotrophic cyanobacteria escape lethal burial.

The soft, irregular biofilm that envelopes a single mineral grain decreases the density of the particle in relation to its actual diameter. This increase in surface area causes increased fluid drag. The coated grain sinks more slowly. In a natural environment, a biofilm-coated sand grain is more affected by turbulence than by laminar settling (Middleton and Southard 1984; Denny 1993; Church 2003; Komar 2003, and references therein).

In conclusion, microbial mats develop under calm conditions and can withstand high erosive stress. However, microbial mats cannot form during constant reworking of the sediments, even if the reworking is just moderate. The following section investigates how microbial mats react to deposition of sediment.

II.2.1.1.1.4.3

The Responsive Behavior of Benthic Cyanobacteria to Deposition – the Lower Limit of the Dynamic Window

By definition, deposition of sandy sediment occurs when particles fall out from the water. This fall-out takes place as the velocity of the current drops below the suspension threshold of the grains (e.g., Middleton and Southard 1984). The biological response of benthic cyanobacteria to deposition of sediment is defined as 'baffling and trapping' (Black 1933). It is characterized by a predominantly vertical orientation and movement of microbial cells and filaments. Epibenthic microbial mats of the lower supratidal zone must be able to respond to the deposition of thick storm layers, or to a muddy, light-blocking suspension load. Endobenthic microbial mats in the upper intertidal areas are well adapted to bed load transport caused by the daily tidal currents. (Note that binding is the reorganization of microbial mat fabrics as soon as sedimentation ceases). Baffling and trapping will be explained in the following text.

II.2.1.1.1.4.3.1

Epibenthic Microbial Mats of the Lower Supratidal Zone

The lower supratidal zone is generally dominated by two dynamic effects: *(i)* the sudden and hefty deposition of sand layers during a storm, and *(ii)* the deposition of fine grained, clay-rich sediments during the slack water current of spring high tides (e.g., de Vries Klein 1977; Dalrymple and Choi 2003).

If too much sediment is deposited at once onto the tidal surface, epibenthic microbial mats cannot survive. Although many cyanobacterial species are motile, *M. chthonoplastes* seems unable to reach the new sedimentary surface of a fresh deposit. On Hatteras Island, North Carolina, USA, hurricane Isabel made landfall in 2003. Epibenthic microbial mats on this island did not recover from burial by a >20 cm thick hurricane deposit. The deposits were too thick for *M. chthonoplastes*.

However, in laboratory experiments, Gerdes et al. (1991) and Gerdes and Klenke (2003) demonstrated that hormogonia (pieces of cyanobacterial filaments capable of vegetative regeneration) of *Microcoleus chthonoplastes* were able to migrate vertically through sand.

In the natural environment, freshly deposited sand, such as an overwash fan, is recolonized over many months by the lateral migration of *Microcoleus chthonoplastes* from surrounding areas. Similar observations were made for sites on Andros Island, Bahamas (Black 1933; Hardie and Garrett 1977; on Mellum Island (Gerdes et al. 1994), and on Plum Island (northeast coast of USA; Cameron et al. 1985).

The fall-out of fines (mud) in the aftermath of spring tides causes a second problem for epibenthic microbial mats. Fine grained material can cover photoautotrophic microbial mats like a deadly drape, blocking essential sun light (e.g., Kuehl and Joergensen 1992, 1994). To escape this lethal burial, cyanobacteria orientate vertically and reach upward into the supernatant water (Consalvey et al. 2004). The presence of vertically oriented filaments in the water column above the microbial mat surface may increase the dynamic viscosity of the water in this layer, and enhance the fall-out of small particles as soon as they arrive in this near-surface area. Following Black 1933, this behaviour is termed baffling and trapping, (Fig. II.19).

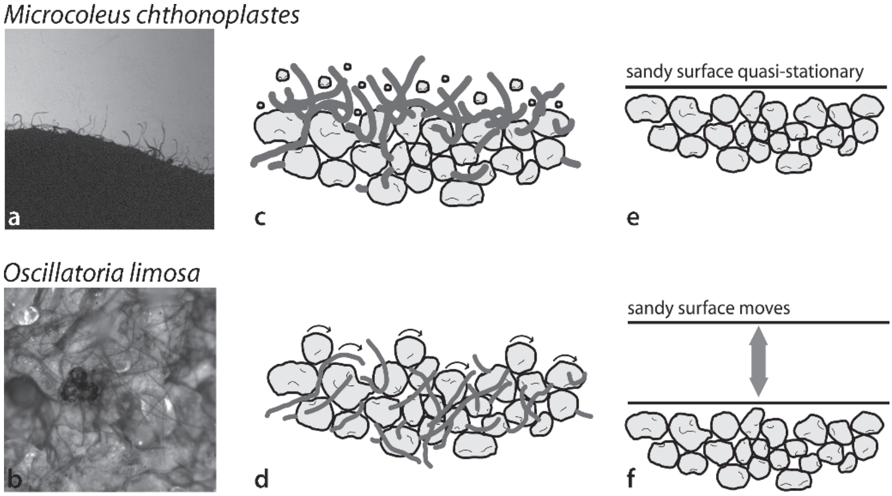


Fig. II.19. Baffling of silt and sand by benthic cyanobacteria. Epibenthic microbial mats baffle silt sized particles by vertical orientation of their filaments. Endobenthic microbial mats baffle sand bed load by rapid migration. Upper part (**a**, **c**, **e**): Epibenthic microbial mats constructed by *Microcoleus chthonoplastes* react to silt suspension load typical for the lower supratidal zone (photo in **a** after Noffke et al. 2001b). **a** and **c** show how the filaments of *Microcoleus chthonoplastes* orientate themselves perpendicularly to the depositional surface. Here they reach into the water and baffle suspended particles. **e** Note that the sandy surface is stationary and not moving upward, downward or laterally by hydraulic reworking. Lower part (**b**, **d**, **f**): In **b** and **d**, endobenthic microbial mats composed of the highly mobile trichomes of *Oscillatoria limosa* keep up with bed load transport typical for this tidal zone. The sand grains are moved by water currents laterally, some grains are deposited, some grains are eroded. Silt-sized particles do not occur. **f** Note that the sandy surface is mobile. It moves upward, downward or laterally

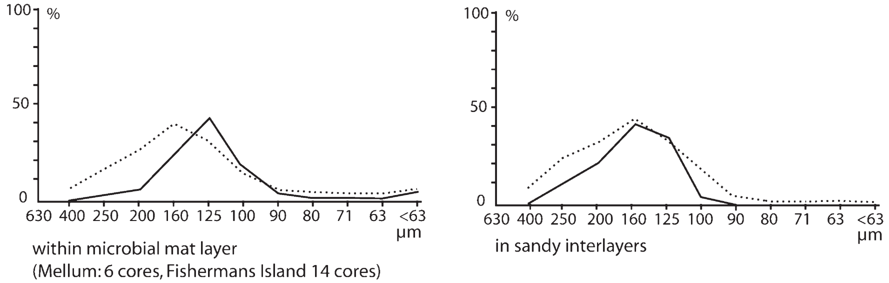
The concentration of small particles is highest close to the mat surface, as shown by the observed deposition of the smaller particles in presence of microbial mats. The ‘sticky fly paper’-effect of the adhesive EPS certainly supports the adsorption of fines. As long as the clay fraction is less than about 5%, the microbial mats can adapt to small regions of local light occlusion. However, a thicker covering of fine cohesive material is much more damaging. In consequence, cyanobacteria avoid areas of higher input of mud. Microbial mats seem to preferentially colonize clear, translucent sand (Watermann et al. 1999; fossil examples Noffke et al. 2002, and discussion therein).

The interaction of the microbenthos with this twofold sediment dynamic is reflected by internal sedimentary structures and textures. Epibenthic microbial mat layers often include fine sand grains. The layers between the mat laminas are composed of medium to coarse grained quartz sand (Fig. II.20).

II.2.1.1.1.4.3.2
Endobenthic Microbial Mats of the Upper Intertidal Zone

The upper intertidal zone is mainly affected by bed load transport, although during ripple formation sand grains are suspended (saltation) for short periods of time (e.g., de Vries Klein 1977; Dalrymple and Choi 2003). At most study sites, fine suspended load is not usually deposited in this tidal zone because of relatively high current ve-

a Epibenthic microbial mat



b Endobenthic microbial mat

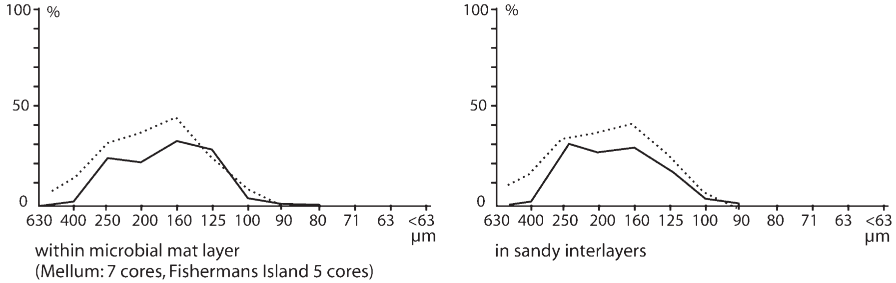


Fig. II.20. Grain size distribution in epibenthic and endobenthic microbial mats. For this grain size analysis the sand grains of individual microbial mat lamina and of sandy interlayers were collected separately. The analyses were conducted by dry sieving. *Lines:* Sediment cores from Mellum, North Sea (Noffke 1997). *Stippled lines:* Sediment cores from Fishermans Island, collected 2002. **a** In epibenthic microbial mats from the lower supratidal zone the main grain size is 125 µm, whereas in the sandy interlayers the predominant grain size is 160 µm. **b** In endobenthic microbial mats from the upper intertidal zone the grain sizes show a peak distribution around 250 µm, 160 µm, and 125 µm. The sandy interlayers are predominantly composed of sand particles of 250 µm and 160 µm

locities. Consequently, endobenthic microbial mats have to respond to bed load transport. Bed load transport is lateral transport and the rolling of sand grains (Fig. II.19). Cyanobacteria react to the hydraulically driven rolling of grains by constant upward, downward and lateral migration. *Oscillatoria limosa* is a particularly quick mover and successfully keeps up with the constantly rising or falling sedimentary surface (e.g., Park 1976; Kruschel and Castenholz 1998; Gerdes et al. 1991; Browne et al. 2000; Sumner 2000; Noffke et al. 2003a; Gerdes and Klenke 2003; Shephard et al. 2004, Consalvey et al. 2004). Light seems to be the predominant trigger for the movement of cyanobacteria. However, a reaction to burial without the influence of light has also been noted, so pressure changes might also cause a reaction (e.g., Seong-Joo et al. 2000; Toker-Nielson and Molin 2000). As soon as bed load transport ceases, endobenthic microbial mats reestablish their mat fabrics within a few hours. This process is called 'binding', and is strictly differentiated from baffling and trapping. A quick response to dynamic changes in the upper intertidal zone is of great importance for the survival of endobenthic mat communities (Villbrandt 1992; Noffke 1998). Thin-sections from epoxy-hardened microbial mats of this type do not display a discrete, mat-bound small grain population (as in the epibenthic microbial mats). There is little difference in size between mat lamina-bound sand grains, and grains of the sandy interlayers (Fig. II.20).

Storms also affect intertidal flats. In the case of sudden burial by a thick layer of sand, endobenthic microbial mats (in contrast to epibenthic microbial mats) migrate rapidly upward towards the new surface, even if the sediment layer is as thick as 15 cm. Once the microorganisms arrive at the new sedimentary surface they reestablish (bind) new mat fabrics quickly. Similar observations were made by Black (1933), and Hardie and Garrett (1977) on the Bahamas, by Villbrandt (1992) on Mellum Island, or by Seong-Joo et al. (2000) for the Great Sippewissett Salt Marsh, Massachusetts (USA).

Vertical movement is also observed in other microphytobenthos, such as diatoms and euglenids (e.g., Palmer and Round 1965; Harper 1977; Joint 1981; Round 1981; de Vos et al. 1988; Consalvey et al. 2004).

In summary, baffling and trapping are:

i) During periods of quasi-stagnant dynamic conditions (velocities of water current close to 0 cm s^{-1}), no grains as large as sand are moved. However, smaller, silt-sized particles remain in suspension. Suspended mineral matter affects the penetration of light through water. The photoautotrophic microbial filaments orientate perpendicularly to the microbial mat surface, and reach up into the supernatant seawater. Here, they passively comb out (baffle) the suspended silt-sized mineral particles. Overall, the sedimentary surface, here defined as the surface created by all sand-sized grains, does not rise due to input of sand-sized grains. Only silt-sized particles accumulate. This baffling behaviour is typical for epibenthic microbial mats in lower supratidal zones.
ii) During periods of deposition of sandy sediment, the surface rises, and also slowly moves laterally at the same time. The microorganisms actively keep up with the moving sedimentary surface by quick movement in an upward and semi-lateral direction. Endobenthic microbial mats show this type of baffling.
iii) Trapping is the deposition of aerially transported grains and detritus during ebb tides, when tidal flats are subaerially exposed. Grains and detritus are bound to the mat surface by sticky EPS (sticky fly paper effect).

II.2.1.1.2

Towards a Definition of Cyanobacterial Modification of Physical Sedimentary Dynamics: the First Step to Classify MISS

From the low to the high water lines of a coastal area, a lateral succession of different populations of biofilms and microbial mats develops. Biofilms and microbial mats occur in response to the long-term hydraulic pattern. Following the nomenclature for lateral soil successions (soil catena), this succession of microbenthos is called biofilm-catena. Each population that forms a member of a biofilm-catena is well adapted to the specific sediment-dynamic condition that prevails at their specific site of colonization. The benthic cyanobacteria respond to the prevailing sediment dynamics by biostabilization, baffling and trapping, as well as binding and growth (Fig. II.21). Biostabilization is the response of the benthic microorganisms to an erosive environment. In contrast,

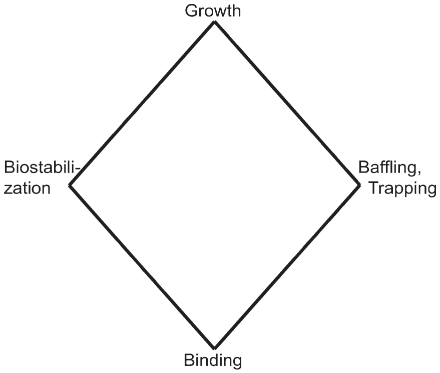


Fig. II.21.
Microbial growth, baffling, trapping, biostabilization, and binding form the end members of a continuum of bacterial behaviour triggered by physical sediment dynamics. This diamond shaped diagram is the basis for the classification of MISS in the next chapter

baffling and trapping are responses to deposition of sediments (reaction to suspension load and bed load). Binding differs from baffling and trapping, because the formation of a mat fabric occurs during the latencies (time periods of no erosion or deposition). Growth includes the enrichment of biomass by cell replication and by EPS secretion. Therefore growth is not only a function of the sedimentological context, but also of environmental parameters such as light, nutrient availability, temperature, etc. For this reason, growth is not binding, but constitutes an extra parameter, forming one of the four corners of the diamond-shaped diagram in Fig. II.21.

Note that each microbial behaviour is related to a specific dynamic condition. Why do cyanobacteria react in such a specific manner to their depositional environment?

It appears that biofilms and microbial mats engineer their own sedimentary habitat by buffering erosion and deposition. They moderate the natural dynamic environment to promote the survival of the microbenthos. From the sedimentological perspective, this biotic influence can be expressed as a modification of the sediment continuity equation (SCE). How can microbial activities be distinguished from physical sedimentary processes that lead to sedimentary structures in tidal flats? Physical sedimentary dynamics, such as the displacement of sand grains by water currents, cause physical sedimentary structures, such as ripple marks. When sandy sediments are overgrown by biofilms or microbial mats, ripple marks differ in appearance. How can microbial modification of ripple marks be determined? To understand the relationship between purely physical processes and structures, and biotic-physical processes and structures, the physical environment must first be considered. Sediment transport in siliciclastic environments can be described generally by the SCE, which defines erosion and deposition of sand within a given area (e.g., Bridges 2003):

$$\text{sediment continuity equation SCE: } (1-\zeta)\,\mathrm{d}h/\mathrm{d}t = \mathrm{d}c/\mathrm{d}t + \mathrm{d}q/\mathrm{d}x$$

where ζ is the porosity of sediment; h is the height of sedimentary surface (in m); t is time (in s); c is the concentration of sediment in water column (in kg m^{-3}); q is sediment discharge (in m^3 s^{-1}), and x is the downstream distance (in m). This SCE is manifested in the geomorphology of tidal flats and sedimentary structures such as ripple marks (Fig. II.22). The equation states that the depositional surface rises or falls over time only if the flow accelerates or decelerates in time ($\mathrm{d}c/\mathrm{d}t$), or in space ($\mathrm{d}q/\mathrm{d}x$). It

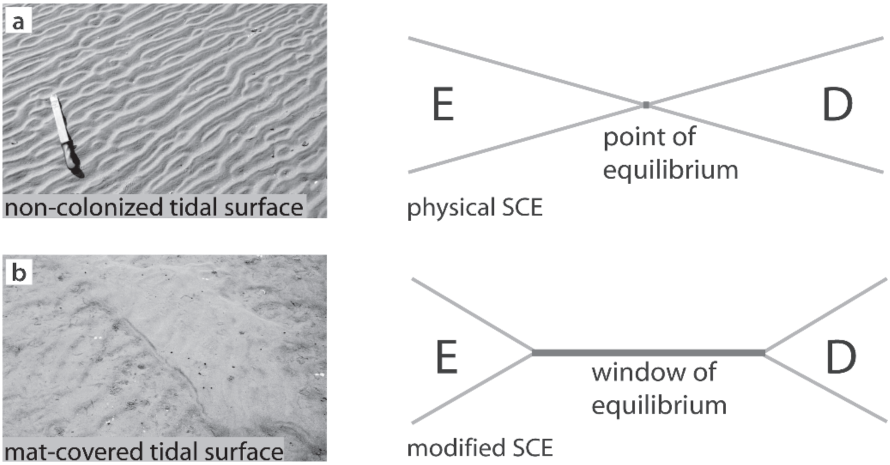


Fig. II.22. For a long time sedimentologists believed that natural depositional environments are governed exclusively by physical sedimentary processes. This physical sedimentary dynamics is expressed by the sediment continuity equation (SCE). The SCE is a continuum between erosion and deposition in a given area. This continuum allows only a transient moment of equilibrium between erosion and deposition (**a**). Physical sediment dynamics generate ripple marks as shown in the photo **a**. However, in presence of biofilms or microbial mats, the ripple marks are modified (photo in **b**). This modified appearance is result of microbial-physical sediment dynamics. In the sketch (**b**), biostabilization shifts the limiting value of the boundary erosion/equilibrium to the left, and baffling and trapping shifts the limiting value of the boundary equilibrium/deposition to the right. Consequently, the equilibrium is no longer a transient point, but a window. This dynamic window allows the establishment of microbenthos, and its protection against mechanical destruction. The microbenthos engineers its own sedimentological habitat to ensure survival

describes a continuum between the parameters 'erosion' and 'deposition'. If the current becomes steady in time and uniform in space, it would go on without eroding or depositing; for every grain that would fall out of the current, one would be deposited in its place. In nature, currents are rarely steady in time or uniform in space, so the point of equilibrium between erosion and deposition is transient (Fig. II.22). However, only during complete equilibrium are microbial mats able to bind or grow. In theory, this means that only during transient moments of complete equilibrium between erosion and deposition could growth and binding occur. Such a dynamic system would be indicated by the exclusive presence of physical sedimentary structures. In reality, microbial mat-overgrown tidal flats do exhibit MISS. These MISS show that microbial mats affect physical sedimentary dynamics. Mats enlarge the transient moment of equilibrium into a window of equilibrium. They do so by biostabilization, which counteracts erosion, and by baffling and trapping, which facilitates deposition. The SCE is microbially modified.

The microbial activities shift *(i)* the limiting value of the boundary erosion/equilibrium of the SCE to the left, and *(ii)* the limiting value of the boundary equilibrium/deposition to the right (Fig. II.22). It appears that microbial mats, in order to survive, buffer erosion and deposition, and generate their own, favorable dynamic environment. Simply, microbial action improves the dynamic life conditions for growth and binding (compare Noffke and Krumbein 1999; Noffke et al. 2003a).

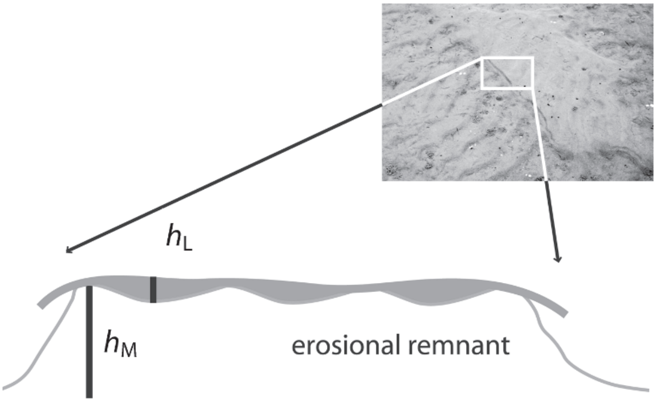


Fig. II.23.
Modification of the sedimentary surface by a microbial mat. In the photo, the mat-covered surface area is higher than non-colonized surface areas. This difference in height is (h_M). The ripple valleys are smoothed by the growing biomass of the mat. The valleys become shallower (h_L)

Biofilms and microbial mats influence the SCE in the following way: Biostabilization types I and II counteract erosion, so the mineral grain concentration in the water is decreased relative to a given current velocity. Baffling and trapping accumulate sediment on the tidal surface. Consequently, tidal surface areas covered by microbial mats are morphologically higher than non-colonized surface areas (Fig. II.23). Such higher areas are 'erosional remnants' (Noffke 1999). Field measurements of the tidal surface document that erosional remnants are up to 25 cm higher than non-colonized areas (Noffke and Krumbein 1999). Additionally, ripple marks are smoothed by growth, and the accumulation of sediment particles by baffling and trapping (Noffke and Krumbein 1999). Following the empirical fieldwork of Noffke and Krumbein (1999), the SCE for the presence of microbial mats can be modified as follows:

$$\mathrm{SCE}_{\mathrm{MOD}}\colon (1-\zeta)\,(k+\mathrm{d}h_S)\,/\,\mathrm{d}t = \mathrm{d}c\,/\,\mathrm{d}t + \mathrm{d}q\,/\,\mathrm{d}x \;\; ; \quad k = [h_M + h_L]$$

In this modified $\mathrm{SCE}_{\mathrm{MOD}}$, k represents biostabilization, and baffling and trapping. h_M is the height of an erosional remnant (Fig. II.23); h_L is the thickness of the microbial mat cover of leveled ripple marks (Fig. II.23). The coefficient k therefore considers that all microbial activities shape the tidal morphology. (The effect of biostabilization type III is not considered, because as stated above, it is not measurable on MISS in the field.) On Mellum and Fishermans Island, values of k, where $h_M = 0.1$–25 cm, plus $h_L = 0.5$–5 mm are indicative of epibenthic microbial mats throughout the year. $h_M = 0.1$–5 cm and $h_L = 0$ are indicative of endobenthic microbial mats with minimum values in January, and maximum values in September (field data for Mellum Island, Noffke and Krumbein 1999).

II.2.1.1.3
The Ecological Window – Summary

Cyanobacteria colonize tidal flats, marshes or sabkhas, and lagoons. On continental shelves, the photoautotrophic microbial mats are restricted to the photic zone. Cyanobacteria prefer finely grained quartz sand, deposited in a moderate hydraulic setting (Fig. II.24). This is described in detail as follows:

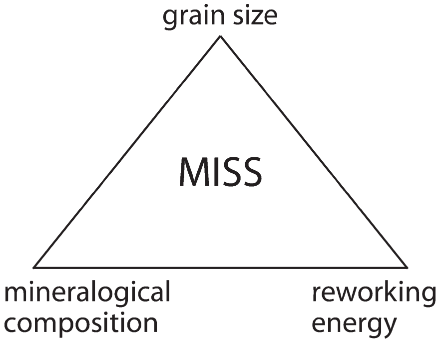


Fig. II.24.
The occurrence of MISS is a function of three sedimentological parameters: a finely grained sand, a quartz mineral composition, and moderate hydraulic conditions

Fine Sand Grain Size. Cyanobacteria prefer finely grained sand. This is probably due to an optimal relationship between the relatively large cyanobacteria, and the fine sediment grains. While cyanobacteria are able to move actively through sand, they cannot penetrate mud. Mud is too strongly adhesive. The filaments are adsorbed to the clay particles and cannot drag the sticky mass of clay with them. Cyanobacteria also avoid substrates of grain sizes that exceed medium sand. If the sand grains are too big, cyanobacteria cannot build up their characteristic microbial mat fabrics. Only biofilms form. Simply, the grains are too big to be embraced by the cyanobacteria.

Mineral composition. Mineral composition of the substrate is also important. Modern and ancient microbial mats prefer sand that consist at least of 95% clear (translucent) quartz grains. Like lenses or glass fiber cables, the quartz grains conduct light into deeper layers of the microbial mat. This light channeling system of quartz grains allows thicker microbial mats to develop. The mat thickness corresponds to the depth of light penetration (photic thickness of a microbial mat).

Moderate hydraulic reworking. In a given area of a depositional environment, waves and currents of moderate reworking energy almost always accumulate sand. The moderate water motion is strong enough to prohibit the fall-out of fines ('mud'). On the other hand, the water movement is strong enough to transport sand grains. Such areas of gentle water motion are overgrown by photoautotrophic microbial mats. When mud covers photoautotrophic microbial mats, it blocks essential sun light. This might be lethal for the microorganisms. Vigorous waves might destroy the microbial mats. Endobenthic mats can withstand currents of up to 60 cm s^{-1} velocity. Epibenthic microbial mats can withstand currents of up to 160 cm s^{-1} velocity. In field studies, an average 10–25 cm s^{-1} current velocity is characteristic for microbial mat sites. Such moderate dynamic conditions are recorded by small scale ripple marks of about 3–8 cm.

II.2.1.2
The Taphonomic Window: Primary and Secondary Processes of MISS-Preservation

This section describes how microbial mats and their MISS become fossilized. In paleontology, preservation processes that lead to the formation of a fossil or structure are described by taphonomy. There are primary and secondary preservation processes.

II.2.1.2.1
To Overcome the Problem of Taphonomic Selection

By definition the fossil record is incomplete. Geoscientists know that most of Earth history is unknown, and that the geological record is full of gaps. Taphonomy, the process of fossilization, is selective. In a rock, only limited information about the original world is preserved. Only a minor percentage of species that comprised an ancient population became fossilized. During their transformation into sedimentary rocks, sediments were overprinted by diagenetic alteration, weathering, and other processes. Sedimentary rocks also provide information about the ancient environment. The reconstruction of ancient environments is difficult, because not every environmental parameter of the original ecosystem is recorded. Not every environmental parameter has affected the sediments by their time of deposition, so not all parameters of an ecosystem have left a signature in the deposits. An example of an environmental parameter that leaves no signature is solar radiation. Sunshine does not leave foot prints in the sand. In contrast, water currents cause ripple marks by moving and accumulating sand grains. Fossil ripple marks are common structures in sandstones. They allow conclusions about an ancient water current system. Clearly, the record of paleoenvironments is only a record of environmental parameters that syndepositionally have imprinted the sediments. Geobiologists who investigate modern environments in order to understand the ancient, usually focus only on sediment-shaping environmental parameters. Only the sediment constitutes the fossil record. Only the sediment becomes preserved.

How do microbial mats in a sandy tidal flat become fossilized? Two taphonomic steps are distinguished. First, there are preservation processes that take place immediately at the time of deposition of sediment. These are the syndepositional, or primary processes. Second, there are preservation processes that take place later, after burial of the sediment. These processes are termed postdepositional, or secondary.

Primary and secondary processes produce macroscopic structures and microscopic textures (Fig. II.25). Examples of structures are multidirected ripple marks (Fig. I.3g,h). This macroscopic structure occurs on sandstone surfaces. An example of a microscopic texture would be a fossil bacterial filament in a rock. In order to study microscopic textures, thin-sections of sedimentary rocks must be made. (One can also make thin-sections of epoxy-hardened fresh sediment). Thin-sections are between 5–30 μm thin slices of rock that are mounted on a glass slide. They allow geoscientists to use a petrologic light microscope to examine any texture present. In MISS, two groups of micro-

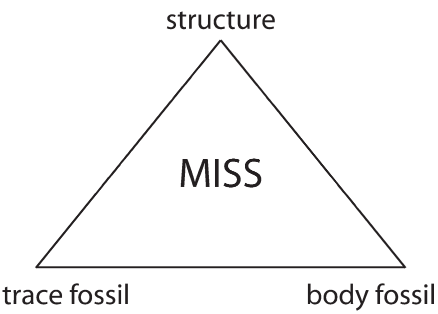
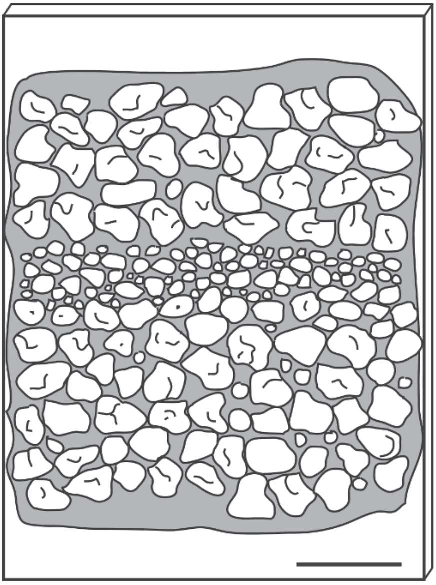


Fig. II.25.
Fossil MISS are a complex combination of structure, trace fossils, and body fossils. This complex nature differentiates them from common sedimentary structures, as well as from common fossils

Fig. II.26.
Thin-section that displays a microscopic texture caused by a microbial mat in sandy sediment. The mat layer itself is not visible anymore, because it is decayed. However, the layer of fine grains in the center shows that once there must have been a microbial mat. The fine grains were accumulated by baffling and trapping. This layer of fines is a microscopic trace fossil; (scale: 0.5 cm)



scopic textures occur. The first group includes textures that represent fabrics in a sedimentary rock caused by microbial activity. For example, syndepositional baffling and trapping by an ancient microbial mat has enriched a layer of small grains in otherwise coarser grained sand. In this case, the former microbial mat itself is not preserved. This texture of fine grained sand is a microscopic trace fossil. Microbial trace fossils are textures of type (i); (Fig. II.26). The second group of textures represents the *in situ* preserved ancient microbial mat itself. These textures rise from *in situ* replacement of the original organic matter by minerals. Microbial mat textures are composed of fossil coccoid cells, filaments, EPS, and other biological elements. Textures of this type (ii) are body fossils (Fig. II.27).

Because of their specific mode of formation and preservation, MISS are a complex combination of macroscopic structure, microscopic trace, and microscopic body fossils (Fig. II.25). This ternary nature differentiates MISS from both common sedimentary structures, and common fossils.

II.2.1.2.2
Primary Processes of MISS-Preservation

Primary processes of preservation of a microbenthic community include all physical ('mechanical') processes that lead to the formation of sedimentary structures or textures without the *in situ* preservation of the organic material itself. The primary processes set the stage for any subsequent secondary processes.

The primary taphonomic path for MISS comprises a very specific series of sedimentological events (compare Fig. III.41, next chapter). This series defines the taphonomic window for MISS (Noffke et al. 2002). First, during a pause in sedimentation, sand is colonized by a microbial mat. Second, the microbiota baffle and trap very fine grains suspended in sea water. These fine grains are bound into the mat fabrics and accumulated as a layer. Third, new sediment is deposited on the mat surface. Because of its biostabilization properties, the mat is not eroded during this placement of fresh deposits. However, it decays over time, leaving behind only the discrete layer of baffled and trapped fines (Fig. II.26). Forth, after consolidation of the deposits, this layer of fine grains separates the deposits into two sedimentary rock beds. On these newly formed bedding planes, MISS such as wrinkle structures can be preserved.

Microbial trace fossils, such as a layer of fines left behind by a microbial mat, are textures of type (i). In vertical thin-section through the sediment, the microbially accumulated finer grains form a discrete layer in the sediment fabrics, indicating the former presence of a mat (Fig. II.26).

II.2.1.2.3
Secondary Processes of MISS-Preservation

Secondary processes of MISS preservation are chemical processes that lead to the *in situ* preservation of biofilms and microbial mats. This fossil microbenthos represents textures of type (ii) (Fig. II.27).

The secondary processes are divided into *(i)* destructive biomineralization during early diagenesis, and *(ii)* recrystallization during late diagenesis. Diagenesis is the sum of sediment alterations that take place during transformation to consolidated sedimentary rock.

Textures that represent fossil microbial mats include all biological and sedimentological components of ancient microbial mat fabrics. These components include filaments, coccoid cells, trapped and bound quartz grains, EPS, and others (Fig. II.26), (Noffke 2000; Noffke et al. 2002, 2003b, 2006a,b, 2008). It is astonishing that even in billion year old sandstones, a fossil mat is clearly recognizable. Sandstones are usually not known for their favorable fossil preservation properties!

In thin-section under light microscope, individual fossil microbes are lined by opaque minerals of brownish or black colour. When opaque structures are viewed using a microscope that illuminates from behind ('transmitted light'), they appear very dark. In reflected light, opaque minerals may appear bright red, golden, or silver (Fig. II.27).

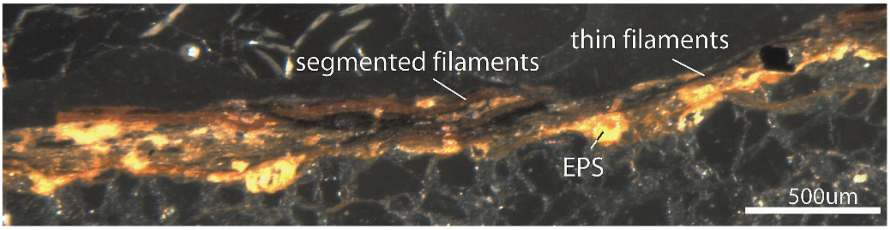


Fig. II.27. A fossil microbial mat viewed in thin-section under light microscope. The thin-section is oriented vertically to the microbial mat. In reflected light, two different types of filaments are visible. Large and segmented filaments appear in orange colour. Thin filaments appear in black colour. The filaments form a network identical to the microbial mat fabrics of modern cyanobacteria. In statistical analyses, both ancient and modern mats show the same orientations, thicknesses, and lengths of the filaments. EPS appear as white, 'cloudy' chert particles between the filaments

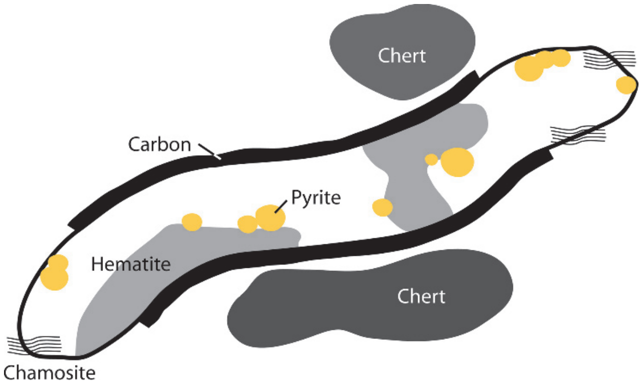


Fig. II.28. Sketch through a fossil cyanobacterium preserved in sandstone from the 2.9 Ga Pongola Supergroup, South Africa. The various organismic components of the filament were replaced by different minerals. Here, pyrite, hematite or magnetite fill in the inner portions of the filaments. Chlorite or chamosite line the outer cell wall. Remains of organic carbon indicate the former presence of a sheath (glycocalix) that surrounded the original filament. In highly metamorphosed rocks such original carbon can be altered to graphite. Chert replaced EPS

Microprobe analyses show that such microbe fossils are composed not only one, but many minerals. This composition of many minerals is not unusual for fossils. Indeed, in paleontology, different types of fossils are distinguished with respect to different mineral composition (e.g., Briggs 2003). Fossils of macroscopic organisms such as fish, plants, etc. are not always completely mineralized. Sometimes the original organic material can still be found as finely dispersed carbon or graphite. Perry et al. 2007 categorize fossils into three types: First, there are organic fossils, in which organic substance is completely preserved as carbon or graphite. Coal is a good example. Second, there are completely mineralized fossils, in which all organic substance is gone, and only minerals can be found. Third, there are mineral-organic fossils, which include organic as well as mineral substance. Many fossil microbes in MISS belong to the group of mineral-organic fossils (Fig. II.28).

In ancient semi-arid paleoclimates, aragonite is a common replacement mineral. Aragonite often lines fossil filaments. Because of the mineralization process, these filaments become strongly dehydrated and rolled-up. These curled up filaments eventually form irregularly shaped carbonate particles in chemical I mats (Krumbein 1979; Gerdes et al. 1994 for an overview on these particles).

Replacement of organic matter by minerals is called 'destructive biomineralization'. The transformation of organic matter is triggered by the activity of heterotrophic bacteria. These bacteria destructively decompose large biomolecules into smaller chemical compounds. The small chemical compounds can react with each other and form mineral precipitates. For example, clay minerals such as chamosite form along the surfaces of decaying bacterial cells (Ferris et al. 1987, 1989; Beveridge 1989; Urrutia and Beveridge 1993b; Konhauser et al. 1994; Schulze-Lam et al. 1996; Douglas and Beveridge 1998). Reiswell 1987, Giblin 1988, or Canfield and Raiswell 1991 describe the precipitation of pyrite on decaying organic matter in reducing chemical environments. Precipitation of silica along organic material is supported by acidic pH-values (Leo and Barghoorn 1976; or Knoll 1985).

It is important to know that these secondary processes foster the *in situ* fossilization of microbial mats even in cold water settings (Noffke 2000). An impressive example for destructive biomineralization is the Circum-Mediterranean Coastal Pleistocene exposed in southern Tunisia. The rock succession includes a 2 m thick unit of finely laminated sandstone. This finely laminated unit is composed of *in situ* lithified microbial mat layers.

Figure II.29 summarizes the secondary taphonomic processes:

a) In close-up, a bacterial cell wall is composed of biomolecules. The large and complex biomolecules are structurally arranged in a fashion that electronegatively charged compounds reach out into the surrounding sea water. All those microsites of electronegativity together contribute to an overall negative charge of a bacterial cell wall. Despite this structural arrangement of the biomolecules, the *de facto* charge of a bacterial cell is neutral. In the course of ATP synthesis, living cells pump out protons. The protons are released into the surrounding microenvironment of the cell, thus equalizing the negative charge.
b) The distribution of protons and electronegative microsites is not always homogeneous. The projecting microsites attract water molecules. Water molecules are strongly polar, having a dielectric constant of 80. They accumulate around the cell, forming a hydrate envelope. This envelope of water is important for the formation of EPS, and also serves to buffer the cell against its chemical environment.
c) Everything has an end. As soon as a bacterial cell dies, the situation changes quickly. The ATP pump stops working. No protons are delivered to the outer cell wall. The cell wall becomes increasingly negatively charged.
d) Sea water contains an enormous amount of dissolved and highly mobile ions. Electropositively charged (metal) ions are attracted by the electronegatively charged microsites of the cell wall biomolecules. The metal ions attach to the microsites, and subsequently attract negatively charged anions from the sea water. First minerals precipitate. Because the water molecules block the microsites of the biomolecules, these first mineral precipitates are hydrated and therefore amorphous. Amorphous means that the molecular structure of these water-rich precipitates is disordered and resembles that of the configuration of atoms in fluid, glass, or gel. No crystalline arrangement of the ions exists. These first amorphous precipitates can be tenorite (FeS – the precursor to pyrite FeS_2) or amorphic aragonite (Krumbein et al. 1979b), and also many others. Which precursor minerals are formed depends on the type of ions provided by the sea water, and therefore is a consequence of the sea water chemistry (Noffke et al. 2001a).
e) In later diagenesis, amorphous precipitates dehydrate. They lose water molecules, releasing them into the sea water. The dehydration is supported by the high binding forces between the ions. The powerful binding forces result into an ordered, crystalline arrangement. A crystalline mineral phase develops. Because the binding forces between the ions and the dipoles of the water molecules are low, the water is released from the crystalline structure. In the increasingly consolidating sediment, the crystalline structure of the mineral phases continuingly adapts to the changing pressure and temperature. Minerals become more crystalline, as dehydration occurs and pressure increases. This stage (e) is a purely abiological process.

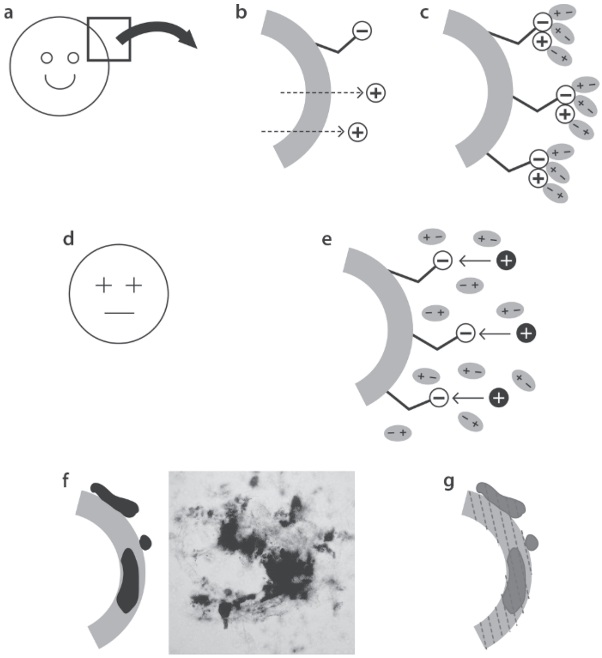


Fig. II.29. Biomineralization of a bacterial cell. **a** A living bacterial cell. **b** In close-up, the cell wall is composed of complex biomolecules. Their structure imparts an electronegative charge to the bacterial cell overall. However, the ATP pump of the living cell produces protons that buffer the electronegativity and generate a neutral charge. **c** Water molecules assemble at the negative microsites of the cell wall. **d** The cell dies, and the ATP pump ceases. Protons are no longer pumped into the surrounding sea water. The biomolecules that compose the cell wall now present a negative charge. Metal ions in the sea water are attracted by the electronegative microsites. Positive ions bind to the negative microsites of the biomolecules. **f** The biomolecules start to decompose. Decomposition is often supported by the catalytic activity of heterotrophic bacteria. The first mineral precipitates fall out. Because of the envelope of water molecules adhered to the bacterial cell, those early precipitates are amorphous. The photo on the right shows a decaying filament covered by black tenorite, the precursor mineral to pyrite. **g** Because of the enormous binding forces between negative and positive ions the mineral precipitates release the water molecules. Over time, an anhydrous, crystalline mineral phase forms

II.2.2
Bringing the Ecological and Taphonomic Window into Alignment: the Search for Biofilms and Microbial Mats in Siliciclastic Settings

Formation and preservation of MISS correspond to the ecological and taphonomic windows (Fig. II.30). In sediments or sedimentary rocks, MISS occur where these two windows overlap. This overlap provides optimum growth and preservation conditions.

In the following, a series of steps is presented that can be used to find microbial mats and to identify MISS in Earth's lithological record. These steps include field procedures, and laboratory analyses. It also provides useful methods and insights for the detection of life on Mars and other planets. The series is composed of 5 steps: search, detection, identification, confirmation, and differentiation.

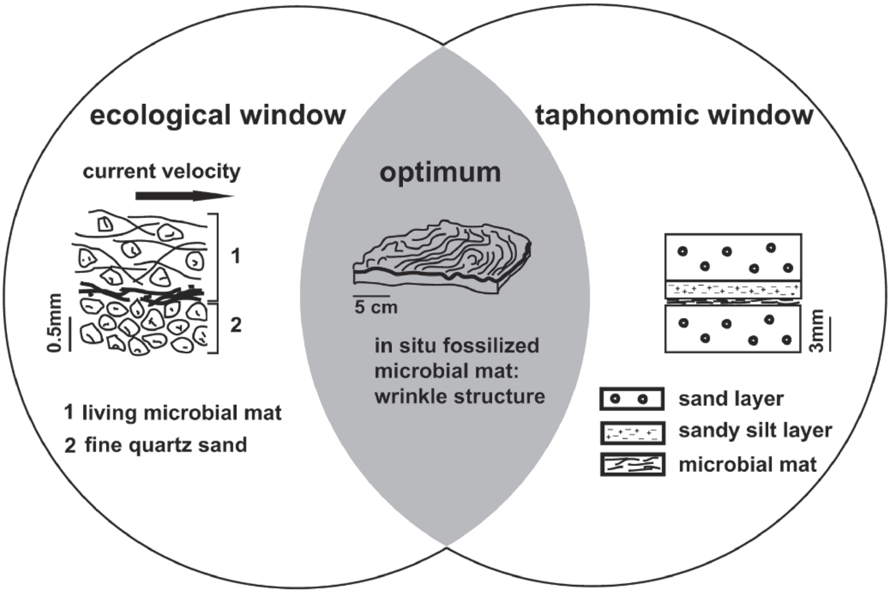


Fig. II.30. The ecological and taphonomic windows overlap, where the sedimentological context of microbial mats is at optimum. In this optimum, MISS can be found. Ecological window: The ecological window is characterized by sediments that constituted favourable substrates for the development of microbial mats. Such sediments are composed of translucent quartz minerals of fine sand grain sizes. The deposits occur at sites where hydraulic reworking is moderate. In order for mats to become preserved, these sediments must undergo a specific set of subsequent sedimentary events (taphonomic window)

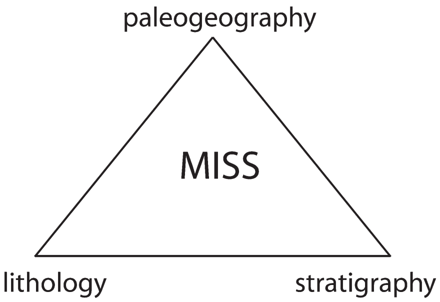
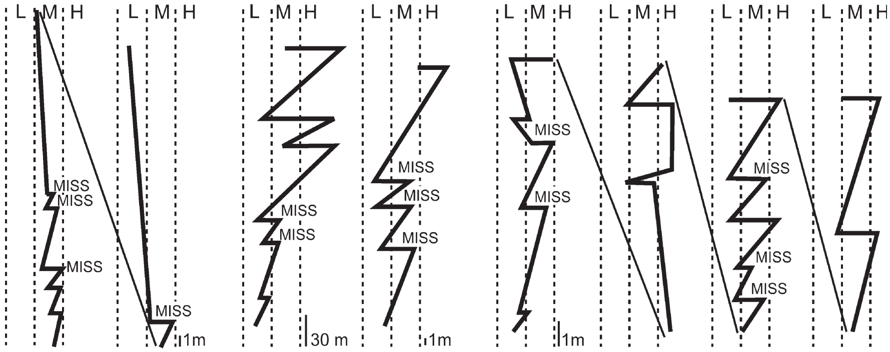


Fig. II.31. In the fossil record, MISS occur only in a specific setting. This setting is defined by three characteristics: the lithology of the rock, the paleoenvironment, and the stratigraphic position with respect to transgressions and regressions

II.2.2.1
Search

The overlap of the ecological and taphonomic windows is a function of a specific sedimentological setting in specific paleoenvironments (Fig. II.31). In these sediments or sedimentary rocks, respectively, MISS occur.

