Sedimentary Controls on the Formation and Preservation of Microbial Mats in Siliciclastic Deposits: A Case Study from the Upper Neoproterozoic Nama Group, Namibia

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Shallow-marine, siliciclastic depositional systems are dominated by physical sedimentary processes, with penecontemporaneous cementation playing only a minor role in sediment dynamics. For this reason, microbial mats rarely form stromatolites in siliciclastic environments; instead, mats are preserved as wrinkle structures on bedding surfaces.

Microbial mat signatures should be widespread in siliciclastic rocks deposited before the Cambrian Period; however, siliciclastic shelf successions of the upper Neoproterozoic Nudaus Formation, Nama Group, Namibia, contain only sparsely distributed wrinkle structures. The facies distribution of observed structures reflects the superposition of a taphonomic window of mat preservation on the ecological window of mat development. Mat colonization is favored by clean, fine-grained, translucent quartz sands deposited at sites where hydrodynamic flow is sufficient to sweep mud from mat surfaces but insufficient to erode biostabilized laminae. During periods of reduced water agitation, microbial baffling, trapping, and binding entrain quartz grains into mat fabrics, increasing the thickness of the living mat layer. Mat preservation is facilitated by subsequent sedimentary events that bury the microbial structures without causing erosional destruction. Pressure originating from sediment loading forms molds and casts at bedding planes, inducing the formation of wrinkle structures.

In storm-influenced shelf successions of the Nudaus Formation, wrinkle structures are restricted to quartz-rich fine sandstone beds, 2–20 cm thick, that alternate with thin interlayers of sandy mud- or siltstones. Such a lithological facies developed only sporadically on the Nudaus shelf, but is common in shallow-marine siliciclastic rocks of older Neoproterozoic age exposed in the Naukluft Nappe Complex. The observed relationship between sedimentary environment and microbial mat preservation can be observed in other Proterozoic and Phanerozoic siliciclastic rocks, as well as in modern environments. This facies dependence provides a paleoenvironmental and taphonomic framework within which investigations of secular change in mat abundance must be rooted. Understanding the physical sedimentary parameters that control the formation and preservation of microbial structures in siliciclastic regimes can facilitate exploration for biological signatures in early sedimentary rocks on Earth or other planets.

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INTRODUCTION

Shallow marine sediments are widely colonized by epibenthic bacteria and cyanobacteria (e.g., Meadows and Anderson, 1966, 1968; Krumbein, 1983; Cohen et al., 1984; Gerdes and Krumbein, 1987; Cohen and Rosenberg, 1989; Golubic and Knoll, 1993; Riding and Awramik, 2000, and literature therein). In carbonate environments, microbial communities may facilitate penecontemporaneous cementation, leading to the accretion of stromatolites (for overviews, see Walter, 1976, 1994; Grotzinger and Knoll, 1999; Reid et al., 2000). Microbial mats also occur in siliciclastic systems, but these communities rarely build stromatolites. Rather, they impart a more subtle sedimentary signature in the form of wrinkle structures (term defined by Hagadorn and Bottjer, 1997; for overview on microbial mats in siliciclastic rocks see Schieber, 1998; contributions in Hagadorn et al., 1999; for modern counterparts see Gerdes et al., 2000; Noffke et al., 2001).

During the Proterozoic Eon, microbial carpets are thought to have induced biostabilized "mat grounds" in siliciclastic depositional areas that, like stromatolites in carbonate environments, covered large areas of the shallow seafloor (Seilacher and Pflueger, 1994; contributions in Hagadorn et al., 1999). A broad post-Proterozoic decline of stromatolites is generally attributed to grazing pressure and competition for space by diversifying metazoans (Garrett, 1970; Awramik, 1971; Moore and Fritsche, 1976; Walter and Heys, 1985; Semikhatov and Raaben, 1996), prompting the prediction that mat signatures in siliciclastic rocks should show a comparable record of decline (Seilacher and Pflueger, 1994; Pflueger and Gresse, 1996; Hagadorn and Bottjer, 1997, 1999; Gehling, 1999; Pflueger, 1999; Seilacher, 1999; Simonson and Carney, 1999). Evaluation of this prediction, however, demands that we understand the conditions under which microbial mats form and those under which they become preserved as wrinkle structures.

This paper reports on a geobiological investigation of siliciclastic deposits in the terminal Proterozoic Nama

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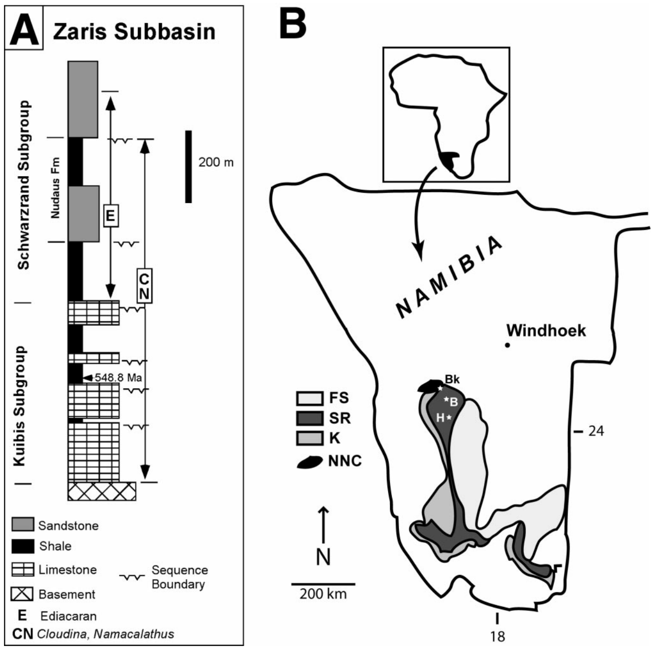


FIGURE 1—Study Location. (A) Generalized stratigraphy of the studied successions of the Nama Group (terminal Proterozoic to Cambrian), Namibia. (B) Map showing exposure area of Nama Group and localities discussed in the text. K=Kuibis Subgroup, SR=Schwarzrand Subgroup, FS=Fish River Subgroup, NNC=Naukluft Nappe Complex. Locations of measured stratigraphic sections, Nudaus Fm.: B=Bullsport, H=Harughas; unspecified Neoproterozoic age: Bk=Blasskranz.

Group, Namibia, as well as purportedly Vendian strata in the tectonically adjacent Naukluft Nappe Complex. Lithological data document (1) ecological parameters that controlled the development and distribution of microbial mats, and (2) the taphonomic path that led to the preservation of mat signatures. Together, these ecological and taphonomic windows are hypothesized to control the distribution of mat structures in siliciclastic environments.

GEOLOGICAL SETTING, STUDY LOCATIONS, AND METHODS

The Nama Group is a foreland basin succession deposited during collision and uplift of the Damara and Gariep belts near the center of Gondwana (Germs, 1983, 1995; Germs and Gresse, 1991; Gresse and Germs, 1993; Grotzinger et al., 1995; for tectonic evolution, see e.g., Miller, 1983). In most exposures, basal Nama sandstones rest on peneplaned crystalline basement, and most Nama rocks are only moderately deformed. The lower Nama Group is divided by a flexural high into the northern Zaris, and the southern Witput basins (Germs, 1974).

Stratigraphically, the Nama Group consists (from base to top) of the Kuibis, Schwarzrand, and Fish River subgroups (Germs, 1974, 1983; Germs and Gresse, 1991; Gresse and Germs, 1993; Germs, 1995; Fig. 1). Radiometric dates on intercalated ash beds, Ediacaran trace and body fossils, acritarch assemblages, and carbon-isotope profiles individually and collectively identify the Kuibis and most of the overlying Schwarzrand subgroups (Nudaus and Urusis formations) as terminal Proterozoic, or Neoproterozoic III in age (Germs et al., 1986; Grotzinger et al., 1995, 2000).

