Earth's earliest microbial mats in a siliciclastic marine environment (2.9 Ga Mozaan Group, South Africa)

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ABSTRACT

This study provides evidence for the existence of filamentous (cyano-) bacteria forming sediment-stabilizing mats in shelf environments at 2.9 Ga—the oldest known occurrence of microbial mats in siliciclastic rocks. The Mesoarchean Mozaan Group, South Africa, features fine-grained quartzites of an ancient shallow-shelf environment. These sandstones contain wrinkle structures, which in thin section reveal filamentous textures forming carpet-like microbial mat fabrics. The textures resemble the trichomes of modern cyanobacteria, chloroflexi, or sulfur-oxidizing proteobacteria. Mineralogical, geochemical, and isotopic analyses are consistent with a biological origin of the filament-like textures. Carbon filaments with biogenic isotopic signatures ($\delta^{13}C = -24.2‰ \pm 0.5‰$) are closely associated with hematite, goethite, and chert minerals, which may derive from the former presence of oxygen within the microbial mats. Detrital quartz, zircon, and rutile in the mats could indicate baffling, trapping, and binding of the bacterial communities.

Keywords: microbially induced sedimentary structures, cyanobacteria, Pongola Supergroup, Archean, siliciclastic rocks.

INTRODUCTION

The fossil record of the Archean is meager, and only rarely are body fossils of bacteria, biogenic sedimentary structures, or biomolecules preserved (see reviews by Knoll, 1999; Nisbet and Sleep, 2001; and controversial discussions of Brasier et al., 2002; Schopf et al., 2002). Mesoarchean life is recorded by body fossils of microbes in cherts, or by stromatolites in carbonate rocks. However, the identities of the fossil bacterial groups are mostly unknown, and even the first occurrence of cyanobacteria ca. 2.7 Ga is debated (Brocks et al., 1999; Schopf, 1999).

Previous studies on Mesoarchean fossils and stromatolites have focused on chert or carbonate rocks that record marine paleoenvironments, where chemical precipitation led to rapid lithification of the bacterial cells or to the formation of stromatolites (see overview by Nisbet and Sleep, 2001). In contrast, this investigation presents evidence for biogenic features in siliciclastic (nonchemical) marine deposits. Siliciclastic depositional areas are governed only by the physical dynamics of water motion. Little or no in situ mineral formation takes place. Therefore, stromatolites are not formed, and bacterial cells or complex biomolecules are rarely preserved.

In modern siliciclastic environments, benthic microbiota form planar, soft (unlithified) organic layers that cover the seafloor like a carpet. These carpets, microbial mats, are composed of bacterial cells and their mucous extracellular polymeric substances (EPS). Microbial mats that colonize siliciclastic depositional areas are subject to erosive traction by water currents or to sudden deposition of sediment. Therefore, siliciclastic regimes can be regarded as extreme environments, where benthic microorganisms have to adapt to nonfavorable life conditions. Of special significance is the ability of the microbiota to construct a mat fabric that is sufficiently coherent to resist mechanical destruction by erosion (Noffke, 1998; Noffke and Krumbein, 1999). The dense microbial mat cover shelters the sediments underneath, an effect known as ''biostabilization'' (Paterson, 1994). But the benthic microbiota have to react to depositional events as well. Especially important for the survival of light-sensitive, photoautotrophic microbiota is the physiological ability to incorporate the deposited mineral particles into their mat fabrics by ''baffling, trapping, and binding'' (Black, 1933).

The activities of benthic bacterial populations in response to erosional and depositional dynamics in marine environments produce a variety of characteristic microbially induced sedimentary structures (Noffke et al., 2001, 2003). Microbially induced sedimentary structures can be observed in modern and ancient environments. Such structures are regarded as counterparts to stromatolites, e.g., wrinkle structures (Hagadorn and Bottjer, 1997), which are crinkled upper bedding planes interpreted as loading structures caused by burial of microbial mats. Wrinkle structures have been detected until now only in siliciclastic shelf successions of Neoproterozoic and younger ages (contributions in Hagadorn et al., 1999; Noffke et al., 2002).

Because Mesoarchean life is mostly recorded as fossils or structures in chemical lithologies such as chert and carbonates, our aim was to detect biogenic phenomena in siliciclastic rocks of the same ages and to investigate whether the phenomena provide information on the bacterial evolution.

STUDY LOCATION

The study focused on the 2.9 Ga Pongola Supergroup, South Africa. Because carbonate successions contain stromatolites (Beukes and Lowe, 1989), contemporaneous siliciclastic sections potentially could include biogenic structures such as microbially induced sedimentary structures.