In order to find fossil MISS, a geobiologist first conducts a thorough geological survey. Of specific interest is to find ancient tidal flats, lagoons, and continental shelves. In these environments, microbial mats could have developed.



Bibane Dam Section,
Pongola Supergroup,
Meso-Archean,
South Africa

Haruchas and Bullsport
Sections, Nama Group,
Neo-Proterozoic,
Namibia

Gres et Schistes de la Cluse de l'Orb
Section, Ordovician, Montange Noire,
France

Fig. II.32. The distribution of MISS correlates with transgressions in sandstone successions. During times of high sea level, shallow-marine areas are especially wide. Large portions of the continents are submerged. In this figure, three example outcrops are shown. The rock successions include tidal flats, lagoons and continental shelves of Archean, Neoproterozoic, and Phanerozoic ages

It is important to consider during the field survey that tidal flats, lagoons, and continental shelves widen when the sea level rises. A sea level rise is called 'transgression'. A drop in sea level is called 'regression'. In rock successions, transgressive and regressive phases can be reconstructed. The surveyor must search for such phases. When shallow-marine areas increase due to rising sea levels, the amount of favorable habitat for microbial mat formation also increases. Therefore, the distribution of MISS often correlates with transgressive portions of rock successions, Fig. II.32 (Noffke et al. 2006b).

Once an appropriate paleoenvironment is identified, a suitable sedimentological context for microbial mats must be found. This context includes quartz-rich fine sand formerly deposited in an area of only moderate reworking. Such optimal conditions are preserved as rippled fine sandstone beds of 2–20 cm thicknesses, composed of 95% quartz grains (Noffke et al. 2002).

A survey for aquatic deposits is among the first steps for the search for life on Mars. Once a promising aquatic rock succession is found, the rock succession is analyzed for rock beds that record optimal conditions for the development and preservation of benthic microorganisms.

II.2.2.2
Detection

Unlike stromatolites, MISS are not very prominent structures. The structures conform to the surface of sandstone beds and rarely have a vertical component. How can MISS be detected?

A simple technique enhances visibility of faint structures on sandstones. This technique is used by trace fossil sedimentologists (or trace fossil paleontologists, if someone prefers this term): the experienced surveyor chooses a time of day when bright

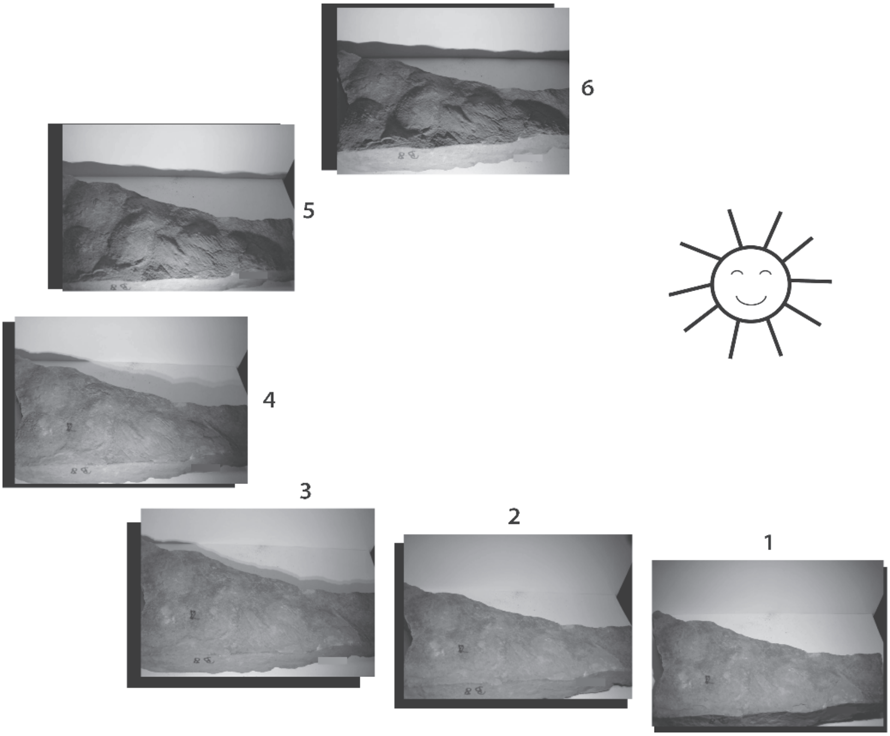


Fig. II.33. A rock surface under different angles of light. From stages *1* to *6*, the light illuminating the rock surface changes from a vertical angle of 90° to a horizontal angle of 180°. Note that with decreasing angle, the rock surface relief becomes more visible. The shadows of irregularities on the rock surface increase the contrast

sunlight illuminates the bedding plane at a low angle. The resulting shadow causes contrast that increases the visibility of a surface relief significantly. On a Mars rover, an artificial light source might be employed to enhance the contrast of irregularities on the depositional surface (Fig. II.33).

Extensive, well exposed bed surfaces would assist the search. However, such surfaces are rare in an outcrop. To find structures, the author quite often has had to climb a lot, painstakingly following individual rock beds centimeter by centimeter, or even millimeter by millimeter.

II.2.2.3
Identification

If a sedimentary structure is detected that potentially could be a MISS, the surveyor must conduct exact measurements of the geometries and dimensions of the structure in question. The objective is to compare the morphology of the fossil structure with the morphology of modern MISS of same type. In order to test similarity, statistical analyses on the morphologies must be conducted. The values are compared against a large data base of known MISS using a computer. This quantitative approach relies not only upon the subjective opinion of the surveyor, but creates real and reproducible data. The identification as MISS is only certain if statistical analyses of the geometries and dimensions of potential MISS correspond to those of modern structures. Examples for quantifications of MISS are provided in Chap. III, where multidirected ripple marks, erosional remnants and pockets, and mat chips are discussed. MISS occur from the early Archean time until today (Fig. I.6). Geobiologists can and should make use of the fact that the structures are of identical morphologies throughout all this time.

Sometimes even this statistical comparison of fossil and modern MISS is not convincing. Examples of potential MISS that often are controversially debated are wrinkle structures. Wrinkled sandstone surfaces can result from tectonics, syndepositional slumping, or other abiotic influences. The identification of a wrinkle structure (or any other MISS) must be confirmed by further analyses. This further analysis is the third step, confirmation.

II.2.2.4
Confirmation

How can the biological origin of a structure be confirmed? It is important to examine whether fossil bacteria are preserved in the MISS in question. Unfortunately, fossil microbes are rarely found in sandstones. In contrast to the well preserved fossil bacteria known from chert rocks, microbes in sandstone are in poor states of preservation. Confirmation requires a lot of microscope work. As in step 3 (identification), fossil samples are compared with modern MISS. Statistical analyses must confirm the similarity of ancient microbial mat textures with modern mat fabrics.

In order to study modern mat fabrics, cores from fresh tidal sediments are taken (Fig. II.34). These cores are processed in the lab in order to prepare relief casts (Fig. II.15).

Rock samples of potential MISS are collected in outcrops. Samples of fresh rock must be taken using a hammer. Loose rock pieces at the base of an outcrop, or along a road must not be collected.

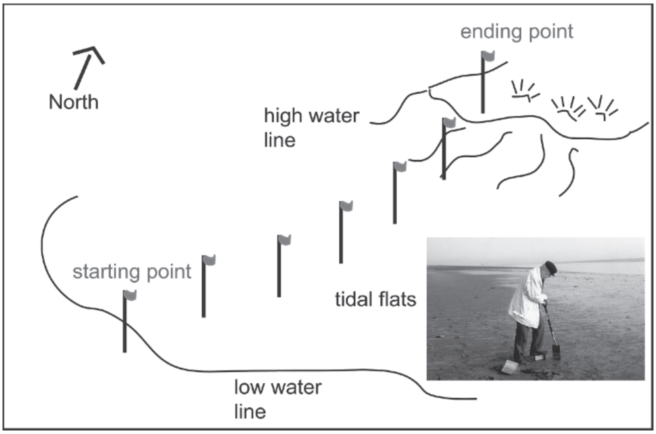


Fig. II.34.
In order to investigate modern MISS, sediment cores are collected. These sediment cores are processed in the laboratory to prepare relief casts. Such casts display sedimentary structures and textures in three dimensions. In the photo, Hans Erich Reineck demonstrates how sediment cores are taken

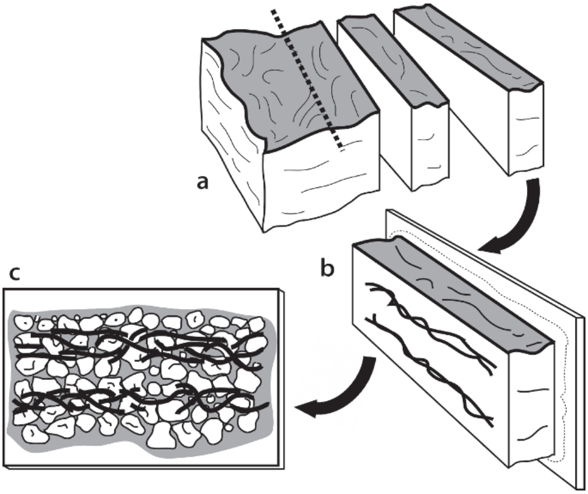


Fig. II.35.
Preparation of thin-sections from a rock or an epox-hardened sediment. **a** A sample is cut into blocks of about 0.5 cm thicknesses. Here the cut is oriented perpendicularly to the sediment surface. **b** The block is glued with resin onto a glass slide. **c** The block then is cut and polished down to a thickness of mere 5–30 µm. Such thin-sections are studied by light microscope, but can also be used for microprobe, Raman spectral analysis and other analytical procedures. The thin-section in (**c**) shows black bacterial filaments in quartz sandstone

Small 2–3 cm blocks are cut from relief casts or rock samples (Fig. II.35). These blocks are then cut into thin-sections. Most thin-sections are directed perpendicularly to the sedimentary surface. One can also experiment with thin-sections oriented in parallel with the surface. Microscopic examination of thin-sections makes detailed study of microscopic textures possible. A variety of microscope techniques are employed.

II.2.2.5
Differentiation

Differentiation is the last step. It is the comparison of potential MISS with structures that are similar in appearance, but not of biologic origin. This final test serves to exclude candidate structures that more closely resemble abiotic structures. Using precise measurements, a computer compares the candidate structure's properties against a large data base of known abiotic structures. The resulting analysis shows the statistical likelihood that the structure under consideration is of abiotic origin.

It is this last step, differentiation, which usually is overlooked. Yet it is important not to proceed too enthusiastically with an interpretation, unless differentiation has been carefully performed. It is always best to objectively consider any other possible origin of a structure before reaching a conclusion.

It is prudent to compare a potential mat fabric with a hydrothermal vein, or with stylolites like those shown in Fig. III.9 of the next chapter (Noffke et al. 2008). Hydrothermal veins are minerals that precipitate from hot, mineral-rich water circulating through fine cracks in the rock. In contrast to fossil mat laminas, hydrothermal veins are predominantly vertically oriented, and they frequently switch directions. Microbial filaments show an orientation of 0–45°. Stylolites are zig-zag lines that result from vertical pressure on a rock during its lithification. In contrast to microbial mat laminae, stylolites lack any internal fabrics of filaments, EPS, etc. Statistical analyses on as many thin-sections as possible are necessary to differentiate microbial mat laminae from abiotic hydrothermal veins or stylolites (Fig. II.36).

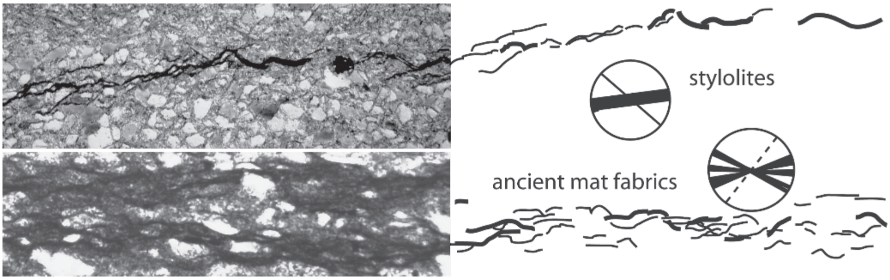
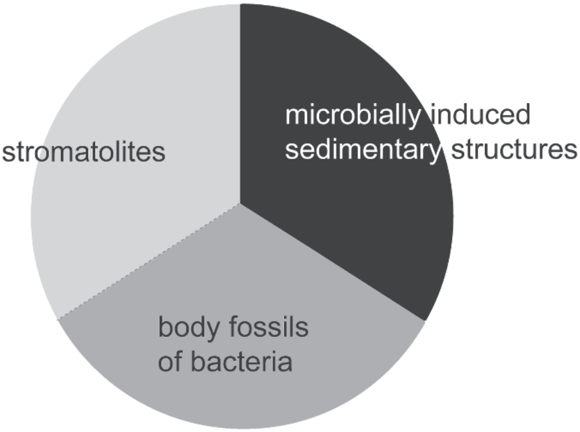


Fig. II.36. Biogenic or abiogenic microscopic fabrics viewed in thin-section. If the filament-like textures are stylolites, statistical analyses of the orientation of filaments reveal a main orientation of 180°. However, true microbial mat fabrics composed of filaments of cyanobacteria display an arrangement of filaments of 45° to each other (after Noffke et al. 2008)

Fig. II.37.
MISS constitute a third avenue to understanding early life. The structures form the complement to stromatolites, and body fossils of bacteria



II.2.3
The Criteria for Biogenicity of MISS

The five steps of identification of biogenic structures established a set of criteria for biogenicity of MISS (Noffke 2009). As explained in the proceeding sections, geobiologists face the problem of taphonomic selection. In older rocks, more original fossils and sedimentary structures have been eliminated by processes that alter the deposits from the moment of their placement to the moment they are studied. The fossil record for the Archean Era is therefore especially sparse. A large volume of Archean rocks are sandstones. MISS constitute a largely unexplored archive, a resource of major significance for understanding Earth's early life (Fig. II.37).

It is know from studies of Archean rocks that many structures are not fossils or stromatolites, but of abiotic origin (Grotzinger and Rothman 1996; Schopf et al. 2002; Brasier et al. 2002; Schopf et al. 2007). Criteria were developed that must be met by candidate structures or textures before they are confidently considered to be of biological origin. Such criteria are termed 'criteria for biogenicity' (e.g., Buick et al. 1981, 1991; Brasier et al. 2006, and references on this topic therein).

Because criteria of biogenicity have been defined for stromatolites and for microfossils of bacteria, a catalogue of criteria for MISS was established as well (Noffke 2009). The catalogue follows the systematic study by the author on modern, Phanerozoic, Neoproterozoic, and Archean rock successions (Noffke 2000; Noffke et al. 2002, 2003b, 2006a,b, 2008).

II.2.3.1
List of Criteria

1. *Fossil MISS occur in sedimentary rocks that experienced less than low grades of metamorphosis (greenschist facies)*
   In all fossil outcrops studied, the rocks have experienced less than lower greenschist metamorphosis. In such metamorphic grades, traces are excellently preserved. The same is true for fossilized MISS, which are microbial trace fossils.
2. *In stratigraphic sections, MISS correlate with transgressive phases*
   Extensive tidal flats, lagoons, and continental shelves form along passive continental margins as the sea level rises. Today all tidal flats surrounding the North Atlantic Ocean are products of the Holocene transgression. Because the modern shallow-marine coasts are so wide and spacious, microbial mats form one of the world's largest ecosystems. This extensive distribution of microbial mats in shallow-marine areas is also reflected in fossil rock successions. In all sandstone successions studied so far, the distribution of MISS correlates with transgressive phases.
3. *MISS occur in a defined 'microbial mat depositional facies' that facilitates the development and preservation of photoautotrophic microbiota*
   Mats develop only in a specific sedimentary facies favourable for the growth and preservation of photoautotrophic microbial mats. This facies comprises the ecological and the taphonomic windows. A suitable microbial mat depositional facies must provide three parameters: a fine sand grain size; a predominantly quartz mineral composition; and a moderately reworked hydraulic setting.
4. *The distribution of MISS is not random, but reflects the average hydraulic and meteorological pattern in a defined area*
   MISS are restricted to tidal, lagoonal and shallow shelf environments. Within these settings, the distribution of MISS reflects the average hydraulic pattern of currents and waves. Meteorological fluctuations such as seasonal rains, storm frequencies, and periods of desiccation also affect the distribution of microbial mats (MISS, respectively).
   - *Distribution of MISS on continental shelves.* Statistical analyses were conducted on the distribution of wrinkle structures on the ancient continental shelf of the Ordovician of the Montagne Noire, France. This study documents that transparent wrinkle structures record fossilized endobenthic microbial mats that grew in the seafloor area above the storm wave base. Non-transparent wrinkle structures (fossil epibenthic microbial mats) developed in mainly quiet zones below the storm wave base. Transparent and non-transparent wrinkle structures are shown in Fig. III.43 in the next chapter.
   - *Distribution of MISS in lagoons.* The Ordovician of the Montagne Noire, and the Proterozoic Nama Group, Namibia, include lagoonal deposits. The lagoonal rock successions are composed of thinly bedded, 'clean' fine sandstone beds. Each

sandstone bed is separated by a fine siltstone layer from the following one. Atop of each sandstone bed a wrinkle structure occurs. The wrinkle structures are *in situ* fossilized microbial mats. Transparent wrinkle structures record that the floor of the lagoon was reworked by bottom currents from time to time. Deeper seafloor areas of the lagoons remained undisturbed by water motion. Here epibenthic microbial mats grew, now recorded as non-transparent wrinkle structures.

- *Distribution of MISS in tidal flats.* The hydraulic system that governs tidal flats creates a lateral succession of different biofilms and microbial mats from the low to high water line. Such a lateral succession is termed 'biofilm-catena'. Each type of biofilm or microbial mat of this catena causes characteristic MISS. One example is the biofim-catena recorded in the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa. This stratigraphic section includes an ancient, sandy tidal flat. As in tidal flats today, endobenthic microbial mats developed in the upper intertidal zone. Epibenthic microbial mats occurred in the lower supratidal zone. Each mat type left characteristic MISS. The location of the fossil MISS corresponds to the location of the same MISS in present tidal settings.

Another example of biofilm-catena can be studied in the sabkha Bahar Alouane, Tunisia. Fossil counterparts include Pleistocene successions from south Tunisia (Noffke et al. 2001a), and Devonian successions of the Muth Formation in the Himalaya (Draganits and Noffke 2004).

5. *In statistical analyses, the geometries and dimensions of fossil MISS correspond to those of modern MISS*

The geometries and dimensions of MISS can be easily measured in modern tidal settings. The change of their morphologies during the course of a year can also be determined (e.g., Noffke 1998, 1999; Noffke and Krumbein 1999). The same morphologies must be shown by fossil MISS. A well-founded comparison conducts statistical analyses on both fossil and modern MISS.

As an example, statistical analyses were made for 'erosional remnants and pockets' (Fig. I.3c,d). The geometry of this surface structure is expressed by the 'MOD-I, the modification index' (Noffke and Krumbein 1999). This is an index number that indicates the degree of microbial influence in the formation of erosional remnants and pockets. The MOD-I is composed of three subindices expressing: *(i)* the extent of a mat-covered surface portion in a given study area; *(ii)* the degree of the angle of slope of the erosional remnants; and *(iii)* the degree of leveling of ripple marks expressed as the thickness of a microbial mat in ripple valleys. Endobenthic or epibenthic microbial mats and their seasonal variations exhibit different values for MOD-I. The values range from 0 for no microbial influence, to 1 for maximum microbial influence. The same MOD-I can be established for ancient erosional remnants and pockets, indicating the position of the MISS on the ancient tidal flat, the seasonality of the paleoclimate, and the possible mat type (a good example is described in Noffke et al. 2008).

Compaction and dewatering processes during the lithification (transformation) of sand to sandstone do not affect the shapes of MISS. Sand composed of quartz grains is very resistant to high pressure and temperature. Metamorphosis of greenschist grade does not alter sandstone except those containing silica-rich cement. Silica is water-rich, and its crystalline structure is more affected by pressure and temperature. In such sandstones, the slight compaction of the silica cement may cause stylolites (Noffke et al. 2008). This minor, microscopic compaction does not affect the macroscopic morphology of MISS. In general, MISS are 1 : 1 preserved.

6. *MISS include textures that either represent, have been caused by, or are related to biofilms or microbial mats*
   In thin-sections, MISS must include textures that are either related to, have been caused by, or represent biofilms or microbial mats. Modern microbial mats, or EPS-rich biofilms, reveal 9 main types of textures. All such textures have also been found in fossil MISS. Five groups of these textures are distinguished.
   i) *Textures representing in situ biofilms or microbial mats.* Wavy crinkled laminae serve as a good example. The laminae record stacks of accumulated microbial mat layers up to 2 cm high. Tufts also can occur.
   ii) *Textures caused by microbial baffling and trapping.* Mat-layer-bound small grains constitute a good example. Small grains are accumulated by microbial baffling and trapping. Heavy minerals and mica also may be present.
   iii) *Textures related to binding of biofilms and microbial mats.* Sinoidal structures serve as good examples. Sinoidal structures are former biofilms or mat laminas that coat ripple marks.
   iv) *Textures related to biostabilization of biofilms and microbial mats.* Sponge pore fabrics constitute a nice example. This structure is a layer of very high porosity in sandstone. This porosity results from gases accumulating beneath a sediment-sealing microbial mat.
   v) *Textures caused by the interference of all microbial activities.* Microsequences are good examples. These sequences are cm-scale, upward fining sand layers, each capped by a microbial mat. Such microsequences result from microbial interaction with gradually changing sediment dynamics.

II.2.3.2

The Criteria for the Biogenicity of MISS in the Context of the Criteria for Stromatolites

There are many good discussions on the biogenicity of stromatolites. The contribution by Buick et al. (1981) is the most applicable model for MISS. In their essay on biogenicity of stromatolites, Buick et al. demand the study of both the paleoenvironmental setting of the stromatolitic structure in question, and the morphology and internal texture of the structure. The above criteria suggested for the biogenicity of MISS are separated into these two categories. Four criteria are related to environmental parameters that control the development and preservation of biofilms and microbial mats. Two criteria describe and quantify morphologies and internal microstructures of MISS.

Buick et al. require the identification of a host rock of a stromatolite to be of sedimentary origin. Further, the stromatolite in question must have formed syndepositionally. MISS are very distinctive, and their morphology cannot be mimicked by physical sedimentary processes. However, a geological field survey of the exact position of a MISS in its paleoenvironmental context is important. MISS are clearly a result of both biological activities (intrinsic factors of biofilms) and physical processes (extrinsic factors of biofilms). The structures cannot be studied without considering their environmental surroundings.

Buick et al. recommend the comparison of fossil structures with modern ones. They prefer the occurrence of a fossil stromatolite in an ancient shallow-marine and photic setting. Comparison of modern stromatolites with the simple, cone-shaped stromatolites of the early Archean Era is difficult. In modern stromatolites, cyanobacteria and various eukaryotic microbes play a significant role. Cyanobacteria and eukaryotes probably did not exist before 3.5 Ga.

Stromatolites have been well investigated, however to date no comparative analyses between Archean, Proterozoic, Phanerozoic, and modern stromatolites have been conducted. In contrast, our research has developed a new concept. Our geobiological perspective has been informed by our comparative analyses of MISS from deposits of 3.2 Ga age to the present. This comparison of MISS of all Earth ages with each other is not only possible, but essential for a comprehensive understanding. It is required for all criteria, except the first criterion.

Buick et al. differentiate stromatolites that include fossil microbial filaments from updomed, but possibly abiogenic structures that lack filaments. This is different from MISS. All MISS include textures (criterion 6). If fossil mat fabrics or filament-like textures are not present, one of the other textures ii–v must occur. Bacterial cells might

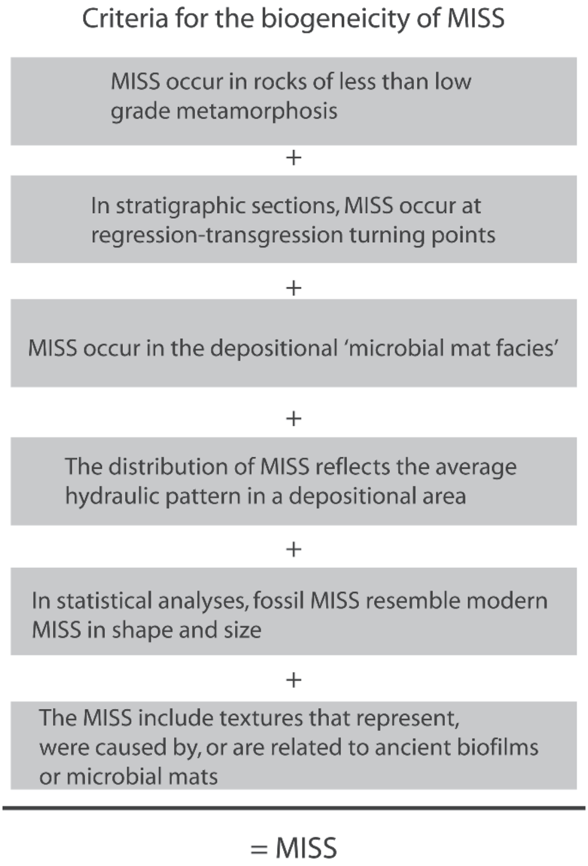


Fig. II.38.
The criteria for the biogenicity of MISS. Only if all six criteria are met, a fossil sedimentary structure in question can be defined as MISS

not be preserved. However, microbial activities such as baffling and trapping, or binding can create traces. Traces include typical textures such as 'oriented grains' (textures of type ii).

The geobiological concept has clearly defined the characteristics of MISS, and the experience and data gathered by our systematic study have developed the criteria for their biogenicity. MISS such as wrinkle structures may be related to abiotic processes such as water motion in sand, desiccation, or tectonic overprint (Noffke 2000). However, all discussions on the biogenicity of a structure in question are unnecessary, if this catalogue of criteria of biogenicity is followed faithfully. The criteria are summarized in Fig. II.38.

Chapter III Classification

Chapter III

Classification

III.1
The Classification Diagram of MISS

This chapter elucidates the classification of MISS. MISS constitute the fifth group of sedimentary structures in the classification of primary sedimentary structures by Pettijohn and Potter (Noffke et al. 2001b). The latest classification of MISS is presented here (Noffke 2009).

MISS comprise 17 main types. The types are summarized in a diamond-shaped classification scheme (Fig. III.1). The scheme includes five categories of microbial activities. Each activity forms a set of characteristic MISS.

The 5 categories are: *(i)* structures arising from growth, *(ii)* structures arising from biostabilization, *(iii)* structures arising from baffling, and trapping, *(iv)* structures arising from binding, and *(v)* structures arising from the interference of all microbial activities. These categories refer to the genesis of the structures.

The individual structures in each category are given descriptive terms, such as ‘multidirected ripple marks’. This term describes the morphology of the structure. The term is descriptive. It assists the identification of structures in the field. Even if the investigator has little knowledge about the formation of MISS, the morphology of the structure can still be described.

Definition of Growth

In the context of this book, growth is the enrichment of biomass by cell replication. The production of EPS may or may not be involved. Growth is controlled not only by sedimentological parameters. Growth also results from favourable sunlight, temperature, humidity, and available nutrients.

Definition of Biostabilization

Three types of biostabilization are distinguished:

1. Biostabilization is the response by benthic microbiota to erosion. Cyanobacterial filaments are oriented horizontally, and the EPS (if present) change their chemical structure to a more erosion-resistant phase.
    I. Biostabilization by epibenthic microbial mats
    II. Biostabilization by endobenthic microbial mats
    III. Biostabilization by biofilms

N. Noffke, *Geobiology*, DOI 10.1007/978-3-642-12772-4_3,

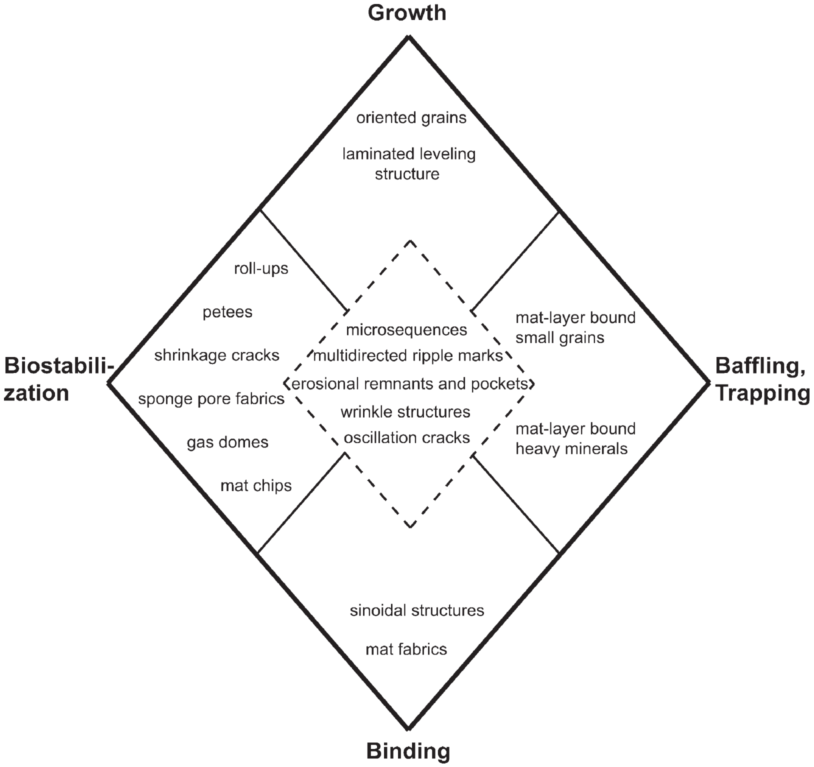


Fig. III.1. Classification of microbially induced sedimentary structures. The diagram shows the formational relationship of all MISS. The structures are induced by growth, biostabilization, baffling, trapping, or binding. The center of the diagram includes MISS caused by the interference of all biotic-physical interactions

2. Biostabilization is the flexible, biologically controlled deformation of otherwise brittle sediment composed of loose sand grains.
3. Biostabilization is sealing of the sedimentary surface so that any exchange of gases between sediment and atmosphere or water is prohibited.

Definition of Baffling and Trapping

Baffling is the response by benthic microbiota to the deposition of sediment. Vertical orientation of cyanobacteria results from phototaxis (movement in order to reach optimal light conditions), and sometimes sediment load pressure. Growth does not play a role. Two types of baffling are distinguished:

1. Sedimentary particles suspended in the supernatant seawater are 'combed out' by vertically oriented filaments during low dynamic periods. This baffling is typical for epibenthic microbial mats. Mats enrich silt-sized particles that otherwise would remain in suspension.

2. Endobenthic microbial mats move actively and quickly through the sediment to keep up with rising (and sometimes laterally migrating) sedimentary surfaces. Sediment grains that become incorporated by this microbial mat type are of same sizes as those of the background deposit.

Trapping is the effect of sticky EPS on the surfaces of microbial mats. Small sized mineral particles are glued to the mat surfaces.

Definition of Binding

Binding is the formation of a mat fabric by active movement of cyanobacteria. These microorganisms communicate, arranging an organic, meshlike network. Biomass production by cell replication does not play a role. The production of EPS may or may not be involved. In contrast to growth, binding is controlled only by sedimentological parameters. A mat fabric is formed only during calm dynamic conditions. Nutrient availability, solar radiation, water temperature, etc., does not affect this process of binding.

III.2
The Five Categories of MISS

III.2.1
Structures Arising from Microbial Growth

This section introduces all MISS that arise from microbial growth. Growth means both biomass production by cell replication and the possible secretion of mucilages. Rapid *in situ* lithification of organic material is required for the preservation of this type of MISS.

III.2.1.1
Oriented Grains

Description

In thin-sections perpendicular to an epibenthic microbial mat, individual quartz grains become visible. They seem to float in the organic matrix of the mat. The grains have no contact to each other. The sizes of the grains correspond to the sizes of the sandy substrate under the microbial mat. In contrast to the randomly oriented grains of the sandy substrate, however, the mat-embedded grains are predominantly arranged with their long axes parallel to the sedimentary surface (Fig. III.2).

Etymology

Oriented grains were first described by Noffke et al. 1997a in modern microbial mats from Mellum Island, North Sea. Fossil examples have been detected in the 3.2 Ga sandstones of the Moodies Group, South Africa (Noffke et al. 2003b), the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa (Noffke et al. 2008), and the Upper Neoproterozoic Nama Group, Namibia (Noffke et al. 2002).

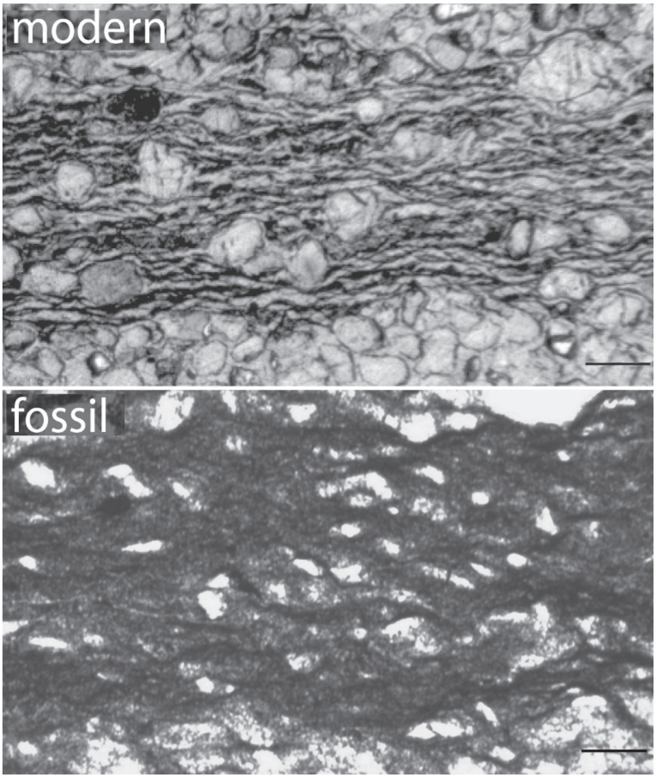


Fig. III.2.
Oriented grains in microbial mat layers as seen in thin-sections perpendicular to the bedding plane. *Modern:* Oriented grains in a microbial mat from Mellum Island. *Fossil:* The same texture of oriented grains entangled by filaments in a Paleoarchean microbial mat from the 3.2 Ga Moodies Group, South Africa; (scales: 0.2 mm)

Genesis

The genesis of 'oriented grains' was demonstrated in laboratory experiments (Noffke et al. 2001b). When cyanobacteria initially colonize freshly deposited sand, they form thin biofilms around each individual sand grain in the uppermost millimeter of the sedimentary surface, Fig. III.3. If calm conditions persist, the envelope of biofilm around each grain grows and thickens equally. Over time, the constantly growing biofilm envelopes push the grains upwards, separating the particles from each other. The grains no longer have grain-to-grain contact, but float independently in the soft organic matrix. Finally, a lateral continuous microbial mat layer is established on the sedimentary surface. In this mat layer, the grains have rotated into a bed-parallel position. The particle orientation may result from low friction between the mineral grains and the surrounding organic matrix. Probably the grains rotate with respect to gravity. In the sandy substrate beneath the microbial mat, the quartz particles are grain-supported. Here, no preferred orientation of the grains occurs, because rotation is not possible in closely packed sediments.

In conclusion, 'oriented grains' derive originally from the sandy substrate under a microbial mat, and have been dragged upward by the developing biomass during mat formation. The grains therefore are not baffled and trapped.

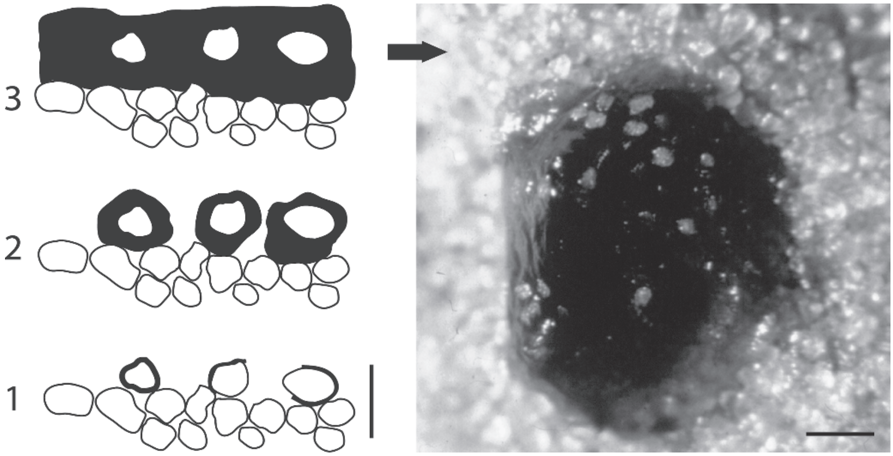


Fig. III.3. Formation of oriented grains. The sketch on the left illustrates the steps of formation in three stages: *Stage 1:* Thin biofilms (*black*) start to envelope individual quartz grains of the sedimentary surface. *Stage 2:* The initial biofilms become thicker, and lift the grains they colonize. *Stage 3:* The biofilms are so thick that they form a laterally continuous layer in the sediment. The grains in this soft organic layer rotate and orient parallel to the bedding plane. Right: The photo shows a top view of a small patch of microbial mat (*dark*) developing on a quartz sand surface. This laboratory experiment was a closed system to exclude contamination by allochthonous grains. Note the white spots in the dark mat patch. These spots are individual quartz grains embedded in the mat's soft organic matrix. The grains are not in direct contact. Photo taken by binocular microscope; (scales: 2 mm)

Paleoenvironmental Distribution and Seasonal Variations

'Oriented grains' are typical textures in epibenthic microbial mats. Their occurrence coincides with that of epibenthic mats of the lower supratidal zone. Because it takes a few months to develop an epibenthic microbial mat, the presence of oriented grains (modern and fossil) indicates a more mature mat community. Epibenthic mats are perennial.

Diagnosis

Oriented grains are identified in thin-sections cut perpendicularly through a microbial mat. The grains have no contact with each other, and they are oriented parallel to the bedding. The orientation must be documented statistically in rose diagrams (see Fig. III.4).

The composition and sizes of the mat-bound grains must correspond to that of the particles that compose the substrate beneath the microbial mat. This correlation must be documented in grain size analyses.

In ancient cold water settings, the organic matter of microbial mats was replaced by pyrite (or hematite, if oxygenized), goethite (a weathering product), chamosite and other chlorite minerals, as well as muscovite. Silica (chert) also might be present. In ancient, hot-arid climates, fossil microbial mats are lined by aragonite, calcite, or dolomite. All fossil microbial mats are organo-mineral fossils, and have an organic C isotope signature.

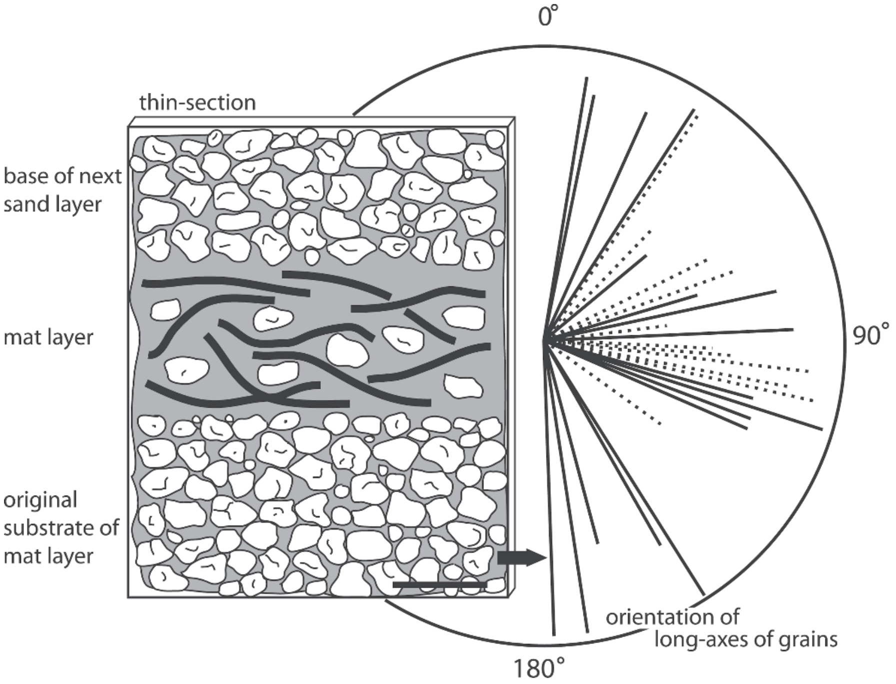


Fig. III.4. Orientation of quartz grains in a microbial mat layer, viewed in thin-section. The thin-section is oriented perpendicularly to the mat laminae. Left: At the base, the thin-section shows the original sandy substrate of the microbial mat composed of randomly oriented quartz grains. The microbial mat layer is visible in the center of the thin-section. This layer is composed of filaments interweaving individual quartz grains. The individual quartz grains seem to float independently from each other in the organic matrix. Their long-axes show a preferred orientation parallel to the bedding. The top of the thin-section shows the next sand layer that was deposited onto the microbial mat. Here the grains are randomly oriented. Right: Orientation of visible long axes of grains transferred into a circular chart. In statistical overview, the stippled lines indicate orientation of grains in mat layers

Example Specimen

A thin-section that displays 'oriented grains' is stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540864.

Application

Oriented grains are an indicator for epibenthic microbial mats. Their fossilized textures serve as an important indicator when evaluating MISS biogenicity. This texture assisted the identification of epibenthic microbial mats from 3.2 Ga sandstones of the Moodies Group, South Africa (Noffke et al. 2003b), the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa (Noffke et al. 2008), and the Upper Neoproterozoic Nama Group, Namibia (Noffke et al. 2002).

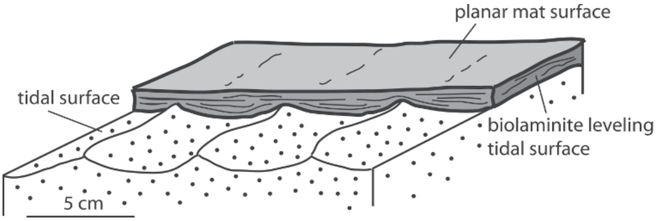


Fig. III.5.
Laminated leveling structure. The sketch shows the planar mat surface. Viewed in vertical cross-section, the ripple valleys are filled in by mat laminae

III.2.1.2
Laminated Leveling Structure

Description

This structure is composed of two geometrical elements (Fig. III.5):

i) Seen from above, a planar mat surface covers the original depositional surface. The prior sedimentary surface structures such as ripple marks are not visible anymore;
ii) In cross-section, laterally continuous mat laminae are visible. The laminae are wavy-crinkled in < mm scale.

The type of laminated leveling structure depends on the climate. In cold water environments, the laminae occur as individual layers that alternate with fine sand layers. In hot, arid climates, biovarvites are common. Biovarvites are composed of two different types of laminae. Each type is composed of different cyanobacterial species (Gerdes et al. 1991). One lamina is formed during summer, the other lamina is formed during winter. Wavy crinkled laminae are nicely described by Schieber (1999). In many examples, the laminae increase in numbers towards the sedimentary surface (Fig. III.6).

In fossil laminated leveling structures, the laminae are composed of pyrite (or hematite, if oxygenized), goethite (a weathering product of pyrite), chamosite and other chlorite minerals, as well as muscovite. Silica (chert) also might be present. In an ancient semi-arid, hot sedimentary system, organic matter is predominantly replaced by carbonate minerals such as aragonite, calcite, siderite and others. Fossil microbial mats are organo-mineral, and have an organic C isotope signature.