The focus of this study was rocks of the Nudaus Formation, a shallow-marine, storm-dominated succession within the lower Schwarzrand Subgroup of the Zaris Basin (Germs, 1983; Saylor et al., 1995, 1998; Grotzinger unpubl. observ.; Fig. 1A). The Nudaus Formation consists of the Niederhagen and the Vingerbreek members. In the southern part of the Zarin Basin, the Niederhagen Member is interpreted as a highstand deposit, whereas the Vingerbreek Member includes shallowing-upward cycles deposited in a transgressive systems tract (Saylor et al., 1995). Both members include two sequences of nearshore to mid-shelf shale, siltstone, and sandstone beds topped by pro-deltaic sandstones (Saylor et al., 1995). Three stratigraphic sections in the northern Zaris Basin were measured in outcrops on the farms Bullsport (Niederhagen Member) and Harughas (Vingerbreek Member) (Fig. 1B). Older Neoproterozoic siltstones and sandstones of isolated stratigraphic position that crop out in the area of the farm Blasskranz also were investigated (Fig. 1B). These rocks belong to the Pavian Nappe within the Naukluft Nappe Complex, considered by Hoffmann (1989) to be "lower Vendian," and occur in a succession that contains glacially influenced strata.

RESULTS

Stratigraphic Sections of Bullsport (I) and Harughas (II)

Section I, Bullsport

A 32-m stratigraphic section through the Niederhagen Member was measured near the Bullsport farmhouse. The succession occurs in a structurally overturned position beneath the Naukluft Nappe Complex (Fig. 2). Lithology and sedimentary structures document deposition within a storm-dominated shelf environment. Thick and massive, mature quartz sandstone beds mark the base and the top of the section, whereas a monotonous succession of sandy shales intercalated with fine sandstone beds dominates the middle part (Fig. 2).

The basal part of the section includes: (1) two minor upward-thickening parasequences that contain sandy shales and planar-laminated, fine sandstone beds; and (2) amalgamated, hummocky cross-stratified quartz sandstone beds 40 to 160 cm thick. The fine sandstone beds are composed of about 97% angular quartz grains, with about 3% mica; they are about 5–12 cm thick and display current ripple marks on upper bedding surfaces, as well as 0.5–1.5-cm mud clasts on bed soles. The fine sandstone beds alternate regularly with finely laminated sandy shales, forming 0.5–10-cm couplets.

Above these basal beds follow thinly laminated sandy shales that give the succession a homogeneous appearance. Only a few, 2-to-10-cm-thick, fine sandstone beds occur in alternation with 5-to-10-cm-thick, shaly interlayers. The middle part of the succession is truncated by thick (up to 2 m) mature quartz sandstone beds marked by hummocky cross-stratification. The top of the section contains three minor upward-thickening parasequences, much like those of the section's base.

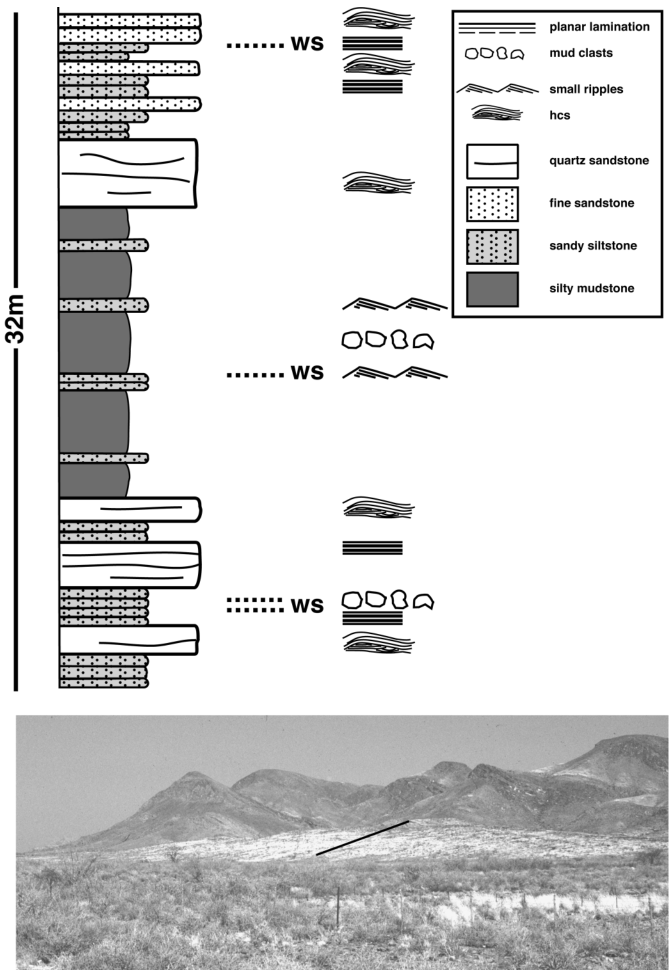


FIGURE 2—Measured stratigraphic section of the Nudaus Formation at Bullsport. Photograph shows study site at southern rim of Naukluft Nappe Complex, and the path of measured section. WS= wrinkle structures.

Section II, Harughas

A stratigraphic section of about 78 m was measured near the mountain "Sattelberg" on the Harughas farm (Fig. 3). Geomorphologically, the sandy siltstones form gentle slopes, whereas the quartz sandstones produce the characteristic flat-topped summits of the hills (Fig. 3). As at Bullsport, these sediments were deposited on a storm-dominated shelf. The section at Harughas records three major upward-thickening parasequences that coarsen from sandy siltstones through fine sandstone beds, to thick, amalgamated quartz sandstones (Fig. 3). Furthermore, six minor parasequences can be distinguished within the entire section. The sandy siltstones that form the lower, monotonous parts of the major parasequences are finely laminated and show no other physical sedimentary structures. Higher in the section, the sand content of the shales increases, and thin sandy beds with rippled surfaces become more abundant. Planar or wavy lamination is visible only in thicker sandy beds.

The fine sandstone beds of the middle parts of the parasequences have sharp planar bases and rippled tops. Their internal structures are dominated by wavy or plane lamination. Mud clasts are commonly observed on bed soles. The sandstone is composed of about 95% angular quartz grains and 5% mica. The 2-to-20-cm-thick beds alternate with siltstone layers a few to a maximum of 15 cm thick. Some of the sandstone beds contain the Neoproterozoic fossil *Archaeichnum* (Glaessner, 1963) preserved three-dimensionally as hollow or infilled tubes up to 4 cm long and 0.5 cm thick.

Sedimentary structures are not commonly visible in the massive, mature quartz sandstone units; nonetheless, parting lineation, planar lamination, and well-developed hummocky cross-stratification are all present. The massive appearance reflects the homogeneity of grain sizes and composition. The beds are from 40 to 200 cm thick. The most prominent unit of this rock type forms the top of the third major parasequence.

Within Section II, a thin interval of wrinkle structure-bearing rocks was measured in greater detail (Fig. 3, compare lithology in Fig. 6). The detailed section is 1.90 m thick and consists of silty mudstones, sandy siltstones, and fine sandstones.

Lithofacies in Sections I and II

The stratigraphic sections record three different lithofacies types (Fig. 4A, B) defined by prevailing depositional energy. The lithofacies types correspond to three main environmental zones (I-III) of the shelf.