We have studied the Mozaan Group (Fig. 1A) that forms the upper part of the Pongola Supergroup. The studied stratigraphic sections involved the 1500-m-thick Ntombe Formation (Beukes and Cairncross, 1991) that crops out in road cuts close to the Bibane River Dam (Fig. 1B). These units comprise siltstone and shale that alternate with rippled, fine-grained quartzites (Fig. 1C). The lithologies and sedimentary structures record a shallow-marine, storm-dominated shelf. The succession has been weakly metamorphosed to low-grade greenschist facies. The maximum age of deposition is 2985 ± 1 Ma (Hegner et al., 1994), whereas the minimum age is older than 2837 ± 5 Ma (Gutzmer et al., 1999).

METHODS

We measured the stratigraphic sections and sampled the wrinkle structures. We conducted optic-petrological investigations on thin sections of the wrinkle structures by using a Zeiss Axioskop 2 Plus microscope.

For the electron-microprobe analysis, we employed standard thin sections for semiquantitative analyses and composition maps with ± 2 μm resolution. Analyses were obtained with a JEOL 8900 electron

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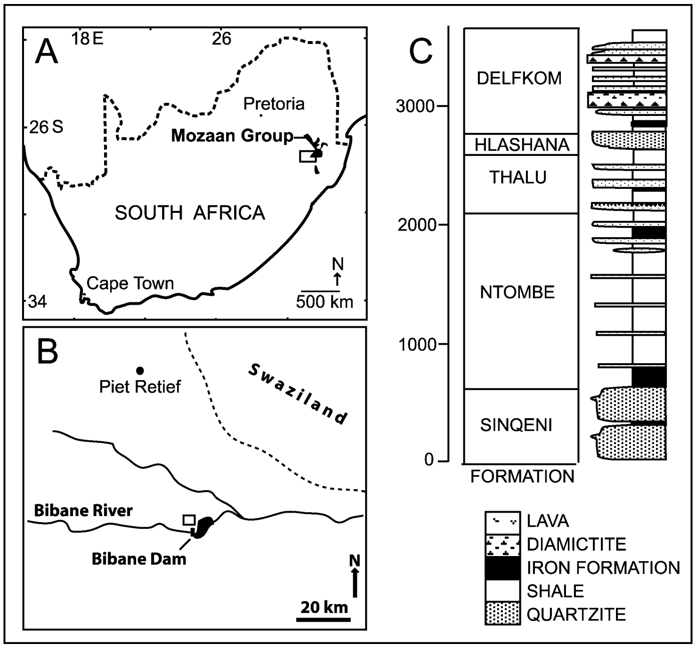

Figure 1. Setting of study area. A: Study site within Mesoarchean (2.9 Ga) Mozaan Group, Pongola Supergroup, South Africa. B: Location of studied sections of Ntombe Formation. C: Stratigraphic setting of Ntombe Formation. Lithologies record shallow shelf environment.

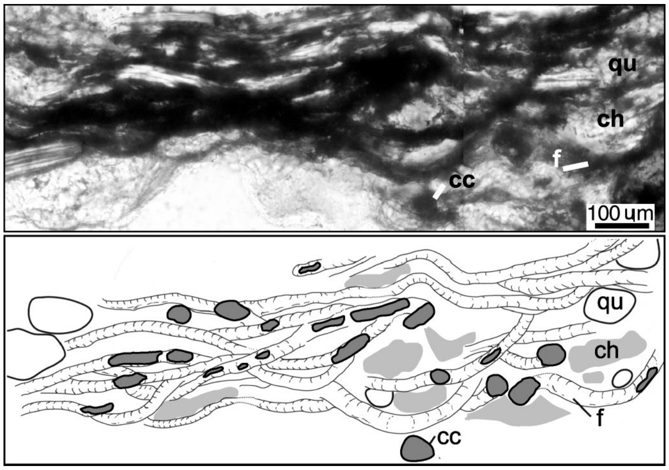

Figure 3. Mat fabrics in fine sandstones of Mozaan Group, as seen in thin section (photograph and sketch). Filament-like microstructures (f) resemble trichomes of bacteria or cyanobacteria. They entangle detrital quartz grains (qu) and in situ–formed chert particles (ch) and construct carpet-like fabrics characteristic of filamentous mats. In bottom sketch, dark areas (cc) are cuts through filaments.

microprobe with five wavelength-dispersive spectrometers for qualitative maps of elemental composition and quantitative point chemical analyses and an energy-dispersive spectrometer for quantitative point measurements of elemental abundance. Analyses were performed at 15 keV (Boyce et al., 2001).