Etymology

The term 'laminated leveling structure' is a name composed of two earlier terms. The earlier terms originally were applied to two discrete structures. The two structures are now considered as one. The first term 'leveling' by itself was introduced by Noffke et al. 2001b for planar mat-covered sedimentary surfaces. Sedimentary surface structures such as ripple marks are 'leveled' by the growing microbial mat until the sedimentary surface is planar. The second term 'biolaminite' was applied to the internal lamination visible in vertical cross-section through such leveled sediment (Gerdes et al. 1991). The terms actually mean the same structure, but seen from two different angles: one from above, and one from the side. These two terms leveling and biolaminite are fused into the new name laminated leveling structure.

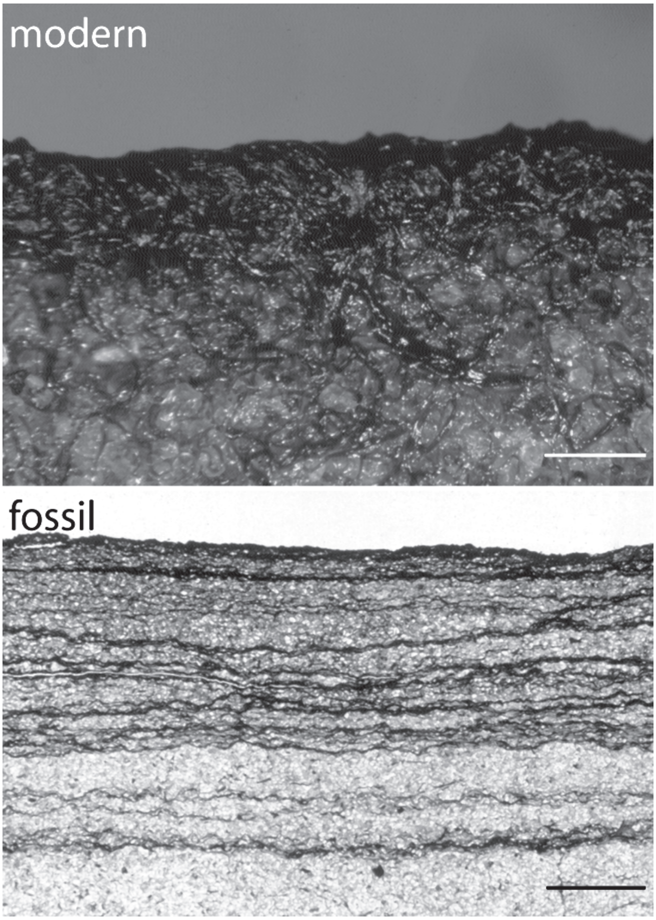


Fig. III.6.
Vertical thin-sections through modern and fossil microbial mats. Note that the density of microbial mat laminae increases towards the sedimentary surface; (scales: 0.5 cm)

Genesis

Seen from above, the developing biomass of a microbial mat overgrows the sandy sedimentary surface until any prior surface structures such as ripple marks become invisible. Planar surfaces are typical for epibenthic microbial mats. This mat type establishes in the course of several months (Hardie and Garrett 1977 for microbial mats on the Bahamas). In vertical cross-sections, older mat generations are overgrown by younger ones, until a stack of organic layers (biolaminite) is formed (Gerdes et al. 1991). Sandy layers between the mat laminae record episodical burial of prior mat generations. Biovarvites are stacks of organic layers composed by at least two different mat generations that mirror seasonal cyclicity: one mat generation for the summer predominantly constructed by *Synechnococcus* sp., one mat generation for the winter predominantly built by *Microcoleus chthonoplastes* (Gerdes et al. 1991). The reason for the predominance of *Synechnococcus* in summer is that this cyanobacterium has protective, UV-blocking pigments (carotenoids). In contrast is *Microcoleus chthonoplastes*, able to endure the poorer light conditions in the darker winter months.

Paleoenvironmental Distribution in Space and Seasonal Variations

Modern laminated leveling structures are typical for epibenthic microbial mats in supratidal zones. In the fossil record, they are typical for non-transparent wrinkle structures. The structures are distributed in dynamically quiet areas (Noffke 2000; Noffke et al. 2001b, 2006a). Biovarvites indicate a semi-arid, hot climate.

Diagnosis

Seen from above, a planar sedimentary surface always suggests a laminated leveling structure possibly caused by an epibenthic microbial mat. This assumption must be confirmed by a vertical cut through the sedimentary surface (modern) or in thin-sections oriented perpendicular to the bedding plane (fossil). The vertical cross-section must reveal the laminated pattern of this structure. The laminae are laterally continuous, alternate with fine sand interlayers, or form stacks of laminae of great inherence (biolaminite). Biovarvites show an alternating lamination of two different microbial communities each composed of different cyanobacterial species.

In microscopic close-up, laminated leveling structures may include filaments, EPS, allochthonous small grains, oriented grains, and heavy minerals. Note that EPS might be abundant. They may even constitute the main material of the build-up.

Example Specimen

Thin-sections that display biolaminates and biovarvites are stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540865, USNM 540866.

Application

The laminated leveling structures are strong indicators of former microbial mats (Fig. III.7). The laminae assisted the identification of microbial mats from the 3.2 Ga sandstones of the Moodies Group, South Africa (Noffke et al. 2003b), the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa (Noffke et al. 2008), and the Upper Neoproterozoic Nama Group, Namibia (Noffke et al. 2002).

III.2.2
Structures Arising from Microbial Binding

This section introduces MISS that arise from microbial binding. Growth plays a minor role. Rapid *in situ* mineralization of organic material is required for the preservation of this type of MISS.

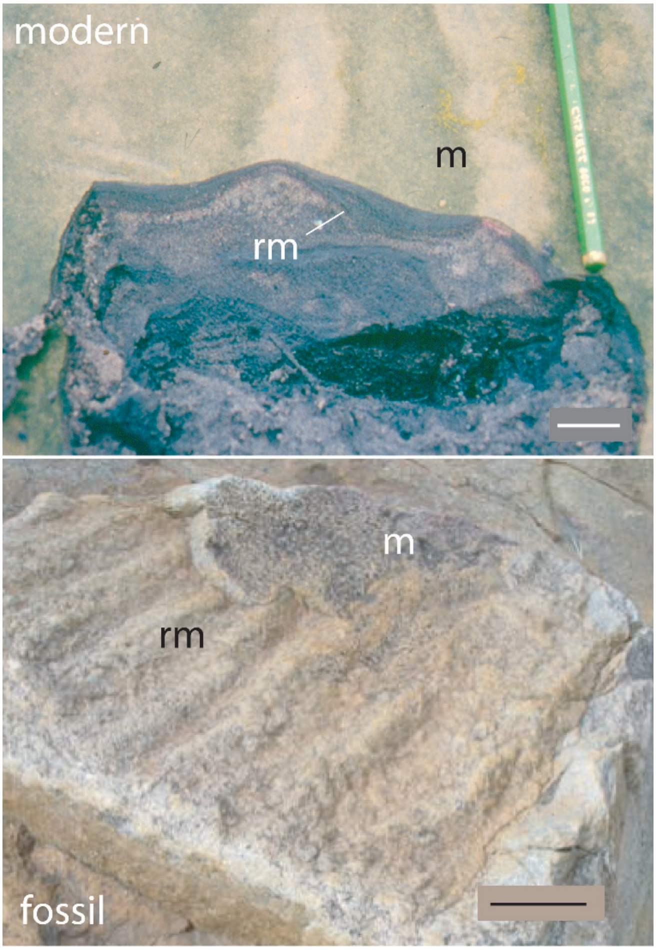


Fig. III.7.
Laminated leveling structures assist the detection of fossilized microbial mats. The two photos show a modern and a fossil example. *M* = microbial mat; *rm* = ripple marks; (scales about 4 cm)

III.2.2.1
Mat Microfabrics

Description

In vertical cross-sections through a microbial mat (either modern or ancient), laterally continuous mat laminae are visible. In microscopic close-up, a lamina displays typical mat microfabrics (Fig. III.8). The microfabrics include: *(i)* the cyanobacteria themselves; *(ii)* their EPS; *(iii)* mineral particles formed *in situ* by decaying organic matter; and *(iv)* detrital, often silt-sized grains enriched by trapping and baffling. Oriented grains also might be present.

The microfabrics of endobenthic and epibenthic microbial mats differ slightly. Under magnification, the laminae of *endo*benthic microbial mats are predominantly composed of filament-like textures, intertwined in angles ranging from 0–45° (Fig. II.36).

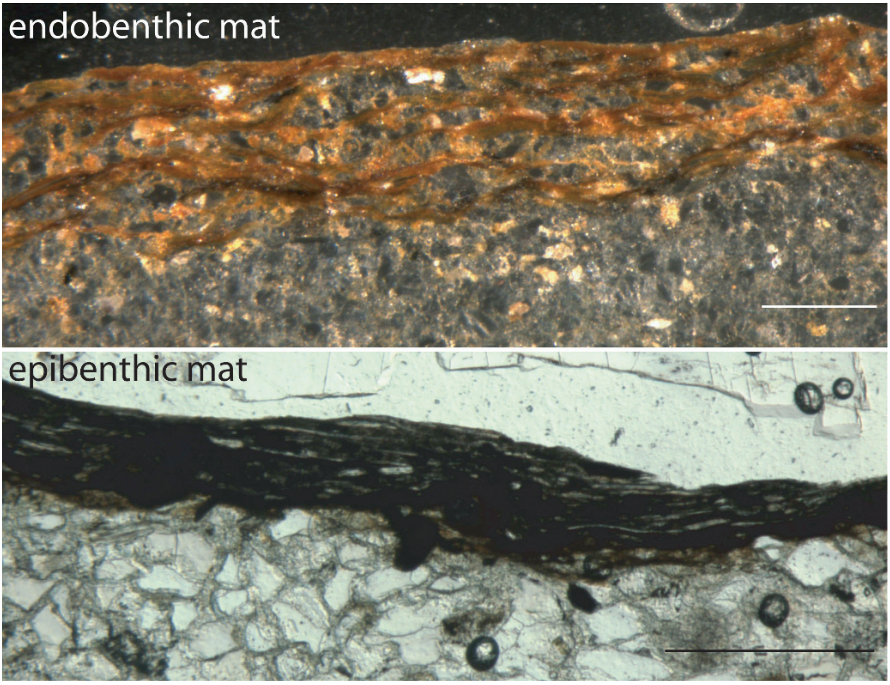


Fig. III.8. The mat fabrics of endobenthic and epibenthic microbial mats, displayed in thin-sections. The endobenthic microbial mat shown in the upper photo is situated in the uppermost millimeter of sandy sediment. The fossil filaments appear red in reflected light. Note the many grains visible in this mat type. In contrast, the epibenthic microbial mat shown in the lower photo is situated on top of sandy sediment. The opaque fossil filaments appear black in transmitted light. Note that this mat type is mostly composed of organic matter, although grains do rarely occur; (scales: 1 mm)

While this organic network interweaves the sandy particles, the grains still have grain-to-grain contact.

In *epi*benthic microbial mats, the typical arrangement of the filaments in 45° angles is not always visible. This is because the density of filaments in an epibenthic mat is much higher than in an endobenthic mat. Individual filaments can not be distinguished.

Under a petrologic microscope, fossil filament-like textures are brownish and opaque. Their outlines are not sharply defined, but cloudy. The textures are normally 5–20 µm wide. The length has been estimated to be about 200–300 µm. Length value estimates are vague, because of overlapping textures. Even in very thinly cut thin-sections, filaments are not clearly visible (Noffke et al. 2003b). The textures are composed of iron oxides (such as hematite), iron hydroxides (goethite), chlorite minerals, clay, sometimes titanium oxide, and a little carbon. In semi-arid, hot sedimentary systems, pyrite and carbonates as primary minerals replaced the original organic matter. Importantly, the filaments often are not purely mineral, but have an organic component as well (organo-mineral preservation).

In cold water settings, EPS are preserved as chert (silica). In semi-arid, hot climates, micritic carbonate or clay are the predominant replacement minerals. Two or 3 cm thick, fossil microbial mats in the 2.9 Ga tidal Pongola Supergroup record ubiquitous EPS.

Etymology

Fossil mat microfabrics in cold water settings first were described in Noffke et al. 2000. Microfabrics serve as diagnostic tool for the identification of fossil mats in Noffke et al. 2002, 2003b, 2006a,b, 2008. Their geometric elements were quantified in Noffke et al. 2008. Chemical I examples are shown in Noffke et al. 2001a, and 2008.

Genesis

Mat fabrics are formed by binding, the active arrangement of mobile filaments into a network during quiet hydraulic conditions. As soon as waves and currents cease, cyanobacteria move through the deposits toward the settled sedimentary surface. Here, they form a mat fabric that ensures optimal exposure of the filaments to light. Biomass production by cell replication does not play a role, however epibenthic microbial mats secrete EPS. This EPS secretion is particularly important in the lower supratidal zone, where mats are exposed to rapidly changing hydrological and meteorological conditions.

In silica-rich sandstones, filaments of both endo- and epibenthic microbial mats are often preserved in three dimensions. They are not flattened by postdepositional pressure. This shows that the lithification of the organic material by destructive biomineralization took place quickly. The organic material is preserved *in situ*, because it was decomposed rapidly by heterotrophic microbes after the microbial mats died. This destructive biomineralization released ions that reacted immediately with ions in the surrounding sea water. An example of this might be the reaction of Fe^{2+} with S^{2-}, and the subsequent formation of pyrite (FeS_2) (Giblin 1988). Later, weathering might affect those primary minerals, and therefore hematite might form, or even goethite. Sometimes, the organic matter induces clay minerals such as chamosite, or chlorites (Ferris et al. 1987; Beveridge 1989; Schulze-Lam et al. 1996). In epibenthic microbial mats, the ubiquitous EPS often recrystallized into silica (chert), or carbonate, especially in ancient semi-arid, hot environments.

Paleoenvironmental Distribution and Seasonal Variations

As a rule of thumb, epibenthic microbial mats form in tidal flats and on continental shelves at sites of longer lasting latencies. Endobenthic mats develop at sites of short latencies, often under more turbulent hydraulic conditions. Microfabrics are only visible in magnification of mat laminae. Analyses of mats from both modern and fossil environments show distinctive microfabrics that help differentiate epibenthic and endobenthic mats. These mats always show a specific distribution (Noffke 2000; Noffke et al. 2002, 2003b, 2006a,b, 2008). The type of preservation allows conclusions about the ancient local climate, with carbonate minerals dominating in semi-arid, hot paleosettings.

Diagnosis

In both modern and fossil settings, mat fabric is microscopically observed as the internal texture of a mat lamina. It includes trichomes or filaments, EPS, and mineral particles. Mineral particles can be *in situ* mineralized particles, or detrital particles. A candidate fossil filament is either organo-mineral, or purely mineral.

The first step is an optical study of the mat textures using a petrologic microscope. In thin-section perpendicular to the bedding, a mat microfabric includes elongated, filamentous textures that have a cloudy appearance. Their cloudy appearance is because the outer wall of filaments is not discretely defined. The opaque textures are brownish, showing no pleochroism under crossed nicols (polarized light). In reflected light, filaments may appear bright red or bright silver.

The elongated textures form the typical carpet-like meshwork around sand grains. Measurements of the filament-like textures are taken from as many thin-sections as possible. Statistical analyses of these measurements show whether they exhibit the orientation and arrangement that characterize mat fabrics. In endobenthic mats, filaments are oriented between 0–45° with respect to a horizontal line (Fig. II.36). The interwoven sand grains have grain-to-grain contact. Such grains are generally the same size as the grains of the substrate under the mat layer. Epibenthic microbial mats include similar filament-like textures. Commonly, a vast bulk of filaments mask the orientation of individual textures. This may give the misleading impression that the textures are horizontally oriented. Unlike in endobenthic mats, baffled and trapped silt-sized grains, and sometimes heavy minerals are common. Note individual sand-sized particles apparently floating in the mat matrix. Such 'oriented grains' indicate a mature epibenthic mat. Any differences in grain size must be documented in grain size analyses.

It is important to consider that abiotic processes also may form very similar laminae. Stylolites and hydrothermal veins are good examples of abiotic textures (Fig. III.9). Stylolites are pressure solution textures, resulting from loading pressure during lithogenesis. Lithogenesis means 'formation of a rock'. Basically it is the transformation of fresh, loose sediment (e.g., sand), into a consolidated sedimentary rock (such as sandstone). Pressure and temperature play important roles in lithogenesis. High pressure may partly dissolve some minerals that composed the fresh sediment. Insoluble mineral residues accumulate along zig-zag lines, perpendicular to the main pressure direction. These lines are called 'stylolites'. In contrast, hydrothermal veins are lines of minerals secreted by hot water circulating through rock. On a large scale, hydrothermal mineral precipitation may create ore deposits.

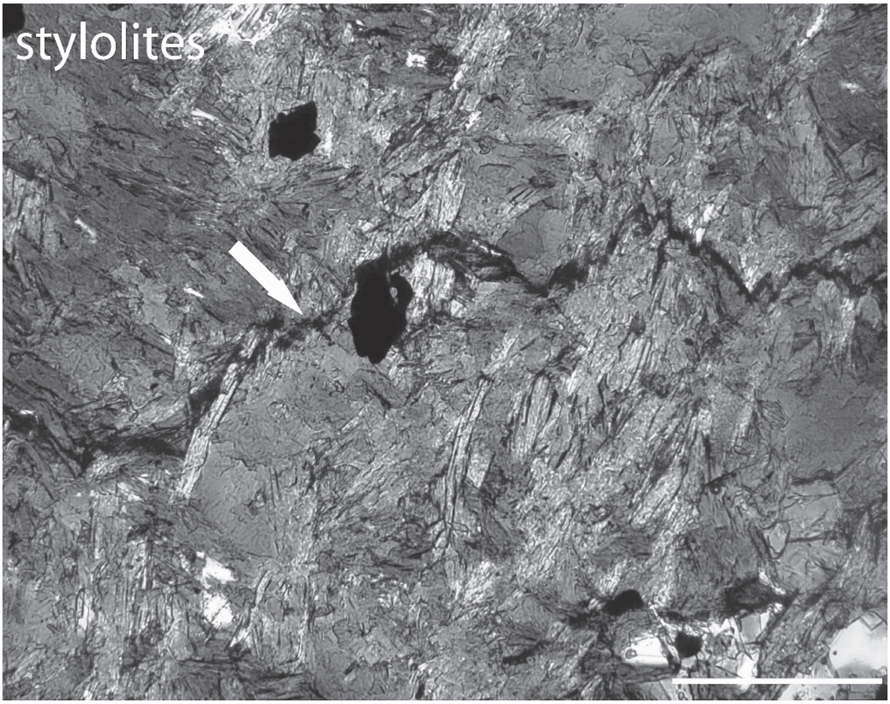
Example Specimen

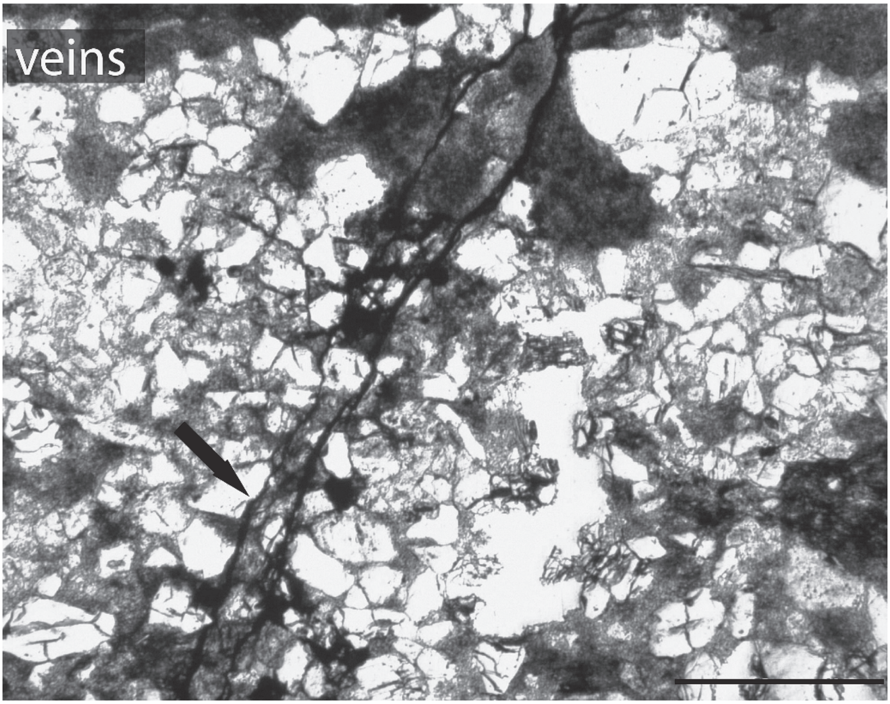
Thin-sections that display microbial mat textures are stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540867, USNM 540868, USNM 540869.

Application

Mat microfabrics are relevant diagnostic criteria for establishing the biogenicity of fossil MISS (Fig. III.10). Mat textures reflect latency. Endobenthic mats form in a few hours (such as endobenthic microbial mats built by *Oscillatoria limosa*, Villbrandt 1992). Epibenthic microbial mats may require weeks to form, although in the laboratory, mats constructed by *Microcoleus chthonoplastes* may grow in a few days (Gerdes et al. 1991).

The mineralogical composition of textures records the paleoclimate. The predominance of iron sulphides and oxides, clay and chlorites, indicates a cool paleoclimate. The predominance of carbonate minerals such as aragonite, carbonate, and siderite is typical of semi-arid, hot conditions.


stylolites


veins

◀ **Fig. III.9.** When studying fossil mat textures, it is important that abiotic sedimentary textures are not mistakenly interpreted as of biological origin. Typical abiotic textures visible in thin-sections include stylolites (upper photo) and hydrothermal veins (lower photo). Although the textures may resemble mat laminae, they are of non-biological origin. Stylolites are composed of clay minerals and some carbon, which appear as dark coloured, zig-zag lines (*arrow*). The hydrothermal vein (*arrow* in lower photo) may be composed of iron oxides. Such veins are formed by hot, mineral-rich water circulating through rock, releasing minerals along the way. Sometimes, the water follows original mat layers. The released minerals imprint the mat microstructure. This makes later identification of an ancient mat difficult. Luckily, veins often change their orientation. They rarely are bedding-parallel. Vertical veins as shown above are most common; (scales: 1 mm)

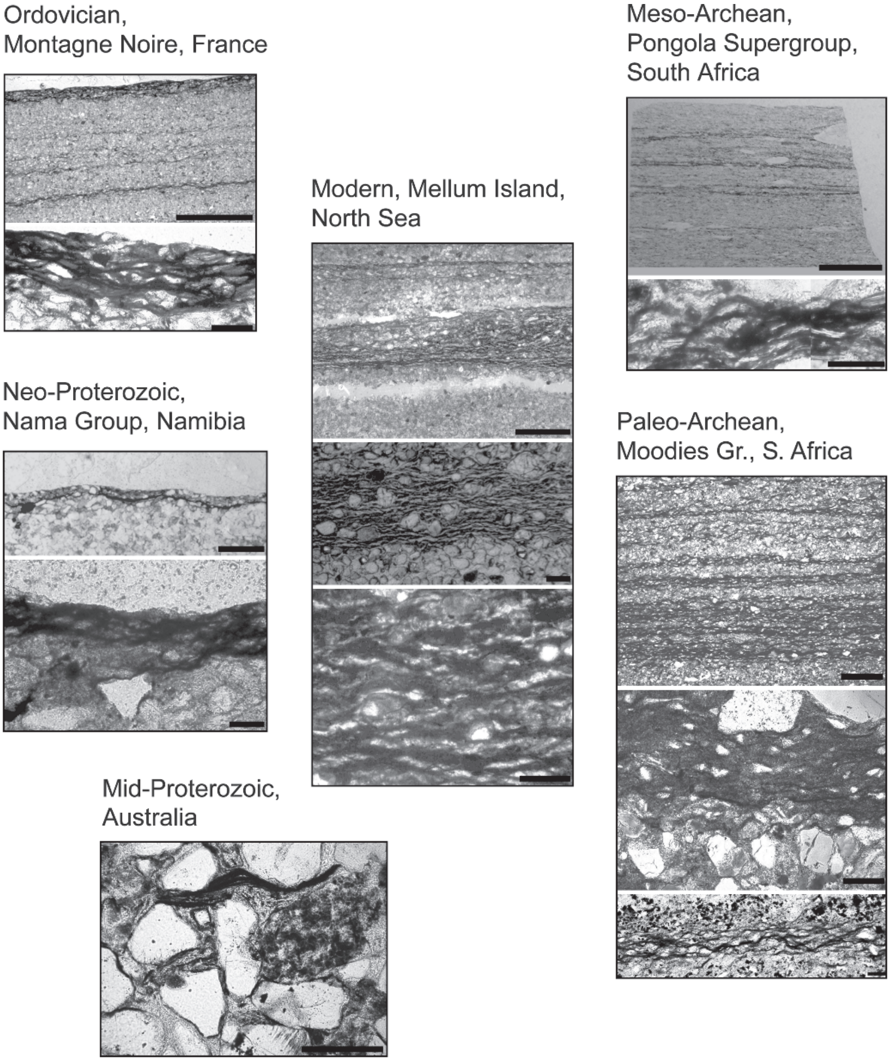


Fig. III.10. Microbial mat textures in thin-sections. Note that the textures of microbial mats have not changed since the Archean. All examples derive from cool paleosettings

III.2.2.2
Sinoidal Structure

Description

Individual, sinoidal shaped laminae may be visible in thin-sections and sediment cores. They consist of organic material (modern), or of organic-mineral or mineral substance (fossil). Laminae coat the troughs and lee faces of buried ripple marks (Fig. III.11). The sinoidal structures are laterally discontinuous, and between 2 to 8 cm in lengths.

Etymology

The term was introduced to describe buried ripple marks that were once overgrown by biofilm (Noffke et al. 1997b), Fig. III.11.

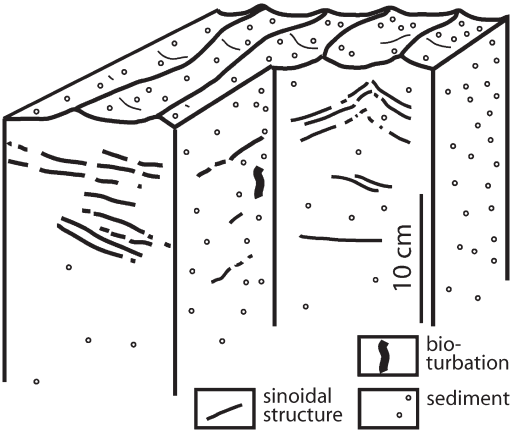
Genesis

Thin-sections or sediment cores from tidal flats composed predominantly of sand do not display buried ripple marks very well. Such sandy tidal flats lack the mud layers that favor ripple mark preservation (Visscher 1980). In intertidal zones, ripple marks are overgrown by the quick moving cyanobacterium *Oscillatoria limosa.* This species establishes an initial mat within the few hours between two floods. The returning second flood can no longer rework the ripple marks, because they are biostabilized by *O. limosa*. However, the ripple marks can be buried. In sediment cores or thin-sections, these buried ripple marks are visible because of the biofilm coating.

Paleoenvironmental Distribution and Seasonal Variations

Sinoidal structures are very common in the upper intertidal zone. Here they form especially during the summer, when biofilms and endobenthic mats are abundant (Fig. II.15). Sometimes they also occur in the lower supratidal zone, and can be as thick as 1 cm.

Fig. III.11.
Sinoidal structures in a sediment core are displayed in three dimensions (after Noffke et al. 1997b)



Diagnosis

Sinoidal structures can easily be detected in sediment cores of fresh tidal deposits, especially from the upper intertidal zone. The sinoidal laminae are black. In order to detect sinoidal structures in a rock, polished cross-sections, or thin-sections perpendicular to the bedding are made. In cool water deposits, the fossil laminae are composed of pyrite (or hematite, if oxygenized), goethite (a weathering product), chamosite and other chlorite minerals, as well as muscovite. Silica (chert) also may be present. In hot, semi-arid paleosettings, carbonate minerals such as aragonite, siderite, and calcite occur. Fossil biofilms have an organic C isotope signature.

Example Specimen

A relief cast which shows sinoidal structure is stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540870.

Application

Sinoidal structures serve well in the detection of buried mat laminae (Fig. III.12). Only biofilms or thin mats can line ripple marks in this characteristic sinoidal fashion.

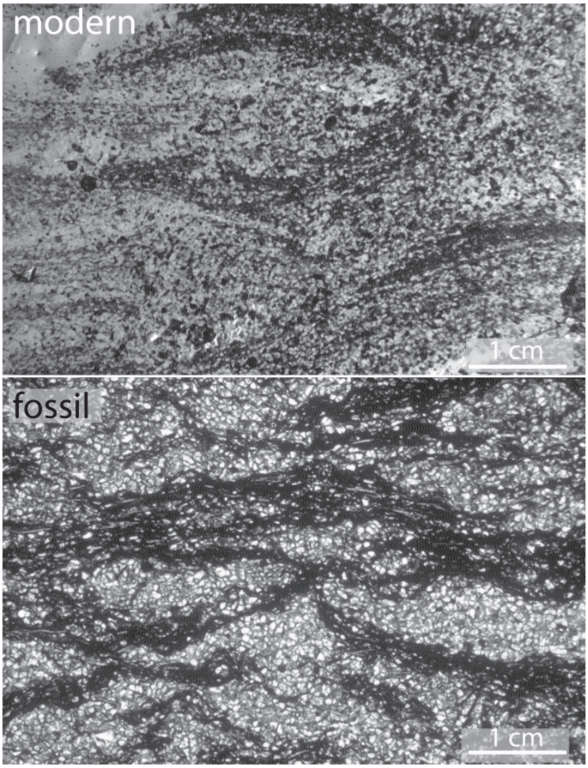


Fig. III.12. Sinoidal structures in thin-sections, perpendicular to bedding planes. Sinoidal structures are dark coloured, bent lines that represent biofilms or thin microbial mat laminae. The laminae developed in ripple mark valleys, hence the structures are bent. Later these ripple marks were buried

III.2.3
Structures Arising from Biostabilization

This section introduces MISS that predominantly, if not exclusively, arise from biostabilization. Biostabilization is

i) the response by benthic microbiota to erosion (I–III);
    I. Biostabilization by epibenthic microbial mats
    II. Biostabilization by endobenthic microbial mats
    III. Biostabilization by biofilms
ii) the flexible deformation of brittle sediment (such as loose sand) bound by biofilms or microbial mats;
iii) the sealing of the sedimentary surface by EPS to reduce the exchange of gases between the deposits below and the water or atmosphere above.

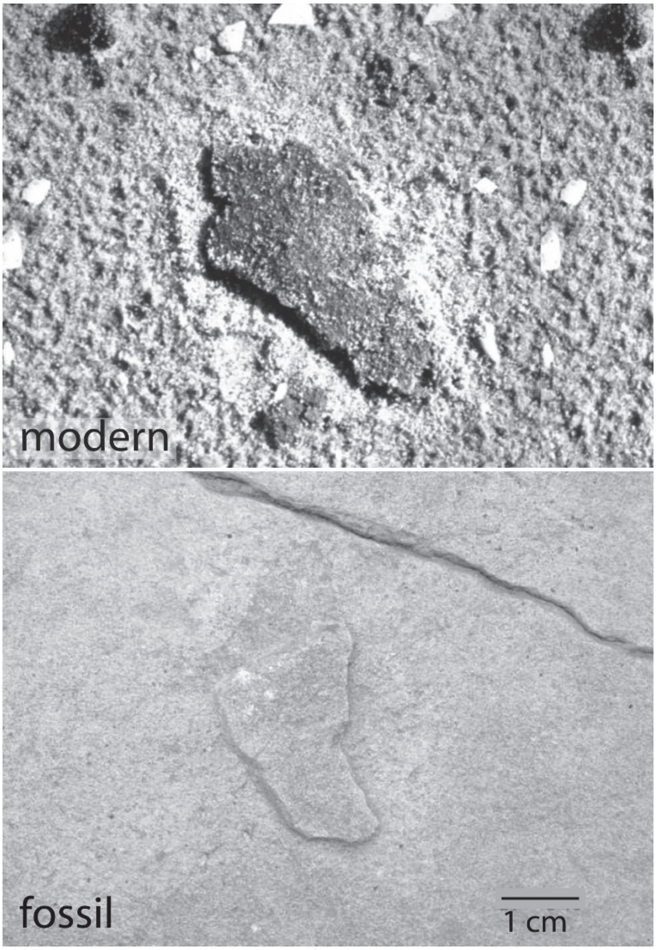


Fig. III.13. Examples of microbial mat chips. Note the rounded edges of the mat chips, both modern and fossil

III.2.3.1
Mat Chips

Description

Mat chips are cm-scale fragments of microbial mats, scattered all over sedimentary surfaces (Fig. III.13). In the modern tidal flats of Mellum Island, two main types of mat chips can be distinguished. Mat chips type I are formed by epibenthic microbial mats. Mat chips type II are formed by endobenthic microbial mats (Noffke 1997).

On Mellum Island, mat chips of type I are fragments of 0.5–5 cm in diameter, and of 0.25 to 0.5 cm thickness (Fig. III.14). In thin-section, the mat chips are composed of an organic top layer and a mineral layer underneath.

The mat lamina can include oriented grains, as well as silt-sized, previously baffled and trapped silt particles. The sandy layer underneath the microbial mat is firmly attached by EPS.

Type II mat chips are smaller. On Mellum Island, they range from 0.3 to 2 cm in diameter. In contrast to type I mat chips, they are composed only of one layer. This layer is entirely composed of sand grains entangled by cyanobacterial filaments. All grains have similar sizes. Oriented grains or silt particles do not occur.

Some mat chips are over folded. This shows flexible deformation of the mat-bound sand. Many chips have rounded edges, thus differ in geometries from mud clasts. Mat chips often have clover-like outer shapes.

Etymology

'Microbial mat chips' have been described in Noffke et al. 1996. Independently, Pflueger and Gresse 1996, described fossil 'microbial sand chips' from the Nama Group, Namibia. Flexible deformation of brittle sand is described in Noffke 2000.

Genesis

Mat chips are fragments of microbial mat that are ripped off by bottom currents. Along the edges of erosional remnants, sand underneath the microbial mat is washed away. The fringes of the undermined mat tear and break off into pieces. These fragments are transported by currents and distributed at random on the depositional surface. The rounded edges of mat chips may result from erosion during transport across the sedimentary surface, or from continuous growth of the mat. Microbial mats

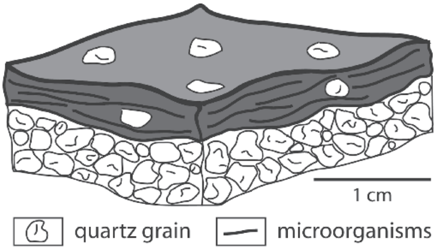


Fig. III.14.
Microbial mat chip, type I. It is composed of the mat laminae on top, and the original sand substrate underneath. The sand grains of the substrate are still glued to the mat laminae by mucilages. Note that oriented grains occur in the mat lamina

may continue to grow even after separation from their parent site. Schieber (2007) describes a beautiful laboratory experiment, where he documents this 'healing' of the edges of mat chips by growth. Note that mat chips do not form by desiccation such as mud clasts do, and therefore they have different shapes. Because of the way they are formed, mat chips are related to biostabilization (i), type I or II. In tidal flats, and on continental shelves, mat chip accumulation is often a consequence of storm events. Over folded chips represent biostabilization (ii).

Paleoenvironmental Distribution and Seasonal Varieties

Modern mat chips are distributed at random on the tidal surface. On Mellum Island, type I mat chips concur with epibenthic microbial mats in the lower supratidal zone. Studies by the author show that mat chips are usually distributed within 200 m from their sites of origin. Type II mat chips originate from endobenthic microbial mats. They are released most abundantly in fall, and are distributed over greater distances.

In the fossil record, mat chips are also found in subtidal areas, but not on outer continental shelves (Noffke 2000). Mat chips are most often released in fall, when storm frequency increases. Mat chips having a more rounded shape have been separated longer from their originating site. They have been rounded during transport and regrowth. In the fossil record, mat chips are the most abundant MISS, ranked only behind wrinkle structures.

Diagnosis

Mat chips have a characteristic outline different from that of mud clasts (Fig. III.15). Mat chips are preserved in pure sandstone even where no mud layer is present. Because of their origin, and deposition as individual entities, the identification of mat chips is easy. It is important to be precise, and to conduct further analyses. Statistical analyses on possible fossil mat chips from the 3.7 Ga Isua Greenstone Belt, Greenland demonstrate how identification can be made. The fossil chips were compared with both modern mat chips from present tidal flats and fossil mat chips from an ancient tidal flat (2.9 Ga Pongola Supergroup, South Africa). All mat chips were then compared with modern mud clasts.

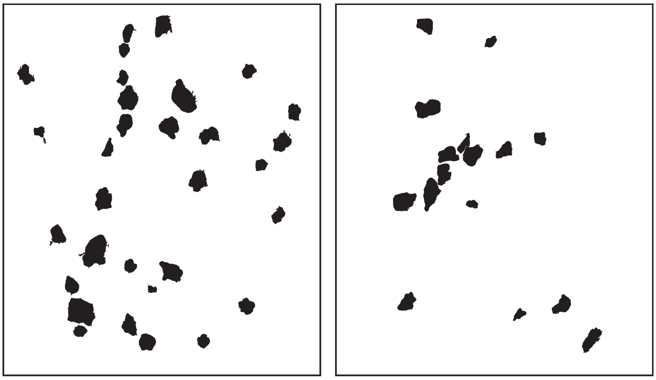
Three indices were developed to describe the morphologies of the chips and clasts: Index 1 is the longest axis of a clast divided by the axis, which runs through the central point of the long axis in a 90 degree angle. Index 2 is the longest axis divided by the absolute shortest axis. Index 3 is the length of circularity of the clasts divided by the longest axes (Fig. III.16).

The results show that the fragments of biofilms from all 3 study sites are not significantly different in pair-wise comparisons, whereas the mud clast population is significantly different (Table III.1).

Example Specimen

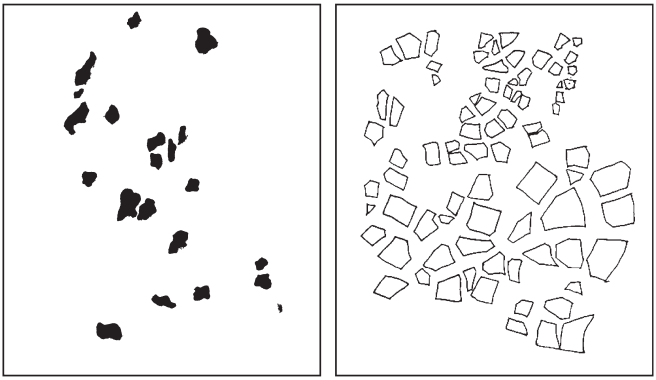
Modern mat chips from Portsmouth Island, North Carolina, and fossil mat chips from the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa, are stored by the

Fig. III.15.
Statistical analyses of shapes of microbial mat chips, and comparison with mud clasts. The outline of chips and fragments was digitally analyzed with an imaging program



modern mat chips

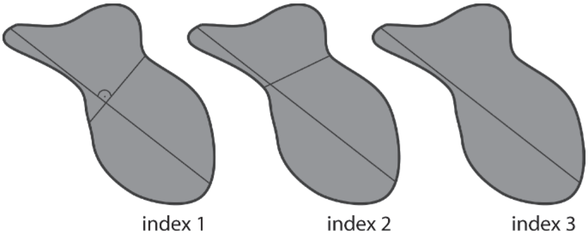
Pongola



Isua Greenstone Belt

modern mud fragments

Fig. III.16.
Three indices describe the morphometry of microbial mat chips. For explanation see text



Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540871, USNM 540872.

Application

In the fossil record, microbial mat chips distributed on tidal or continental shelf deposits include information on ancient storms and current systems. They allow reconstruction of the prevailing current directions and storm intensities. Because the production of mat chips coincides with increasing storm frequency, information

Table III.1.
Example of statistical analyses of microbial mat chips and mud clasts. Three populations of mat chips (modern; 2.9 Ga Pongola Supergroup, South Africa; 3.7 Ga Isua Greenstone Belt, Greenland), as well as modern and ancient mud clasts (Outer Banks, USA; 3.2 Ga Moodies Group, South Africa) were compared (*SD:* standard deviation)

Index	Group	*n*	Mean	SD
1	Isua	55	1.64	0.50
1	Pongola	55	1.72	0.45
1	Modern	55	1.75	0.51
1	Mud	50	1.41	0.24
2	Isua	45	1.74	0.52
2	Pongola	45	1.88	0.62
2	Modern	45	2.01	0.61
2	Mud	47	1.19	0.17
3	Isua	16	0.52	0.11
3	Pongola	16	0.57	0.14
3	Modern	16	0.53	0.12
3	Mud	16	0.76	0.04
Clast morphologies – P-values				
Index 1	Isua	Pongola	Modern	Mud
1		0.9421	0.7486	0.0483
2			0.9992	0.0033
3				0.0008
4				
Index 2	Isua	Pongola	Modern	Mud
1		0.7349	0.0711	<0.0001
2			0.7628	<0.0001
3				<0.0001
4				
Index 3	Isua	Pongola	Modern	Mud
1		0.6060	0.9993	<0.0001
2			0.8550	<0.0001
3				<0.0001
4				

about the seasonal paleoclimate may be gathered. Together with wrinkle structures, they constitute the most abundant MISS in the fossil record. They are especially helpful in field work when a quick analysis of the paleoenvironment and biota is necessary.

III.2.3.2
Roll-up Structure (Mat Curl)

Description

Two types of roll-up structures (or mat curls) are differentiated. The types are related to their genesis:

i) Viewed from the side, roll-ups are upwardly bent type I mat chips. The degree of bending ranges from slightly lifted edges to completely up-rolled examples ('finger rolls'), (Fig. III.17). Roll-ups are always bent towards the organic layer of the mat chip. A nice photo of fossil mat curls is shown by Eriksson et al. 2007, from the 1.8 Ga Waterberg Group. The sizes of roll-ups correspond to the sizes of type I mat chips.
ii) The second type of roll-up is generated by the transport and up-rolling of chips or larger mat pieces by bottom currents. Sometimes mat tissues of several meters extension are rolled up by strong storm currents. These mat curls truly resemble rolled up carpets (Fig. III.18)!

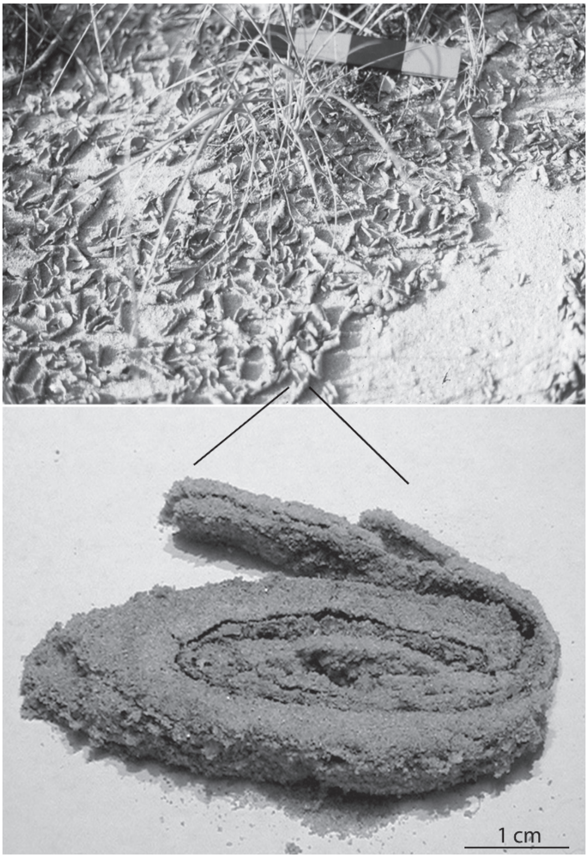


Fig. III.17.
Roll-ups (or mat curls) from Portsmouth Island, USA. The upper photo shows curled up structures that result from mat chip desiccation; (scale: probably around 10 cm). Photo below: This roll-up displays its internal structure very nicely; (scale: 1 cm; after Noffke et al. 2006b)

Fig. III.18.
Roll-ups (or mat curls) in modern tidal flats, Portsmouth Island, USA. The photo above is a roll-up structure of just a few cm in size. The photo below shows a much larger roll-up structure. It resembles a rolled up carpet. Compare the person for scale. The close-up photo reveals the internal structure of this carpet roll. Huge roll-ups like this one are typical post-hurricane phenomena

Etymology

The term mat curl was introduced for bent or even rolled-up mat chips (Noffke et al. 1996). The word 'roll-ups' is a synonym also in use (Simonson and Carney 1999).

Genesis

Roll-ups or mat curls of both types are result of biostabilization (ii). Type I microbial mat curls are the result of desiccation of the organic portion of the mat chip. Most curls are type I mat chips (epibenthic microbial mat). Mat chips consist of an organic, water-rich mat layer over a sand layer. These materials (mat and sand) react differently to desiccation. During dehydration, the organic material (microbial mat) shrinks more than the drier, sandy layer underneath.

The direction of contraction is usually parallel to the main orientation of the filaments. The sandy portion of the mat chip does not contract significantly. The two mat chip layers are adhered to each other. As the chip dries, the organic layer shrinks more than the sandy layer. The difference in the amount of shrinkage deforms both layers unequally, causing the mat chip to curl.

Mat curls are not always a result of desiccation. Mat chips can also roll-up during transport by bottom currents. Typically, these type II mat curls are rolled up many times. Severe storms can roll up several m^2 of mat. On Portsmouth Island, North Carolina, USA, mat curls of huge dimensions witness the strength of hurricane Isabel, churning its way through the island in 2003.