Lithofacies I is dominated by fine-grained background sedimentation recording an offshore environment of generally low hydrodynamic energy (Fig. 4A, B). About 80–85% of the strata are sandy siltstones; the remainder are fine sandstone beds 2–15 cm thick. In the fine sandstone beds, minor bottom currents are indicated by a few symmetric or asymmetric, small-scale current ripples, along with small (0.5–1 cm) mud clasts. Little evidence of storm-induced sediment reworking is observed.

Lithofacies II is characterized by a higher abundance of fine sandstone beds (35–75%) that alternate regularly with shales (22–47%) (Fig. 4A, B). Mature quartz sandstone event beds (2–17%) also occur. The fine sandstone beds are 2–25 cm thick and exhibit planar lamination, ripple marks, and abundant mud clasts of larger sizes. They indicate moderate hydrodynamic reworking in a depositional environment below fair weather- and above storm-wave base.

Lithofacies III consists of mature quartz sandstone beds up to 2 m thick (33–66%) that record major storm events in a shallow, high-energy depositional environment. Shales (1–6%) and fine sandstones (26–64%) are relatively minor lithologies within this lithofacies (Fig. 4A, B).

Wrinkle Structures of Stratigraphic Sections I (Bullsport) and II (Harughas)

Occurrence of Wrinkle Structures in the Stratigraphic Successions

In both stratigraphic sections, wrinkle structures occur only within lithofacies II, that is, in depositional environments marked by moderate erosional and depositional energy (Fig. 4A, B).

At Bullsport, fine sandstone layers in both the basal and

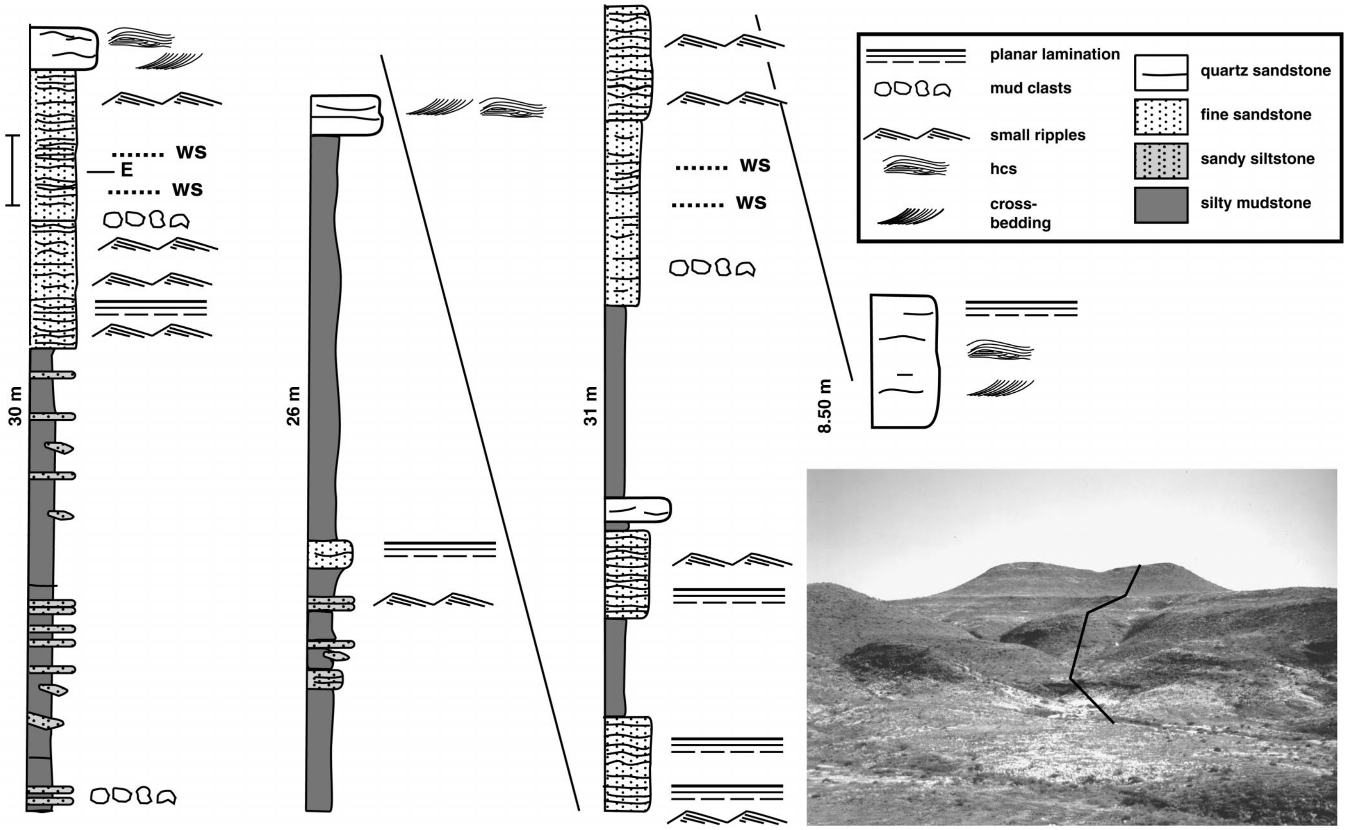


FIGURE 3—Measured stratigraphic section of the Nudaus Formation at Harughas. Photograph shows study site and the path of measured section. Sandy siltstones form gentle slopes, whereas thick sandstones produce the flat-topped summits of the hills. WS= wrinkle structures; E= Ediacaran fossils. Note location of detailed section (bar) shown in Fig. 6.

upper parts of the section are covered by wrinkle structures, as are some beds in the middle portion. Despite this mode of occurrence, however, wrinkle-marked beds make up no more than about 3% of the whole succession. All wrinkle structure-bearing beds are fine sandstones 5–12 cm thick (with one 20-cm-thick outlier) that are interbedded with 5-to-15-cm siltstone and shale layers (Fig. 5).

At Harughas, fine sandstone beds in the middle parts of the parasequences have wrinkled surfaces. The thicknesses of wrinkle structure-bearing beds range from 3 to 17 cm (Fig. 5), and intercalated 0.5-to-7-cm-thick siltstone layers are characteristic. Wrinkle structure-bearing beds make up less than 1% of the whole succession.

Within the detailed stratigraphic section at Harughas, wrinkle structures can be found in 2-to-17-cm-thick, fine sandstone beds that alternate with sandy, finely laminated siltstones 0.5 to 5 cm thick (Fig. 5). The fine sandstone is mature, containing 99% angular quartz grains (mean grain size 137 μm; range 90–300 μm). Within this limited section, wrinkle structures are relatively common; wrinkled rock layers comprise 26% of all strata.

Types of Wrinkle Structures

Within the detailed stratigraphic section at Harughas, we found 25 specimens of wrinkle structures (Fig. 6; compare Fig. 3 for location). The structures vary widely in appearance; nonetheless, they can be grouped into two main types. Type A are wrinkles composed of casts and molds that cover but do not obscure ripple marks of the original sediment surface that provided substrates for mat development. One example (specimen i, Fig. 6; Fig. 7A) shows very fine, irregular crinkles that cover a subjacent rippled surface like a skin. Other examples (specimens ii and iii, Fig. 6; Fig. 7B) reflect more fulsome mat development that has partially but not completely smoothed the underlying ripple surface. Round structures that could record microbial overgrowth of an Ediacaran organism were found on one wrinkled bedding plane (Fig. 7B).

In Type B wrinkle structures, no antecedent bedding surface morphology is visible beneath the crinkled mat (e.g., specimens iv, v, and vi in Fig. 6; Figs. 7C, D). Figure 7C shows a regular pattern of shallow casts and molds on an otherwise planar bedding surface. In contrast, the bedding surface illustrated in Fig. 7D appears to be irregularly folded like a tissue; crinkle crests are 0.5–2 mm high.