Paleoenvironmental Distribution and Seasonal Varieties

Mat curls are littered across tidal flats, and sometimes pile up and accumulate around current obstacles, such as plants. In cool, moderate climate zones, mat curl formation peaks in fall when many mat chips are released. In semi-arid, hot areas, breakage of shrinkage cracks during long lasting dry seasons induces mat curl formation. Roll-ups are typically observed on tidal flats after strong storms or hurricanes. Roll-ups are very likely to be transported into subtidal areas.

Diagnosis

Mat curls have dimensions of a few cm^2 to several m^2. The structures are preserved in pure sandstone, even lacking clay-like material. The morphology of mat chips is very distinct. Microscopic examination serves to exclude abiotic clay chips.

Example Specimen

A cross-section through a dried, modern mat curl from Portsmouth Island, USA, is stored in the Smithsonian Natural History Museum, Washington, DC, Noffke Collection no. USNM 540872.

Application

In the fossil record, type I mat curls indicate subaerial exposure of a tidal area. Curls or roll-ups are indicative of an ancient climate with dry periods. Desiccation and subsequent mat curl formation may take up to a week (see ‘shrinkage cracks’).

Large type II curls that resemble rolled carpets indicate strong, episodic storms that push seawater far into the supratidal zone. The currents that fold up mat pieces of several meters in diameter have enormous strengths. Current velocities must be higher than 1.60 m s^{-1} – the critical shear stress velocity for erosion of epibenthic microbial mats.

The structures are especially helpful for field work when conducting a quick analysis of the paleoenvironment and biota.

III.2.3.3
Shrinkage Cracks

Description

During dry seasons, a subaerially exposed microbial mat in a supratidal zone desiccates and cracks. The edges of the crack curl up, and sandy sediment beneath the mat is exposed (Fig. III.19). Cracks like this are between 1 cm and several dm long, and sometimes of sinoidal shape.

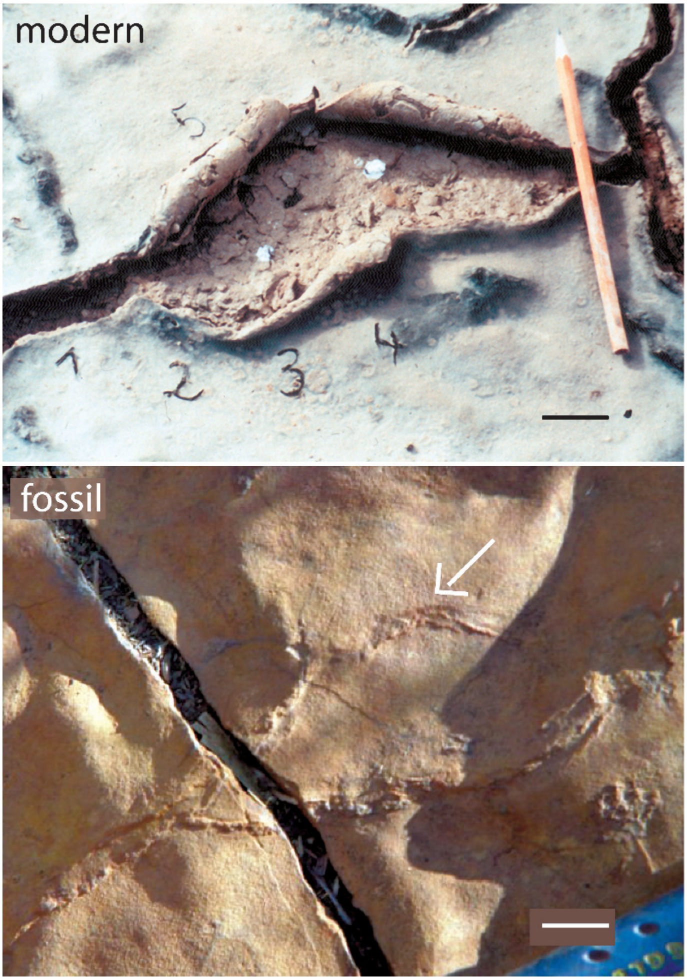


Fig. III.19. Shrinkage cracks: The upper photo shows a modern example from the tidal flats of southern Tunisia. The numbers *1*, *2*, *3*, *4* and *5* indicate different stages of formation from the first rupture of the microbial mat, to the final rolling-up of the mat margins; (scale: 5 cm). The photo below shows a fossil example (*arrow*) from the 2.9 Ga old Brixton Formation, South Africa; (scale: 1 cm)

Etymology

'Shrinkage cracks' were first described in modern microbial mats from the tidal flats of southern Tunisia (Noffke et al. 2001a). Fossil examples are known from the 2.9 Ga old Brixton Formation, South Africa (Noffke et al. 2006a).

Genesis

Shrinkage cracks result from subaerial exposure and desiccation of microbial mats. On Mellum Island, the first cracks in a microbial mat developed after 3 days of subaerial exposure. In southern Tunisia, thick mats seem to develop cracks after two weeks of subaerial exposure. Characteristically, a mat shrinks laterally up to ⅓ of its original lateral extension – a fine example of biostabilization (ii). The edges of cracks curl up. They sometimes break off as highly convoluted mat curls. The reason for the curling is that the mat layer atop the sediment shrinks significantly more than the sandy substrate underneath.

Paleoenvironmental Distribution and Seasonal Varieties

Shrinkage cracks occur in endobenthic and epibenthic microbial mats of the upper intertidal to lower supratidal zone. In semi-arid hot climates, shrinkage cracks are frequent in spring, when the dry season starts and many microbial mats decompose.

Diagnosis

Shrinkage cracks resemble synaeresis cracks, or desiccation cracks in mud. Care must be taken not to misinterpret them. In vertical cross-section, the profile of a microbial mat crack is U-shaped. Only the mat margin is curled up. The sandy bottom remains flat. In contrast, mud cracks are V-shaped. In the fossil record, shrinkage cracks are preserved in sandstone even if no clay-like material was present. Because of this origin, identification of shrinkage cracks is easy.

Example Specimen

A beautifully preserved shrinkage crack pattern on a 1.8 Ga sandstone bed from Australia is stored at the Smithsonian Natural History Museum, Washington, DC (donation by Ed Simpson, Kutztown University, PA, USA), USNM 540000.

Application

Fossil shrinkage cracks record subaerial exposure of a tidal flat surface (Fig. III.19). They are important indicators for the former presence of microbial mats, even if the original microbial mat is not preserved. Sand, composed of loose grains, does not crack as mud does. Desiccation cracks occur only if the grains are bound by a cohesive medium, such as a microbial mat. Shrinkage cracks are especially helpful for field work when conducting a quick analysis of the paleoenvironment and biota.

III.2.3.4
Petees

Description

Petees occur on the surface of microbial mats. They are cauliflower-like elevations of 0.5–2 cm heights. They can be individual upheavals, but most often are arranged in a polygonal pattern (Fig. III.20). In vertical cut through a petee, the microbial mat forms a folded arch above the sediment, producing a hollow cavern. In the fossil, this cavern is filled by *in situ* precipitated carbonate (Noffke et al. 2001a).

Etymology

Petees were first described by Reineck et al. 1990. The authors created this word in order to differentiate the structures from tepees. Tepees bound by a microbial mat are termed petees. Reineck et al. 1990 differentiate into several types of petees, depending on the content of evaporate minerals in them.

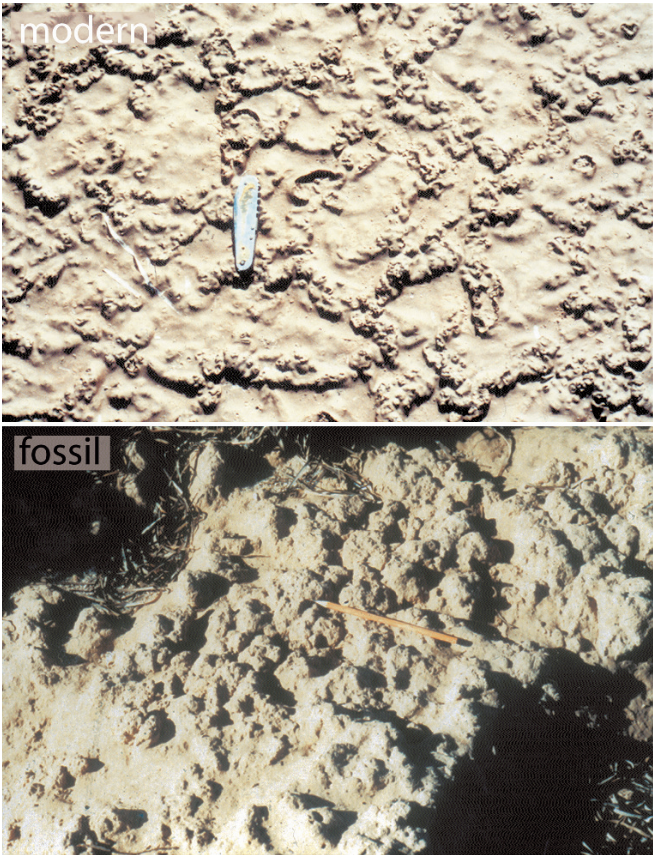


Fig. III.20.
Petees. The photo above shows modern petees from microbial mats composed by the cyanobacterium *Synechnococcus* sp. This cyanobacterium causes the rose colour of this mat. Photo taken in Tunisia, summer 1995. The photo below shows similar petees from a fossil microbial mat of the Circum-Mediterranean Pleistocene, Tunisia

Genesis

Petees result from evaporite pumping that characterizes sabkha-like tidal flats in semiarid, hot climates. Evaporite pumping means that incoming seawater penetrates sedimentary deposits as rising ground water. The flood current does not flow across the tidal surface, but is moving in the sediment. Solar heating of the tidal surface causes some flood water to ascend as capillary water, dissolving salty minerals such as gypsum and halite. Minerals can precipitate as soon as the water reaches the depositional surface upon which microbial mats occur. Eventually, microbial mats growing on the depositional surface incorporate the evaporate crystals. Rising sea water periodically supplies the evaporitic system with surface minerals that continue to accumulate. The repetition of this combined process between mineral formation and microbial mat growth causes the petees. Petees are products of biostabilization (ii). A microbial mat is arranged into folds, because mat portions exposed to sunlight grow at different rates than surface portions protected in the fold. Many coccoid cyanobacteria such as *Synechnococcus* sp. are resistant to solar radiation and desiccation, so they predominate along the exposed petee surface portions. Filamentous taxa such as *Oscillatoria limosa* or *Microcoleus chthonoplastes* occur in the folds of a petee (Fig. III.21).

Paleoenvironmental Distribution and Seasonal Varieties

In southern Tunisia, petees occur in the morphologically higher portions of the Bahar Alouane. They form during the dry season, but can be dissolved when water covers the tidal surface, for example after a storm or heavy rain.

Diagnosis

Both modern and fossil petees have the characteristic cauliflower shape (Fig. III.20). Loose grains of sand do not fold up in such a fashion, unless they are bound by a cohesive medium – a microbial mat. Therefore, petees are very characteristic of MISS.

Example Specimen

A modern mat that displays petees is stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection no. USNM 540873.

Fig. III.21. Genesis of petees in stages. *Stage 1:* Lateral growth of a microbial mat pushes up portions of the mat lamina. This upward growth is supported by minerals that crystallize in the roof area of this domed mat layer. *Stage 2:* At sites where little sunlight reaches the microbial mat, bacterial growth is inhibited. Therefore, the petee continues to grow upward. *Stage 3:* The petee starts to form its characteristic cauliflower shape. Each deformation in shape varies the amount of sunlight that reaches other parts of the mat. Mat portions receiving the most light grow more rapidly. Evaporite minerals precipitate in well exposed areas of petees. *Stage 4:* The height of a mature petee is controlled by the height that ascending capillary water reaches (after Noffke 1997)

Application

Petees are significant facies indicators, and help determine the narrow facies zones of tidal flats. They record the hydraulic and climatological conditions of ancient tidal flats in detail (Noffke et al. 2001a). Petees are especially helpful for field work, if a quick analysis of the paleoenvironment and biota is necessary.

III.2.3.5
Gas Domes

Description

Gas domes are hemispherical or roundly conical elevations, 0.5 to 25 cm high elevations (Fig. III.22). The diameter of the base is not in a specific ratio to the height. The most prominent gas dome the author has seen was 25 cm high with just 30 cm diameter at its basis. In vertical cross-section, a gas dome is an upward buckled microbial mat with a hollow cavern underneath. In fossils, this cavern is not always visible. Often fossil gas domes are collapsed, and only a triple junction-shaped crack records their former presence (see Chap. IV). Gas domes may or may not occur together with sponge pore fabrics.

Etymology

Gas domes were originally termed 'domal upheavals' (Noffke et al. 1996), but now the simpler term 'gas dome' is used.

Genesis

In modern tidal settings, gas domes are common features. They occur with thick, epibenthic microbial mats that seal tidal deposits. The structures are caused by biostabilization (iii). Gas domes develop under EPS-rich microbial mats, such as those constructed by *Microcoleus chthonoplastes*. Mucilages of these microbial mats prohibit the exchange of gases between tidal deposits, and water or atmosphere above. Consequently, gas accumulates underneath the sediment-sealing mat. Locally, the increasing gas pressure lifts the microbial mat, which loses contact with its underlying substrate. This generates a hollow cavern, which is visible in vertical cross-section through a gas dome (Fig. III.22). Depending upon the size of the gas dome, this hollow cavern is typically about 1–3 cm long, however, lengths up to 20 cm were measured in thick, biolaminated Tunisian mats. Analyses by gas chromatograph showed that the hollow caverns are filled with H_2S, H_2, CO, CO_2, CH_4, and others. These gases are products from the decay of underlying organic matter in tidal sediments.

Gas domes typically occur along the normal high water line. They indicate spots where gases escape the sand. The gases are pushed upward by the rising tide. The mucilages of microbial mats block the quick escape of gases. These gasses become trapped underneath mats. These bouyant gasses exert localized pressure that forms convex domes in the microbial mat. Eventually, the dome tips rupture, and triple junction-shaped cracks open. The gases escape, and the gas domes collapse. This breakage

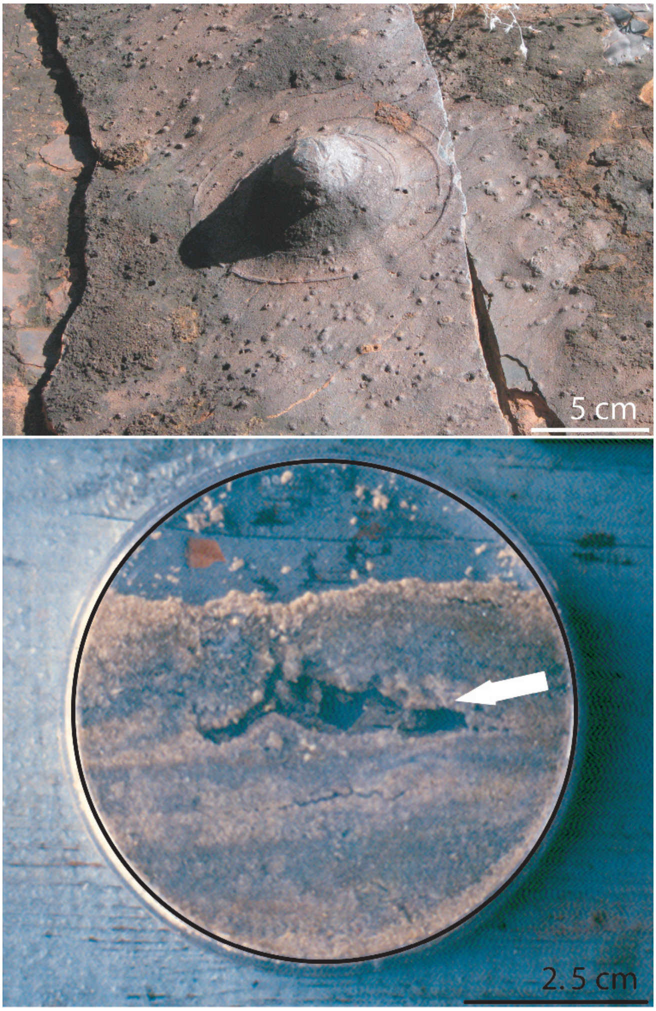


Fig. III.22.
Gas domes. Above: The view of this fossil tidal surface shows a gas dome projecting from the sedimentary surface. Below: In the modern tidal flats of Mellum Island, North Sea, a vertical cut through a gas dome shows a hollow cavern (*arrow*). In this hollow cavern gases accumulate that push the microbial mat upward

occurs because the mat loses its contact with the damp, underlying substrate. Once mats dry out, their biostabilization properties are reduced, and their organic material becomes brittle. Gas dome roofs typically have a brownish colouration, indicating drier conditions. Diatoms may assemble here.

At the coast of southern Tunisia, gas domes are related to polygonal oscillation cracks in lower supratidal zones. The domes form with the opening of the cracks.

Paleoenvironmental Distribution and Seasonal Varieties

On Mellum Island, gas domes are always associated with the normal high water line. They are temporary structures that persist for only a few hours. Occasionally, a few semi-permanent gas domes can be observed, but only in lower supratidal zones.

Diagnosis

Gas domes are hemispherical or roundly conical elevations of 0.5 to 25 cm. In vertical cross-section, modern gas domes have a hollow cavern underneath the up domed roof. In fossil samples, this hollow cavern might be filled in by precipitated minerals, or not visible at all. Sand, composed of loose grains, cannot trap gas bubbles in such a fashion, unless the sand grains are bound by a cohesive, sealing medium – a microbial mat. Gas domes are very characteristic. If hollow caverns are not preserved in candidate fossil mat samples, then the sample must be differentiated from sand stromatolites.

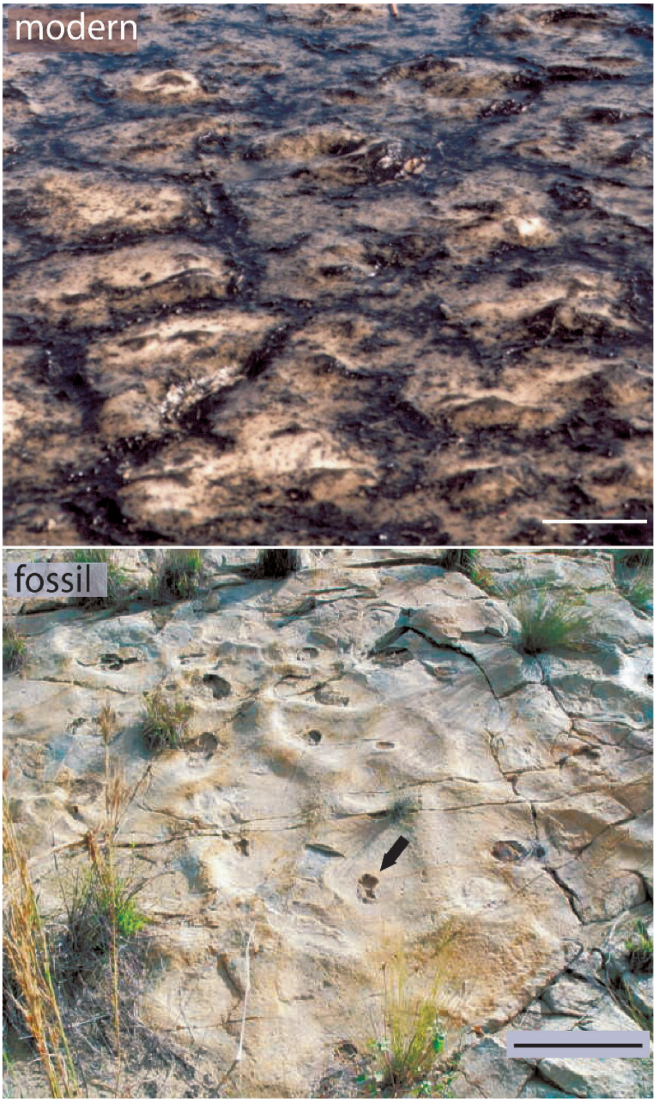


Fig. III.23.
Gas domes. The upper photo displays modern gas domes formed in a *Microcoleus chthonoplastes* dominated mat in southern Tunisia. The gas domes are temporary. They last just a few days. The domes collapse as soon as their roofs rupture. The gases include methane, CO_2, H_2S, and other impolite smelling compounds. The photo below shows fossil examples in an ancient, epibenthic mat that grew in a similar tidal setting (2.9 Ga Pongola Supergroup, South Africa; scales: 25 cm)

Example Specimen

Gas domes occur on the modern tidal flats of Mellum Island, North Sea, as well as the Sabkha Bahar Alouane, Tunisia (Noffke et al. 2001a). Fossil examples are exposed in the Nhlazatse Section, White Mfolozi River Gorge, Pongola Supergroup, South Africa (Noffke et al. 2008). At the time of this writing, no sample is stored yet by the Smithsonian Natural History Museum.

Application

Gas domes are significant indicators for narrow facies zones in tidal settings. They indicate the normal high water line. In the chemical I sedimentary system, they record periodic desiccation and decay of microbial mats in sabkha-like tidal flats. A great example of application of such fossil gas domes is the Nhlazatse Section, Pongola Supergroup, South Africa (Noffke et al. 2008), Fig. III.23.

III.2.3.6
Sponge Pore Fabrics

Description

In vertical cross-section through sediment cores, sandy layers between microbial mat laminae are visible (Fig. III.24). Within these sandy interlayers, pores of 0.5–3 mm sizes occur. The pores are arranged in a pearlstring-like pattern. The number of pores increases towards the sedimentary surface. In the fossil, the pores might be filled in by minerals such as sparite.

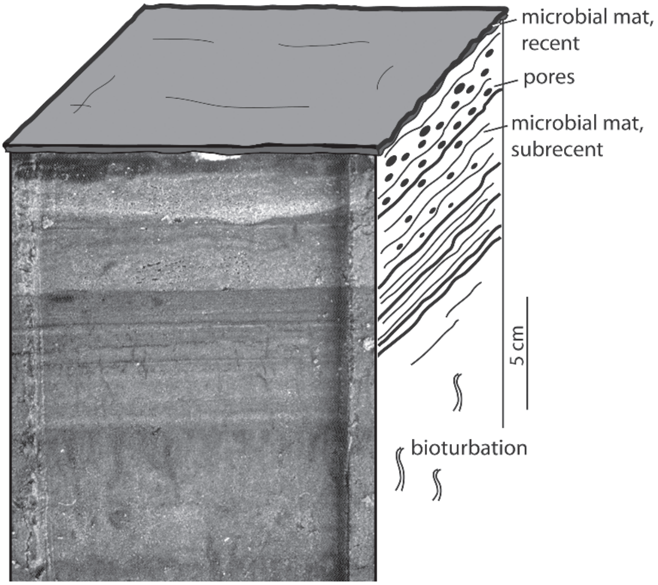


Fig. III.24.
Sponge pore sand. The vertical cross-section through modern tidal sediment displays subrecent (buried) microbial mat laminae alternating with sandy layers. The sandy interlayers contain pores, which are arranged in a pearlstring-like pattern. The pores form as the pressure of gases accumulating underneath the sediment-sealing microbial mat layer increases

Etymology

In carbonate sedimentology, such pores in tidal deposits are known as 'fenestrae fabrics' (Tebutt et al. 1965). Because of the lack of early mineral precipitation in siliciclastic deposits, the term 'sponge pore fabrics' is used (Noffke et al. 1996, 2001b).

Genesis

A microbial mat that covers a sandy substrate functions like a sealing plastic tissue, and prohibits the escape of gas from the underlying sediment (biostabilization type (iii)). Intra-sedimentary gas, however, migrates through sandy layers, pushed through the tidal deposits by rising flood water. The gases accumulate underneath the mat layers, especially along the high water line. The increasing gas pressure causes the pores in the sand layers. Gases result from the decay of organic matter in marine sediment. A core taken from fresh tidal flat sediment smells impolite. Gas analyses show the presence of H_2S, H_2, CO, CO_2, CH_4, and other gases.

The degree of intrasedimentary porosity was determined by artificial compaction of cores of tidal sands in laboratory experiments. Cores from tidal deposits along the high water line of Mellum Island revealed an intrasedimentary porosity of up to 30%. Tidal sediments from the intertidal zone showed a porosity of only 13%.

Paleoenvironmental Distribution and Seasonal Varieties

Sponge pore sand can occur together with gas domes, but not always. Pore-rich sands develop under epibenthic microbial mats in the lower supratidal area, mostly along the high water line. A hiker crossing a tidal flat can 'feel' the position of the high water line. The foot steps sink into the sand more than at other sites.

In specific cases, sponge pores can be also present much higher in the upper supratidal zone. This can especially be observed in overwash fans in the months after a severe storm. A storm might have deposited large amounts of sand onto the land. Such sand can be overgrown by a microbial mat. The decaying organic debris can cause similar sponge pore fabrics in the sandy sediments.

Diagnosis

In modern tidal deposits, a vertical cross-section through the upper 25 cm of sediment reveals an intrasedimentary structure composed of laminae of buried, subrecent microbial mats, and sandy layers in between them. The sandy interlayers include pores that are arranged like a string of pearls. From the base to the top of the vertical cross-section, the pores increase in diameter. Sponge pore fabrics can be nicely displayed in relief casts that show internal sedimentary structures in three dimensions. Fossil sponge pore fabrics can best be detected in polished rock samples (see Noffke et al. 2001b); Fig. III.25.

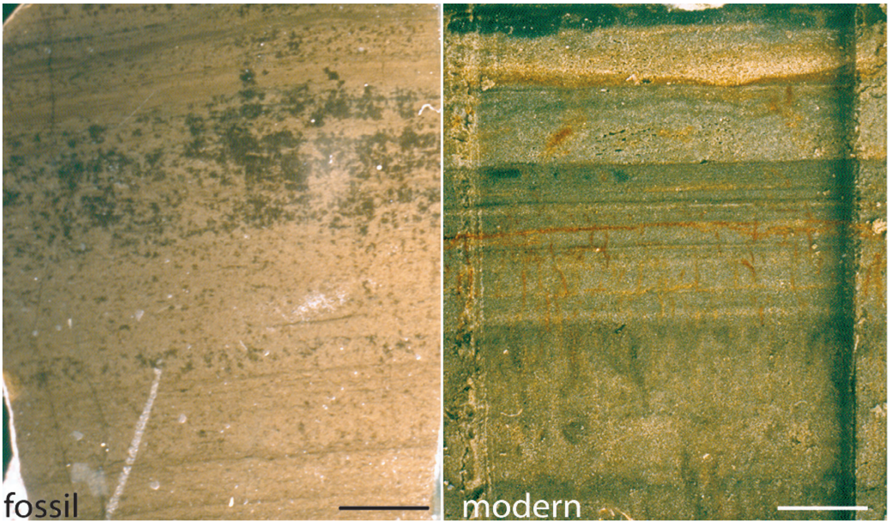


Fig. III.25. A fossil and a modern sponge pore fabric. The left photo is a polished rock slab that displays laminae and fenestrae (i.e., carbonate mineral-filled, ancient pores). This rock sample is from the Triassic close to Tuebingen, Germany. The right photo is a fresh sediment core taken from modern tidal flats on Mellum Island, North Sea; (scales: 5 cm)

Example Specimen

A relief cast of a modern tidal sand core with typical sponge pore fabrics is stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection no. USNM 540874.

Application

Sponge pore sand can only become preserved at sites of rapid diagenetic mineral precipitation. Otherwise, the pores collapse quickly. In the fossil record, such a porous fabric is therefore visible only in chemical I sandstones. However, the fabrics allow conclusions about the position of ancient high water lines.

III.2.4

Structures Arising from Baffling and Trapping

This section introduces all MISS that predominantly, if not exclusively, arise from baffling and/or trapping. Baffling is a response by benthic microbiota to the deposition of sediment. Overall, cyanobacteria move in a vertical direction. Their vertical orientation is result of phototaxis (movement in order to reach optimal light conditions). It is not induced by growth.

Two types of baffling are described. Silt-sized sedimentary particles suspended in supernatant seawater are ‘combed out’ by vertical filaments during periods of calm dynamic conditions. This type of baffling is typical of epibenthic microbial mats. In this case, the sedimentary surface is not rising. As water motion increases, sand grains are transported as bed load along the sedimentary surface. Consequently, the sedimentary surface rises and moves laterally. Active benthic microbiota move rapidly through the sediment to keep up with the sedimentary surface. This behaviour is typical of endobenthic microbial mats.

Trapping differs from baffling. Trapping results from the cohesive effect of EPS, which acts to adhere particles to microbial mat surfaces.

III.2.4.1

Mat Layer-Bound Small Grains

Description

Thin-sections vertical through an epibenthic microbial mat show that silt-sized quartz grains occur exclusively in the organic matrix (Fig. III.26). In contrast to sand-sized 'oriented grains', the much smaller, silt-sized particles show no preferred orientation of their long-axes. The mat layer-bound small grains can occur by themselves, or together with microsequences, oriented grains, and laminated leveling structures.

Etymology

Mat layer-bound small grains were first described by Noffke et al. 1997a.

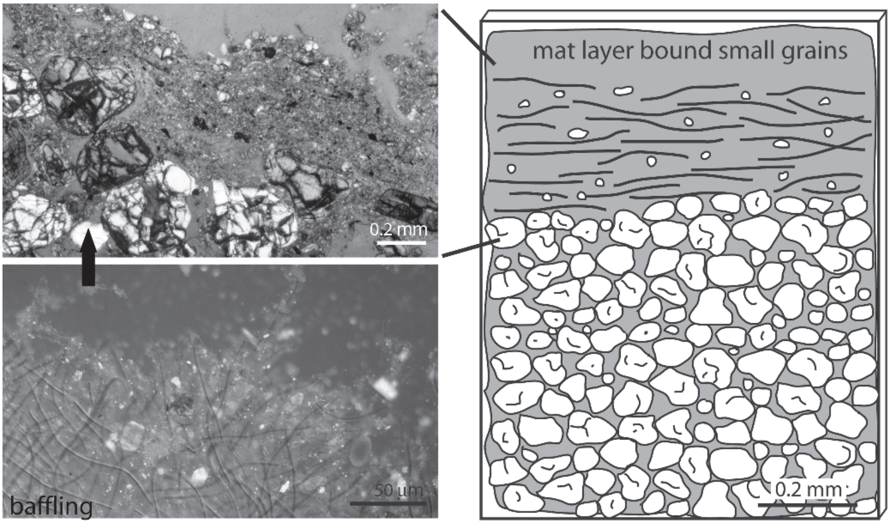


Fig. III.26. Mat layer-bound small grains. Photo on the lower left: Vertical cyanobacterial filaments and their EPS baffle and trap silt-sized particles from the water column. Photo on the upper left: In thin-section, silt-sized particles are finely distributed in a modern microbial mat. The sketch on the right further describes this texture

Genesis

Mat layer-bound small grains are result of baffling type I, or of trapping. Filamentous cyanobacteria orient perpendicularly to the microbial mat surface, and reach into supernatant seawater. They comb out fine particles suspended in the water. The filaments create micro-zones of lower current velocity that allow silt-sized grains to settle.

In tidal flats, grains can also be transported by wind. As soon as grains are deposited on a microbial mat, they glue to the sticky EPS. This trapping can be observed especially in lower supratidal zones.

Paleoenvironmental Distribution and Seasonal Varieties

Mat layer bound small grains are typical of epibenthic microbial mats. They do not occur in endobenthic mats. Therefore, the MISS occur in lower supratidal zones. Seasonal variation is unknown, although it is possible. Seasonal variations in the local sediment supply control baffling and trapping.

Diagnosis

In grain size analyses, mat-bound grains are smaller (silt-sized) than those of the underlying substrate. (Mat substrate commonly is composed of sand). Oriented grains, microsequences, and laminated leveling are commonly associated. A search for additional MISS in the surrounding area could support biogenicity.

Example Specimen

A thin-section with mat layer-bound small grains is stored by at the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540874.

Application

In sandstones, where no organic matter is preserved, and no organo-mineral or mineral fossils occur, any layer of silt-sized grains could be indicative of an ancient mat.

III.2.4.2
Mat Layer-Bound Heavy Minerals

Description

Mat layer-bound heavy minerals are, as the name says, heavy minerals such as rutile, tourmaline, hematite, magnetite, and others enriched in microbial mats. The grain size is comparable to silt-sized particles, but can be much smaller.

Etymology

Mat layer-bound heavy minerals in modern microbial mats are described by Gerdes et al. 2000b.

Genesis

The specific weight of heavy minerals is much higher than that of quartz grains. Heavy minerals are deposited before quartz sand. Baffling by microbial mats also triggers the fall-out of heavy minerals. It is not true that cyanobacteria actively accumulate heavy minerals, as sometimes expressed. Cyanobacteria are photoautotrophic, and would not cover themselves with opaque sediment. Rather, these microbes respond more rapidly to the deposition of opaque minerals than to deposition of translucent quartz grains.

Paleoenvironmental Distribution and Seasonal Varieties

Mat layer-bound heavy minerals occur in epibenthic microbial mats. They have not been detected in endobenthic microbial mats. Seasonal variations might be possible, but have not yet been documented.

Diagnosis

Thin-sections through tidal sediment show mat lamina-bound layers of heavy minerals. A search for additional MISS in the surrounding area could support biogenicity.

Example Specimen

A thin-section with mat layer-bound heavy minerals is stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection USNM 540875.

Application

In sandstones, where no organic matter is preserved, and no organo-mineral or mineral fossils occur, any layer of heavy mineral grains could be indicative of an ancient mat.

III.2.5
Structures Arising from the Interference of All Microbial Activities Interacting with Physical Sediment Dynamics

This section introduces all MISS that arise from interference of growth, baffling, trapping, and binding, as well as biostabilization.

III.2.5.1
Erosional Remnants and Pockets

Description

Erosional remnants and pockets are composed of two geometric elements (Fig. III.27). The structure includes elevated surface portions that are flat-topped, or that display strongly leveled ripple marks. These surface portions are erosional remnants. The structure also includes deeper lying, V-shaped, rippled depressions. These are erosional pockets.

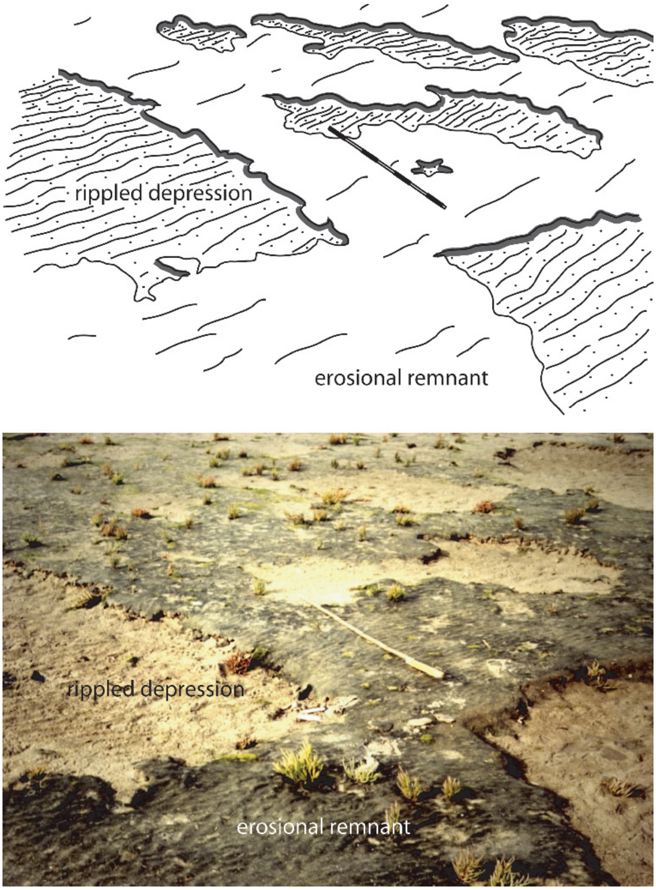


Fig. III.27.
Erosional remnants and pockets. This tidal surface morphology consists of elevated, flat-topped surface portions that are overgrown by microbial mat, and of deeper lying surface portions that are ripple marked and not colonized by microbes; (scale: 1 m)

Erosional remnants are overgrown by epibenthic or endobenthic microbial mats. The remnants are elevated on the remaining tidal surface with a slope angle of 5 to 90° depending on the mat type. Their lateral extension is between 5 cm^2 to several tens of meters. Vertical cross-sections through remnants reveal internal laminated patterns of buried microbial mat laminae, alternating with sand layers.

Erosional pockets are commonly not overgrown by microbial mats. Only individual cells of diatoms or cyanobacteria are present. These V-shaped depressions are between 25 cm to 0.5 cm deep. The bottom of an erosional pocket is never level. The deepest parts are the peak, and the lateral sides of the 'V'. Along a line from the peak of the 'V' towards the opening, the bottom of an erosional pocket rises with an average gradient of about 3.5%. Ripple marks in the erosional pocket are oriented approximately in a 45° angle to the sides of the 'V'. The ripples indicate the direction of the tidal currents that form the erosional pocket. Most often the main structure-forming current is the tidal flood current. Erosional pockets extend laterally between 5 cm^2 to several tens of meters. Some depressions cover larger parts of the tidal surface, and show irregular outlines. They consist of many joined V-shaped pockets.

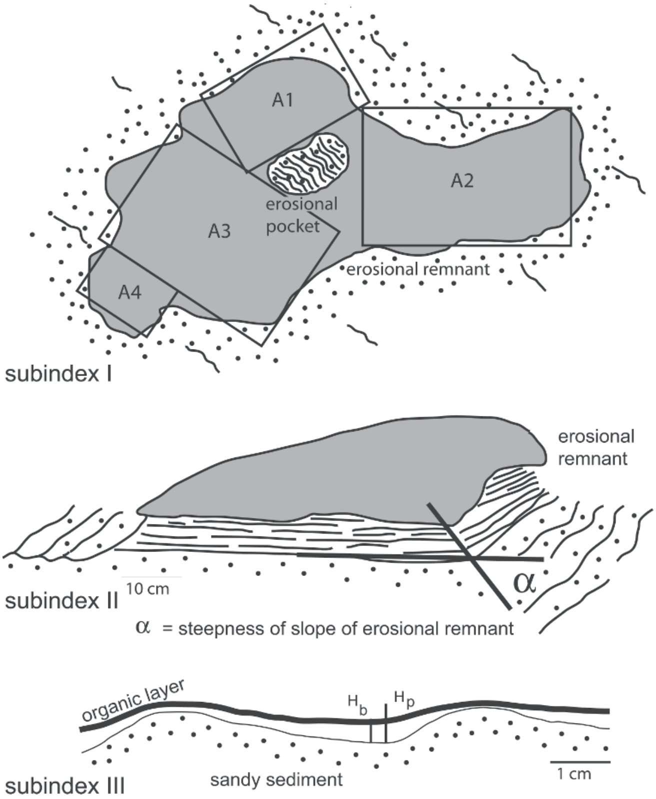


Fig. III.28.
Three subindices describe the three geometric elements of erosional remnants and pockets. See text for explanation

The geometries and dimensions of erosional remnants and pockets are defined by a modification index (MOD-I) (Noffke and Krumbein 1999). The MOD-I expresses the degree of microbial influence on the formation of such structures. It can be applied to structures at any chosen site, on any tidal flat. The MOD-I allows tidal sites to be compared. It also allows comparison between modern and ancient tidal flats. The MOD-I is composed of three subindices, Fig. III.28:

i) the proportion of the mat-covered tidal surface area related to a defined area of investigation

$$I_A = (A_m / A_i)$$

ii) the degree of steepness of the slope angles of the erosional remnants

$$I_S = \sin \alpha$$

iii) the degree of microbial leveling of a rippled sedimentary surface

$$I_N = [(H_p - H_b) / H_p]$$

Taken together, the subindices define the MOD-I as follows:

$$\text{MOD-I} = (A_m / A_i) \cdot \sin\alpha \cdot 1 - [(H_p - H_b) / H_p] \quad \text{with} \quad H_p > 0$$

Values approaching 0 express little or no microbial influence, values approaching 1 express maximum microbial influence on the morphology of the sedimentary surface.

Etymology

The term 'erosional remnants and pockets' has been introduced by Reineck 1979, Wunderlich 1979, and Gerdes et al. 1993. The name derives from the mode of formation. Erosion causes ripple marked erosional pockets in an otherwise mat-stabilized depositional surface.

Genesis

The genesis of erosional remnants and pockets has been monitored and quantified in Noffke 1999, and Noffke and Krumbein 1999. The equation for the MOD-I expresses the overlap of all microbial activities in the formation of such structures.

Growth and binding level the original sedimentary surface. Microbial mats covering a tidal deposit smooth any prior surface relief. Baffling, and trapping of mineral grains contributes to the thickness of microbial mats.

Microbial mats biostabilize tidal deposits. Careful examination of the slopes of erosional remnants can help quantify the effects of biostabilization. Erosional remnants with higher slope angles indicate microbial mats with higher biostabilization properties than remnants having lower slope angles. Low slope angles reflect low biostabilization properties.

Erosional remnants and pockets exhibit type I biostabilization. This type of biostabilization is the response of microbial mats to erosion. Epibenthic microbial mats induce type I biostabilization, whereas endobenthic microbial mats induce type II biostabilization.

Field observations in modern tidal flats reveal the stages of erosional remnant and pocket formation (Fig. III.29). Initially, a sediment-stabilizing microbial mat overgrows a tidal surface. Then, the microbial mat is locally disturbed, such as a mollusk shell is deposited on top. The shell may cause a local shadow. The photoautotrophic cyanobacteria react by migrating away. Consequently, the mat texture around the shell becomes less coherent. Tidal currents can then erode sand grains.

The V-shaped pattern of erosional pockets indicates that as soon as the tidal current hits the shell, the current is divided into two branches. Each branch flow is diverted away from the obstacle at 45° (model by Peabody 1947). Within each branch, greater amounts of water flowing over the same surface area create zones of higher current velocities (Fig. III.30).

The increased velocities cause more erosion in these branches. This erosion sculpts the characteristic V-shape of erosional pockets. The peak of the 'V' usually is the deepest point of erosional pockets. The sediment eroded from the zones of highest current velocities is redeposited behind the obstacle. This dynamic causes the slight rising of the bottom of the pocket from the peak of the 'V' towards the opening.

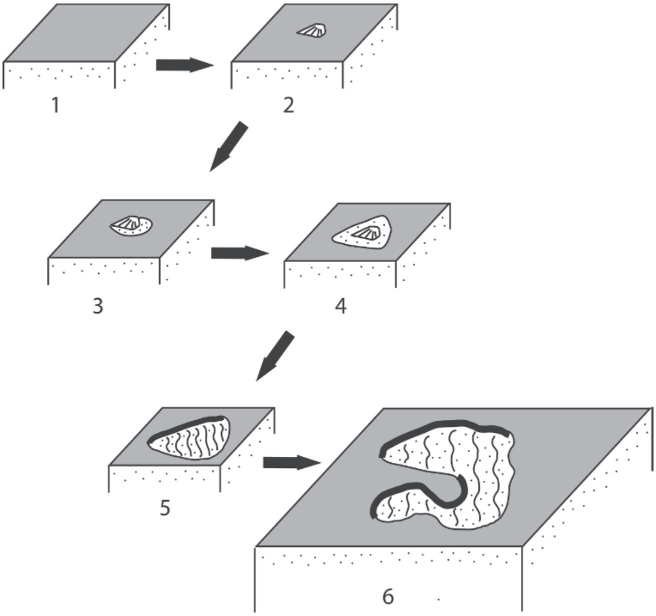


Fig. III.29.
Formation of erosional remnants and pockets. *Stage 1:* Undisturbed microbial mat covers sandy sediment. *Stage 2:* An obstacle (here a clam) is deposited on mat surface. *Stage 3:* Around this obstacle, erosion sets in. *Stage 4:* Erosion is highest in front of the obstacle, and on both sides behind the obstacle (compare Fig. III.30). *Stage 5:* Obstacle is removed by currents. Erosional pocket enlarges laterally. *Stage 6:* Several erosional pockets join (after Noffke 1999)

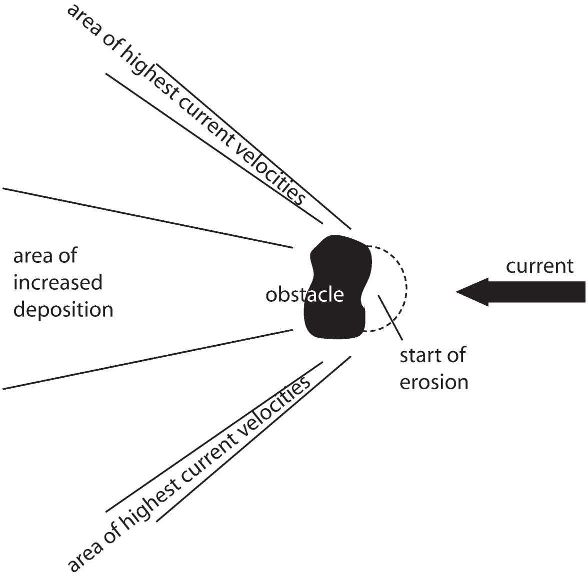


Fig. III.30.
Formation of an erosional remnant and pocket. Erosion is triggered by obstacles deposited onto mat surfaces. Obstacles block available light, and weaken the underlying microbial mat. Cyanobacteria move away from darkened zones, leaving behind weak mat fabrics. Such weakened mats experience erosion by tidal currents. A current is separated into two main streams that pass the obstacle on both sides. At these two zones, the erosion causes V-shaped appearances of erosional pockets (after Noffke 1997)

Most erosional pockets are oriented with the peak of the ‘V’ away from the shoreline. The current ripples at the bottom of erosional remnants indicate shoreward water flow. Together with the orientations of the V-shaped erosional pockets, they show that tidal flood current is the primary agent in the genesis of erosional remnants and pockets.

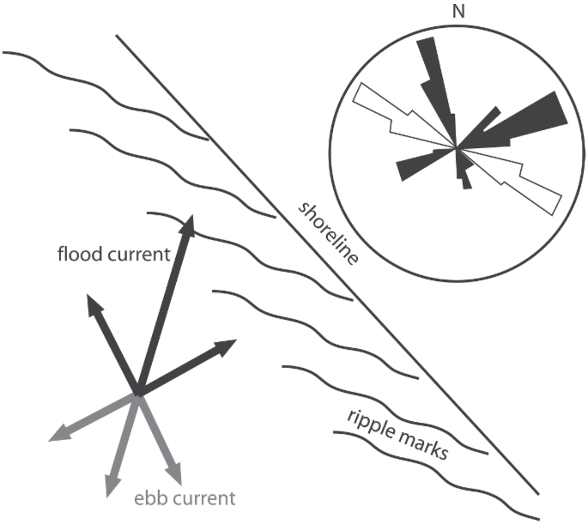


Fig. III.31.
Flood and ebb currents form erosional remnants and pockets. Because the currents are reflected by the shore line, the erosional remnants and pockets are asymmetric. This asymmetry is presented in the rose diagram on the right. The white directions represent the direction of ripple marks along the shore. The black directions represent the sides of the V-shaped erosional depressions. Note that the directions of ripple marks and sides of the 'V' do not form 45° angles (after Noffke 1999)

On Mellum Island, a few erosional pockets are oriented the other way around. Such pockets are less well visible. They are caused by the weaker ebb current.

Eventually, erosional pockets may join the neighboring pockets (Fig. III.29). Tidal flats are not only inclined towards the ocean (remember Fig. II.12), but also slightly tilted. Due to this, erosional remnants and pockets commonly are slightly asymmetric.

Statistical analyses of the morphologies of erosional pockets on Mellum Island revealed that the sides of the 'V' are not precisely oriented at a 45° angle to the flood currents. The ripple marks at the bottom of the 'V' are also not precisely at a 45° angle to the sides of the pockets. These two asymmetries are result of resonance and deflection of currents that ascend obliquely towards the inclining tidal flat surface (Noffke 1999), Fig. III.31.

Paleoenvironmental Distribution and Seasonal Variations

On Mellum Island, erosional remnants and pockets are typical in the lower supratidal and the upper intertidal zone. They do not develop in the lower intertidal zone. The dimensions of erosional remnants and pockets are a function of their location on the tidal flats, the microbial mat type, and the season (Fig. III.32). This relation was shown by Noffke and Krumbein 1999.

The lower intertidal zone is characterized by MOD-index values approaching zero, both in winter and in summer. During the time of observation (years 1994–1996), the maximum MOD-I has been just 0.02. This implies that microbial influences in this tidal zone are negligible. No leveling of the tidal sedimentary surface by growth, or by baffling and trapping could be observed. The tidal deposits are merely overgrown by biofilms. Only type III biostabilization occurs.

The biofilms are formed by coccoid cyanobacteria such as *Merismopedia punctata*. Cyanobacteria cannot form mats in the lower intertidal zone, because the sediments are reworked too often.

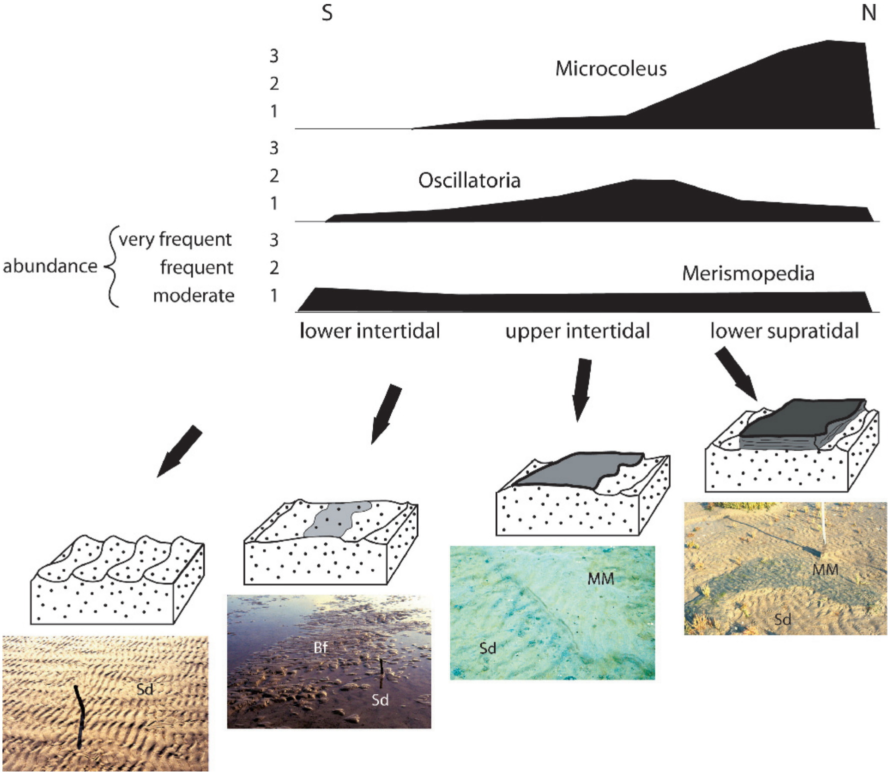


Fig. III.32. Change of surface morphology of a tidal flat from the lower intertidal to the lower supratidal zone, Mellum Island, North Sea (study period 1994–1996). From left to right, the photos document the microbial colonization of the tidal surface by mat-forming cyanobacteria. The sketches above the photos characterize, how the biofilms and microbial mats overgrow the tidal surface. The graph above summarizes the abundance of cyanobacterial species that form the biofilms and mats. In the lower intertidal zone (photo on the far left) only biofilms develop. These are dominated by *Merismopedia punctata* (see the graph of abundance above). In the lower and upper intertidal zones (two photos in the center) endobenthic microbial mats form. The mats are dominated by *Oscillatoria limosa*. The lower supratidal zone (photo on the far right) is dominated by epibenthic microbial mats. The mats are constructed by *Microcoleus chthonoplastes*. The figure shows the situation for the summer. However, seasonal variations in the pattern of colonization can be distinguished (detailed study is Noffke and Krumbein 1999)

The upper intertidal zone shows low MOD-I in winter (0.03–0.1), and higher values in summer (0.12–0.3). The erosional remnants have angles of slopes of 30–60°. The tidal flats are overgrown by endobenthic microbial mats constructed predominantly by *Oscillatoria limosa*. Whereas these mats flourish in summer, they decompose in fall. This endobenthic mat type biostabilizes its substrate by forming the typical carpet-like, organic meshwork. Baffling, and trapping takes place as response to the movement of the sand grains entrained by the daily flood currents. That is the microbes move actively to keep up with the laterally migrating sandy surface. The microbes do not accumulate fine material such as silt. Such fine debris would contribute to the leveling of the original depositional surface. Endobenthic mats grow within the sediment, not on top of it. Ripple marks underneath the microbial mat remain visible. However, they are less pronounced than the ripple marks of the remaining, non-colonized tidal surface barren of mats.

The lower supratidal zone is characterized by high MOD-I. Winter values are around 0.55, summer values 0.6. This tidal zone is overgrown by *Microcoleus chthonoplastes*, which forms thick, epibenthic microbial mats. These mats do not decompose in fall. However, they might suffer from erosion by strong storms that are frequent during this season. The biostabilization properties of epibenthic microbial mats are high. The mats withstand even currents of 1.60 $m\ s^{-1}$.

The slopes of the erosional remnants are 60–90°. In contrast to endobenthic microbial mats formed by *Oscillatoria limosa*, *Microcoleus chthonoplastes* actively accumulates fine material in its mat fabrics. This fine material together with the high amount of biomass of epibenthic mats levels the tidal sedimentary surface significantly. Typically, the mat surface is planar.

Diagnosis

Erosional remnants and pockets are composed of two geometrical elements: elevated, flat-topped surface areas, and deeper lying, rippled surface areas. Both geometrical elements must be preserved on the same depositional surface. In thin-sections through the erosional remnants, the presence (or former presence) of sediment-stabilizing microbiota must be confirmed. Microsequences, and laminations occur. Associated MISS are microbial mat chips, and sometimes gas domes. Measurements on erosional remnants and pockets must be conducted to express the microbial influence in their formation as MOD-I. Ancient erosional remnants and pockets can be directly compared with modern ones.

Example Specimen

A rock sample of cm-scale erosional pockets is stored as Noffke Collection no. USNM 540000 by the Smithsonian Natural History Museum, Washington, DC. This sample is from the 2.9 Ga Brixton Formation, Witwatersrand Supergroup, South Africa (Noffke et al. 2006b).

Erosional remnants and pockets occur on the modern tidal flats of Mellum Island, North Sea (Reineck 1979; Wunderlich 1979; and Gerdes et al. 1993). Fossil erosional remnants and pockets are exposed in the Nhlazatse Section, Pongola Supergroup, South Africa, and in the Cretaceous Dakota Sandstone, Dinosaur Ridge, Colorado, USA (Fig. III.33).

Application

In the fossil record, erosional remnants and pockets allow researchers to reconstruct flood and ebb-currents in an ancient tidal flat.

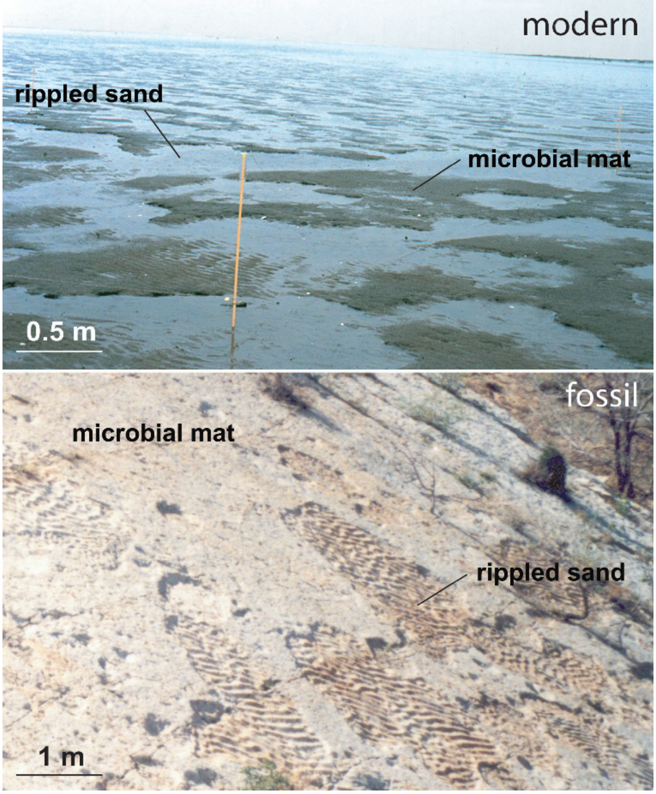


Fig. III.33.
Erosional remnants and pockets, modern and fossil. The upper photo is a view of modern tidal flats on Mellum Island, North Sea. The tidal flats of the North Sea coast are very extensive. Large areas display this surface morphology. The photo below shows a beautifully preserved fossil example exposed at the site 'Dinosaur Ridge' in Colorado, USA. The site is famous for its dinosaur tracks that cross an ancient, Cretaceous tidal flat

III.2.5.2
Multidirected Ripple Marks

Description

A chaotic-like pattern of dm-scale patches that each display ripple marks of a different direction covers modern or ancient tidal flats (Noffke 1998). Such a pattern is called multidirected ripple marks. The ripple marks are current ripples with 3–8 cm crest-to-crest distance. The crests of the ripple marks of neighboring patches join. All ripple marks are on one and the same tidal surface (Fig. III.34).

Usually, 2 to 4 main ripple mark directions can be distinguished on the same surface. Each ripple direction is characterized by a microbial population of distinct maturity (Fig. III.35). In modern settings, adjacent patches of different shades of green indicate mats in different stages of development.

Etymology

Because of the chaotic-like pattern of ripple marks, the term 'multidirected ripple marks' was introduced (Noffke et al. 1996; quantification in Noffke 1998).

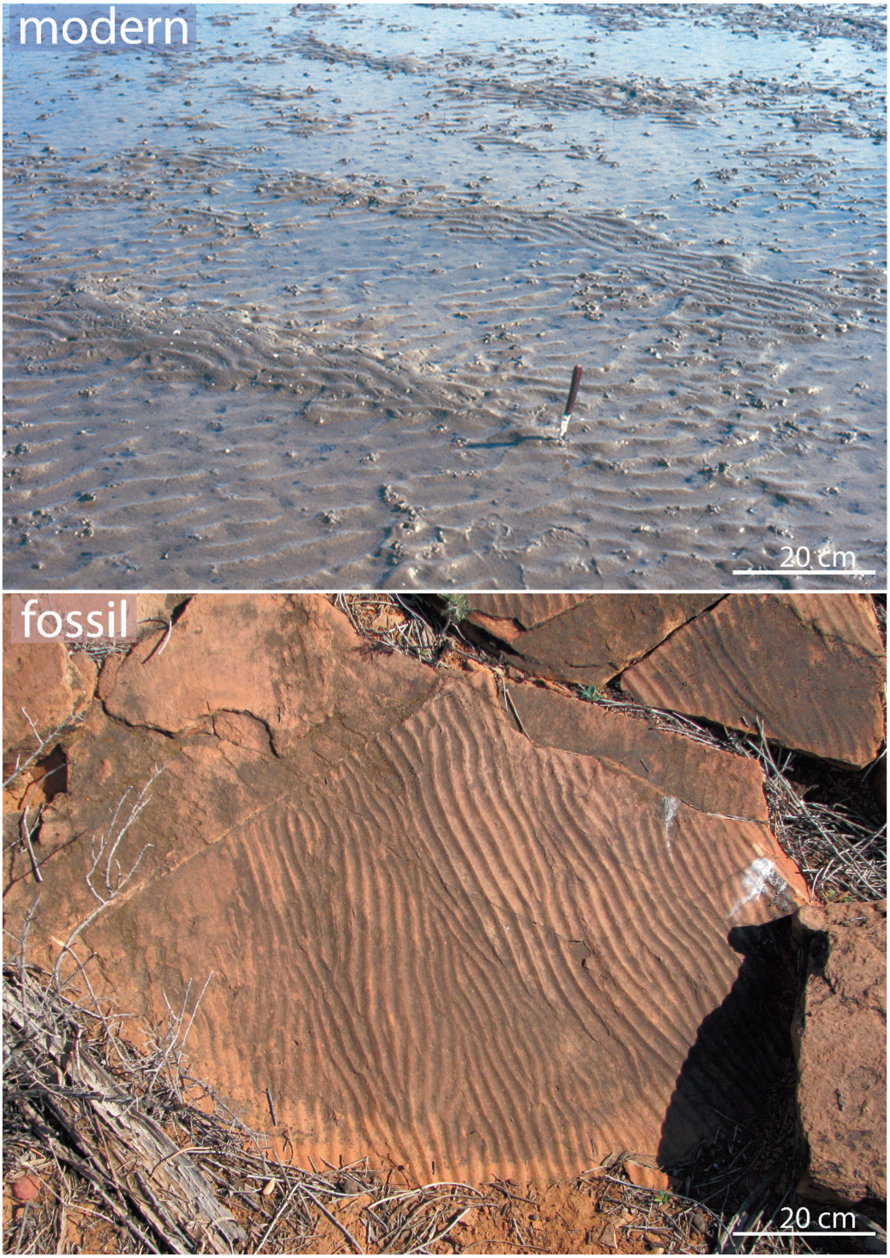


Fig. III.34. Multidirected ripple marks, modern and fossil. The upper photo is a view of a tidal flat on Mellum Island, North Sea (summer 1995). The sandy surface nicely displays ripple marks of two different orientations. The ripple marks are grouped into elongated patches. Note that the orientations of the two groups of ripple marks are at an angle of about 45° to each other. The photo below shows a similar situation on a fossil sandstone surface (Australia, age unknown)

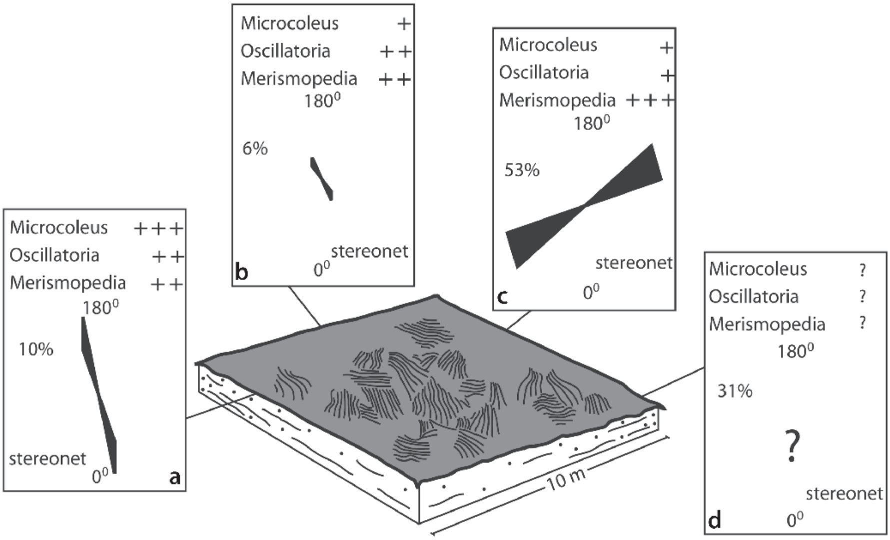


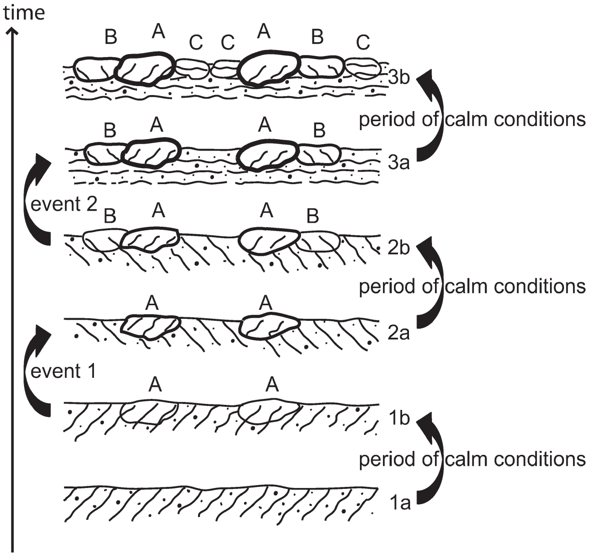
Fig. III.35. Multidirected ripple marks from the Westplate (the sandy lower supratidal zone), Mellum Island, North Sea, 1994. An area of 10 × 10 m showed three categories (**a, b, c**) of similar ripple mark orientations, each covered by cyanobacterial populations of similar stages of development. Category **d** contains indistinct ripple orientations and varying microbial communities of transition zones, or of zones destroyed by humans. **a, b, c** Species compositions of microbial assemblages that cover ripple marks having distinct orientation. Three classes that characterize the abundance of cyanobacterial species are distinguished: + seldom; ++ frequent; +++ dominant. In stereonet plots, the primary orientation of ripple marks becomes obvious. The areas covered by specific ripple generations are given in % from 100. 1% of the surface in the area of investigation is also represented by 1° of the equator of the stereonet (after Noffke 1998, modified)

Genesis

Field studies monitored the development of multidirected ripple marks in the modern tidal flats of Mellum Island, North Sea. The study showed that this surface pattern evolves over the course of half a year, from spring to fall (Noffke 1998). The specific ripple mark orientations correlate with specific stages of development of cyanobacterial communities. Multi-directed ripple marks form in several steps (Fig. III.36).

During winter months, microbial mats may decompose or be eroded away by strong storms. In spring, storms are less frequent, thus providing opportunites for microorganisms to recolonize tidal flats. During high tide, the lower supratidal zone is covered by water having a depth of a few cm. Water motion generates landward directed current ripple marks of direction A (Fig. III.36). On Mellum Island, the first cyanobacteria that reestablish after the winter is *Merismopedia punctata.* It forms biofilms. The surface of the tidal flats is slightly uneven, showing a few millimeters variation in height. This slight variation affects the water currents passing the surface, and consequently the colonization by microbes. The degree to which sedimentary surfaces are disturbed by ascending flood waters varies at different locations on tidal flats. *Merismopedia punctata* preferentially colonizes slight elevations on tidal sur-

Fig. III.36.
Formation of multidirected ripple marks from spring to fall. This chaotic-like pattern of ripple marks occurs from interference of mat growth with storm events. During storms sedimentary surfaces are reworked. In the calm periods between storms microbial mat patches grow. The mats stabilize the sands. Detailed explanation in text (after Noffke 1998, modified)



faces. Biofilms contribute to biostabilization of sediment (type III biostabilization; MOD-I 0.02). Over time, other cyanobacterial species join the microbenthos. *Oscillatoria limosa* establishes its typical carpet-like meshwork. Although *Oscillatoria limosa* is able to move quickly with shifting sands, it preferentially colonizes slightly elevated, partially biostabilized tidal flat surfaces. Consequently, initial microbial colonization of tidal surfaces is patchy.

Over time, *Oscillatoria limosa* forms a thin, primary endobenthic microbial mat. The higher tidal flat sites overgrown by endobenthic mats show a higher erosional stability of the sediment (type II biostabilization). The first generation of ripple marks, oriented in direction A is now well protected, whereas the ripple marks on the remaining tidal surface are less stabilized.

During the following high spring tide, the water currents rework these less well stabilized tidal surfaces again. This reworking creates a new ripple mark generation of a new direction (B). However, the patches overgrown by endobenthic microbial mats still show the first ripple mark generation A. The ripple marks remain unchanged, because they are biostabilized to a higher degree.

After the tidal flats drain, endobenthic microbial mat patches continue to develop. Microbial mat patches extend laterally and start to overgrow the area covered by the newly formed ripple marks of direction B. Before microbial mats can cover the tidal surface completely, a third high spring tide occurs. This third flooding event reworks all those surface areas still not overgrown by a microbial mat. Consequently, a third ripple generation C forms. This third direction differs from the directions A and B.

In the following period of quiet dynamic conditions, the endobenthic microbial mats that formed the initial mat patches mature. What does this mean? It means that many other cyanobacterial species join the primary mat communities. An important prerequisite for other microbes to join the mat community is an immobile substrate. Once the sand is stabilized by *Oscillatoria limosa*, *Microcoleus chthonoplastes* can establish and participate effectively in sand fixation. Indeed, the name *chthonoplastes* means 'soil forming' (Bang 1813 in Krumbein 1987). *M. chthonoplastes* joins endobenthic mats of ripple mark direction A. The endobenthic microbial mats mature into epibenthic ones. The patches covering ripple marks A are now elevated surface areas. They force ascending flood waters to flow around them. Consequently, the elevated sediment patch is even less reworked by water, thus more cyanobacteria join the mat community. A view of the tidal flat now shows a patchy pattern of different shades of blue-green, representing different stages of mat maturity. In fall, several ripple mark generations (each characterized by a different ripple direction and by a different mat) cover the tidal surface – multidirected ripple marks.

Paleoenvironmental Distribution and Seasonal Variations

Multidirected ripple marks occur in the upper intertidal and lower supratidal zones, at somewhat sheltered locations. Whereas multidirected ripple marks develop during the growth season (on Mellum Island from May to September), the final multi-hued, blue-green patchy appearance of such tidal flats is usually seen in the late fall (October). As winter nears, the microbial mats recess, and the patchy ripple mark patterns disappear by December.

Diagnosis

Multidirected ripple marks occur in the same sedimentary surface, in both modern and fossil settings. In fossil outcrops, care must be taken not to consider ripple marks as 'multidrected ripple marks' that actually are preserved in very thin, yet different, rock beds. Multidirected ripple marks must be documented in rose diagrams. The presence (or former presence) of sediment-stabilizing microbiota in or on the depositional surface must be verified in thin-sections.

Example Specimen

The first example of modern multi-directed ripple marks was described from Mellum Island, North Sea (Noffke et al. 1996; quantification in Noffke 1998). The fossil example is preserved in the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa.

Application

Fossil multidirected ripple marks indicate a seasonal paleoclimate. An ancient tidal surface that displays only two ripple mark directions might record a late spring. A fossil tidal surface covered by many patches of ripples of different directions might record a fall situation. The varying orientations of multidirected ripple marks permit conclusions about the number of storms that affected the ancient area. The ripple mark pattern shown in Fig. III.35 displays 69% rippled surface in total, of which 10% are of direction A, 6% of direction B, and 53% of direction C. It records 3 storms.

III.2.5.3
Microsequences

Description

In thin-sections perpendicular to the sedimentary surface, microbial mat-overgrown tidal deposits show graded sand layers, each some millimeters thick (Fig. III.37). The tops of the layers are formed by microbial mat laminae. The grain sizes in each sand layer decrease from the bottom layer upwards. That is, medium grain sizes at the base, to fine grain sizes close to the top. In the medium sized sand at the base of each layer, hollow cavities occur. These pores average 0.3 mm in diameter. This porosity is called 'sponge pore fabric'. Within the mat laminae on top of each layer, mat layer-bound small grains and/or oriented grains occur. The silt-sized particles can be quartz minerals, or an array of different heavy minerals such rutile, tourmaline, hematite, and others.

Etymology

Each graded sand layer, including the mat on top, is called a 'microsequence' (Noffke et al. 1997a).

Genesis

Each graded sand layer is formed by one spring tide. The fining upward grading records a decrease of flow energy of the ascending flood current. 'Fining upward grading' means

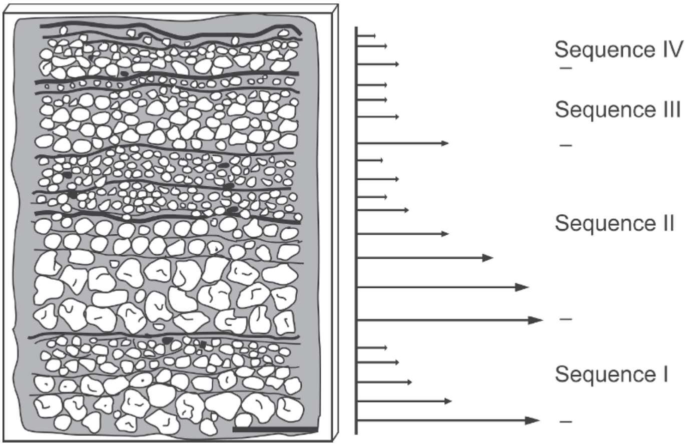


Fig. III.37. Microsequences in thin-section taken vertically to tidal bedding. Each microsequence consists of medium grained sand at its base. The sand grain sizes decrease towards the top. The top of each microsequence is marked by a microbial mat lamina. This thin-section displays 4 microsequences. The *arrows* on the right document the current velocities that prevailed during the time of deposition of each microsequence. The lengths of the *arrows* document the current velocities. Note that the base of each microsequence records stronger current velocities, but that towards the top the current velocities must have decreased. Finally, water motion calmed enough for a microbial mat to form (after Noffke et al. 2008); (scale: 0.5 cm) that the grain sizes decrease from the base of the layer towards the top. On Mellum Island, first only medium sand sized particles are deposited, because the current velocity is high. Over time, the current velocities decrease. Consequently, particles of gradually finer sand sizes are deposited. After hydraulic reworking has ceased completely, the sedimentary surface remains undisturbed. Pioneer microorganisms such as *Oscillatoria limosa* colonize the freshly deposited sand layer, forming a biofilm. This biofilm develops into an endobenthic microbial mat that quickly is joined by *Microcoleus chthonoplastes*. The mat matures into an epibenthic community. During the growth of this microbial mat, the sticky EPS drag some of the sand grains of the tidal surface upward, until these grains 'float' as oriented grains in the biomass. Baffling and trapping induces the fall-out of silt-size particles, which become incorporated into the developing mat matrix as well. The surrounding tidal areas not overgrown by a microbial mat do not include silt-sized particles in the sediment layers.

In the tidal sands of Mellum Island and in fossil sandstones from the Archean Pongola tidal flats, the microsequences include sponge pore fabrics. The pores in the medium sand close to the base of each graded bed are induced by gas (type III biostabilization). The gas derives from decay of prior microbial mat generations buried in the underlying sand. In vertical cross-sections through the tidal deposits, these earlier mats are visible as opaque laminae. The laminae separate each microsequence from the next. The laminae have protected the tops of each microsequence against erosion during placement of the subsequent microsequence above (Fig. III.38). This is a fine example of biostabilization against amalgamation and cannibalism. 'Amalgamation' is the fusion of several layers, because each sediment deposition event erodes some of the prior surface. This sedimentary surface erosion during placement of subsequent deposits is termed cannibalism (Fig. III.38). This effect corresponds to type I biostabilization.

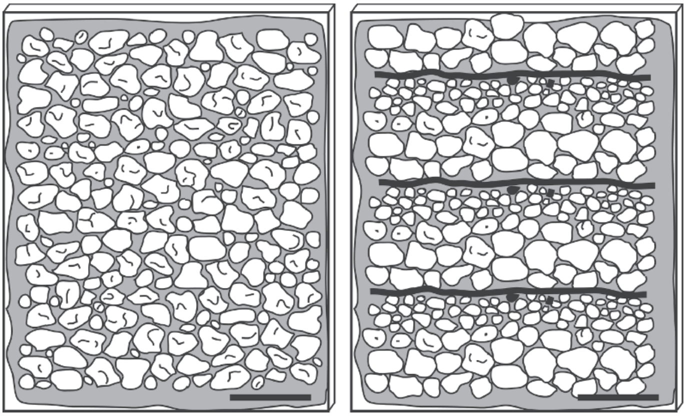


Fig. III.38. Microbial mats protect the sedimentary surface against cannibalism. The thin-section on the left is an idealized presentation of an amalgamated tidal sequence. In sandy sediment lacking microbes, freshly deposited sand causes deep surface erosion. Subsequent depositional events cause amalgamation. None of the individual depositional events would form a discrete sediment layer. However, the sedimentary surface is overgrown by a microbial mat that protects the surface against erosion. Consequently, each depositional event leaves behind one discrete layer (thin-section on the right). Cannibalism does not take place in the presence of microbial mats (after Noffke et al. 1997a); (scale: 0.5 cm)

Paleoenvironmental Distribution and Seasonal Variations

Microsequences have been found in sandy deposits of lower and upper supratidal zones. They record transgressions.

Diagnosis

Microsequences are visible in thin-sections perpendicular to bedding planes. The sandy lower portion of each layer must be graded, with coarser grains at the base and finer grains towards the top. Sponge pore fabrics may be present. The tops of each bed are formed by a microbial mat lamina, which can contain oriented grains and silt size particles. Each microsequence bed is less than 10 mm thick. Several microsequences are stacked together. The presence of graded beds, oriented grains, and mat-layer bound small grains must be documented. The mat-layer bound grain sizes must be significantly smaller than the sizes of the grains composing the base of the subsequent microsequence above. Commonly, mat-layer bound small grains are silt-sized, whereas sand grains at the microsequence base are medium sized.

Example Specimen

A thin-section from the Ordovician tidal flats of the Montagne Noire, France, and a relief cast from a sediment core from modern tidal flats of Fishermans Island, USA display microsequences and are stored as Noffke Collection no. USNM 540876, USNM 540877 by the Smithsonian National Museum of Natural History, Washington, DC.

Application

Microsequences are indicative of a lower and upper supratidal flat. In sediment cores of both modern and ancient deposits they serve to trace the oscillation of the former

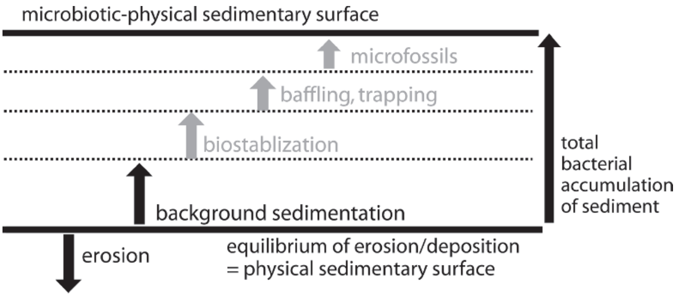


Fig. III.39. Microbial mats influence the depositional and erosional dynamics of a sedimentary basin. This was shown for Lower Arenigian rocks of the Montagne Noire, France. The normal sedimentation dynamics includes background sedimentation and erosion, forming an equilibrium represented by the 'physical sedimentary surface'. Microbial mats influence this equilibrium. Biostabilization acts against erosion; baffling, trapping and binding accumulates mineral particles; and the amount of lithified mat biomass adds to the total sediment. This microbially modified equilibrium is now represented by the 'biotic-physical sedimentary surface'. This surface is elevated compared to the physical sedimentary surface (after Noffke 2000) coast line, with respect to sea level transgression and regression. Examples have been found in the Lower Arenigian, Montagne Noire, France, as well as the Mozaan Group, and the Sinqueni Formation, Pongola Supergroup, South Africa (Noffke 2000; Noffke et al. 2003b, 2008).

In the Ordovician of the Montagne Noire, it was shown that carpet-like microbial mats overgrew large areas of the seafloor, covering the surfaces of continental shelves, lagoons, and tidal flats. Biostabilization by the microbial mats prohibited erosion and cannibalism of the seafloor deposits. In addition, the extensive microbial mats baffled, trapped, and bound mineral grains. These mineral grains and the *in situ* lithified microbial mats added to the accumulation of sediment. Consequently, the microbial mat covered seafloor was relatively higher than it would have been, had it not been colonized by microorganisms (Fig. III.39).

III.2.5.4
Wrinkle Structures

Description

Wrinkle structures occur only in the fossil record, not in modern sediments. Wrinkle structures are crinkled upper bedding planes of fine quartz sandstones. Wrinkle structures occur only on the upper, never on the lower bedding plane. The wrinkles are crests and valleys of irregular directions. The crests are between 0.2 to 2 mm high, the crest-to-crest distance ranges from 0.2 mm to 2 cm. Two main types of wrinkle structures are distinguished (Fig. III.40). There are transparent and non-transparent wrinkle structures. 'Transparent wrinkle structures' means that any underlying physical sedimentary structures, such as ripple marks, are still visible beneath the wrinkles. 'Non-transparent wrinkle structures' describes upper bedding planes covered completely by crinkles. No original, physical surface relief of the bedding plane is visible beneath the wrinkles.

Etymology

The term 'wrinkle structure' was introduced by Hagadorn and Bottjer 1997 to describe any wrinkled sandy surface of biological or non-biological origin. The term is now generally understood to mean an *in situ* fossilized microbial mat. In 2000, Noffke introduced the two types 'transparent' and 'non-transparent'.

Genesis

The genesis of wrinkle structures has been described in detail in Noffke et al. 2002. Wrinkle structures result from the lithification of endobenthic microbial mats (transparent wrinkle structures), or epibenthic microbial mats (non-transparent wrinkle structures) (Fig. III.40). Mat preservation requires a set of specific depositional events (Fig. III.41). This set defines the taphonomic path of microbial mats.

First, quartz sand is deposited (stage 1 in Fig. III.41). Finely grained sand is optimal for colonization by cyanobacteria, because the microbes can move through the sediment without being held back by adhesion forces. Clear, translucent quartz grains

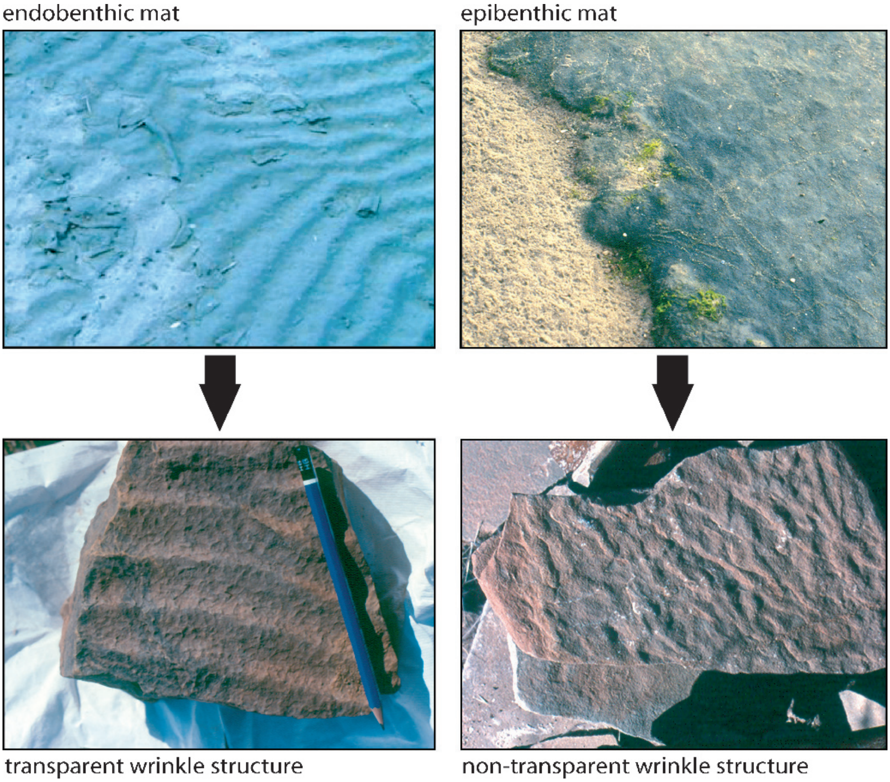


Fig. III.40. The two main types of wrinkle structures arise from the two main types of microbial mats. Left: Endobenthic microbial mats cause transparent wrinkle structures. Right: Epibenthic microbial mats form non-transparent wrinkle structures

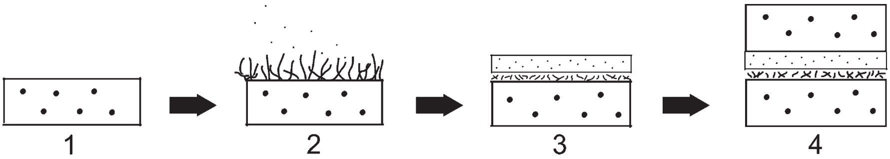


Fig. III.41. Wrinkle structures are *in situ* fossilized microbial mats. The structures arise from burial of sediment-stabilizing microbiota. *Stage 1:* Sand is deposited. Eventually, this sand is overgrown by a microbial mat. *Stage 2:* The mat baffles and traps fine grained, silty particles. These particles become enriched in the mat layer. *Stage 3:* A layer of fine sand is deposited on top of the microbial mat. The mat is buried. *Stage 4:* The loading pressure of subsequently deposited sediments squeezes water out of the mat laminae. The water escapes along the bedding plane, forming channels. This escaping water causes the wrinkly appearance of the fossil structure. Rapid biomineralization of the buried organic matter supports the preservation of microbial mat fabrics (from Noffke et al. 2002)

favor light penetration and provide a favorable substrate for photoautotrophic microbes. During a pause in sedimentation, a microbial mat establishes (stage 2). The microbiota baffle and trap silt-sized particles suspended in the water, and incorporate them into the growing mat (stage 3). A layer of fines is accumulated. In step 4, the sedimentation continues. During the placement of subsequent deposits, no erosion or cannibalism of the mat including its fine-grained particles occurs. The microbial mat is not mechanically destroyed. Subsequent deposits (overburden) are heavy, and squeeze out water from the microbial mat. This water escapes laterally, perpendicularly to the pressure. Wrinkles form along the soft bedding plane. The type of wrinkles (transparent or non-transparent) depends on the type and thickness of the original microbial mat. Epibenthic microbial mats that contain high amounts of EPS produce non-transparent wrinkle structures. Endobenthic (intrasedimentary) mats generally contain only a little EPS. They result in transparent wrinkle structures (Fig. III.40). Postburial diagenetic processes (secondary preservation processes) transform the original organic material (microbial filaments, EPS) into mineral substance. Fossil mat fabrics are not only frequently observed with wrinkle structures, but constitute one criterion for their biogenicity (Noffke 2000, 2009; Noffke et al. 2002, 2003b, 2006a,b, 2008).

Sometimes it is assumed that wrinkle structures reflect the original surface morphology of crinkled microbial mats. While this is a tempting conclusion, it is rarely the case (Fig. III.42). Elephant skin textures are an exception (Gehling and Droser 2009). They arose from tufted microbial mats. High silica content in the Ediacaran ocean may have contributed to this type of preservation (Gehling 1999; Callow and Brasier 2009).

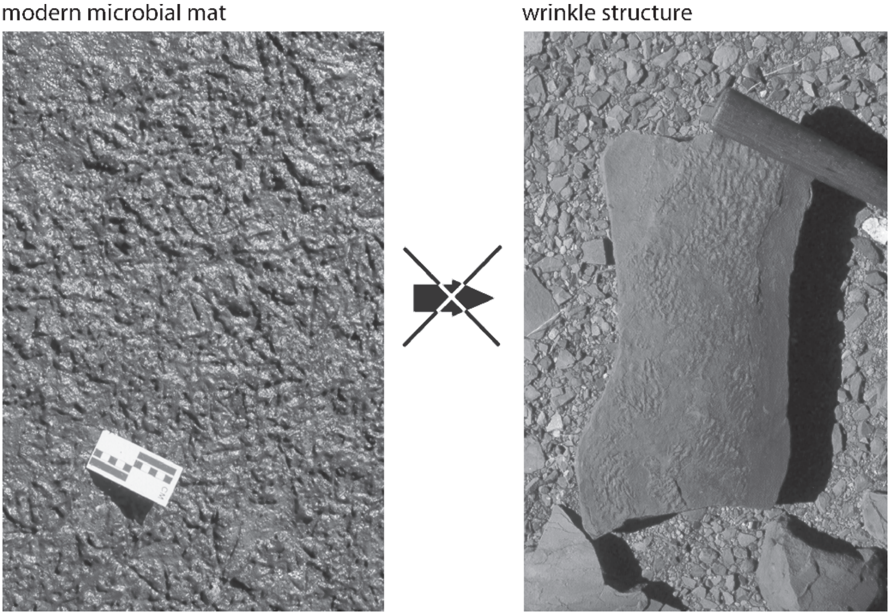


Fig. III.42. Although it may be tempting to assume that wrinkle structures show the original crinkled surface of the living microbial mat, this assumption is incorrect. Wrinkle structures only show that water was squeezed out of the mat during the placement of overburden. An exception are elephant skin textures which arose from tufted microbial mats

Paleoenvironmental Distribution and Seasonal Variations

Wrinkle structures occur in tidal, lagoonal, and continental shelf settings. Throughout Earth history, the distribution pattern of wrinkle structures shows that the structure-forming microbial mats must have been photoautotrophic. At all study sites (Ordovician of the Montagne Noire, France, (Noffke 2000); Neoproterozoic Nama Group, Namibia (Noffke et al. 2002); Meso-Archean Pongola and Witwatersrand Supergroup, South Africa (Noffke et al. 2003b, 2006a); Early Archean Moodies Group, South Africa (Noffke et al. 2006b), wrinkle structures occur exclusively in ancient photic zones (Fig. III.43). Wrinkle structures are particularly important in the exploration of cold water environments, such as these stratigraphic successions. A wonderful overview of the distribution of Phanerozoic wrinkle structures is provided by Mata and Bottjer 2009. Pruss et al. 2004, 2005 and 2006 discuss the response of wrinkle structures to extinction events.

This photic zone includes tidal flats and lagoons, but also shallow continental shelves. Photic means that these areas are so shallow that sun light penetrates the water and reaches the sea floor (approximately 200 m water depth). A survey of the Ordovician sandstones of the Montagne Noire, France, shows that specific wrinkle structures occur in specific facies zones (Table III.2).

However, it is not the paleogeography alone that controls wrinkle structure distribution. Equally important is the presence of a substrate of specific composition, and moderately calm water motion (Noffke et al. 2002). This correlation between substrate, dynamic situation, and wrinkle structure distribution reflects the colonization pattern of the seafloor by cyanobacteria. Cyanobacteria preferentially settle on fine grained sediment, avoiding muddy substrata. Finely grained quartz sand is the most favored substrate (Fig. III.44). Small-scale ripple marks, mud clasts, and planar lamination (not hcs!) record favourable dynamic settings (Fig. III.44). The best way to detect microbial mats in the fossil record is to search for fine sandstone beds of 2–20 cm thickness, composed of quartz (Fig. III.45).

In stratigraphic sections, wrinkled rock beds indicate the turning points of regression-transgressions. Because shallow marine environments form as sea level rises, microbial mats develop especially well during sea water highstands (compare Fig. II.32).

Diagnosis

It is not possible to identify wrinkle structures alone from their macroscopic appearance. There is no geometrical characteristic of microbial crinkles. The first descriptions by the author tried to distinguish between regular and irregular wrinkle types. However, the distinction between these two types could not be quantified, and their evaluation is too subjective. It is more pragmatic to simply differentiate transparent and non-transparent wrinkles.

The criteria for MISS biogenicity serve very well for wrinkle structures (Noffke 2009). A geological survey investigates the situation of the wrinkle structure in question with respect to its paleogeographical, lithological, and stratigraphical context. Wrinkle structures occur in ancient photic zones, in typical microbial mat lithofacies. A stratigraphic position at turning points of regression and transgression is characteristic.