Textures of Wrinkle Structures in Thin-section

In thin-section view, wrinkled surfaces are marked by dark clay-rich laminae about 5 μm thick (Fig. 8A). Commonly, the dark laminae increase in number toward wrinkled bedding surfaces; laminae can show high inheritance or micro-unconformities. Within thicker parts of the laminae, single grains 'float' independently in the opaque matrix (Fig. 8B). In other instances, the laminae form a distinctive mesh-like microfabric around entangled mineral grains (Fig. 8C).

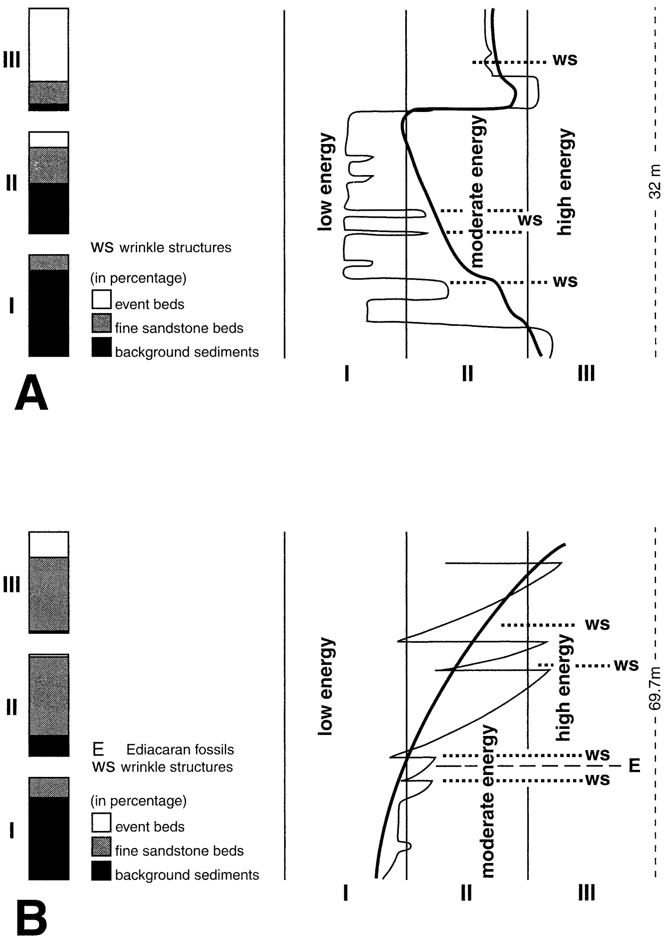


FIGURE 4—Lithofacies types found in stratigraphic sections Bullsport (A) and Harughas (B), Nudaus Fm., Nama Group, Namibia. The stratigraphic section Bullsport (A) shows thickening-upward parasequences at the base and the top, and a thinning-upward parasequence in the middle part of the succession. The stratigraphic section Harughas (B) shows 3 major thickening-upward parasequences recording an overall trend of increasing hydrodynamic energy. At both sections, lithofacies types are defined by depositional energy and correspond to 3 main zones (I-III) within a storm-influenced shelf. I- offshore, low hydrodynamic energy; II- shallow shelf beneath fair weather and above storm wave base, moderate hydrodynamic energy; III- shallow shelf above fair weather wave base, high hydrodynamic energy. Wrinkle structures (WS) and Ediacaran fossils (E) occur at paleoenvironments of moderate hydrodynamic reworking (lithofacies II).

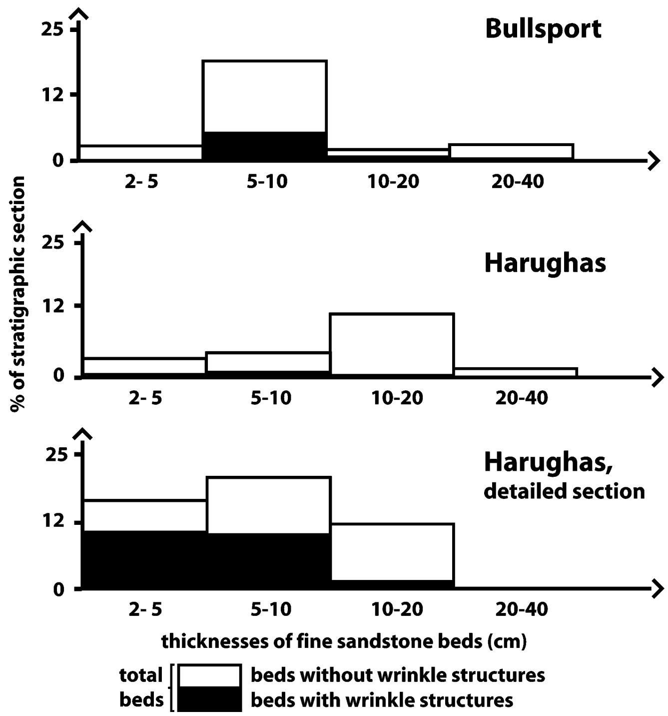


FIGURE 5—Distribution of wrinkle structures as a function of the bedding thickness of fine sandstones in stratigraphic sections at Bullsport and Harughas (including the detailed section at Harughas). Wrinkle structures occur mainly in fine sandstone beds 2–12 (maximum 20) cm thick.

DISCUSSION

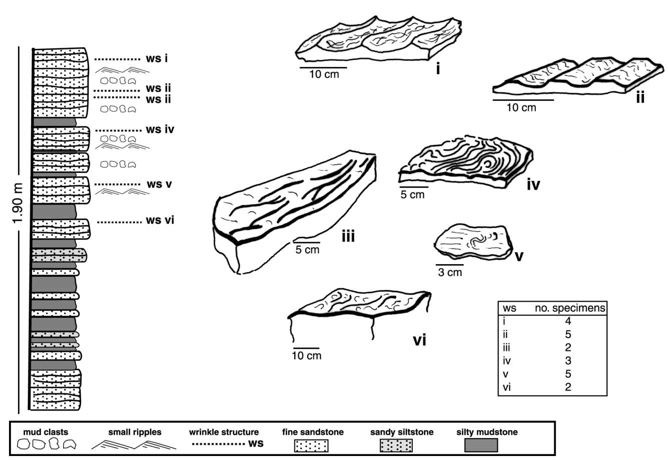
Sedimentological Parameters Controlling Microbial Mat Development and Preservation

Despite an expectation that mat signatures should be widespread in Precambrian siliciclastic rocks, wrinkle structures are rare in the Nudaus Formation. Observed structures are confined to a specific sedimentary facies (Fig. 9) that reflects both ecological conditions favoring microbial mat development and taphonomic conditions that facilitate microbial mat preservation.

Microbial Mat Development: The Ecological Window

In modern environments, mat development is restricted by grazing, bioturbation, and competition for space (including space occupation by algae and halotolerant vascular plants). Even where mats do form, however, sediment surfaces are not ubiquitously covered. Mat-building populations show distinct environmental preferences with respect to substrate and hydrodynamic regime (Noffke, 1997, 1998, 1999; Noffke and Krumbein, 1999; Noffke, in press).

Filamentous mat-builders shelter their substrate against erosion by entangling sand and silt grains along



ws	no. specimens
i	4
ii	5
iii	2
iv	3
v	5
vi	2

FIGURE 6—Detailed stratigraphic section of a part of the Nudaus Formation at Harughas. Wrinkle structures (ws) range from 'transparent' (rippled depositional surfaces visible below crinkles; i-iii) to 'non-transparent' (depositional surface underneath crinkles not visible; iv-vi).