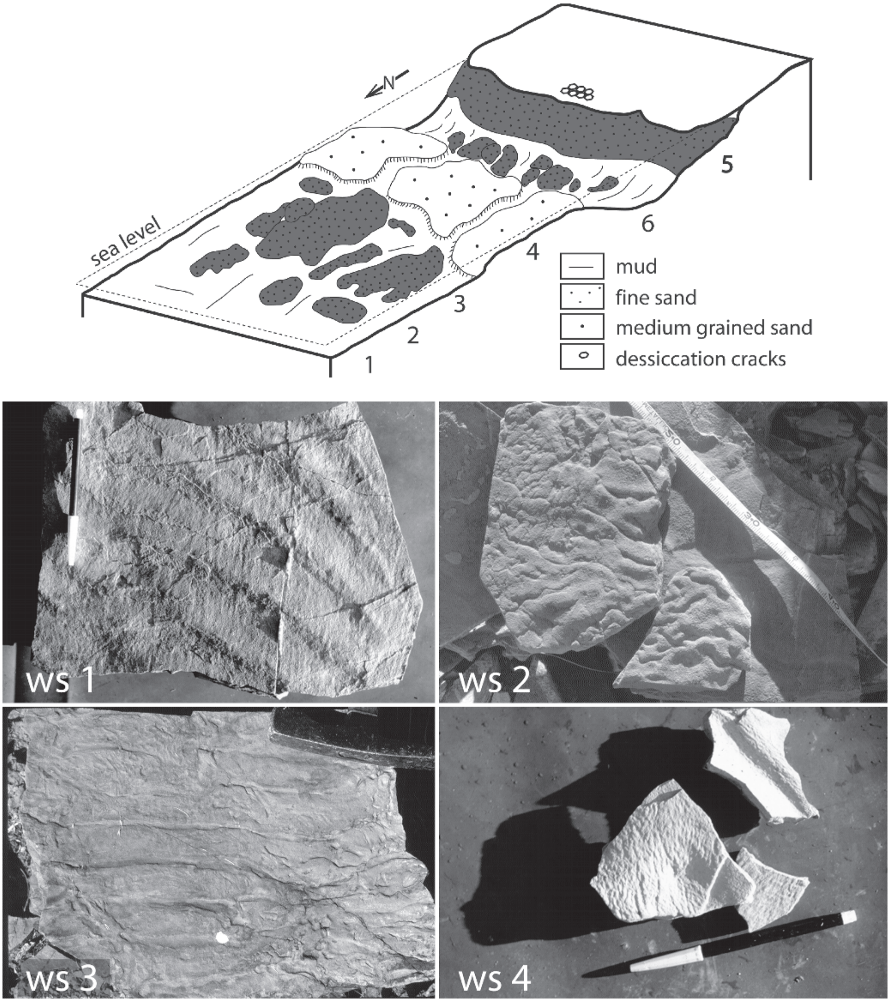


Fig. III.43. Wrinkle structures (*ws*) are *in situ* fossilized microbial mats. A detailed survey of the distribution of different wrinkle structures in the Ordovician of the Montagne Noire, France, revealed that mats occurred exclusively in the photic zone. The preferred substrate was quartz sand. The microbial mats must have been photoautotrophic. Facies zones are: *(1)* outer continental shelf below storm wave base (mainly muddy sediments); *(2)* foreshore zone below the storm wave base (includes fine grain size sand patches); *(3)* foreshore zone above the storm wave base (includes mud, fine sand, and medium grain size sand); *(4)* high-energy barrier bars (medium grain size sand); *(5)* intertidal zone (includes fine sands and some mud); *(6)* subtidal and lagoonal zone with sandy spill-over lobes. In detail, 4 types of wrinkle structures were distinguished: *WS 1:* Transparent wrinkle structure caused by a thin, endobenthic microbial mat in frequently reworked settings; *WS 2:* Non-transparent wrinkle structure caused by a thick, epibenthic microbial mat in dynamically calm areas of the sea floor; *WS 3:* Transparent wrinkle structure that records increased accumulation of biomass in ripple valleys (note, how the ripple crests project from the crinkled valley fillings); *WS 4:* Non-transparent wrinkle structures formed by an epibenthic mat on an ancient slope. At sites where sandy sediments glided down the continental slope, the mats ruptured, and cracks formed (after Noffke 2000, modified)

Table III.2. Distribution of wrinkle structures of types 1 to 4 in a shallow-marine paleoenvironment (from Noffke 2000). Facies zones are: *(1)* outer continental shelf below the storm wave base; *(2)* foreshore zone below the storm wave base; *(3)* foreshore zone above the storm wave base; *(4)* high-energy barrier bars; *(5)* intertidal zone; *(6)* subtidal and lagoonal zone with sandy spill-over lobes. The 4 types of wrinkle structures are pictured in Fig. III.43

Wrinkle structure	**Facies zone**					
	1	**2**	**3**	**4**	**5**	**6**
ws 1	0	21	0	0	0	0
ws 2	0	12	17	0	15	11
ws 3	0	0	3	0	1	1
ws 4	0	0	0	0	22	19

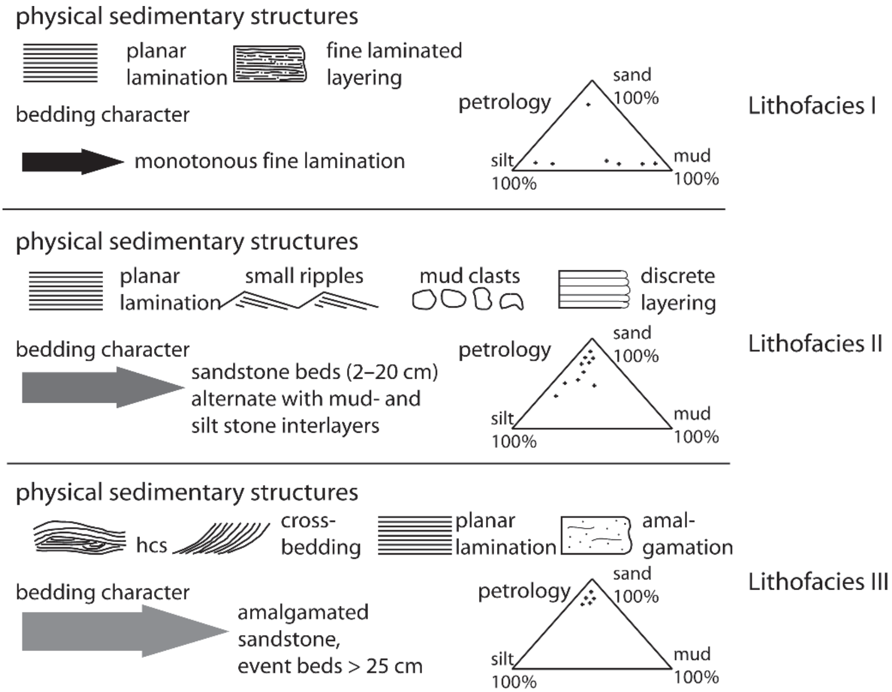
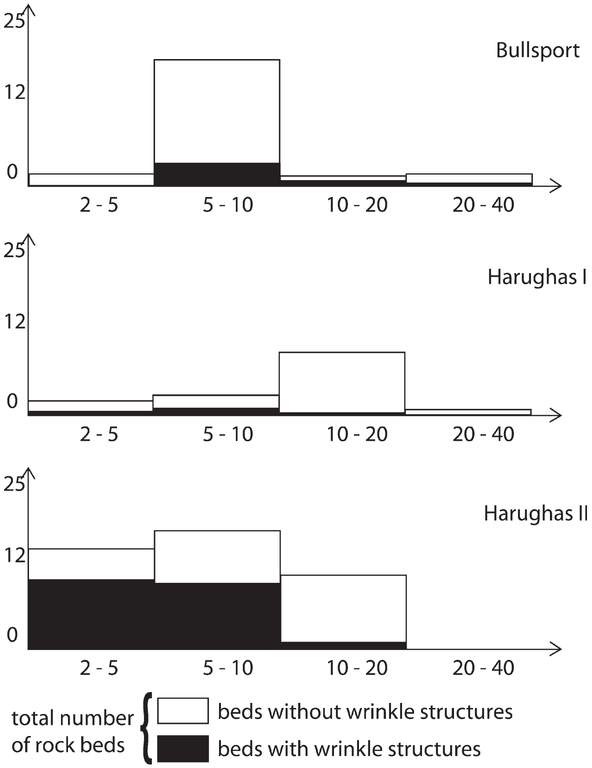


Fig. III.44. Sedimentary parameters define the ecological and taphonomic window of mat development. The lithofacies types I–III are recorded by physical sedimentary structures, bedding type, and the petrological composition of the sediment. In this diagram, the ecological and taphonomic windows of mat development and preservation conform with lithofacies II. Lithofacies I would be too muddy, and lithofacies III would be too energy-rich

It is important to keep in mind that similarly crinkled surfaces can result from purely abiogenic processes, such as dewatering, or tectonic overprint (discussion in Noffke 2000). The former presence of a microbial mat must be verified in thin-sections. Additional criteria

Fig. III.45.
Distribution of wrinkle structures as a function of rock bed thickness. Shown are fine sandstones in the stratigraphic sections of the farms Bullsport and Haruchas, Nama Group, Namibia. Wrinkle structures occur mainly in fine sandstone beds of 2–20 cm (maximum 20) thick (from Noffke et al. 2002)



for biogenicity including *in situ* lithified filaments, EPS, oriented grains, and others must be met. Organic carbon isotopes can be documented in geochemical analyses.

Example Specimen

Transparent and non-transparent wrinkle structures (Mozaan Group, Pongola Supergroup, South Africa) are stored by the Smithsonian Natural History Museum, Washington, DC, Noffke Collection nos. USNM 540878, and USNM 540879.

Application

Wrinkle structures serve in the identification of fossil microbial mats in sandstone successions. Because wrinkle structures are especially frequent on continental shelves, they constitute the most frequent MISS in the fossil record. Wrinkle structures do not occur in the present. The likelihood is great, however, that sediment cores from the ocean seafloor may include crinkled layers of subrecent mats.

Wrinkle structures are useful features when detecting regression-transgression cycles in sections composed of monotonous sand-, silt-, and mudstone. In such clastic lithologies, sea level oscillation is often masked. Only the presence of wrinkled bedding surfaces indicates regression-transgression cycles.

III.2.5.5
Polygonal Oscillation Cracks

Description

Polygonal oscillation cracks are typical MISS of semi-arid, hot climate zones. Seen from above, a thick epibenthic microbial mat can show a pattern of polygons, each between 15 and 50 cm in diameter. Each polygon is defined by 5 to 10 cm wide cracks that cut vertically into the microbial mat (Fig. III.46).

Seen from above, the cracks in modern mats are composed of two parallel ridges of 0.5 to 10 cm elevation. Each ridge marks the outer edge of a mat polygon. A vertical cross-section through one of the ridges shows that this edge is upwardly folded (Fig. III.47). It is composed of a stack of subrecent microbial mat laminae, forming biovarvites. The bottom of the cracks is covered by stacked mat laminae, which are not folded. This flat mat at the bottom is separated from the ridges on both sides by gaps. These gaps are filled by black, impolite smelling gunk.

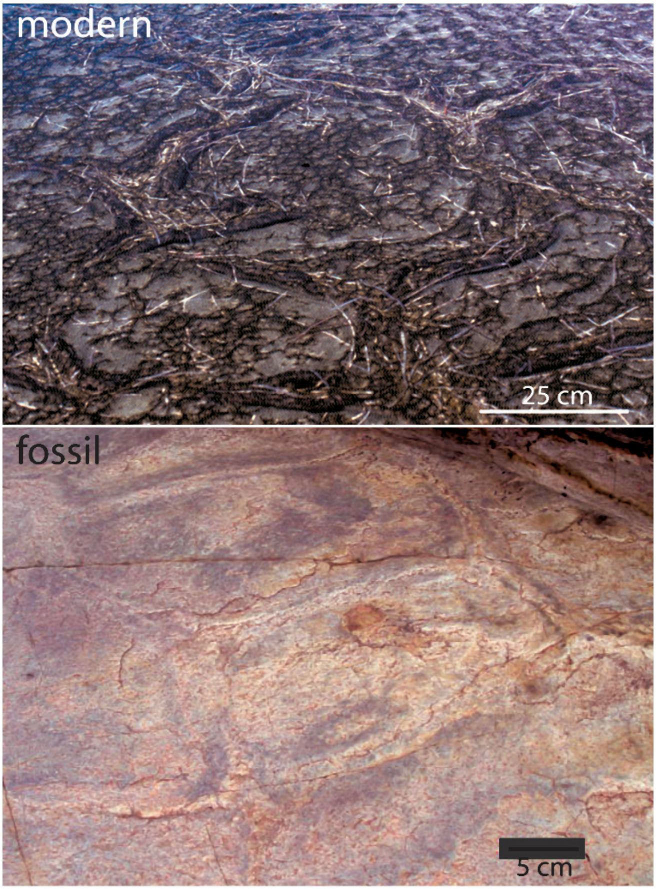


Fig. III.46. Oscillation cracks, modern and fossil. The upper photo shows the surface of a modern microbial mat from sabkha-like tidal flats of southern Tunisia. The mat surface displays a pattern of polygonally arranged cracks. The cracks are not discrete lines, but are composed of two parallel running ridges. Each ridge defines the margin of a mat polygon. The ridges are upwardly folded mat margins. The mat polygons expand laterally, when moist, and shrink when dessiccating. In the lower photo, the same structure of polygonal cracks is visible on a fossil sandstone bedding plane (2.9 Ga Pongola Supergroup, South Africa)

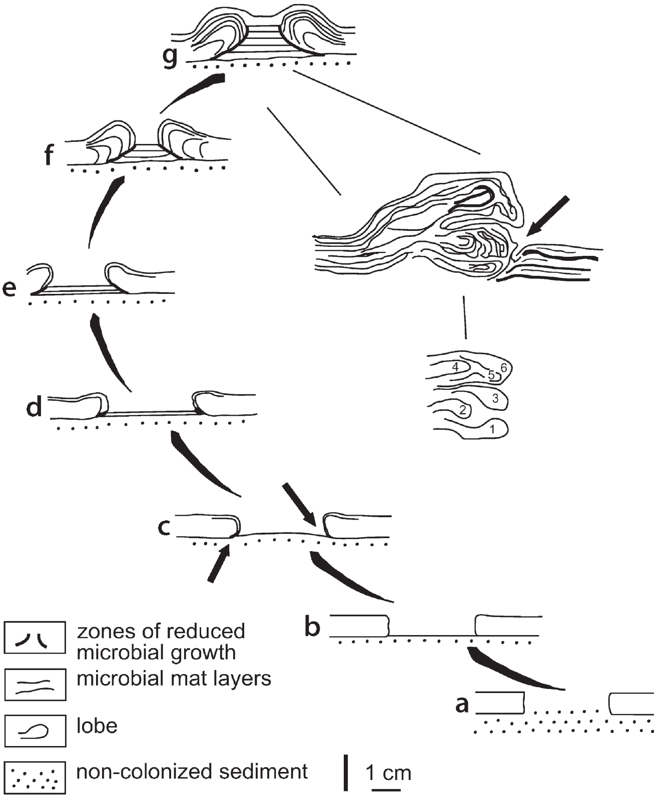


Fig. III.47.
Formation of oscillation cracks in several stages. The sketch shows the vertical cross-section through a crack from its first formation (stage **a**) to its final stage (**g**). The close-up on the right documents the several lobes (*1–6*) that represent lateral expansion of the mat margin during times of increased moisture and the subsequent withdrawal of the mat margin during episodes of desiccation. Further explanation in text

Sometimes, the center of each mat polygon may buckle up, forming a temporary gas dome. In Tunisia, such gas domes can be up to 25 cm high. Gas domes can also be found in the fossil record (Fig. III.22). Most fossil gas domes are not preserved as upheavals. Fossil mat polygons might show a hole just a few cm wide, or a triple-junction shaped crack in their centers. These holes or cracks are where gas escaped and the former gas domes collapsed.

Etymology

The term polygonal oscillation crack was given by Noffke et al. 2001a, and 2008, because of the genesis of this structure. The cracks with their upwardly folded margins arise from oscillation (i.e., lateral back and forth movement) of the margins of the mat polygons.

Genesis

Polygonal oscillation cracks arise from growth, and alternating lateral expansion and contraction of the mat polygons. The oscillation is a response to the changing amount of moisture in microbial mats (type II biostabilization). It is a phenomenon associated with tidal flats in semi-arid, hot climates.

A series of vertical cross-section views through the rim of a mat polygon reveals the stages of oscillation crack formation, Fig. III.47, (Noffke et al. 2001a):

i) A thick microbial mat develops on sandy sediment. During a period of hot, dry weather, the microbial mat cracks into a pattern of polygons – quite similar to the development of mud cracks.
ii) As soon as the moist season returns, the microbial mat recovers. The mat polygons grow and close the cracks. Consequently, the bottom of the crack becomes overgrown by a microbial mat. The crack is healed.
iii) The thin mat layer that drapes the bottom of the crack is separated from the two rims at both edges of the crack by a gap. This gap receives less light. Foul gases escape from underneath the mat finding their way through the gaps.
iv) The original mat polygon margins continue to grow. They fold up and form ridges. Eventually, the mat polygon is bordered by this ridge. Consequently, the crack between mat polygons becomes narrower. The crack width is further reduced as the mat draping the crack bottom grows.
v) Finally, the crack vanishes completely. The polygonal pattern of the mat surface is merely marked by parallel running ridges. Quite often, the original crack is only visible because the mat polygon margins exhibit slight color variations. The gaps between the crack bottom mat and the ridges remain weak zones. In subsequent dry seasons, the microbial mat surface cracks again along these weak zones. The mat polygons shrink again, opening the cracks along the gaps. At the same time, the center of each polygon may rise as underlying gases accumulate and push the mat upward. During the dry season, microbial mats start to decompose. The resulting gaseous decomposition products accumulate under the mat. The increasing pressure probably supports crack formation. As soon as the gas domes collapse, the polygons sink back down, and the cracks close slightly. The repetition of these alternating seasonal changes in moisture and gas production causes corresponding lobes at the margins (Fig. III.47; close-up right).

Paleoenvironmental Distribution and Seasonal Variations

Polygonal oscillation cracks are typical structures for the lower and upper supratidal zones in semi-arid, hot climates. Their formation depends upon seasonal changes in precipitation. During hot and dry seasons, polygonal cracks open, and gas domes may buckle up. In wet seasons, new microbial mat overgrows prior polygonal cracks, which are then barely visible.

Diagnosis

Polygonal oscillation cracks separate microbial mats into mat polygons. Mat polygons are separated by 'U'-shaped cracks into pieces that range in size from 15 to 50 cm. The margins of mat polygons form the rims of polygonal oscillation cracks. These rims form two parallel ridges, one on each side of the crack. A vertical cross-section view through an oscillation crack should reveal a laminated pattern, and particularly the lobes that build up on the rims.

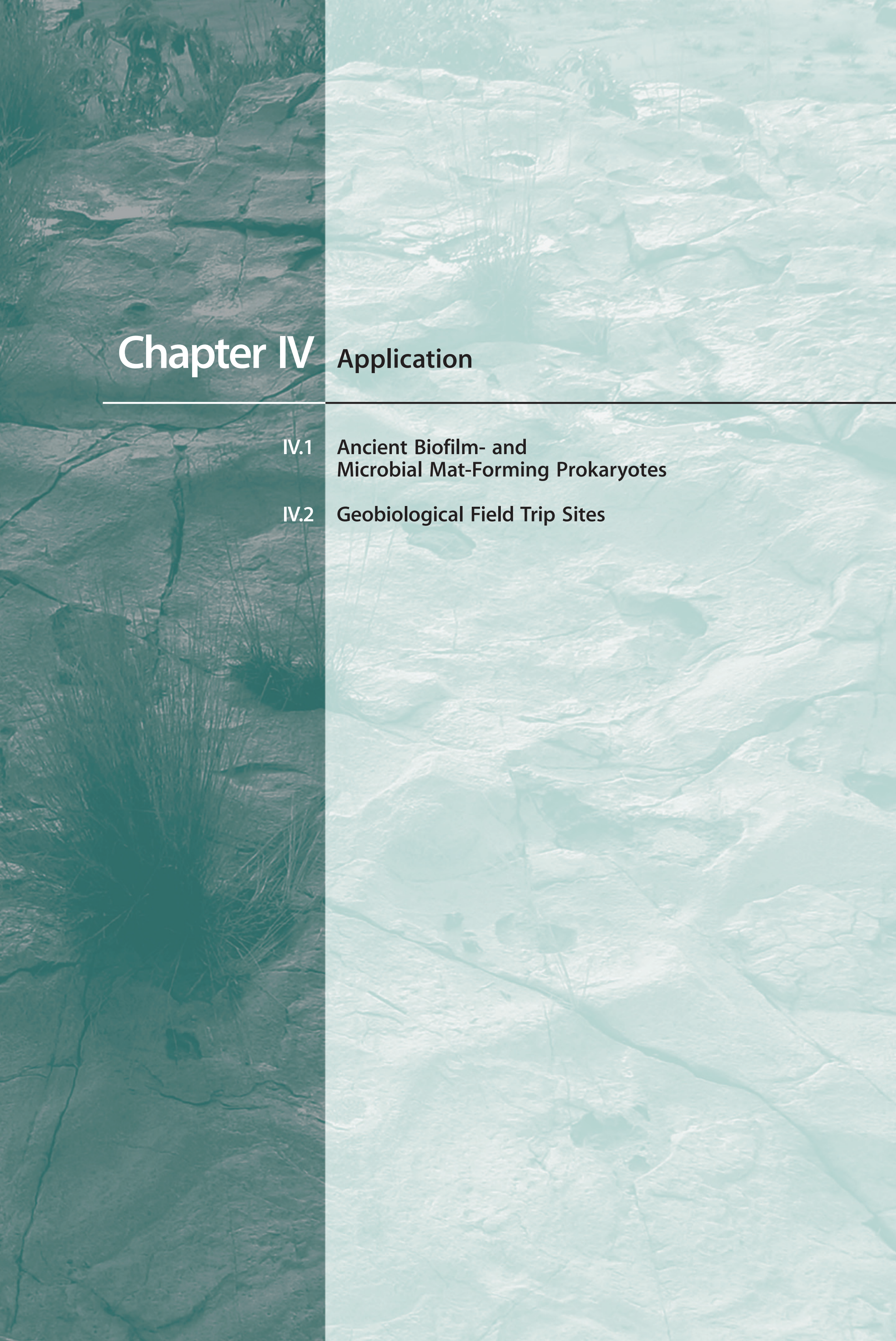
Gas domes may occur in mat polygon centers. Fossilized gas domes are sometimes, but not usually, preserved in three dimensions. Most fossilized gas domes are recorded by holes of a few cm width. Such holes are often triple junction shaped, but are not always present.

Example Specimen

A vertical cross-section through an oscillation crack of a modern microbial mat is preserved in formaldehyde, and stored by the Smithsonian National Museum of Natural History, Washington, DC, Noffke Collection USNM 540880. The original structure is from the sabkha Bahar Alouane, coast of southern Tunisia.

Application

Polygonal oscillation cracks are useful indicators for ancient climates. The structures exposed in the 2.9 Ga Nhlazatse sandstone, Pongola Supergroup, South Africa, record that Earth already had a semi-arid, hot climate belt.



Chapter IV Application

IV.1 Ancient Biofilm- and Microbial Mat-Forming Prokaryotes

IV.2 Geobiological Field Trip Sites

Chapter IV

Application

IV.1

Ancient Biofilm- and Microbial Mat-Forming Prokaryotes

Modern microbial mats and MISS are the keys to understanding the nature of ancient benthic microbiota and their habitats. Most intriguing is the question: which prokaryotes formed biofilms and microbial mats in Earth's past? Geobiologists help to answer the question by studying the present. They are interested to learn how modern organisms interact with their environments. This information provides insight into ancient worlds.

The fossilized, 2.9 Ga old tidal flat of the Pongola Supergroup, South Africa, and the Pleistocene sabkha exposed in Tunisia provide exceptional study sites for understanding MISS. These two sites constitute excellent locations for geological field trips and are visited regularly by scientists, school classes, and members of the interested public. Both fossil sites have modern counterparts. The Pongola tidal flats correspond to modern tidal flats on the North Sea coast, to sabkha-like settings in southern Tunisia, and to sites in the Bahamas. The Pleistocene sabkha in Tunisia corresponds to the modern sabkhas still present at the coast of the Mediterranean Sea.

Comparative studies show that MISS at both fossil and modern sites are of striking similarity, and of similar distribution even on a scale of meters. In thin-section analyses, modern and ancient microbial mats include textures that highly resemble one another. Textures include filament-like and coccoid-like microstructures, EPS, oriented grains, and many others.

The author suggests that the dominant mat-forming prokaryotes at both fossil sites, the Pleistocene of Tunisia, and the Archean Pongola Supergroup, were benthic cyanobacteria. The fossil cyanobacteria have formed the same biofilm-catenae like modern cyanobacteria in the modern environments. The formation of biofilm-catenae is a response by highly specialized microbial communities to long-term hydraulic and meteorological patterns. Each biofilm is highly adapted to its site of colonization that is each member of the biofilm possesses highly adapted physiological abilities. *Oscillatoria limosa* is able to migrate quickly through moving sand in intertidal settings. *Microcoleus chthonoplastes* secretes high amounts of EPS to protect itself against desiccation in frequently subaerially exposed supratidal areas. The biofilm members also must collaborate to function as a biological unit. This collaboration makes it possible for the microorganisms to engineer their own microhabitat. A functional arrangement of different species within biofilms is needed for the effective harvesting of nutrients and sun light. Most likely, similar collaboration

N. Noffke, *Geobiology*, DOI 10.1007/978-3-642-12772-4_4,

by the same members of a biofilm results in the creation of same MISS at specific colonization sites.

From a theoretical perspective, any biological unit has a form, hardware, and an organismic body plan. This is true for any organism, be it clam or dinosaur. This hardware enables controlled chemical reactions to counteract chemical gradients. A biological unit's form is a product of phylogeny, adaptation and growth. Phylogeny is genetic information. Without genetic information, a biological unit cannot construct hardware. Without any mechanism of preserving information, it cannot retain the benefits of natural selection. Adaptation is the response of a biological unit to external environmental conditions. A biological unit proliferates or fails while interacting with its environment. Growth is the morphological change of the hardware of a biological unit. Natural selection favors hardware that maximizes metabolic effectiveness. In the prokaryotic world, a biofilm is a biological unit. The individual microorganisms function like organs, collaborating to create a highly efficient entity. This entity, the biofilm, is a form built to function. Biofilms are manifested in the geological record as MISS. A MISS indirectly records the form of a biofilm. Analogous to any other organism, the form of biofilms is a result of environment, genetic information, and construction (Fig. IV.1). Consequently, biofilms are highly adapted to their specific habitat where they form specific MISS. Only the same biofilm can create the same MISS at specific sites of colonization. Other biofilms constructed by different microorganisms would form different structures in the same habitats.

Both modern and 3 billion year old MISS correspond in morphologies, spatial distributions and internal textures. It is too simplistic to assume that 3 billion years ago completely different groups of microorganisms than cyanobacteria had colonized the same tidal flat zones, created the same MISS under the same environmental conditions, and form the same mat types as in the present. This would be too much of a coincidence! In conclusion the author suggests that cyanobacteria are at least 2.9 Ga old, and had already developed to the same diversity at that time as seen today (Margulis 2009). The following description of two classical study sites supports this conclusion.

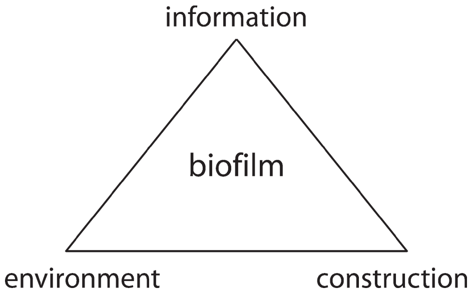


Fig. IV.1. Biofilms are a result of the complex interference of genetic information (phylogeny), environment (adaptation), and construction (growth). Specific information, environments, and biomass accumulations selectively favor the development of specific biofilms. Biofilms recorded as MISS in the same environment and of the same construction require the same genetic information. Consequently, only cyanobacterial biofilms form the same MISS in the same environment. Cyanobacteria are likely to be older than 3 billion years

IV.2
Geobiological Field Trip Sites

IV.2.1
Modern and Pleistocene Catena of Benthic Cyanobacteria in the Bahar Alouane, Southern Tunisia, Africa

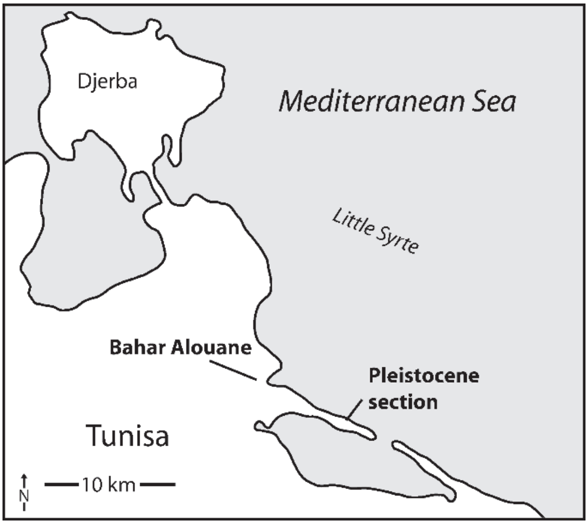
Sabkhas are subaerially exposed coastal areas in hot, arid climate zones. They are rarely flooded. Sabkhas are good examples to show how meteorological conditions also influence benthic microbiota. Cyanobacteria are well adapted to such settings (e.g., the comprehensive study by Gerdes and Krumbein 1987).

Sabkhas can be found along the modern coast of southern Tunisia. In the sabkha 'Bahar Alouane', cyanobacteria form extensive microbial mats of many km^2 (Noffke et al. 2001a) (Fig. IV.2). In the Bahar Alouane, sediments are composed of fine to medium-grained quartz sands, oolitic-bioclastic carbonate sands, clay-rich mud, and evaporite minerals such as anhydrite and gypsum. The tidal range is microtidal (80–150 cm) (Strasser et al. 1989). In the Bahar Alouane, low and high water lines are marked by small cliffs of 5–30 cm heights. The lower supratidal plains that comprise the largest portion of the sabkha include shallow, 5–25 cm deep depressions of some tens of meters in diameter. The depressions, i.e., tidal pools, are episodically covered by 5–10 cm of water. The water runs off slowly. Higher locations towards the upper supratidal zone are rich in salt minerals. Evaporite minerals indicate evaporite pumping. From the low water line to the supratidal zone, a biofilm-catena has formed. It is composed of three characteristic mat communities, as follows.

Simple biofilms colonize tidal channels. The biofilms are composed of individual coccoid cells and filaments of various cyanobacteria. MISS do not form.

Rose coloured, single-layer microbial mats overgrow levees and the step-like cliffs that mark the modern shoreline. These cliffs were carved by waves and currents. This mat

Fig. IV.2.
In southern Tunisia, the modern sabkha Bahar Alouane is widely overgrown by microbial mats. A short Pleistocene age rock succession is exposed at the nearby coast. The rock succession records the same type of sabkha as the modern Bahar Alouane



type is composed predominantly of the coccoid microorganisms *Synechnococcus* sp. and *Aphanothece* sp. The dominant cyanobacterium *Synechnococcus* sp. contains a reddish pigment, a carotenoid that gives the leathery microbial mats their rose colour (Gerdes et al. 1994). This pigment protects the cells against sun light during the absence of a protective water cover. Associated MISS are petees, mat chips, roll-ups, shrinkage cracks, gas domes, and many others.

Dark blue-green coloured, multilayered mats thrive in constantly moist depressions of the lower supratidal area. This mat type includes biovarvites. Vertical sections showed mat layers ranging from 4 cm to 8 cm thickness. In vertical section, the multilayered mat communities are composed of two alternating layers: dark layers formed by *Microcoleus chthonoplastes*, *Lyngbya aestuarii*, *Phormidium fragilis* and others, and light layers composed by *Synechnococcus* sp., *Croococcales* sp., and *Aphanothece* sp. The mats induce polygonal oscillation cracks, tufted mat surfaces, pizza-sized mat chips, and gas domes. It was a great surprise to the author's team to find the same biofilm-catena and the same suite of MISS in an outcrop of Pleistocene rocks (Fig. IV.3). This short stratigraphic section, only 1.5 m, is located close to the modern Bahar Alouane. A comparison of the Pleistocene MISS with the modern MISS in the Bahar Alouane revealed that the structures accurately record, in meter-scale resolution, the hydraulic, meteorological, and depositional conditions of ancient coastal zones (Noffke et al. 2001a). The results of this study constitute the foundation for the description of individual MISS in Chap. III.

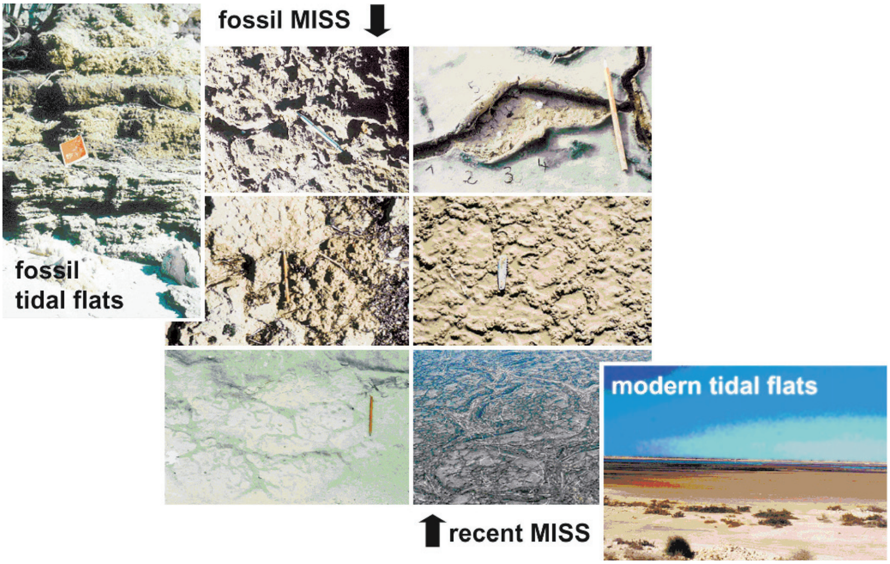


Fig. IV.3. The modern sabkha 'Bahar Alouane' and the nearby Pleistocene rock succession include the same biofilm-catena and the same suite of associated MISS (coast of southern Tunisia). The study sites are good examples of the influence of hydraulic and meteorological parameters on mat development and MISS formation. Left photos show MISS from the Pleistocene outcrop, photos on the right show modern MISS from the Bahar Alouane. From above to below, shrinkage cracks, petees, and polygonal oscillation cracks are pictured

IV.2.2
Earth's Possibly Oldest Fossil Cyanobacteria Preserved in the Nhlazatse Section, 2.9 Ga Pongola Supergroup, South Africa

For a long time, MISS were rarely found in Archean rocks. Therefore, the discovery of abundant, highly diverse and exceptionally well preserved MISS in a 2.9 billion year old rock succession was noteworthy (Noffke et al. 2008).

The Nhlazatse Section, Pongola Supergroup, contains possibly the oldest cyanobacteria preserved in Earth history, and is therefore of great paleontological significance. The outcrop is considered as geoheritage site by the Geological Society of South Africa. The outcrop is visited by scientists, school classes, and interested members of the public.

The name 'Nhlazatse' is taken from the nearby village of the same name. The sandstones that compose the stratigraphic section record an ancient tidal flat. The abundant MISS must have been formed by a great variety of microbial mats. In the following, the most spectacular MISS in the outcrop are described. The original study on this outcrop is Noffke et al. 2008.

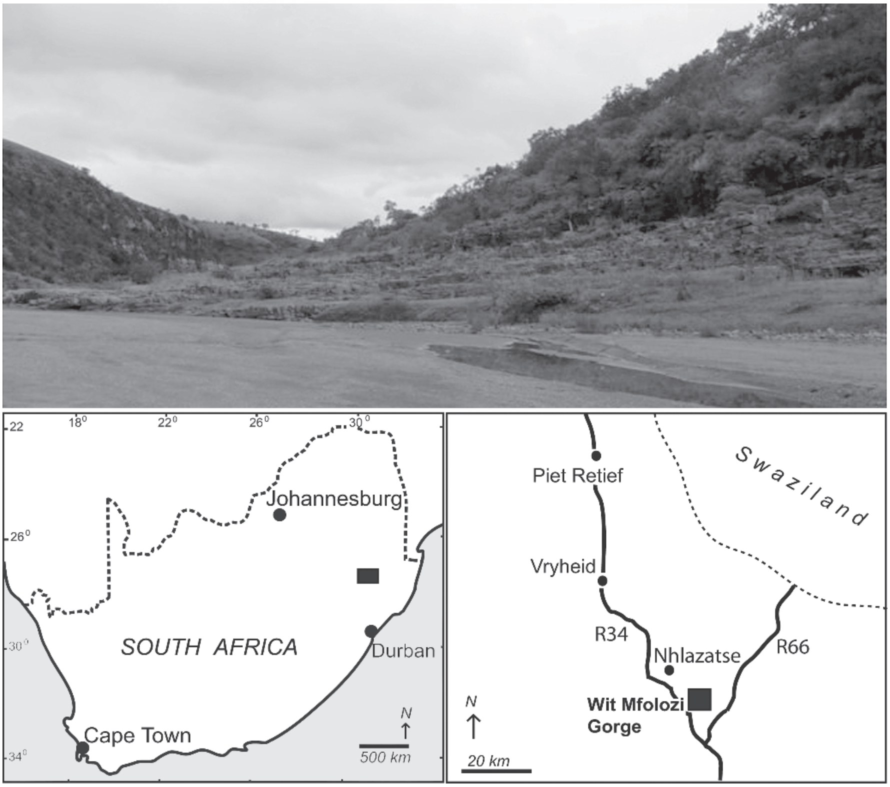


Fig. IV.4. Location of the Wit Mfolozi River Gorge in South Africa. The photo shows a view into the Nhlazatse rock succession that crops out along the river

IV.2.2.1
Location of the Outcrop

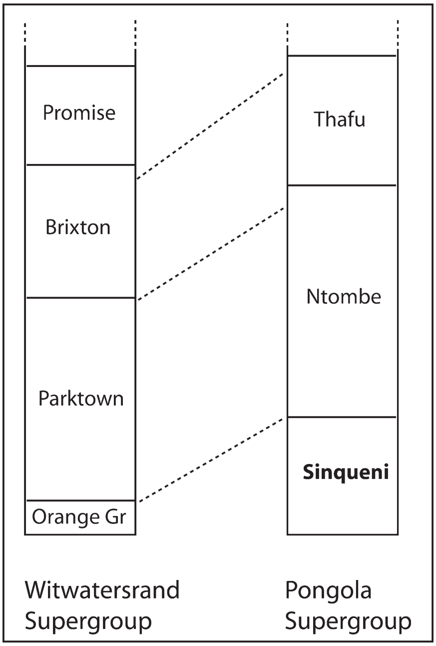
The stratigraphic section is located in the Wit Mfolozi River Gorge, a deep valley framed by vertical cliffs. The Wit Mfolozi River Gorge is located about 70 km south-east of the town of Vryheid, 5 hours from Johannesburg. The exact location is 31°15' E and 28°10' S, on the left side of the road R34 (towards Durban) (Fig. IV.4). The approximately 46 m thick rock succession crops out along the right side of the river. Widely exposed bedding surfaces display the most beautifully preserved Archean age MISS known to date.

The owner of the outcrop must be contacted before any visit. A path leads from the entrance gate downhill into the gorge. Some climbing is necessary. The outcrop is framed by the river of its left, and by the steep cliffs of the gorge on its right. The best time of day to visit is in the late afternoon, because the sun illuminates the bedding surfaces at a low angle.

IV.2.2.2
Stratigraphy

The Nhlazatse Section is part of the Pongola Supergroup, which has an age of 2.9 Ga (Fig. IV.5). The base of the stratigraphic section is formed by 1 to 2 m thick conglomerate bars. Above these, fine sandstone beds occur. They include small ripple marks that indicate ancient water depths of only 1–10 cm. The next rock unit is a set of sandstone beds alternating with mud-rich, siltstone beds. The rocks display desiccation cracks and flaser bedding, recording a tidal flat. The tidal range was microtidal (Matthews 1967; Beukes and Cairncross 1991; Beukes et al. 2002). One reason for the well preserved MISS is the

Fig. IV.5.
Stratigraphic position of the 2.9 Ga Nhlazatse Section, Pongola Supergroup, South Africa



relatively high amount of micritic cement in the Nhlazatse sandstone. This cement is typical of the semi-arid, warm paleoclimate. In contrast, the slightly younger sandstones of the Ntombe Formation, Pongola Supergroup, and the Brixton Formation, Witwatersrand Supergroup, are typical of cool water paleosettings (Noffke et al. 2003b, 2006a). The stratigraphic section is transgressive. Whereas the lower portion of the stratigraphic succession records intertidal and supratidal flats, the top characterizes subtidal settings.

IV.2.2.3
Tectonic Overprint

The Nhlazatse Section has experienced only a low grade of metamorphism to greenschist facies. This low metamorphic alteration is a significant reason that these sedimentary structures are so exceptionally well preserved.

IV.2.2.4
Biofilm-Catena

The Nhlazatse succession records subtidal, intertidal, and lower supratidal paleoenvironments. The tidal zones are defined by physical sedimentary structures such as ripple marks, desiccation cracks, flaser bedding, and many others. From the ancient low to high water lines, different microbial mats established a biofilm-catena. The fossil biofilm-catena corresponds in every detail to modern biofilom-catenae in equivalent tidal flats (compare Noffke and Krumbein 1999; Noffke et al. 2001a).

Non-colonized subtidal and lower intertidal zones. The subtidal and lower intertidal zones do not contain sedimentary structures caused by biofilms or microbial mats. Just as in modern settings, sediments in these tidal zones were constantly reworked by waves and currents. Microbial mats could not form. Sandstone beds alternate with mud- and siltstone layers. Fine to medium grained sandstone beds are covered by ripple marks of about 8–12 cm crest-to-crest-spacing. These ripple marks record quite high current velocities. Many beds show thick cross strata sets. These rock beds were deposited in subtidal areas. Overall, the well sorted sandstone is very quartz-rich with a mineralogical composition of 95% quartz, 5% mica, feldspar and heavy minerals.

Endobenthic microbial mats in the upper intertidal zone. The upper intertidal zone of the Nhlazatse Section is characterized by a slight predominance of sandstone layers over mud- and siltsone beds. The well sorted sandstones are composed of 88–96% quartz with some clay, feldspar, and heavy minerals. Typical tidal sedimentary structures include mud cracks caused by the subaerial exposure of the depositional surface during ebb tides. Flaser bedding records the alternating rhythm of strong flood currents transporting sand, and weak ebb currents releasing mud (Reineck and Singh 1986).

In this upper intertidal zone, endobenthic microbial mats grew. The mats correspond to endobenthic mats that develop in intertidal zones in modern tidal flats.

In thin-section vertical through the endobenthic mat layers, filaments entangle the sand grains. The individual sand particles have grain-to-grain contact. The microbial mat surface must have felt rough, similar to the surface of modern endobenthic mats. Endobenthic mats occupy the uppermost millimeters of sandy deposits, and do not project from the surface. In the present, such endobenthic microbial mats are dominated by mobile cyanobacteria such as *Oscillatoria limosa* sp. (Villbrandt 1992; Golubic and Knoll 1999).

Epibenthic microbial mats in the lower supratidal zone. The lower supratidal zone in the Nhlazatse Section displays beautiful MISS. These structures were formed by epibenthic microbial mats. These are the typical 'algal mats' described from Mellum Island, North Sea, the coast of Tunisia, or the Bahamas. In the Nhlazatse Section, three main types of epibenthic microbial mats can be distinguished:

i) a planar mat type with a flat surface: this mat occurs on the levees of tidal channels and along the edge of the high water line. Frequent splashing of water must have kept the microbial mat substrates constantly moist.
ii) a tufted mat type, which displays a surface spotted by tufts (vertically oriented bundles of filaments). This mat type occurs in morphologically higher tidal flat areas. These areas were subjected to periodical desiccation typical of a semi-arid climate.
iii) a spongy mat type, which is characterized by a very high internal porosity. This mat type occurs in deeper tidal pools, and probably was submerged under water most of the time.

Viewed in thin-section, the microbial mats display various textures. The textures include oriented grains, fossil filaments forming a mat fabrics, and EPS. Abiotic stylolites also occur. The following text explains some of the best preserved MISS in the outcrop.

IV.2.2.5
Exceptionally Preserved Structures in the Nhlazatse Outcrop

IV.2.2.5.1
Cross-Stratification in the Subtidal and Lower Intertidal Zone

In the lower third of the outcrop, about 10–40 cm thick sandstone beds display cross-strata sets (Fig. IV.6). The cross strata sets are unconform at their bases with up to 30 cm of relief. In total, 15% of all measured rock beds of the stratigraphic section belong in this subtidal paleosetting.

IV.2.2.5.2
Endobenthic Microbial Mats Forming Mat Chips in the Upper Intertidal Zone

This site is located in the very right corner of the outcrop, about 5 m above the lowermost rock bed. An approximately 50 cm wide bedding plane displays 4 microbial mat pieces distributed on top of a ripple marked sandy surface (Fig. IV.7). They are angular to subangular in shape, and display faint ripple marks themselves. Their thickness is about 0.25 mm. Please note that the sandstone surface is of the same colour as the mat pieces. The chips are fragments of an endobenthic microbial mat. Such endobenthic microbial mats also form in modern tidal flats, where they colonize upper intertidal zones (Fig. IV.7).