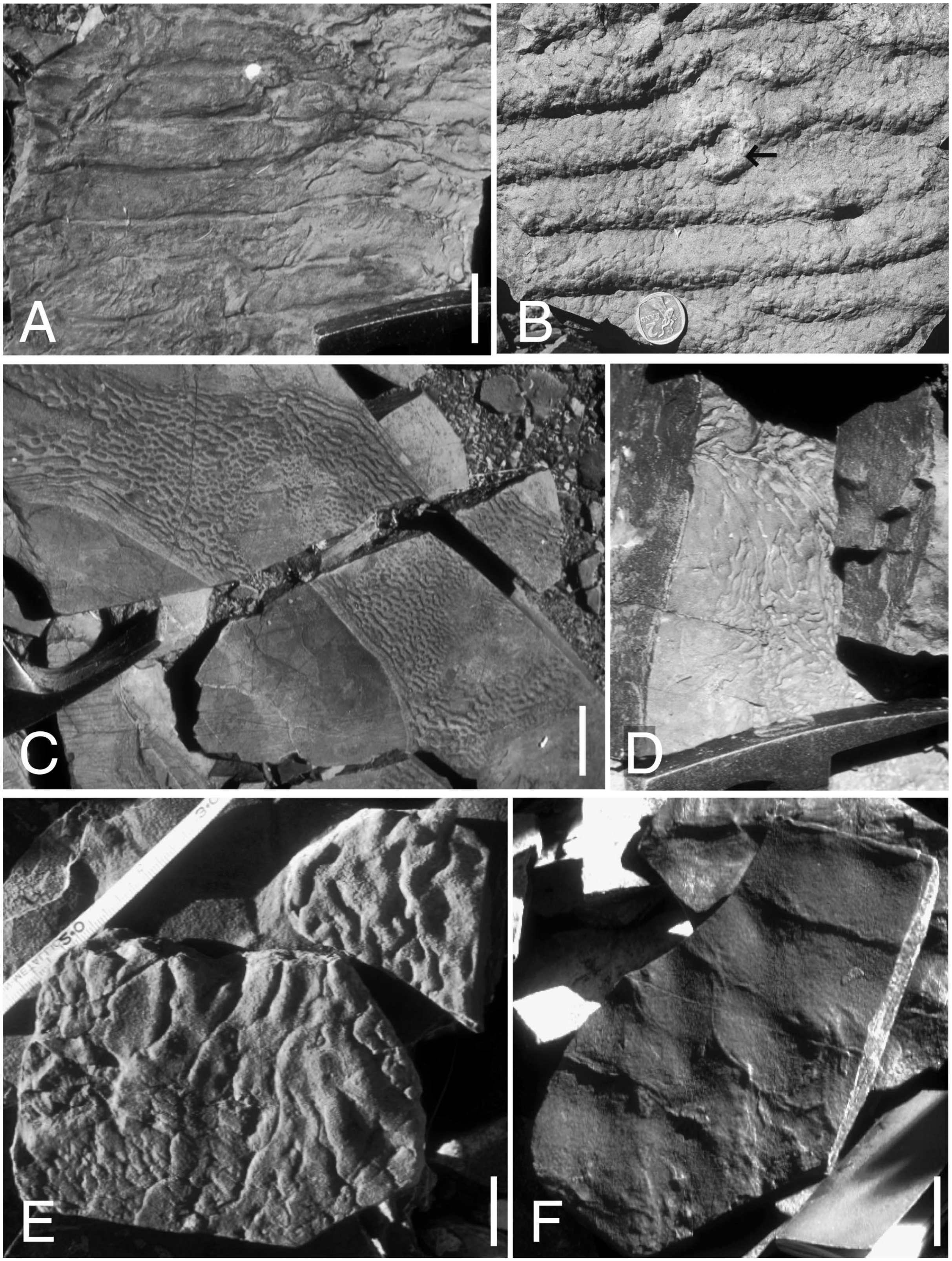


FIGURE 7—Wrinkle structures (ancient microbial mats) from stratigraphic sections at Harughas (A-D) and Blasskranz, Naukluft Nappe Complex (E-F). (A) Transparent wrinkle structure: ripple marks of the ancient depositional surface are visible underneath the wrinkles. Scale: 5 cm. (B) Transparent wrinkle structure showing rounded trace fossils on top. Scale: 2 cm. (C) Non-transparent wrinkle structure: no structures of the depositional surface are visible underneath crinkles. Note regular pattern of molds and casts. Scale: 4 cm. (D) Non-transparent wrinkle structures with irregular molds and casts. Hammer for scale. (E) Non-transparent wrinkle structures with significant crinkles of 0.5 to 2 mm heights. Scale: 5 cm. (F) α-petees. Scale: 5 cm.

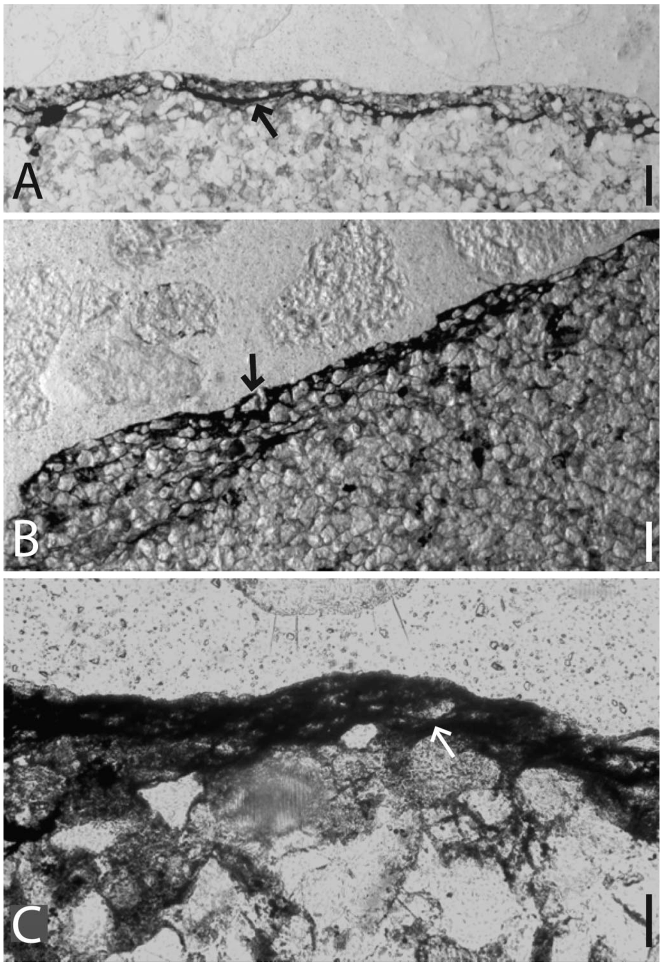


FIGURE 8—Textures of wrinkle structures in thin-sections of beds with wrinkle marks, Nudaus Formation. (A) Dark clay-rich laminae separate sandy interlayers of different grain textures. Scale: 0.5 cm. (B) Single quartz grains 'float' independently from one another in the dark clay-rich matrix. Scale: 0.5 cm. (C) Possible mat fabrics (arrow) woven about sand grains. Vertical section through wrinkle structure. Scale: 2 mm.