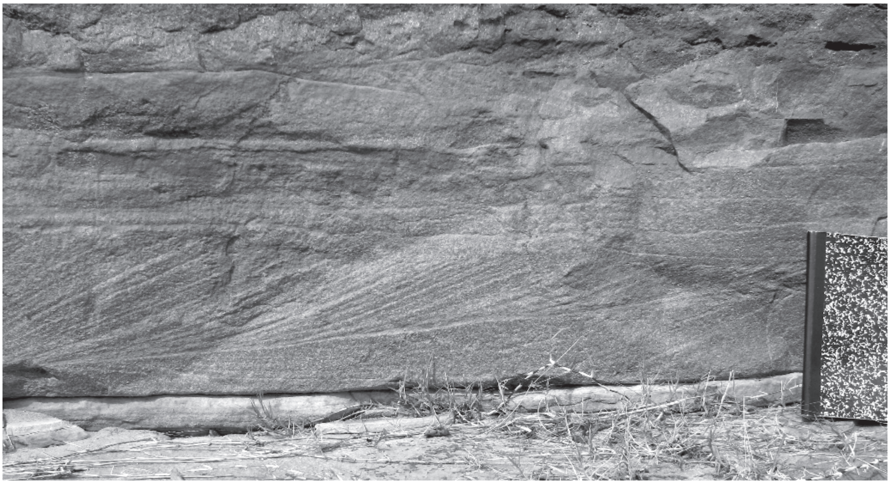


Fig. IV.6. Cross strata in the Nhlazatse Section, Pongola Supergroup. The cross beds record subtidal paleosettings; (scale: note book, 18 cm)

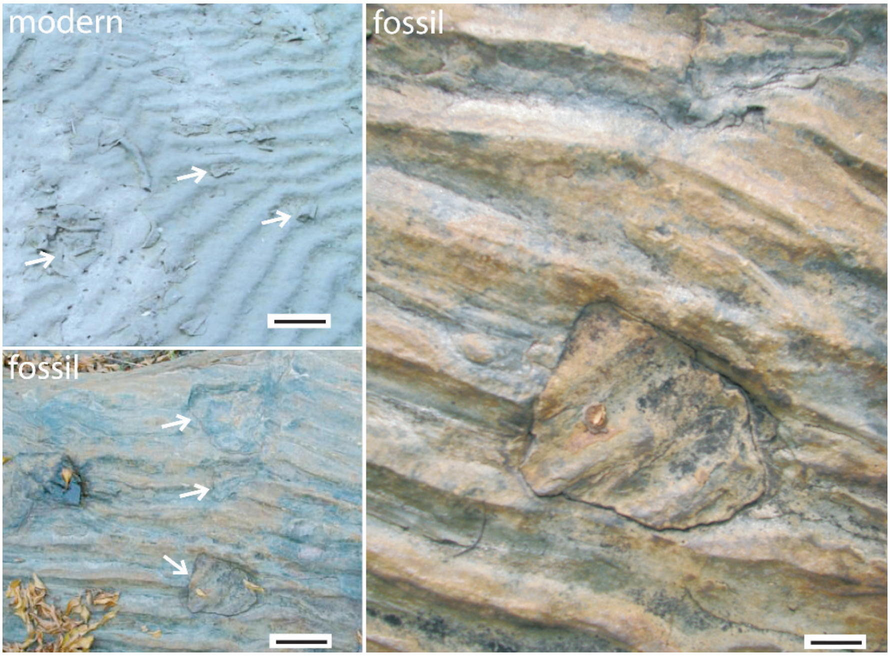


Fig. IV.7. Mat chips released from endobenthic microbial mats in upper intertidal zones, fossil and modern. The upper left photo shows mat chips (*arrows*) of endobenthic mats in an intertidal setting of Fishermans Island, USA. The modern chips were somewhat rolled up by a gentle current. The photo on the lower left shows equivalent mat chips (*arrows*) from the Nhlazatse Section, Pongola Supergroup. The large photo on the right is a close-up of one of the fossil mat chips. Note the ripple marks that are still visible on this mat chip; (scales: 10 cm)

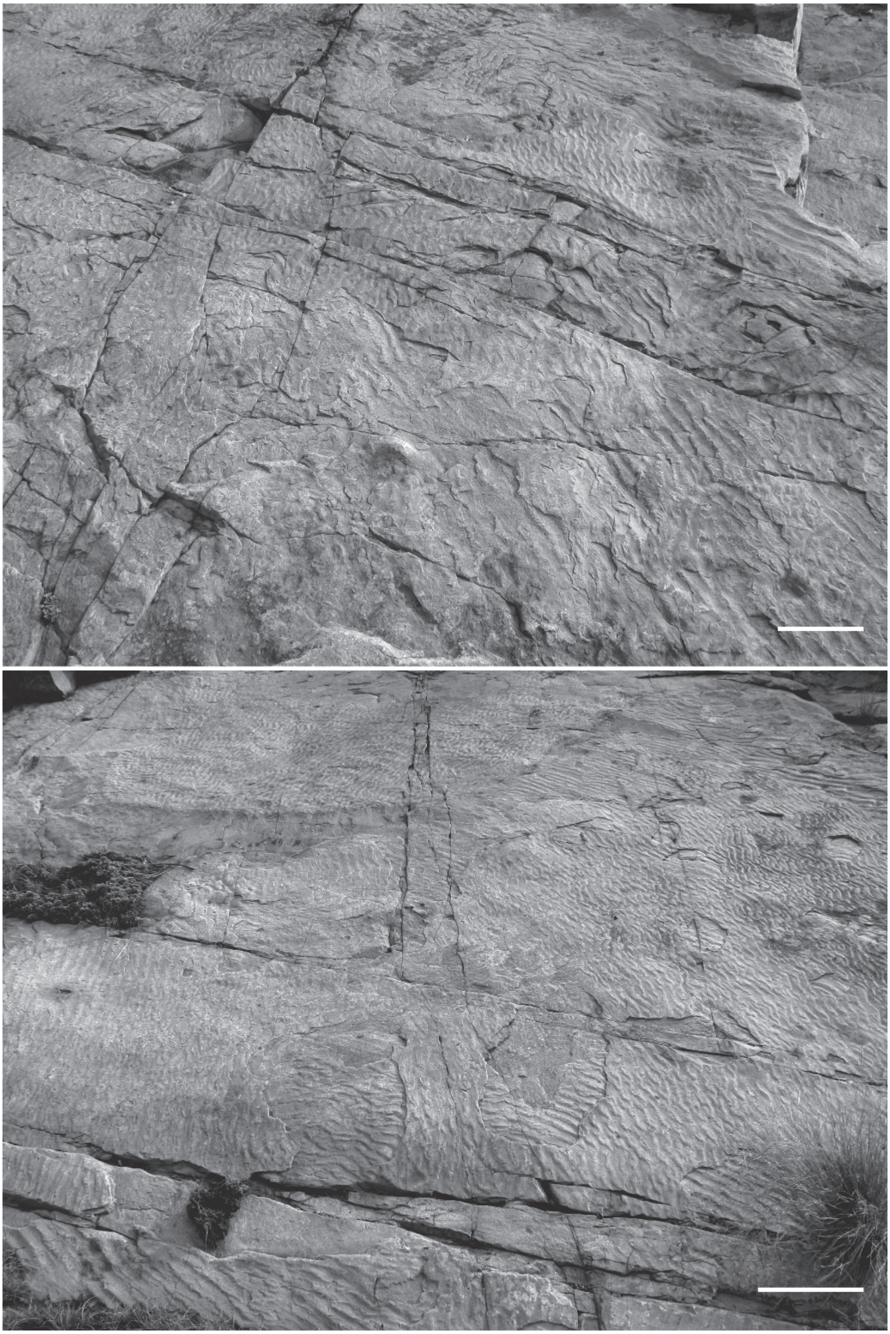


Fig. IV.8. Multidirected ripple marks covering large areas of sandstone beds in the Nhlazatse Section, Pongola Supergroup. Note the gas dome in the front of the upper photo; (scales: 25 cm)

IV.2.2.5.3
Endobenthic Microbial Mats Forming Multidirected Ripple Marks in the Upper Intertidal Zone

Towards the middle of the outcrop, the color of the rock beds becomes reddish. Three several m^2 wide bedding surfaces are covered by ripple marks of many different directions (Fig. IV.8). The ripple marks constitute an exceptional example of 'multidirected ripple marks'. The straight ripple crests have between 2 and 8 cm crest-to-crest distances. The geometries correspond to oscillation or combined flow ripples caused by shallow water motion with short wave lengths. Water has been 10–30 cm deep, and orbital velocities of 25 cm s^{-1} were reached. This pattern of ripple marks in Fig. IV.9 suggests seasonal storms. A sequence of several storms gives rise to different generations of ripple marks.

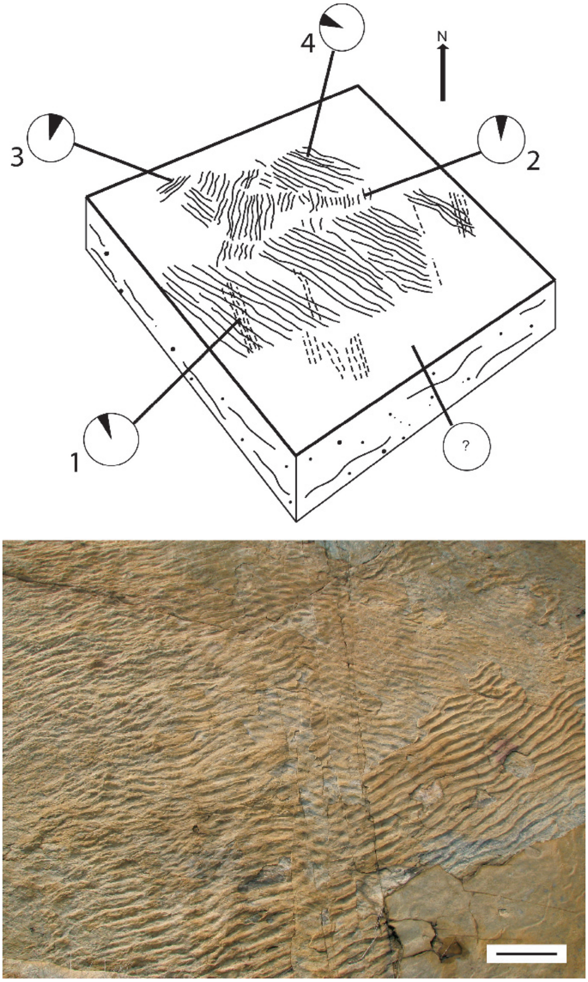


Fig. IV.9.
A bedding plane in the Nhlazatse Section, Pongola Supergroup, displays beautifully preserved, multidirected ripple marks. Analysis of this ripple mark pattern reveals four ancient storms that occurred in the order *1–4*; (scale: 25 cm) (from Noffke et al. 2008)

IV.2.2.5.4
Epibenthic Microbial Mats of Planar Type Forming Erosional Remnants and Pockets and Mat Chips in the Lower Supratidal Zone

Beneath the main cliff of the outcrop, two several m^2 wide bedding surfaces are exposed. The two rock bed surfaces (1 and 2) are about 15 to 20 m apart, and easy to spot. A third bedding plane, only 2 m wide, is exposed under a tree on the far left of the outcrop.

Bed Surface 1

This bed surface is covered by cm to dm wide sand-coloured and blue-green coloured patches (Fig. IV.10). This bed surface constitutes a unique snapshot of erosional remnants and pockets caused by planar microbial mats. Although this rock bed is 3 billion years old, it gives the impression of a view on a modern tidal surface overgrown by living microbial mats!

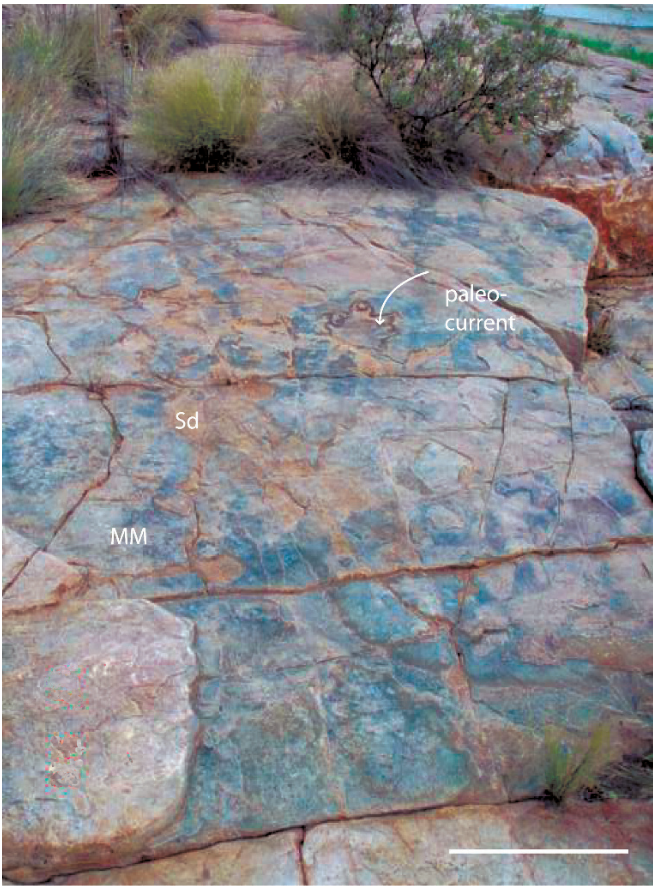


Fig. IV.10. Erosional remnants and pockets, Nhlazatse Section, Pongola Supergroup. The fossil microbial mats (*MM*) appear blue-green. Erosional pockets expose the yellow sand (*Sd*) beneath the ancient microbial mats; (scale: 1 m)

Blue-green patches on the bedding plane are fossilized epibenthic microbial mats. The blue-green colour of the mats is not caused by fossil chlorophyll, but by chlorite minerals that replaced the ancient organic material. The yellow patches of the rock surface are erosional pockets. Ancient currents have eroded the microbial mat so that the sand is now exposed.

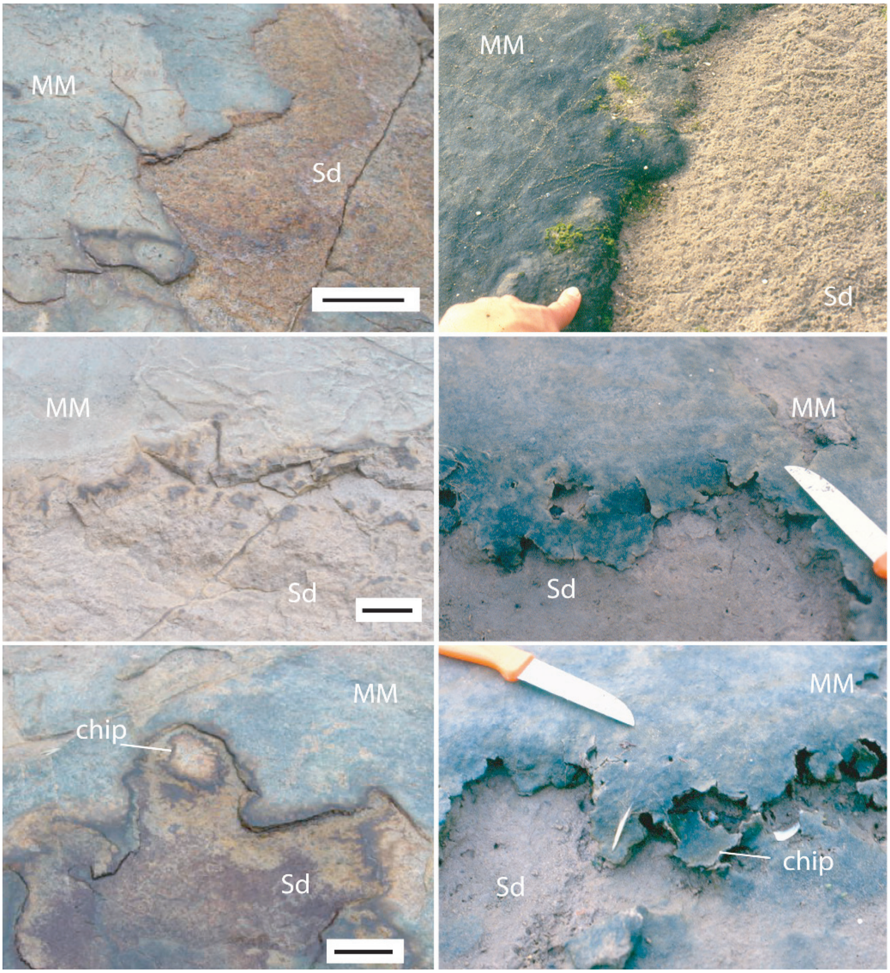


Fig. IV.11. Margins of microbial mats along edges of erosional pockets, left: fossil, right: modern. The microbial mats (*MM*) are in blue-green colour, whereas the sandy bottom (*Sd*) of the erosional pockets are yellowish. Note that the edges of the mat-covered erosional remnants become more pronounced from the top to the lower row of photos. In the uppermost row, microbial mats encroach on the sandy surface. In the middle row, currents have undermined the margins of microbial mats, and erosional pockets start to form. Consequently, the mat margins are fringed and hang down into the erosional pockets. In the lower row, erosion has ripped off individual pieces from the mat margins. These mat chips are deposited along the edges of the erosional pockets. Fossil examples from Nhlazatse Section, Pongola Supergroup, modern examples from Mellum Island, North Sea; (scales: 5 cm)

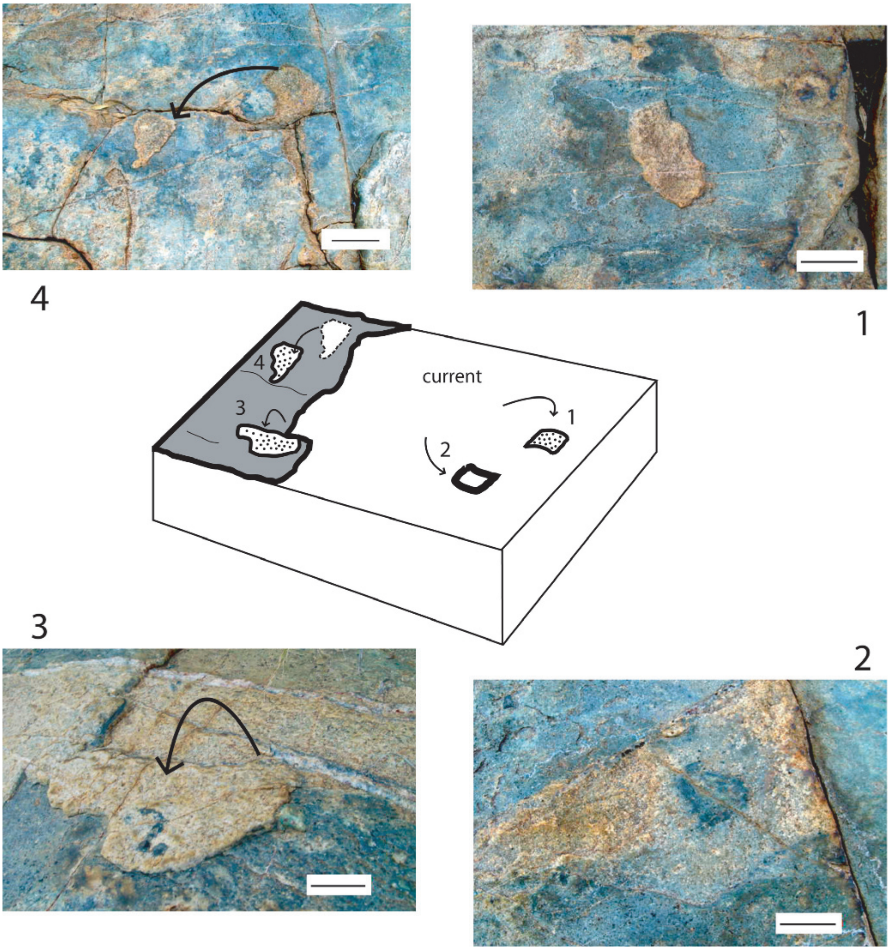


Fig. IV.12. Examples of mat chips scattered at random across bedding surface 1, Nhlazatse Section, Pongola Supergroup. The sketch in the center of the figure summarizes the modes of chip formation. Chip 1 was transported across the tidal surface and deposited face-down on a microbial mat surface. The lower layer of the chip is turned upward. As in modern mat chips, the lower layer was composed of sand agglutinated to the upper mat layer. The mat chip appears yellow in colour because of this sandy layer; (scale: 2.5 cm). Chip 2 was transported across the tidal surface and deposited face-down onto the sandy bottom of an erosional pocket. The sandy substrate of the erosional pocket is yellow in colour. The overturned mat chip should be yellow as well. Note, however, that the edges of this chip are lined by a dark, blue-green rim. As in modern specimens, this rim indicates cyanobacterial migration from the buried, downward pointing chip face towards the face exposed to sun light. The cyanobacteria moved from their mat layer, originally situated on top of the mat chip, towards the sandy layer, originally beneath the mat layer. Note that the center of the now exposed lower mat chip face is still less densely colonized than the dark coloured rim; (scale: 1 cm). Chip 3 is overturned. The sandy base points upward. This chip was not released from its parent site, but is still connected to the edge of an erosional remnant; (scale: 3 cm). Chip 4 is a triangular piece deposited face-down. Note the triangular hole in the mat visible about 10 cm to the right of this chip. The chip was originally released from that hole; (scale: 4 cm)

Fossil erosional remnants and pockets record paleotidal currents and seasonality of paleoclimates. This tidal flat surface in the Nhlazatse Section was buried in an ancient fall. During a season when living conditions for benthic microbiota become less favourable, erosional pockets form and mat chips are released. In modern climates, sun light intensity and duration decreases in fall and winter. Storms can be more frequent. This interpretation of the paleoclimate is supported by the modification index (MOD-I) of this bed surface. The geometries and dimensions of erosional remnants and pockets record the degree of microbial influence on the formation of a tidal surface morphology. This influence is expressed by the modification-index. This fossil tidal flat surface in the Nhlazatse Section shows a MOD-I of 0.35. This value concurs with values measured on modern tidal flats in fall (Noffke and Krumbein 1999).

The geometries of the erosional remnants and pockets also record the ancient predominant current direction (compare Chap. III). In Fig. IV.10, the current moved towards the observer. The observer is standing close to the shore line.

The assumption that the fossil epibenthic microbial mats possibly were constructed by benthic cyanobacteria is strongly supported by the shapes of mat margins along the erosional pockets (Fig. IV.11).

Specific biostabilizing properties of the organic tissues control the way fragments rip and their final shapes. Mat chips scattered at random across bedding surface 1 show geometries and compositions identical to that of chips created by modern mat-forming cyanobacteria (Fig. IV.12; statistical analyses shown in Fig. III.16 and Table III.1).

Bed Surface 2

Bed surface 2 is about 15 to 20 m away from bed surface 1. The wide bedding plane is bluish-green. The surface is slightly crinkled, and resembles a blue-green table cloth. This bed surface represents a planar microbial mat preserved *in situ*. In the center of this bedding plane, an erosional pocket of about 25 cm in length is exposed (Fig. IV.13). This erosional pocket records a paleocurrent from the SW. The MOD-I of this bedding plane is 0.68, consistent with summer conditions in the modern tidal flats of Mellum Island, North Sea (Noffke and Krumbein 1999).

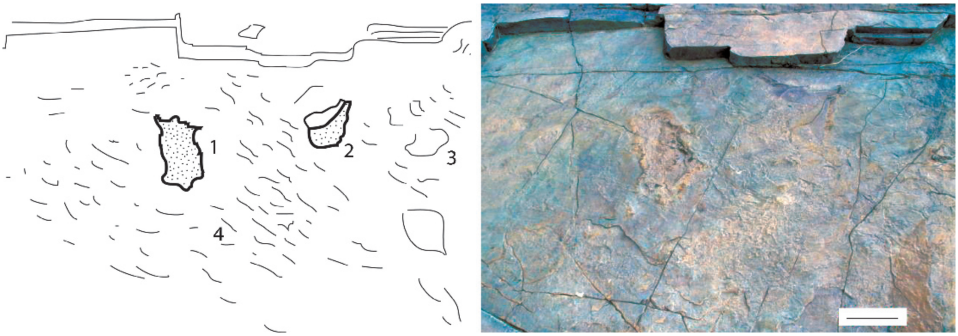


Fig. IV.13. A wrinkled bedding surface in the Nhlazatse Section, Pongola Supergroup. This bedding surface displays an erosional pocket (marked as *1* in sketch), a flipped over, larger mat chip (2), and a desiccation crack (3); (scale: 20 cm)

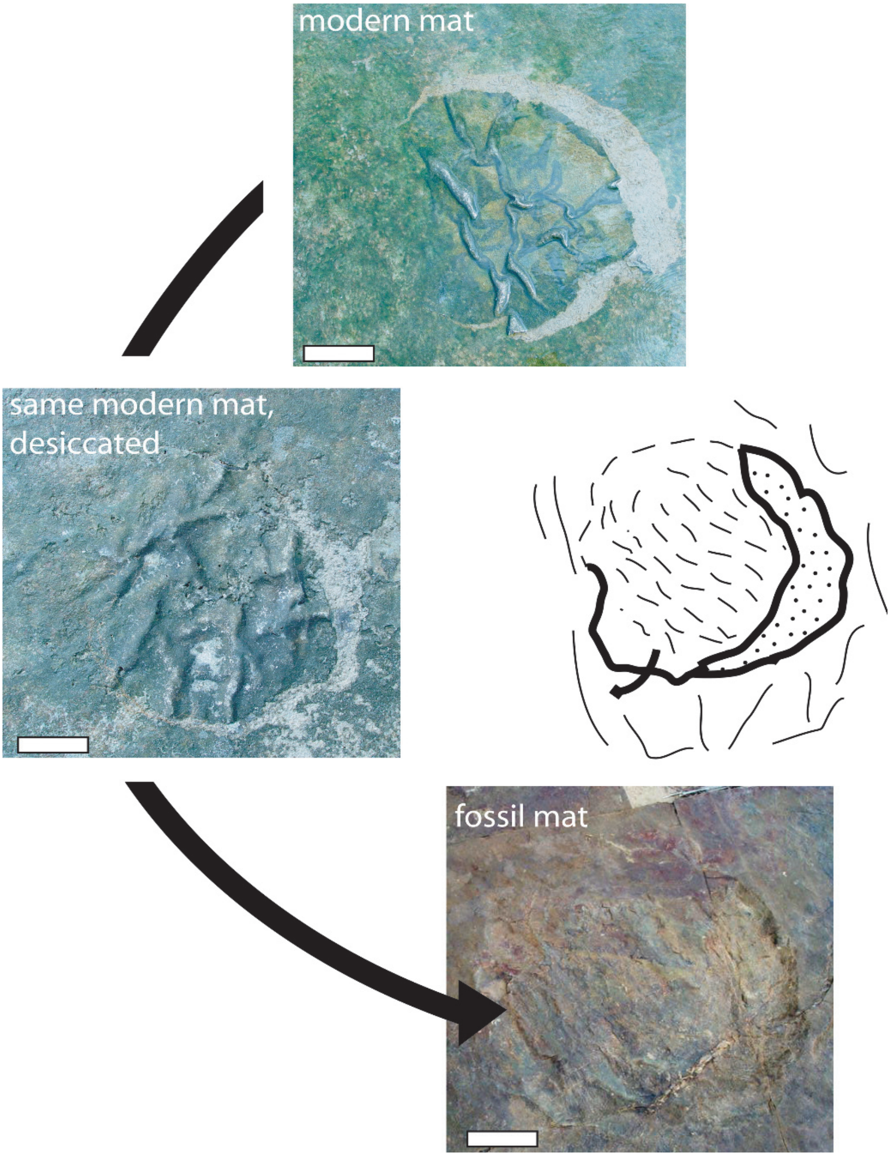


Fig. IV.14. Taphonomy of a mat clast in pictures. The lowermost photo taken in the Nhlazatse Section, Pongola Supergroup, documents a pancake-shaped piece of ancient microbial mat that had been torn off and rotated in a clock-wise direction by a previous bottom current. The sketch above illustrates this MISS and its formation. The top photo is a snapshot of the very same situation taken 3 billion years later in the modern tidal flats of Portsmouth Island, USA. Note the half moon-shaped crack that rose from the rupture and rotation of the mat piece. The sand beneath the mat is visible in this crack. The middle photo shows the same modern mat after two weeks of subaerial exposure. The structure is desiccated, and the mat rigid. One can reasonably assume that this solidified mat might become a fossil structure, such as the one shown far below; (scale: 10 cm)

Bedding plane 2 displays another MISS. A pancake-sized mat piece was dragged laterally in a counter clock-wise direction, and left behind a half moon-shaped crack. The crack exposes the sand originally beneath the ancient microbial mat. The pancake piece was folded during this movement (Fig. IV.14). It so happened that the author detected a very similar structure on the modern tidal flats of Portsmouth Island, Outer Banks, USA.

Bed Surface 3

A few steps to the left from bed surface 2, a third bedding plane is exposed. Microbial mat chips are scattered abundantly across this ancient tidal surface (Fig. IV.15). Statistical analyses on the morphologies of the ancient chips used the indices explained in Chap. III for the description of mat chips. The comparison with modern mat chips shows that both groups have identical shapes. Many mat chips have a cloverleaf-like outline (Fig. IV.15). This results from the re-growth ('healing') of the mat chip edges after deposition. This outline is fundamentally different from that of mud chips. Bedding planes 1 to 3 include many other mat chips. A pile of mat chips were accumulated by an ancient current. The pile is so well preserved that it appears as if it had formed only a few hours ago (Fig. IV.16). Over folded or bent mat chips occur that reflect the ductile deformation of biostabilized sand

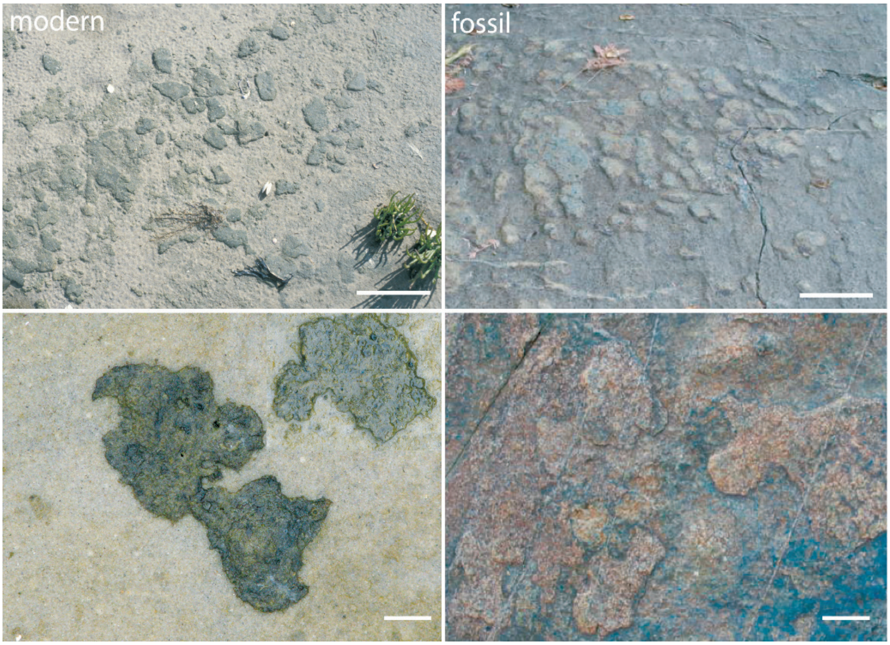


Fig. IV.15. Comparison of modern mat chips from Fishermans Island, USA, (left) with fossil mat chips from the Nhlazatse Section, Pongola Supgergroup (right). The photos at the top display the distribution of mat chips randomly scattered on a tidal surface; (scale: 15 cm). The photos below document the cloverleaf shape typical of many mat chips; (scale: 1 cm)

(Noffke 2000). Other pieces of mat were ripped away from their parent sites, and re-deposited closeby. The outlines of chips and parent sites fit together (Fig. IV.16).

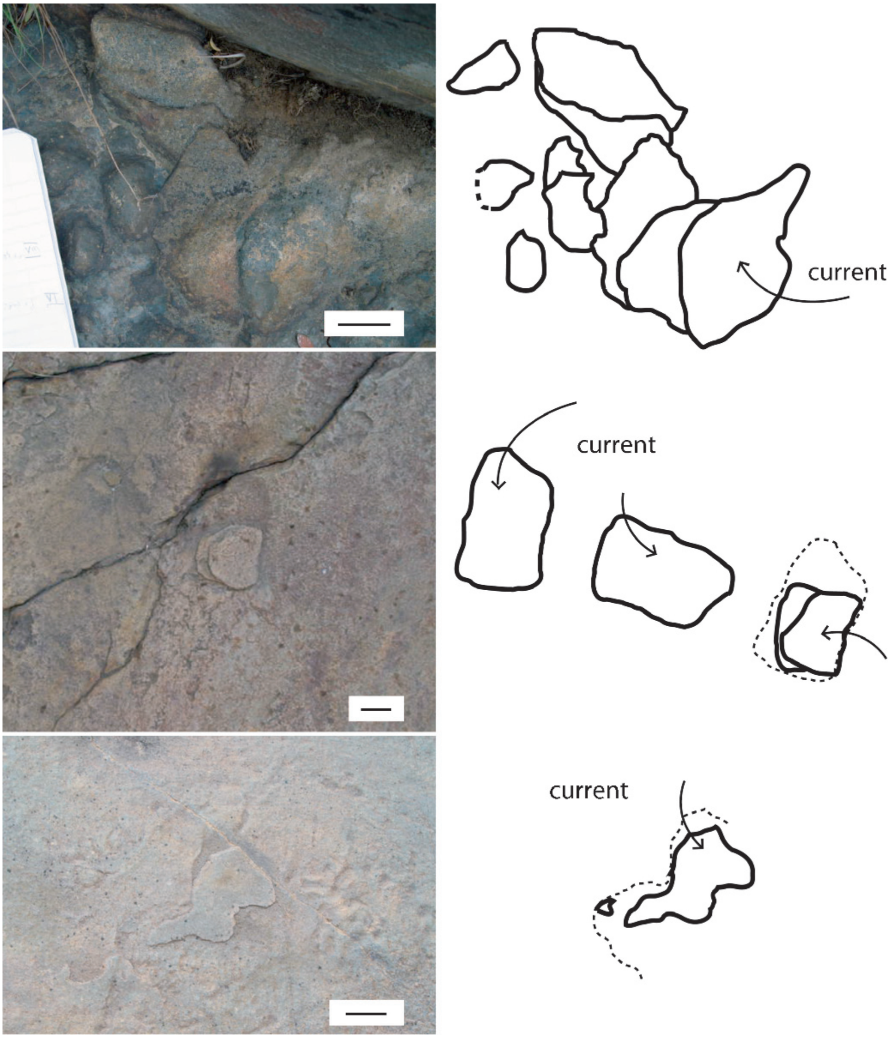


Fig. IV.16. Different scenarios of mat chip deposition preserved in the Nhlazatse Section, Pongola Supergroup. The upper photo shows how mat chips were stacked upon each other by currents. Note that the chips on the left of the photo are somewhat smaller and rounder. These small chips probably originated from an area farther away than the larger, more edgy chips on the right; (scale: 1 cm). In the middle photo, a mat chip is over folded. The original placement of the rounded chip is still visible as dark depression on the bedding surface. The chip was deposited, and then lifted up by a current, rotated, overfolded and re-deposited; (scale: 1 cm). The lower photo documents the moment of mat chip release. The outlines of the parent site and of the chip itself are identical. The older a mat chip becomes, the more the shape of its outline changes. Very old chips can be round or can have clover-leaf-like embayments and lobes; (scale: 1 cm)

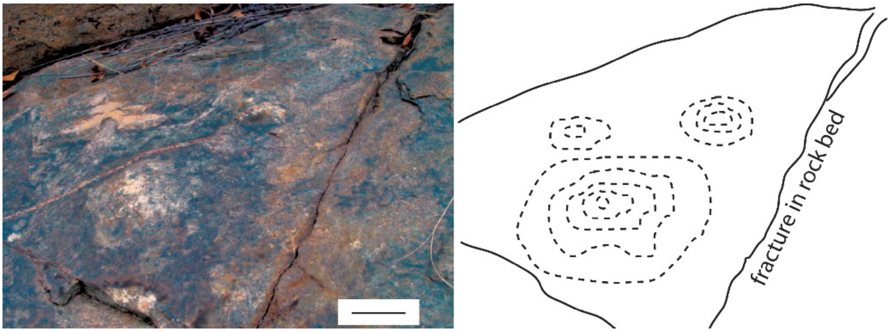


Fig. IV.17. Gas domes on a sandstone surface, Nhlazatse Section, Pongola Supergroup; (scale: 10 cm). Preservation of gas domes in three dimensions is rare in sandy deposits (compare Fig. IV.23)

IV.2.2.5.5
Epibenthic Microbial Mats of Planar Type Forming Gas Domes in the Ancient Lower Supratidal Zone

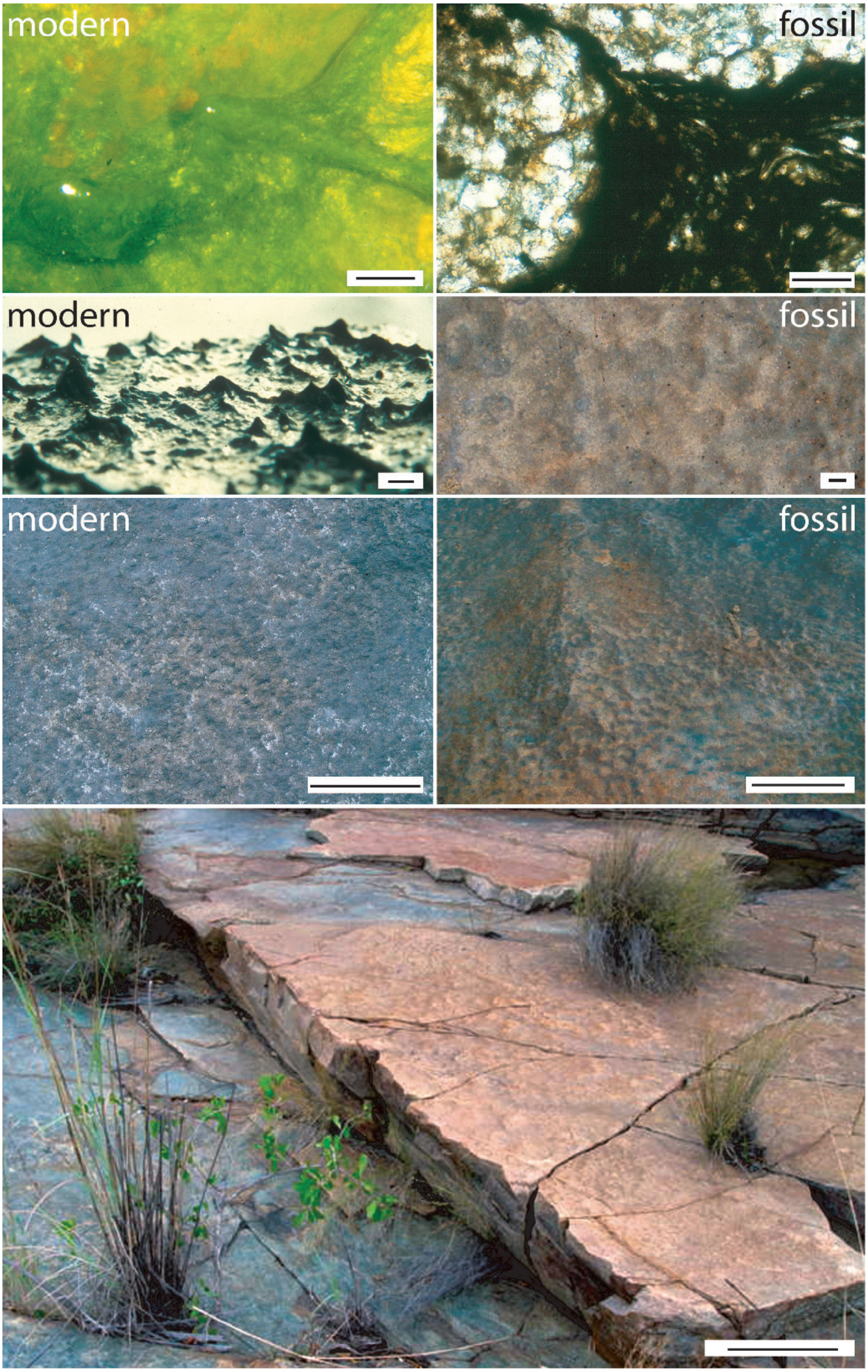
Sandstone beds located at the top of the outcrop show three individual gas domes. It is noteworthy that they are preserved in three dimensions. Gas domes are hollow and in general collapse quickly. The structures in the Nhlazatse Section are rare exceptions. The largest gas dome is 30 cm in diameter at its base, and 3 cm high. The smaller ones are 3 and 4 cm wide, and 0.5 and 1 cm high, respectively, Fig. IV.17. More gas domes occur at the top far left of the outcrop. They are associated with multidirected ripple marks and with storm-influenced erosional remnants and pockets. Three-dimensional preservation results from the rapid *in situ* lithification of organic matter.

IV.2.2.5.6
Epibenthic Microbial Mats Forming Tufted Mat Surfaces in the Lower Supratidal Zone

Below the gas dome site, several rock beds are arranged like stairs. These rock beds have a distinctly spotted surface, which appears reddish or blue-green (Fig. IV.18). In close-up view, each spot is a 'tuft'. Tufts are bundles of vertically oriented filamentous cyanobacteria. Microbial mats that form tufts are called 'tufted mats.' Along the modern southern Tunisian coast, mats develop tufts as high as 2 cm (Noffke et al. 2001a). In the Nhlazatse outcrop, fossil tufts can be felt as little spikes on the sandstone surface. Rapid cementation processes caused the surface structures to be preserved in an upright position (Kah and Knoll 1996).

IV.2.2.5.7
Epibenthic, Tufted Microbial Mats Forming Polygonal Desiccation Cracks in the Lower Supratidal Zone

Towards the river, several about 2 m high cliffs occur in the outcrop. A small, approximately 1 × 2 m sized bedding surface displays exceptionally well preserved polygonal oscillation cracks in tufted microbial mats. The rock bed surface is bluish-green and


modern
fossil
modern
fossil
modern
fossil

◀ **Fig. IV.18.** In the Nhlazatse Section, Pongola Supergroup, step-like sandstone beds display tufted microbial mats. The lower photo gives an impression of the spotted surfaces of such microbial mats in the outcrop; (scale: 25 cm). The smaller photos above are close ups on tufts, scale of first row 10 cm, second row 1 cm. The left column of photos shows modern tufts, the right column shows ancient tufts. The filament bundles project vertically as triangles as much as 2 cm above the mat surface. The topmost photos are microscopic views; (scales: about 0.5 mm). They document how cyanobacterial filaments organize to form a tuft. The fossil tuft is an example from the Lower Ordovician, Montagne Noire, France (after Noffke 2000)

Fig. IV.19. Spectacularly preserved polygonal oscillation cracks ornament this bedding plane in the Nhlazatse Section, Pongola Supergroup. Note that each polygon is lined by two parallel, dark ridges (*arrow 1*). In the center of each polygon is a hole (*arrow 2*). This rock surface unfortunately has been destroyed by erosion by the river Wit Mfolozi. However, some nearby bedding planes display such oscillation cracks as well, although less visible; (scale: 25 cm)

decorated by about 10 polygons (Fig. IV.19). Each polygon is defined by a rim of two parallel lines that record ancient cracks. There is a hole in the center of each polygon. Such oscillation cracks are typical for modern microbial mats in Tunisia (see Chap. III). Sadly, the spectacular surface documented in Fig. IV.19 has since been largely eroded by the Wit Mfolozi River.

IV.2.2.5.8
Pizza-Shaped Mat Chips of Epibenthic, Tufted Microbial Mats

In lower supratidal zones of warmer climates such as in the Mediterranean, microbial mats can become quite thick. When such microbial mats erode, they do not form small mat chips, but pizza-sized clasts. In the Nhlazatse Section, several rock beds include such clasts. The relatively heavy fragments were eroded during storms and re-deposited in all tidal zones, including the subtidal. Some clasts are over folded (Fig. IV.20). The clasts show that the original material that composed them was ductile. Some clasts still display a faint internal lamination. This lamination is due to the build-up of ancient microbial mats. As observed in modern settings, the mats might have been constructed as biovarvites (Fig. IV.20).

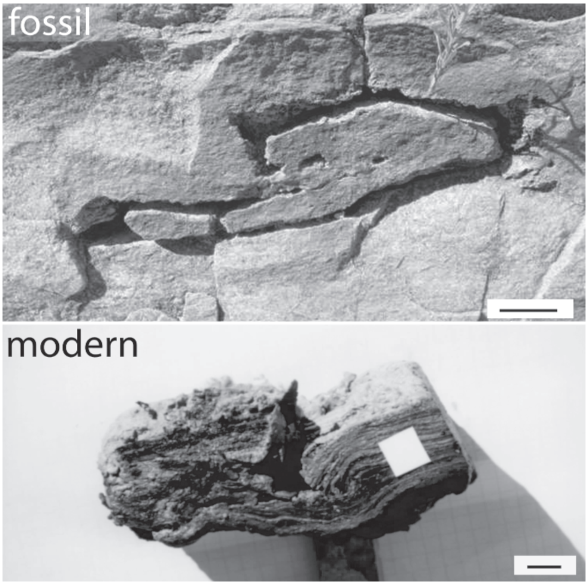


Fig. IV.20.
Pizza-shaped clasts are scattered randomly across the Nhlazatse tidal flats, Pongola Supergroup. The upper photo documents a vertical section through an overfolded microbial mat piece; (scale: 4 cm). Pictured below is a vertical section through a modern microbial mat from southern Tunisia. Dark and light lamina form a stack, a biovarvite; (scale: 1 cm)

IV.2.2.5.9
Epibenthic Microbial Mats of Spongy Type in Tidal Pools in the Lower Supratidal Zone

At the left side of the main cliff in the center of the outcrop, rose coloured rock bed surfaces are exposed. Here, several dark lenses of 0.5 to 3 m in diameter are exposed on the bedding planes (Fig. IV.21). The original study interpreted these lenses as ancient tidal pools, overgrown by very thick, spongy microbial mats. This type of microbial mat occurs in tidal pools of the Bahamas (Hardie et al. 1977). The sandstones are predominantly composed of medium to coarse grained quartz minerals. The dark colour of the fossil microbial mats that flourished in the ancient tidal pools is from hematite-rich cement. The fossil microbial mat has been overturned in some spots, and the spongy mat fabric is visible. The resemblance of the spongy fabrics with Hardie et al.'s air bubble filled algal swamps of *Scytonema*, Bahamas, is astonishing.