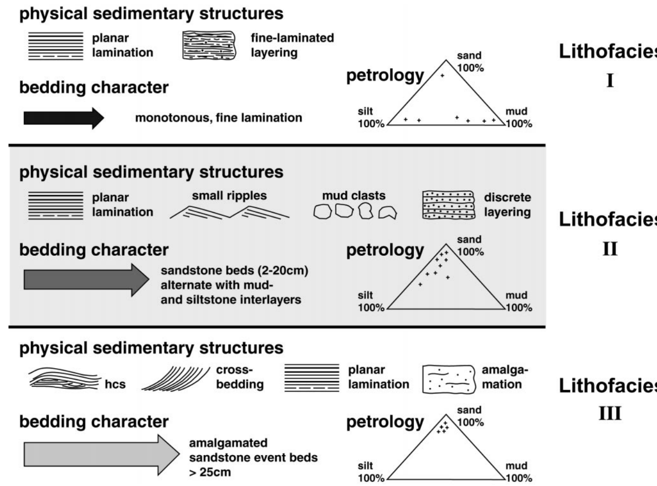


FIGURE 9—Sedimentary parameters define the ecological and taphonomic window of mat development. Lithofacies types I-III are recorded by physical sedimentary structures, bedding type, and petrological composition of sediment. The ecological and taphonomic window of microbial mat development and preservation conforms with lithofacies II.

the sediment surface (Noffke, 1998; Noffke and Krumbein, 1999; Noffke, in press). The microbes also secrete extracellular polymers that further increase the cohesion of surficial sediments (Decho, 1990, 1994, 2000). The resulting biostabilization can be significant, as measured in Recent tidal environments where mat-secured sands are up to 10-fold more resistant to erosion than non-colonized sands (Führboeter and Manzenrieder, 1987; Yallop et al., 1994; Paterson, 1997). Under moderate hydrodynamic conditions, thick mats can build up. In contrast, in environments characterized by large-scale or persistent disturbance, only thin biofilms develop (Noffke, 1998; Noffke and Krumbein, 1999; Noffke, in press). Moderate reworking does not move bacterially bound sand grains, but nevertheless prohibits the deposition of mud that might seal potential photosynthetic mat builders from light.

Deposition, especially of translucent quartz grains, triggers upward growth of microbial mats, producing thicker piles of mat laminae (Gerdes and Krumbein, 1987; Gerdes et al., 1991; Noffke et al., 2001). When ambient hydrodynamic energy is low, microbial mats can facilitate sediment accumulation. The cyanobacterial filaments orient themselves perpendicular to the mat surface, reaching upward into ambient water. In doing so, they form small-scale obstacles that baffle bottom currents like a comb. By producing microzones of reduced current velocities, the filaments cause suspended particles to fall on the mat surface. Grains thus "trapped" become incorporated into the fabric of the growing mat, a microbial effect well known as "baffling, trapping, and binding" (classical description in Black, 1933; for siliciclastic sediments see Noffke et al., 1997a,b; Gerdes et al., 2000).

Sand grains that appear to "float" in a finer-grained mat matrix are common features of Recent mats (Noffke et al., 1997a). The particles are either pulled upward from the substrate (oriented grains, Noffke et al., 1997a) or rain onto the surface from above. Because the penetration depth of light limits the thickness of mat laminae, high amounts of incorporated quartz grains increase the thickness of the living microbial mat.

In the Nudaus Fm., favorable ecological conditions for the development of microbial mats are recorded by lithofacies II, which displays moderate intensity erosional and depositional dynamics similar to those that promote mat development in Recent environments (Fig. 9). Such favorable dynamic conditions are indicated by physical sedimentary structures like planar or wavy lamination, small-scale ripple marks, and mud clasts. Regularly alternating sedimentary dynamics produced sandstone beds of 2–20 cm thickness intercalated by thin, sandy siltstone layers. As occurs in modern settings, the ancient microbial mats are found exclusively in sandstone beds composed principally of clear, fine-grained quartz grains. Of interest are the textures visible in thin sections through wrinkle structures (Fig. 8). In modern mats, sets of different grain textures similar to those shown in Fig. 8A result from biostabilization that counteracts erosion by cannibalism during deposition of sediment onto a mat layer (Noffke et al., 1997a). Grains pushed upward during microbial mat growth are also apparent in thin sections through Nama wrinkle structures (Fig. 8B).

Conversely, microbial mats did not develop in either lithofacies I or lithofacies III, which were characterized by very low or very high current velocities and sediment fluxes, respectively (Fig. 9). In lithofacies I, a continuing fall-out of mud- or silt-sized particles characteristic of quiet water environments produced the finely laminated, regularly bedded shales (Fig. 4). Bottom reworking by traction currents was rare. In contrast, major reworking and amalgamation formed the thick units of mature quartz sands characteristic of lithofacies III. In these beds, physical sedimentary structures like HCS are typical (Fig. 4).

Studies in modern environments show how mobile cyanobacteria react to mechanical disturbance of the mat surface (Villbrandt, 1992). When objects like semisessile macroorganisms are placed on top the mat surface, the cyanobacteria move away and start to grow around the obstacle. By this mechanism, the shape of the obstacle can become imprinted by the mat surface. This behavioral response can explain the round structures illustrated in Fig. 7 B.

Actualistic investigations suggest that the conditions for mat growth apparently are best only when hydrodynamic energy, rate of deposition and sediment composition were all optimal. In concert, therefore, these sedimentological parameters define the "ecological window" of microbial mat development (Fig. 9). In the Nudaus sections, only about 1–3% of the beds examined in continuous vertical succession were found to contain evidence of ancient microbial mats.

Microbial Mat Preservation by Formation of Wrinkle Structures: The Taphonomic Window

The wrinkle structures observed in this study are interpreted as load structures (sensu Kuenen, 1953) arising from the deformation of a hydroplastic sediment in response to loading pressure originated by freshly deposited sediment (physical processes described by Potter and Pettijohn, 1977; Allen, 1985; Pye, 1994). Wrinkle-structure formation additionally reflects the interaction of two different materials. The fluid-rich microbial extracellular polymeric mucilages of the mat show hydroplastic deformation under pressure. Conversely, the water content of non-colonized sands or silt is low. As a response to sudden depositional loading pressure, the degree of liquifaction within the mats must have risen greatly; escaping water formed channels, and the moving water-rich mass induced protrusions that projected upward from the mat surface to displace overlying sediment. Particle movement was highest in these protrusions, where strong pressure resulted in the growth of crests. By this mechanism, the interface between the fluid-rich mass of microbial mats and the freshly deposited sediment was arranged into casts and molds (compare Fig. 7C). After sediment consolidation, such casts and molds were preserved along bedding planes (for the role of cyanobacteria in bedding-plane formation itself, see Noffke, in press). Our interpretation of wrinkle structures as loading structures differs from the idea proposed by Pflueger (1999). In his appealing model, he deduces that 'Kinneyia', a pattern of elongated grooves and casts on upper bedding planes, formed from gas bubbles entrapped underneath a sealing microbial mat layer atop the sediments. In our case, the irregular geometry of the wrinkles on bedding planes does not support this model of formation.

Transparent wrinkle structures (type A) result when thin microbial mats did not fill in the antecedent surface relief of the substrate. Such thin biofilms or mats imprint an antecedent surface morphology without altering the original relief (Noffke et al., 1996; Gerdes et al., 2000; Noffke et al., 2001). Conversely, non-transparent wrinkle structures (type B) that smooth over the antecedent, physical sedimentary surface (compare Fig. 7 C, D, E) originated as thick microbial mats that obscured any influence of substrate surface on the load pattern. In the Recent, the process of microbes overgrowing depositional surfaces and forming a complete planar mat surface over time is termed 'microbial leveling' (Noffke et al., 2001).