IV.2.2.5.10
Epibenthic, Red Microbial Mats Forming Polygonal Oscillation Cracks in a Lower Supratidal Zone

Towards the top of the outcrop, the colour of the sandstone becomes more deeply rose. A very large bedding surface of several tens of m^2 displays about a hundred spectacularly preserved polygons, of 20–40 cm in diameters (Fig. IV.22). The oscillating microbial mat margins of each polygon worked like a bulldozer, moving sand towards the surrounding polygons. However, all polygons oscillated. Consequently, the bulldozing mat margins formed ridges of sand in the space between the polygons. These polygonally arranged sand ridges are still clearly visible – 3 billion years after their accumulation!

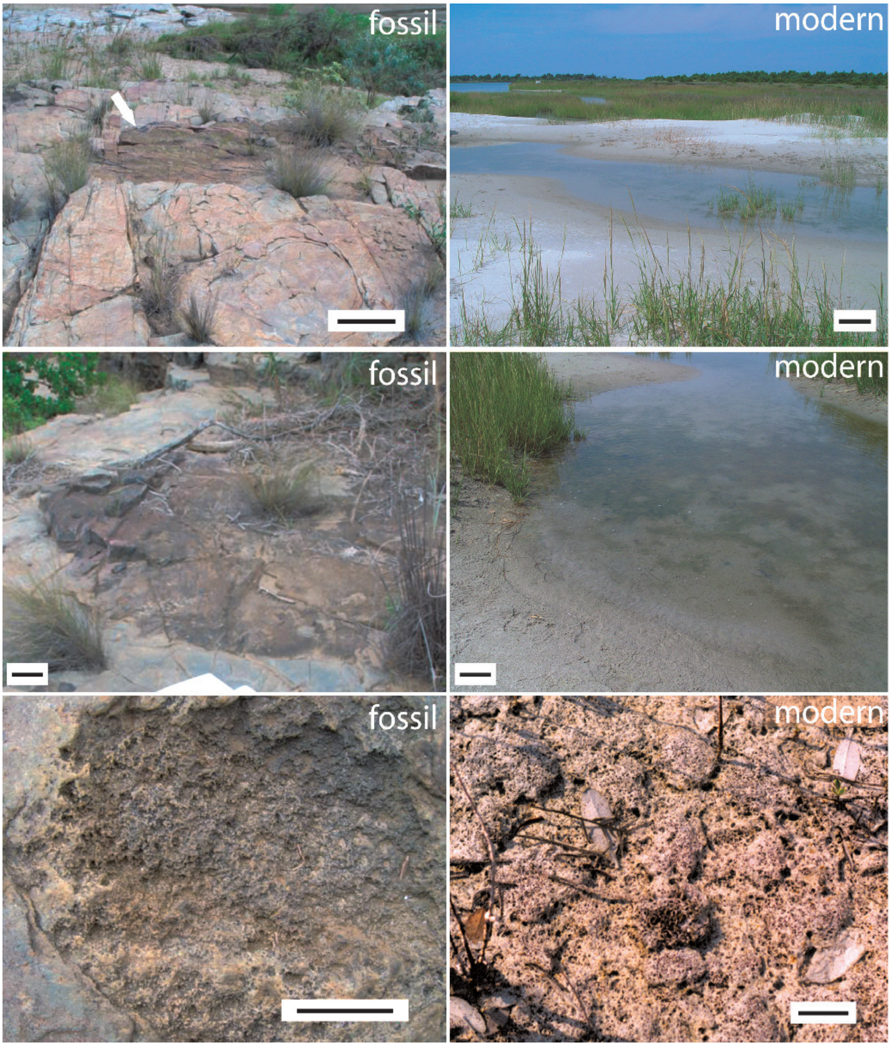


Fig. IV.21. Fossil tidal pools in the Nhlazatse outcrop (left) and modern tidal pools from Portsmouth Island and the Bahamas (right). The upper photos are views into the field; (scales: 1 m). Tidal pools have a sharply defined edge. The middle photos show that the pools are overgrown by microbial mats. The mat cover is patchy; (scales: 15 cm). Note the similarity of these spongy microbial mats composed of filamentous microorganisms in the close-ups (below); (scales: 5 cm)

Many polygons have a hole in their centers (Fig. IV.23). The holes are a few cm wide, and several cm deep. They have sharply defined edges. Modern microbial mats in Tunisia have the same polygonal structures. Gases accumulate under the mat, and gas domes form. The gas domes finally collapse, and the gas exits through the gas dome roof. Some gas domes erupted, leaving a hole behind. Other gas domes simply cracked open. Many holes are still covered by a gas dome roof.

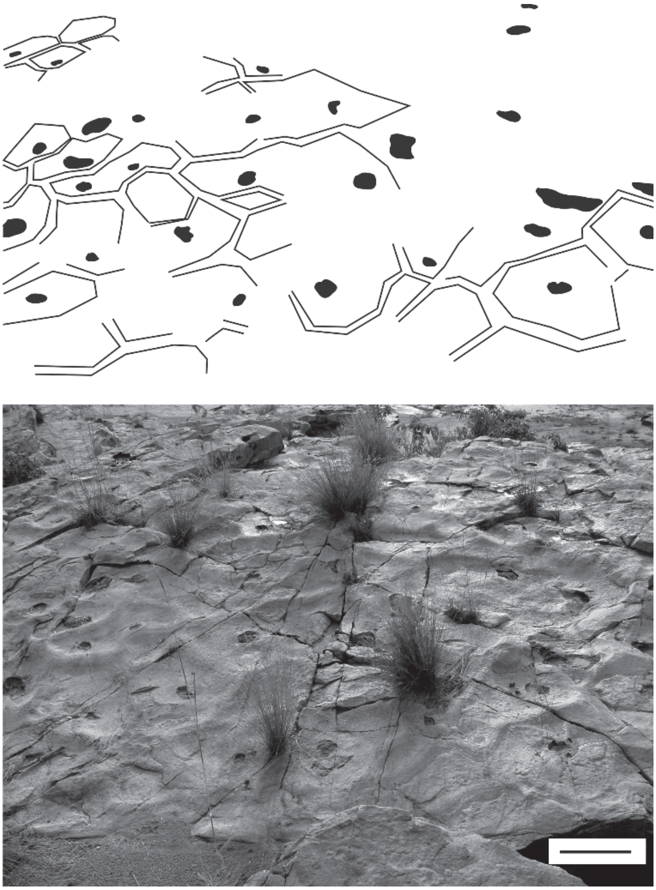


Fig. IV.22. Polygonal patterns on sandstone surfaces record ancient oscillation cracks (Nhlazatse Section, Pongola Supergroup). The individual polygons are defined by sand ridges. Many polygons show a hole in their center; (scale: 50 cm)

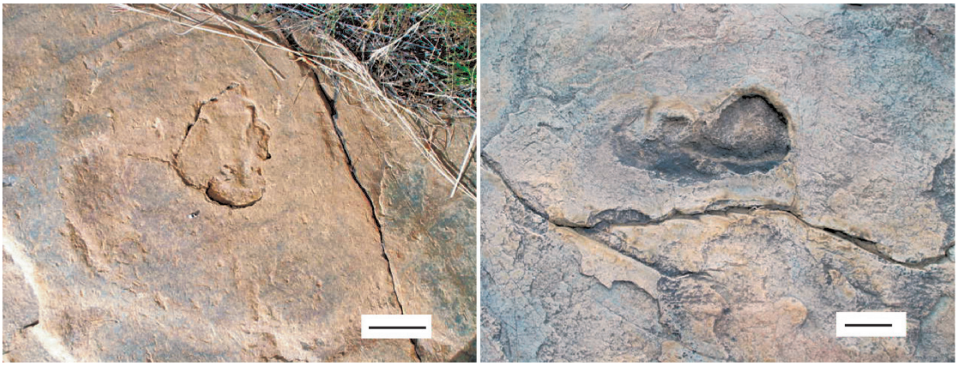


Fig. IV.23. Polygonal desiccation cracks have holes in their centers. Some holes are still covered by microbial mat (left). Most holes, however, are open gaps (right). Nhlazatse Section, Pongola Supergroup; (scales: 10 cm)

IV.2.2.5.11

Endobenthic and Epibenthic Microbial Mat-Forming Erosional Remnants and Pockets in a High Energy Lower Supratidal Zone

Above the wide rock bed surfaces that display multidirected ripple marks, orange-coloured sandstone bedding planes are covered by steep-sloped erosional remnants and pockets (Fig. IV.24). Gas domes signify the presence of thriving microbial mats. The ripple marks in the bottom of the erosional pocket are overgrown by a microbial mat layer. This mat layer is much thinner than that of the erosional remnants. It developed after the pocket was created. The heavily sculptured morphology of deep erosional pockets was probably driven by episodic hurricanes. During subsequent months, new mat generations developed and covered the freshly eroded pockets again.

The examples of MISS documented in this final chapter record the similarity between fossil structures and their facies-related distributions with modern MISS, both with respect to their morphology and facies-related distribution. It is unlikely that similar structures are formed by any bacterial group other than benthic cyanobacteria.

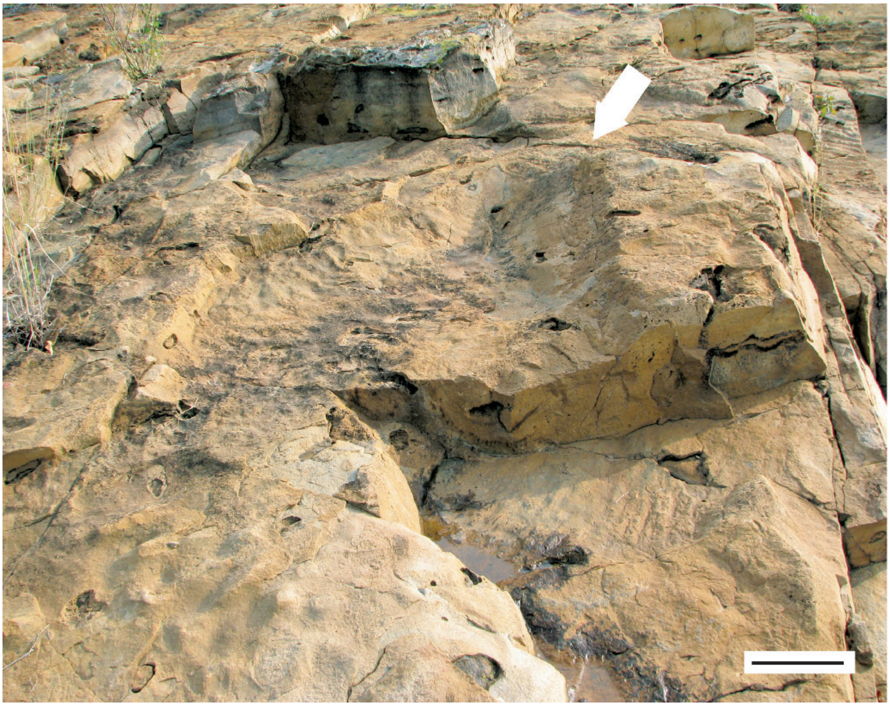


Fig. IV.24. Steep erosional remnants and pockets in the Nhlazatse tidal flats, Pongola Supergroup. The *arrow* points to the tip of a V-shaped erosional pocket. Note the height difference between the erosional pocket and the remnant. The ripple marks in the bottom of the erosional pocket are overgrown by a thin microbial mat layer; (scale: 45 cm)

References

Aitken J (1967) Classification and environmental significance of cryptalgal limestones and dolomites, with illustrations from the Cambrian and Ordovician of southwestern Alberta. J Sediment Petrol 37:1163–1178

Allen J (1997) Simulation models of salt-marsh morphodynamics: some implications for high-intertidal sediment couplets related to sea-level change. Sediment Geol 113:211–223

Altermann W, Kazmierczak J (2003) Archean microfossils: A reappraisal of early life on Earth. Res Microbiol 154:611–617

Beukes N, Lowe D (1989) Environmental control on diverse stromatolite morphologies in the 3 000 Myr Pongola Supergroup, South Africa. Sedimentol 36:383–397

Beveridge T (1989) Role of cellular design in bacterial metal accumulation and mineralization. Annu Rev Microbiol 43:147–171

Black M (1933) The algal sediments of Andros Islands, Bahamas. Philos Trans R Soc Lond Series B 222:165–192

Bottjer D (2005) Geobiology and the fossil record: Eukaryotes, microbes, and their interactions. In: Noffke N (ed) Geobiology: Objectives, concepts, perspectives. Special Issue Paleogeography, Paleoclimatology, Paleoecology 219:5–22

Bottjer D, Hagadorn J, Dornbos S (2000) The Cambrian substrate revolution. GSA Today 10:1–7

Brasier MD, Green OR, Jephcoat AP, Kleppe AK, Van Kranendonk MJ, Lindsay JF, Steele A, Grassineau NV (2002) Questioning the evidence for Earth's oldest fossils. Nat 416:76–81

Brasier MD, Green OR, Lindsay JF, McLoughlin N, Steele A, Stoakes C (2005) Critical testing of Earth's oldest putative fossil assemblage from the 3.5 Ga Apex chert, Chinaman Creek, Western Australia. Precambr Res 140:55–102

Brasier M, McLoughlin N, Green O, Wacey D (2006) A fresh look at the fossil evidence for early Archaean cellular life. Philos Trans R Soc Lond 361:887–902

Bridge J (2003) Rivers and floodplains: Forms, processes, and sedimentary record. Blackwell Publishing, Boston

Briggs D (2003) The role of decay and mineralization in the preservation of soft-bodied fossils. Sci 31:275–301

Brock T (1976) Halophilic-blue-green algae. Microbiol 107:109–111

Brocks JJ, Logan GA, Buick R, Summons RE (1999) Archean molecular fossils and the early rise of eukaryotes. Sci 285:1033

Browne K, Golubic S, Seong-Joo L (2000) Shallow marine microbial carbonate deposits. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Berlin

Buick R (1992) The antiquity of oxygenic photosynthesis: Evidence from stromatolites in sulphate-deficient Archaean lakes. Sci 255:74–77

Buick R, Dunlop J, Groves D (1981) Stromatolite recognition in ancient rocks: An appraisal of irregularly laminated structures in an Early Archaean chert-barite unit from North Pole, Western Australia. Alcheringa: Australas J Palaeontol 5:161–181

Cairns-Smith A (1982) Genetic takeover and the mineral origins of life. Cambridge University Press, Cambridge

Callow R, Brasier M (2009) A solution to Darwin's dilemma of 1859: Exceptional preservation in Salter's material from the late Ediacaran Longmyndian Supergroup, England. J Geol Soc 166:1–4

N. Noffke, *Geobiology*, DOI 10.1007/978-3-642-12772-4,

Cameron B, Cameron D, Jones J (1985) Modern algal mats in intertidal and supratidal quartz sands, northeastern Massachusetts, USA. In: Curran A (ed) Biogenic structures: Their use in interpreting depositional environments. SEPM, Tulsa

Canfield D, Raiswell R (1991) Pyrite formation and fossil preservation. In: Allison P, Briggs D (eds) Taphonomy: Releasing the data locked in the fossil record. Plenum Press

Charaklis WG, Marshall KC (eds) (1989) Biofilms. Brisbane, New York Chichester

Charaklis WG, Marshall KC (1990) Biofilms. Wiley, New York

Church M (2003) Grain size and shape. In: Middleton G (ed) Encyclopedia of sediments and sedimentary rocks. Kluwer Academic Publishers, Dordrecht

Cohen Y, Rosenberg E (1989) Microbial mats: Physiological ecology of benthic microbial communities. American Society for Microbiology, Washington

Cohen Y, Krumbein W, Goldberg M, Shilo M (1977) Solar Lake (Sinai) – Physical and chemical limnology. Limnol Oceanogr 22:597–608

Consalvey M, Jesus B, Perkins RG, Brotas V, Underwood GJC, Paterson DM (2004) Monitoring migration and measuring biomass in benthic biofilms: The effects of dark/far-red adaptation and vertical migration on fluorescence measurements. Photosynth Res 81:91–101

Cooksey K (1992) Extracellular polymers in biofilms. Biofilms – Sci Technol 223:137–147

Costerton JW, Lewandowski Z, Caldwell DE, Korber DR, Lappin-Scott HM (1995) Microbial biofilms. Annu Rev Microbiol 49:711–745

Dalrymple R, Choi K (2003) Sediment transport by tides. In: Middleton G (ed) Encyclopedia of sediments and sedimentary rocks. Kluwer Academic Publishers, Dordrecht

Davies J (1964) A morphogenic approach to world shorelines. Z Geomorphol 8:127–142

Davies DG, Parsek MR, Pearson JP, Iglewski BH, Costerton JW, Greenberg EP (1998) The involvement of cell-to-cell signals in the development of a bacterial biofilm. Sci 280:295

Decho A (1990) Microbial exopolymer secretions in ocean environments – their role(s) in food webs and marine processes. Oceanog Mar Biol 28:73–153

Decho A (2000) Microbial biofilms in intertidal systems: An overview. Cont Shelf Res 20:1257–1273

Decho A, Visscher P, Reid R (2005) Production and cycling of natural microbial exopolymers (EPS) within a marine stromatolite. Palaeogeogr Palaeoclimatol Palaeoecol 219:71–86

Demicco R, Hardie L (1994) Sedimentary structures and early diagenetic features of shallow marine carbonate deposits. SEPM, Tulsa

Denny M (1993) Air and water: The biology and physics of life's media. Princeton University Press, Princeton

Des Marais DJ, D'Amelio ED, Farmer JD, Jørgensen BB, Palmisano AC, Pierson BK (1992) Case study of a modern microbial mat-building community: The submerged cyanobacterial mats of Guerrero Negro, Baja California Sur, Mexico. In: Schopf W, Klein C (eds) The Proterozoic biosphere: A multidisciplinary study. Cambridge University Press, New York

deVries Klein G (1977) Clastic tidal facies. Continuing Education Publication, Champaign

Dill RF, Shinn EA, Jones AT, Kelly K, Steinen RP (1986) Giant subtidal stromatolites forming in normal salinity waters. Nature 324:55–58

Douglas S, Beveridge T (1998) Mineral formation by bacteria in natural microbial communities. FEMS Microbiol Ecol 26:79–88

Draganits E, Noffke N (2004) Siliciclastic stromatolites and other microbially induced sedimentary structures in an early Devonian barrier-island environment (Muth Formation, NW Himalayas). J Sediment Res 74:191

Dravis J (1983) Hardened subtidal stromatolites, Bahamas. Sci 219:385–386

Dunlap P (1999) Quorum regulation of luminescence in *Vibrio fischeri*. J Mol Microbiol Biotechnol 1:5–12

Dyer K (1986) Coastal and estuarine sediment dynamics. Wiley and Sons, Sussex

Eisma D, de Boer P (1998) Intertidal deposits: River mouths, tidal flats, and coastal lagoons. CRC Press, Bocha Raton

Eriksson P, Simpson E, Eriksson E, Bumby A, Stein G, Sarkar S (2000) Muddy roll-up structures in siliciclastic inter dune beds of the 1.8 Ga Waterberg Group, South Africa. Palaios 15:177–183

Ferris F, Fyfe W, Beveridge T (1987) Bacteria as nucleation sites for authigenic minerals in a metal-contaminated lake sediment. Chem Geol 63:225–232

Ferris FG, Schultze S, Witten TC, Fyfe WS, Beveridge TJ (1989) Metal interactions with microbial biofilms in acidic and neutral pH environments. Applied Environ Microbiol 55:1249

Flemming B (2000) A revised textural classification of gravel-free muddy sediments on the basis of ternary diagrams. Cont Shelf Res 20:1125–1137

Flemming B (2003) Tidal flats. In: Middleton G (ed) Encyclopedia of sediments and sedimentary rocks. Kluwer Academic Publishers, Dordrecht

Flemming H, Wingender J (2001) Relevance of microbial extracellular polymeric substances (EPSs)-Part II: Technical aspects. Water Sci Technol 43:9–16

Flemming H, Neu T, Wozniak D (2007) The EPS matrix: The 'house of biofilm cells'. J Bacteriol 189: 7945–7947

Friedman G, Krumbein W, Gerdes G (1985) Hypersaline ecosystems: The Gavish Sabkha. Springer-Verlag, Berlin

Friedman G, Sanders J, Kopaska-Merkel D (1992) Principles of sedimentary deposits: Stratigraphy and sedimentology. Macmillan, New York

Führböter A, Manzenrieder H (1987) Biostabilisierung von Sandwatten durch Mikroorganismen. In: Gerdes G (ed) Mellum – Portrait einer Insel. Kramer, Frankfurt

Fuqua C, Winans S, Greenberg E (1996) Census and consensus in bacterial ecosystems: the LuxR-LuxI family of quorum-sensing transcriptional regulators. Annu Rev Microbiol 50:727–751

Gehling J (1999) Microbial mats in terminal Proterozoic siliciclastics; Ediacaran death masks. Palaios 14:40

Gehling J, Droser M (2009) Textured organic surfaces associated with the Ediacara biota in South Australia. Earth Sci Rev 96:196–206

Gerdes G, Klenke T (2003) Geologische Bedeutung ökologischer Zeiträume in biogener Schichtung (Mikrobenmatten, potentielle Stromatolithe). Mitt Ges Geol Bergbaustud Österreich 46:35–49

Gerdes G, Krumbein W (1987) Biolaminated deposits. Springer-Verlag, Berlin

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

Gerdes G, Krumbein W, Reineck H (1991) Biolaminations – Ecological versus depositional dynamics. In: Einsele G, Ricken W, Seilacher A (eds) Cycles and events in stratigraphy. Springer-Verlag, Berlin

Gerdes G, Krumbein W, Reineck H (1994) Microbial mats as architects of sedimentary surface structures. In: Krumbein WE, Paterson DM, Stal LJ (eds) Biostabilization of Sediments Bibliotheks- und Informationssystem der Universität Oldenburg, Oldenburg

Gerdes G, Klenke T, Noffke N (2000a) Microbial signatures in peritidal siliciclastic sediments: A catalogue. Sediment 47:279–308

Gerdes G, Krumbein W, Noffke N (2000b) Evaporite microbial sediments. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Berlin

Giblin A (1988) Pyrite formation in marshes during early diagenesis. Geomicrobiol J 6:77–97

Ginsburg RN (1991) Controversies about stromatolites: Vices and virtues. In: Müller DW, McKenzie JA, Weissert H (eds) Controversies in modern geology. Academic Press Limited, London, pp 25–36

Golubic S, Hofmann H (1976) Comparison of Holocene and mid-Precambrian Entophysalidaceae (Cyanophyta) in stromatolitic algal mats: Cell division and degradation. J Paleontol 1074–1082

Golubic S, Knoll A (1993) Prokaryotes. In: Lipps J (ed) Fossil prokaryotes and protists. Blackwell, Boston

Grotzinger J, Knoll A (1999) Stromatolites in Precambrian carbonates: Evolutionary mileposts or environmental dipsticks? Annu Rev Earth Planet Sci 27:313–358

Grotzinger J, Rothman D (1996) An abiotic model for stromatolite morphogenesis. Nat 383:423–425

Hagadorn J, Bottjer D (1997) Wrinkle structures: Microbially mediated sedimentary structures common in subtidal siliciclastic settings at the Proterozoic-Phanerozoic transition. Geol 25:1047

Hagadorn J, Bottjer D (1999) Restriction of a late Neoproterozoic biotope; Suspect-microbial structures and trace fossils at the Vendian-Cambrian transition. Palaios 14:73

Hagadorn W, Pflueger F, Bottjer D (1999) Unexplored microbial worlds. Palaios Special Issue 14, 120 p

Hardie L, Garrett P (1977) Sedimentation on the modern carbonate tidal flats of Northwest Andros Island, Bahamas. John Hopkins University Press, Baltimore

Harper M (1977) Movements. In: Werner D (ed) The biology of diatoms. Blackwell, New York

Harrison J, Turner R, Marques L, Ceri H (2005) Biofilms. Am Sci 93:508–515

Heubeck C (2009) An early ecosystem of Archean tidal microbial mats (Moodies Group, South Africa, ca. 3.2 Ga). Geology 37:931–935

Hofmann HJ, Grey K, Hickman AH, Thorpe RI (1999) Origin of 3.45 Ga coniform stromatolites in Warrawoona Group, Western Australia. Geological Society of America Bulletin 111:1256–1262

Hofmann Bang N (1818) Densu confervorium in oeconomia naturae. In: Hormemann JW (ed) Flora Danica. Copenhagen, pp 13–16

Horodyski R, Bloeser B, Vonder Haar S (1977) Laminated algal mats from a coastal lagoon, Laguna Mormona, Baja California, Mexico. J Sediment Petrol 47:680–696

Joint I (1981) Growth and survival of estuarine microalgae. In: Jones N, Wolff W (eds) Feeding and survival strategies of estuarine organisms. Plenum Press, New York

Joubert L, Wolfaardt G, Botha A (2006) Microbial exopolymers link predator and prey in a model yeast biofilm system. Microb Ecol 52:187–197

Kah L, Knoll A (1996) Microbenthic distribution of Proterozoic tidal flats: Environmental and taphonomic considerations. Geol 24:79–82

Kalkowsky E (1908) Oolith und Stromatolith im norddeutschen Buntsandstein. Z Dtsch Geol Ges 60:68–125

Kelley JT, Belknap DF, Jacobson Jr GL, Jacobson HA (1988) The morphology and origin of salt marshes along the glaciated coastline of Maine, USA. J Coast Res 4:649–666

Kieber R, Zhou X, Mopper K (1990) Formation of carbonyl compounds from UV-induced photodegradation of humic substances in natural waters: Fate of riverine carbon in the sea. Limnol Oceanogr 35:1503–1515

Klausen MM, Thomsen TR, nielsen JL, Mikkelsen LH, Nielsen PH (2004) Variations in microcolony strength of probe-defined bacteria in activated sludge flocs. FEMS Microbiol Ecol 50:123–132

Knoll A (1985) Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats. Philos Trans R Soc Lond Series B, Biol Sci:111–122

Knoll A (2003) Life on a young planet: The first three billion years of evolution on Earth. Princeton University Press, Princeton

Knorre H, Krumbein W (2000) Bacterial calcification. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Berlin

Kolenbrander PE, Andersen RN, Kazmerzak K, Wu R, Palmer Jr RJ (1999) Spatial organization of oral bacteria in biofilms. Methods enzymol 310:322–332

Komar P (2003) Grain settling. In: Middleton G (ed) Encyclopedia of sediments and sedimentary rocks. Kluwer Academic Publishers, Dordrecht

Konhauser K (2007) Introduction to geomicrobiology. Blackwell Publishing, Boston

Konhauser KO, Schultze-Lam S, Ferris FG, Fyfe WS, Longstaffe FJ, Beveridge TJ (1994) Mineral precipitation by epilithic biofilms in the Speed River, Ontario, Canada. Applied Environ Microbiol 60:549

Kropp J, Block A, von Bloh W, Klenke T, Schellnhuber HJ (1997) Multifractal characterization of microbially induced magnesian calcite formation in Recent tidal flat sediments. Sediment Geol 109:37–51

Krumbein W (1979) Photolithotropic and chemoorganotrophic activity of bacteria and algae as related to beachrock formation and degradation (Gulf of Aqaba, Sinai). Geomicrobiol J 1:139–203

Krumbein W (1983) Stromatolites – The challenge of a term in space and time. Precambr Res 20: 493–531

Krumbein W (1986) Biotransfer of minerals by microbes and microbial mats. Biomineralization in lower plants and animals, pp 55–72

Krumbein WE (1987) Die Entdeckung inselbildender Mikroorganismen. In: Gerdes G, Krumbein WE, Reineck HE (eds) Mellum – Portrait einer Insel. Kramer, Frankfurt/Main, pp 62–76

Krumbein W (1994) Paracelsus und die muciliginischen Substanzen – 500 Jahre EPS-Forschung. Deutsche Gesellschaft für Mikrobiologie 1993:8–14

Krumbein W, Paterson D, Stal L (1994) Biostabilization of sediments. BIS Oldenburg, Oldenburg

Kruschel C, Castenholz R (1998) The effect of solar UV and visible irradiance on the vertical movements of cyanobacteria in microbial mats of hypersaline waters. FEMS Microbiol Ecol 27:53–72

Kuhl M, Jorgensen B (1992) Microsensor measurements of sulfate reduction and sulfide oxidation in compact microbial communities of aerobic biofilms. Applied Environ Microbiol 58:1164

Kuhl M, Jorgensen B (1994) The light field of microbenthic communities: radiance distribution and microscale optics of sandy coastal sediments. Limnol Oceanogr 1368–1398

Kvale E (2003) Tides and tidal rhythmites. Kluwer Academic Publishers, Dordrecht

Lawrence J, Neu T, Swerhone G (1998) Application of multiple parameter imaging for the quantification of algal, bacterial and exopolymer components of microbial biofilms. J Microbiol Methods 32:253–261

Leo R, Barghoorn E (1975) Silicification of wood. Bot Mus Leaflets Harvard University 25:1–46

Lowe D (1980) Stromatolites 3400-myr old from the archean of Western Australia. Nat 284:441–443

Margulis L (2009) Pavements along memory lane and castles of sand long before 'Man'. Earth Sci Rev 96(3):1–5

Marshall K (1976) Interfaces in microbial ecology. Harvard University Press, Cambridge

Mata S, Bottjer D (2009) The paleoenvironmental distribution of Phanerozoic wrinkle structures. Earth Sci Rev 96(3):181–195

Middleton G, Southard J (1984) Mechanics of sediment movement. SEPM, Tulsa

Miller M, McCave I, Komar P (1977) Threshold of sediment motion under unidirectional currents. Sedimentol 24:507–527

Møller S, Sternberg C, Andersen JB, Christensen BB, Ramos JL, Givskov M, Molin S (1998) In situ gene expression in mixed-culture biofilms: Evidence of metabolic interactions between community members. Applied Environ Microbiol 64:721

Mopper K, Zhou X, Kieber RJ, Kieber DJ, Sikorski RJ, Jones RD (1991) Photochemical degradation of dissolved organic carbon and its impact on the oceanic carbon cycle. Nat 353:60–62

Nealson K, Berelson W (2003) Layered microbial communities and the search for life in the universe. Geomicrobiol J 20:451–462

Neu TR (1994) Biofilms and microbial mats. In: Krumbein WE, Paterson D, Stal L (eds) Biostabilization of sediments

Neumann A, Gebelein C, Scoffin T (1970) The composition, structure and erodability of subtidal mats, Abaco, Bahamas. J Sediment Petrol 40:274–297

Noffke N (1997) Mikrobiell induzierte Sedimentstrukturen (M.I.S.S.) in siliziklastischen Wattablagerungen. PhD Thesis University of Oldenburg, 127 p

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

Noffke N (1999) Erosional remnants and pockets evolving from biotic-physical interactions in a Recent lower supratidal environment. Sediment Geol 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). Sediment Geol 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. pp 439–441

Noffke N (2003b) Bacteria in sediments. In: Middleton C (ed) Encyclopedia of sediments and sedimentary rocks. pp 37–39

Noffke N (2003c) Epibenthic cyanobacterial communities counteracting sedimentary processes within siliciclastic depositional systems (present and past). In: Paterson D, Zavarzin G, Krumbein WE (eds) Biofilms through space and time. Congress Proceedings, Kluwer Academic Publishers, pp 265–280

Noffke N (2005) Geobiology – A holistic scientific discipline. Palaeogeogr Palaeoclimatol Palaeoecol 219:1–3

Noffke N (2008) Turbulent lifestyle: Microbial mats on Earth's sandy beaches – Today and 3 billion years ago. GSA Today 18:4–9

Noffke N (2009) The criteria for the biogenicity of microbially induced sedimentary structures (MISS) in Archean and younger, sandy deposits. Earth Sci Rev 96:173–180

Noffke N, Krumbein W (1999) A quantitative approach to sedimentary surface structures contoured by the interplay of microbial colonization and physical dynamics. Sedimentol 46:417–426

Noffke N, Paterson D (2008) Microbial interactions with physical sediment dynamics, and their significance for the interpretation of Earth's biological history. Geobiol 6:1

Noffke N, Gerdes G, Klenke T, Krumbein WE (1996) Microbially induced sedimentary structures-examples from modem sediments of siliciclastic tidal flats. Zbl Geol Palfiont Tell I 1:307–316

Noffke N, Gerdes G, Klenke T, Krumbein WE (1997a) A microscopic sedimentary succession of graded sand and microbial mats in modern siliciclastic tidal flats. Sediment Geol 110:1–6

Noffke N, Gerdes G, Klenke T, Krumbein WE (1997b) Biofilm impact on sedimentary structures in siliciclastic tidal flats. Cour Forsch Senckenberg 201:297–305

Noffke N, Gerdes G, Klenke T, Krumbein WE (2001a) Microbially induced sedimentary structures indicating climatological, hydrological and depositional conditions within Recent and Pleistocene coastal facies zones (southern Tunisia). Facies 44:23–30

Noffke N, Gerdes G, Klenke T, Krumbein WE (2001b) Microbially induced sedimentary structures: A new category within the classification of primary sedimentary structures. J Sediment Res 71:649

Noffke N, Knoll A, 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 17:533

Noffke N, Gerdes G, Klenke T (2003a) Benthic cyanobacteria and their influence on the sedimentary dynamics of peritidal depositional systems (siliciclastic, evaporitic salty, and evaporitic carbonatic). Earth Sci Rev 62:163–176

Noffke N, Hazen R, Nhleko N (2003b) Earth's earliest microbial mats in a siliciclastic marine environment (2.9 Ga Mozaan Group, South Africa). Geol 31:673

Noffke N, Beukes N, Gutzmer J, Hazen R (2006a) Spatial and temporal distribution of microbially induced sedimentary structures: A case study from siliciclastic storm deposits of the 2.9 Ga Witwatersrand Supergroup, South Africa. Precambr Res 146:35–44

Noffke N, Eriksson KA, Hazen RM, Simpson EL (2006b) A new window into Early Archean life: Microbial mats in Earth's oldest siliciclastic tidal deposits (3.2 Ga Moodies Group, South Africa). Geol 34:253

Noffke N, Beukes N, Bower D, Hazen RM, Swift DJP (2008) An actualistic perspective into Archean worlds-(cyano-)bacterially induced sedimentary structures in the siliciclastic Nhlazatse Section, 2.9 Ga Pongola Supergroup, South Africa. Geobiol 6:5

Palmer J, Round F (1965) Persistent, vertical-migration rhythms in benthic microflora. I. The effect of light and temperature on the rhythmic behaviour of *Euglena obtusa*. J Mar Biol 45:567–582

Park R (1977) The preservation potential of some recent stromatolites. Sedimentol 24:485–506

Paterson D (1994) Microbial mediation of sediment structure and behaviour. In: Stal L, Caumette P (eds) Microbial mats. Springer-Verlag, Berlin

Paterson D (1997) Biological mediation of sediment erodibility: Ecology and physical dynamics. In: Burt N, et al. (eds) Cohesive sediments. Wiley, London

Peabody FE (1947) Current crescents in the Triassic Moenkopi Formation. J Sed Petrol 17:73–76

Perry RS, McLoughlin N, Lynne BY, Sephton MA, Oliver JD, Perry CC, Campbell K, Engel MH, Farmer JD, Brasier MD, Staley JT (2007) Defining biominerals and organominerals: Direct and indirect indicators of life. Sediment Geol 201:157–179

Pettijohn F, Potter P (1964) Atlas and glossary of primary sedimentary structures. Springer-Verlag, Berlin

Pflüger F, Gresse P (1996) Microbial sand chips – A non-actualistic sedimentary structure. Sediment Geol 102:263–274

Pia J (1927) Pflanzen als Gesteinsbildner. J Geol 35:477–478

Prave A (2002) Life on land in the Proterozoic: Evidence from the Torridonian rocks of northwest Scotland. Geology 30:811–815

Pruss S, Fraiser M, Bottjer D (2004) Proliferation of Early Triassic wrinkle structures: Implications for environmental stress following the end-Permian mass extinction. Geol 32:461–464

Pruss S, Corsetti F, Bottjer D (2005) The unusual sedimentary rock record of the Early Triassic: A case study from the southwestern United States. Palaeogeog, Palaeoclimatol, Palaeoecol 222:33–52

Pruss SB, Bottjer DJ, Corsetti FA, Baud A (2006) A global marine sedimentary response to the end-Permian mass extinction: Examples from southern Turkey and the western United States. Earth Sci Rev 78:193–206

Purser B (1973) The Persian Gulf: Holocene carbonate sedimentation and diagenesis in a shallow epicontinental sea. Springer-Verlag, New York

Raiswell R (1987) Non-steady state microbiological diagenesis and the origin of concretions and nodular limestones. Geol Soc Lond Spec Publl 36:41–54

Reid RP, Macintyre IG, Browne KM, Steneck RS, Miller T (1995) Modern marine stromatolites in the Exuma Cays, Bahamas: uncommonly common. Facies 33:1–17

Reid RP, Visscher PT, Decho AW, Stolz JF, Bebout BM, Dupraz C, Macintyre IG, Paerl HW, Pinckney JL, Prufert-Bebout L, Steppe TF, DesMarais DJ (2000) The role of microbes in accretion, lamination and early lithification of modern marine stromatolites. Nature 406:989–992

Reid RP, Dupraz C, Visscher PT, Sumner DY (2003) Microbial processes forming modern marine stromatolites: Microbe-mineral interactions with a three-billion-year rock record. Fossil and Recent Biofilms – A Natural History of Life on Earth, pp 103–118

Reineck H (1979) Rezente und fossile Algenmatten und Wurzelhorizonte. Nat Mus 109:290–296

Reineck H, Singh I (1986) Depositional sedimentary environments. Springer-Verlag, Berlin

Reineck HE, Gerdes G, Claes M, Dunaijtschik K, Riege H, Krumbein WE (1990) Microbial modification of sedimentary surface structures. In: Heling D (ed) Sediments and environmental geochemistry. Springer-Verlag, Berlin

Richter D, Herforth A, Ott E (1979) Brackish blue-green algal bioherms composed by *Rivularia* haematites in Pleistocene deposits of the Perechora Peninsula near Korinthos (Greece). Neues Jahrb Geol Palaontol 159(1):14–40

Round F (1981) The ecology of algae. Cambridge University Press, New York

Ruby E (1996) Lessons from a cooperative, bacterial-animal association: The *Vibrio fischeri-Euprymna scolopes* light organ symbiosis. Annu Rev Microbiol 50:591–624

Runnegar B, Fedonkin M (1992) Proterozoic metazoan body fossils. The Proterozoic Biosphere 369–388

Sarkar S, Banerjee S, Samanta P, Jeevankumar S (2006) Microbial mat-induced sedimentary structures in siliciclastic sediments: Examples from the 1.6 Ga Chohat Sandstone, Vindhyan Supergroup, M.P. India. J Earth System Sci 115(1):49–60

Schidlowski M, Hayes J, Kaplan I (1983) Isotopic inferences of ancient biochemistries – Carbon, sulfur, hydrogen, and nitrogen. In: Schopf J (ed) Earth's earliest biosphere: Its origin and evolution. Princeton University Press, Princeton

Schieber J (1989) Facies and origin of shales from the mid-Proterozoic Newland Formation, Belt Basin, Montana, USA. Sedimentol 36:203–219

Schieber J (1999) Microbial mats in terrigenous clastics; The challenge of identification in the rock record. Palaios 14:3–13

Schieber J, Bose F, Eriksson P, Banerjee J, Sakar S, Altermann W, Catuneanu D (2007) Atlas of microbial mat features preserved within the siliciclastic rock record. Elsevier Science, Oxford

Schooling S, Beveridge T (2006) Membrane vesicles: An overlooked component of the matrices of biofilms. J Bacteriol 188:5945

Schopf J, Packer B (1987) Early Archean (3.3-billion to 3.5-billion-year-old) microfossils from Warrawoona Group, Australia. Sci 237:70–74

Schopf JW, Kudryavtsev AB, Agresti DG, Wdowiak TJ, Czaja AD (2002) Laser-Raman imagery of Earth's earliest fossils. Nat 416:73–76

Schopf JW, Kudryavtsev AB, Czaja AD, Tripathi AB (2007) Evidence of Archean life: Stromatolites and microfossils. Precambr Res 158:141–155

Schultze-Lam S, Fortina D, Davisa BS, Beveridgea TJ (1996) Mineralization of bacterial surfaces. Chem Geol 132:171–181

Seilacher A (2007) Trace fossil analysis. Springer-Verlag, Berlin

Seilacher A, Reif W, Westphal F (1985) Sedimentological, ecological and temporal patterns of fossil Lagerstätten [and discussion]. Philos Trans R Soc Lond 311:5

Seong-Joo L, Browne K, Golubic S (2000) On stromatolite lamination. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Berlin

Stal L (2000) Cyanobacterial mats and stromatolites. In: Whitton B, Potts M (eds) The ecology of cyanobacteria: Their diversity in time and space. Kluwer Academic Publishers, Dordrecht

Stal L, Caumette P (1994) Microbial mats: Structure, development and environmental significance. Springer-Verlag, Berlin

Staley J, Bryant M, Pfennig N (1989) Bergey's manual of systematic bacteriology. Williams & Wilkins, Baltimore

Stanier R, Cohen-Bazire G (1977) Photosynthetic prokaryotes: The cyanobacteria. Annu Rev Microbiol 31:225–274

Stanier R, Adelberg E, Ingraham J (1976) The microbial world. Prentice Hall, Englewood Cliffs

Stolz J (2000) Structure of microbial mats and biofilms. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Berlin

Stoodley P, Sauer K, Davies DG, Costerton JW (2002) Biofilms as complex differentiated communities. Annu Rev Microbiol 56:187–209

Strasser A, Davaud E, Jedoui Y (1989) Carbonate cements in Holocene beachrock: Example from Bahiret el Biban, southeastern Tunisia. Sediment Geol 62:89–100

Strauss H (2003) Sulphur isotopes and the early Archaean sulphur cycle. Precambr Res 126:349–361

Summons R, Hope J, Logan G (1996) 2-Methylhopanoids as biomarkers for cyanobacterial oxygenic photosynthesis. Nat 400:554–557

Sumner D (2000) Microbial vs environmental influences on the morphology of Late Archean fenestrate microbialites. In: Riding R, Awramik S (eds) Microbial sediments. Springer-Verlag, Heidelberg

Sutherland I (1990) Biotechnology of microbial exopolysaccharides. Cambridge Univ Press, New York

Sutherland I (2001) The biofilm matrix–an immobilized but dynamic microbial environment. Trends Microbiol 9:222–227

Tait K, Sutherland I (2002) Antagonistic interactions amongst bacteriocin-producing enteric bacteria in dual species biofilms. J Appl Microbiol 93:345–352

Tebbutt G, Conley C, Boyd D (1965) Lithogenesis of a distinctive carbonate rock fabric. Rocky Mt Geol 4:1

Tolker-Nielsen T, Molin S (2000) Spatial organization of microbial biofilm communities. Microb Ecol 40:75–84

Urrutia M, Beveridge T (1994) Formation of fine-grained metal and silicate precipitates on a bacterial surface (*Bacillus subtilis*). Chem Geol 116:261–280

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

Vos P, De Boer P, Misdorp R (1988) Sediment stabilization by benthic diatoms in intertidal sandy shoals: Qualitative and quantitative observations. In: DeBoer P, et al. (eds) Tide-influenced sedimentary environments and facies. Reidel, Dordrecht

Walsh M, Lowe D (1985) Filamentous microfossils from the 3 500-Myr-old Onverwacht Group, Barberton Mountain Land, South Africa. Nat 314:530–532

Warren J (1999) Evaporites: Their evolution and economics. Blackwell, Oxford

Watermann F, Hillebrand H, Gerdes G, Krumbein WE, Sommer U (1999) Competition between benthic cyanobacteria and diatoms as influenced by different grain sizes and temperatures. Mar Ecol 187:77–87

Westall F, de Wit MJ, Dann J, van der Gaast S, de Ronde CEJ, Gerneke D (2001) Early Archean fossil bacteria and biofilms in hydrothermally-influenced sediments from the Barberton greenstone belt, South Africa. Precambr Res 106:93–116

Wharton R (1994) Stromatolitic mats in Antarctic lakes. In: Bertrand-Sarfati J, Monty C (eds) Phanerozoic stromatolites II. Kluwer, Dordrecht

Whitton B, Potts M (2000) The ecology of cyanobacteria: Their diversity in time and space. Kluwer Academic Publishers, Dordrecht

Wimpenny J, Manz W, Szewzyk U (2000) Heterogeneity in biofilms. FEMS Microbiol Rev 24:661–671

Wunderlich F (1979) Die Insel Mellum (südliche Nordsee), dynamische Prozese und Sedimentgefüge. I. Südwatt, Übergangszone und Hochfläche. Senck Marit 11:59–113

Yallop ML, de Winder B, Paterson DM, Stalb LJ (1994) Comparative structure, primary production and biogenic stabilization of cohesive and non-cohesive marine sediments inhabited by microphytobenthos. Estuar Coast Shelf Sci 39:565–582

Zhang X, Bishop P, Kupferle M (1998) Measurement of polysaccharides and proteins in biofilm extracellular polymers. Water Sci Technol 37:345–348

Zobell C (1946) Marine microbiology. The Chronica Botanica Co, Waltham

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