Observations of the detailed stratigraphic section at Harughas, (Fig. 4) show that only a very specific succession of sedimentary events leads to formation and preservation of wrinkle structures in this outer shoreface environment (Fig. 10; for lithology compare Fig. 9). The first stage is deposition of sediment of appropriate grain size (fine sand) that facilitates the establishment of bacterial carpets. During a period of no sedimentation and no disturbance by water agitation, a microbial mat develops and expands across the depositional surface (stage 2). In some cases, the mat becomes enriched in mineral particles by baffling, trapping, and binding. The bacterial community must then become buried suddenly by a layer of sediment thick enough to block continued photosynthesis by the covered microorganisms and to prevent even mobile species from migrating upward toward the new depositional surface (stage 3). Sedimentation must occur without erosion or cannibalism; otherwise, the surface-stabilizing microbial carpets will be destroyed. Thus, grain-sizes in the overlying sediments tend to be finer or, at most equivalent, to those of the mat substrate, recording a degree of hydrodynamic reworking too low to disturb the underlying surface. During the final stage (4), further sedimentation generates loading pressure that enhances dewatering and crinkling of the buried microbial mat, and casts and molds are formed at the bedding plane during later diagenesis. Only when this succession of depositional events was complete, did wrinkle structures form and preserve. Therefore, these sedimentological parameters define a narrow taphonomic window for wrinkle structures.

Bringing the Ecological and Taphonomic Windows into Alignment

Favorable Ecological and Taphonomic Conditions for Microbial Mat Development and Preservation: The Siliciclastic Succession at Blasskranz

In contrast to the Nudaus sections at Bullsport and Harughas, shallow-marine siliciclastic rocks of the Naukluft Nappe Complex exposed on Blasskranz farm (see Fig. 1B) contain abundant mat structures that record the repeated confluence of favorable ecological and taphonomic conditions for wrinkle structure development and preservation. These rocks are inferred to be of shallow-marine origin. More specific interpretation is not possible owing to limit-

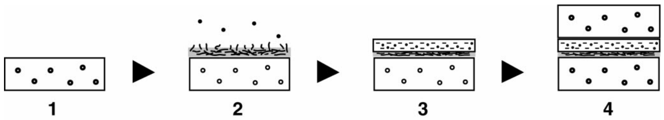


FIGURE 10—Taphonomic path of microbial mat preservation in siliciclastic environments. A distinct succession of subsequent sedimentary events is necessary to produce wrinkle structures: (1)- deposition of fine sand of optimal grain size for cyanobacterial colonization. (2)- period of no sedimentation during which microbial mat is established. Baffling, trapping and binding of suspended mineral particles contributes to increased mat thicknesses and a higher degree of biostabilization. (3)- sudden burial of epibenthic community by finer grained deposits, without erosion of buried mat surface. (4)- pressure from sediment loading forms wrinkle structures along bedding plane. Not drawn to scale.

ed outcrop exposure and the isolated nature of the outcrop with respect to both adjacent strata and its structural position within the Naukluft Nappe Complex. The strata that were examined are structurally, and perhaps stratigraphically, overlain by rocks of glaciogenic origin.

Stratigraphic Section (III), Blasskranz

The section (Fig. 11A) is 7.2 m thick. Thick beds of consolidated conglomerate occur at its base and top. The conglomerates are poorly sorted, with subangular to well rounded clasts. The middle part of the section is a 3.8-m-thick pile of regularly alternating, thin sand- and siltstones. Within this middle interval, four minor thinning-upward parasequences can be distinguished (Fig. 11A). No macrofossils have been observed.

The fine sandstone beds are composed of about 94% angular quartz grains, as well as mica, feldspar, and heavy minerals. The average grain size is 102 μm (range = 90–250 μm); bed thickness ranges from about 0.5 to 4 cm. The beds are planar and weather into even plates of decimeter dimensions. The fine sandstones alternate regularly with sandy siltstone layers 0.5 mm to 2 cm thick. Toward the top of the succession, the sandstones coarsen, displaying both ripple marks and crossbedding, and intercalated conglomerates are increasingly common. Meter-thick conglomerate beds cap the succession.

In this stratigraphic section, three main lithofacies types that record different levels of sediment flux and hydrodynamic energy are identified (Fig. 11B). The interbedded thin sandstones and sandy siltstones (lithofacies I) record an environment of moderate hydrodynamic reworking. Sands were transported by low-velocity traction currents, whereas the fine-grained fraction of the sandy siltstone interlayers was suspended in the water column and deposited only following waning of the traction currents. Stronger, wind-driven flows produced the coarser-grained sand beds that display both unidirectional and wave oscillation ripples. Lithofacies I contains ca. 38% sandy siltstone and 62% fine sandstone.

The thinning-upward sequences of the silt-rich lithofacies II record a migration of the depositional area towards a more distal setting. Whereas silt was deposited steadily, the input of sandy sediment was less than in lithofacies I. Reworking by wave action was rare, as documented by paucity of ripple cross-stratification. Conversely, finely laminated siltstone beds predominate. Lithofacies II is characterized by 57% siltstone, forming layers up to 7 cm thick, and 43% fine sandstone. Strongly increasing depositional energy is recorded by conglomerate beds that are typical for lithofacies III.

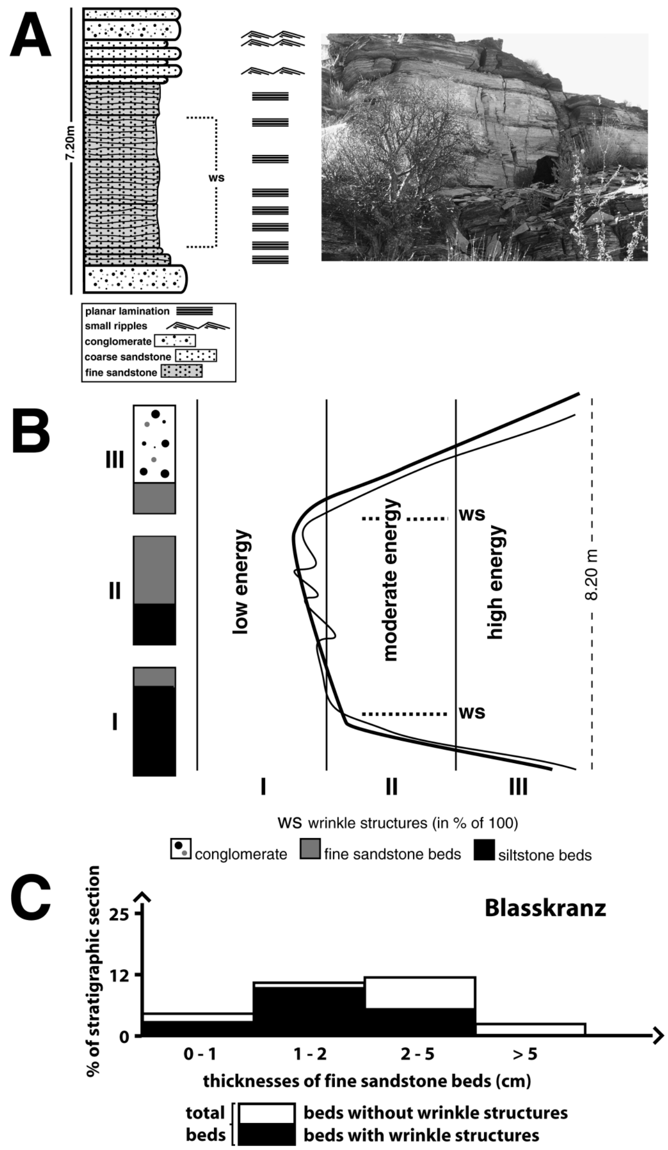


FIGURE 11—Measured stratigraphic section of Neoproterozoic siliciclastic rocks at Blasskranz, NNC, Namibia. (A) Cross-section of succession. Photograph shows outcrop. Note thin, planar sandstone beds that regularly alternate with sandy siltstone interlayers. The succession contains abundant wrinkle structures (WS), suggesting optimal ecological and taphonomic conditions. (B) Lithofacies types found in the stratigraphic section at Blasskranz. The middle part of the succession includes four minor parasequences. The bases and middle portions of the sequences (lithofacies I) record moderate hydrodynamic energy, and wrinkle structures (WS) are abundant. The top of the sequences document deposition in quiet water (lithofacies II), and wrinkle structures are less common. The stratigraphic section contains conglomerate at its base and top (lithofacies III), indicating high-energy deposition; no wrinkle structures occur in these beds. (C) Distribution of wrinkle structures related to bed thicknesses in the stratigraphic section at Blasskranz. Wrinkle structures occur mainly in fine sandstone beds 0.5–2.5 cm thick.

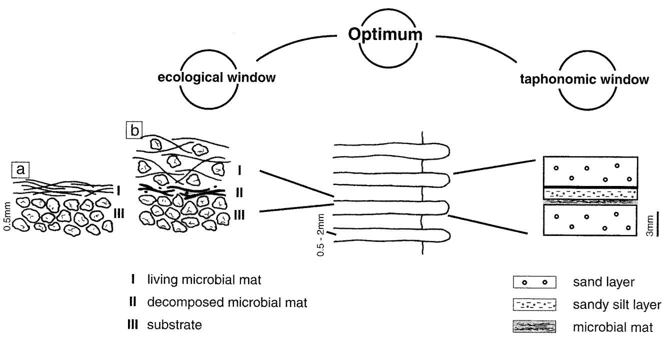


FIGURE 12—Occurrence and preservation of microbial mats under optimal conditions, recorded within the stratigraphic section at Blasskanz. The optimal ecological window is defined by a substrate of 'clear,' fine-grained sandstones appropriate for colonization by photosynthetic microbes. Initially, thin microbial mat layers (a) thicken through the incorporation of quartz grains into the mat fabrics by baffling, trapping, and binding. The translucent quartz grains channel light into deeper parts of the mat and thus contribute to increased mat thickness (b). Erosion by bottom currents was subordinate to biostabilization, but water movement was sufficient to prohibit deposition of inhibitory mud-sized particles on the mat surface. However, sudden burial of the microepibenthos led to *in situ* preservation of mat communities. Repetition of the complete succession of subsequent sedimentary events necessary for wrinkle structure formation (optimal taphonomic path, compare Fig. 10) leads to an abundance of mat signature-bearing bedding planes in the stratigraphic section.

Wrinkle Structures of Section III (Blasskranz)

As at Harughas and Bullsport, type A (transparent) and type B (non-transparent) wrinkle structures can be observed at Blasskranz. Type B wrinkle structures are particularly well developed here (Fig. 7E). A third wrinkle structure (type C) α-petees (sensu Reineck et al., 1990), is found only at this site. There are interpreted as overfolded soft-mat margins (Fig. 7F). Like non-transparent wrinkle structures, petees rise from thick microbial mats.

Unlike the stratigraphic sections at Bullsport and Harughas, the Blasskranz succession contains abundant wrinkle structures. Nearly 70% of all fine sandstone beds (35% of all rock strata) are wrinkled. In particular, within lithofacies I, nearly every 0.5-to-2.5-cm-thick, fine sandstone layer is covered by wrinkle structures (Fig. 11C). Grains within the mature, fine sandstones are clean and translucent, and the rock beds alternate very regularly with sandy siltstone interlayers a few mm to cm thick. Microbial mats are less abundant in lithofacies II, and no examples have been observed in lithofacies III.

Observed differences between the Nudaus and Nama Naukluft successions with respect to the abundance of mat signatures can be understood in terms of the previously discussed environmental windows for mat development and preservation. At Blasskranz, clean quartz sands of appropriate grain size spread repeatedly across the seafloor, facilitating bacterial colonization. Siliciclastic influx was episodic and limited in volume, allowing initially thin microbial mat layers to thicken by incorporating light-channeling mineral particles into the mat fabrics (Fig. 12). Ambient currents were too weak to erode mat layers, but strong enough to sweep potentially lethal muds from mat surfaces. Episodic influxes of sandy silt buried and preserved the mats. The succession of sedimentary events necessary for wrinkle-structure formation (compare Fig. 10) occurred repeatedly, giving rise to the wrinkle-rich interval preserved in these Naukluft strata (Fig. 12).

Toward a Global Explanation of Wrinkle-Structure Distribution

Given the older age of the Blasskranz section and uncertainities of more specific environmental interpretation, we cannot eliminate the possibility that the dawn of animal or macroalgal evolution interfered with mat development, resulting in a paucity of wrinkle structures in the younger Nudaus section. Nevertheless, the abundance of wrinkle structures in the Blasskranz section is consistent with predictions drawn from our observations in the Nudaus section, that a balance between hydrodynamic energy, sediment flux, and sediment composition is required to promote and preserve microbial mats. Together, the Nudaus and Blasskranz successions provide support for the hypothesis that ecological and taphonomic windows in tandem govern the distribution of microbial mat signatures in siliciclastic rocks.

This superimposition of ecological and taphonomic windows appears to explain the abundance of mat structures in other successions, including the terminal Proterozoic Ust-Pinega Formation, White Sea, Russia (Fedonkin, 1992; Runnegar and Fedonkin, 1992); the approximately coeval Wilpena Group, South Australia (Gehling, 1999); and terminal Proterozoic silicilcastics of the Great Basin, USA (Hagadorn and Bottjer, 1997). Phanerozoic occurrences appear to follow similar rules of formation and preservation; examples include the Cretaceous Dakota Sandstone, Colorado (McKenzie, 1968); a number of Cambrian sucessions in North America (Hagadorn and Bottjer, 1997); the Silurian of Libya (Pflueger, 1999); and the Ordovician of the Montagne Noire, France (Noffke, 2000, in press).

An observed paucity of wrinkle structures in Cambrian and younger siliciclastic successions led Seilacher and Pflueger (1994; see also Hagadorn et al., 1999) to hypothesize that radiating metazoans restricted the distribution of microbial mats to extreme biotopes in the Phanerozoic. Our experience in the Nama Group indicates that preserved mat structures can be rare in Proterozoic successions for reasons other than competition or grazing, requiring that evolutionary arguments be based specifically on facies where one would expect wrinkle structure to be found. In carbonate environments, significant microbial build-ups remained important in shallow marine environments until well into the Ordovician Period (Pratt, 1982, Kennard and James, 1986; Grotzinger, 1990), and occurred sporadically (largely, but not entirely, in restricted coastal environments) after that time (e.g., Pratt, 1982; Schubert and Bottjer, 1992; Grotzinger and Knoll, 1995; Soja et al., 2000).

CONCLUSIONS

From the evidence of stromatolites, we know that microorganisms were widely distributed on shallow seafloors of the Proterozoic Eon. However, coherent mats formed only where permitted by substrate and current conditions. Wrinkle structures can be abundant in facies where ecological facilitation is matched by pattern of sedimentation that enhances the probability of preservation. Under most circumstances, however, conditions for mat development and/or preservation were not met, resulting in strata with few or no wrinkle structures.

The facies specificity of mat structures must be taken into account in any attempt to track these biosedimentary features through time. A paucity of wrinkles need not reflect metazoan grazing or competition for substrate occupation. In Proterozoic (and perhaps many Phanerozoic?) examples, it can be explained by a combination of microbial preferences and physical processes observable today. By understanding these processes, we can search more effectively for microbial signatures in ancient rocks of Earth or on Mars.

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