Isotopic measurements of $\delta^{13}C$ were made by using a Carlo Erba elemental analyzer interfaced with a Finnigan DeltaPlusXL continuous-flow isotope-ratio mass spectrometer via the Cinflo II interface. The sample was prepared by immersion of powdered sandstone in a CsF solution (Cody et al., 2002). Demineralization reactions were carried out in the presence of two immiscible liquids: an aqueous CsF solution and a dioxane + CS_2 mixture. Total carbon concentration is ~0.1 mg per 1 g of sandstone, although carbon constitutes >2 wt% in the vicinity of the mat features. After extraction of the insoluble carbon-rich residue in methanol, these carbon-rich samples were dried under a stream of N_2 in silver boats at 50 °C. Isotope compositions were determined by measuring three separate fractions of the samples relative to high-purity, calibrated reference gas standards.

RESULTS

In three stratigraphic sections of the Ntombe Formation, we found five wrinkle-structure specimens ~5 × 10 cm in area and three wrinkle-structure specimens ~20 × 40 cm in area (Fig. 2A). The host sandstone is a well-sorted, fine-grained (~120 µm) quartzite with subangular quartz (~85%), alkali feldspar (~10%), and minor rock fragments (~2%), mica (~1%), rutile, and zircon (<1%).

The wrinkle structures are composed of irregular crinkles that cover the upper bedding plane. The wrinkle crests are ~0.5–1 mm high with a spacing of 3–5 mm. The wrinkle structures resemble a crinkled tissue that covers the bedding plane in a way that no primary surface structures such as ripple marks can be seen (non-transparent wrinkle structure; Noffke, 2000). Only one sample shows wrinkle structures that are thinner, so that the sandstone's surface relief is slightly visible (transparent wrinkle structure; Noffke, 2000). None of the wrinkle structures record any syndepositional erosion. The specimens have been detected on rippled quartzite beds 3–20 cm thick that intercalate with siltstone layers 2–10 cm thick. The associated physical sedimentary structures such as oscillation ripple marks record a shallow-shelf environment above the fair-weather wave base (moderate hydrodynamic energy).

Thin sections cut perpendicular to the wrinkle structures reveal dark laminae 100–300 µm thick (Fig. 2B). These laminae alternate with intercalated sandstone layers 0.5–10 mm thick. The intercalated sandstone layers contain pores filled by secondary chert. The ellipsoidal pores have diameters ranging from 0.5 to 3 mm in length and from 0.5 to 1 mm in height (Fig. 2B). Their long axes are oriented parallel to the bedding plane.

In magnification, the internal laminae texture is composed of filament-like, interwoven microstructures (Fig. 3). These filament-like microstructures appear reddish to dark brown, and serial thin sections

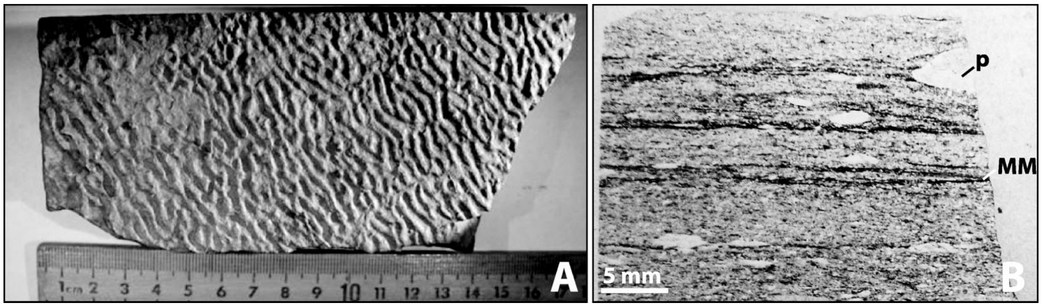

Figure 2. Ancient microbial mats constructed by benthic bacteria; fine sandstones of Mozaan Group. A: Wrinkle structures represent buried microbial mats of high cohesiveness. They are well known from similar paleoenvironments of post-Archean ages. B: In thin section, dark laminae comprising filamentous microstructures represent microbial mat layers (MM). They alternate with sandy interlayers of high secondary porosity. Pores (P) result from pressure of gas trapped beneath sediment-sealing microbial mat layers.

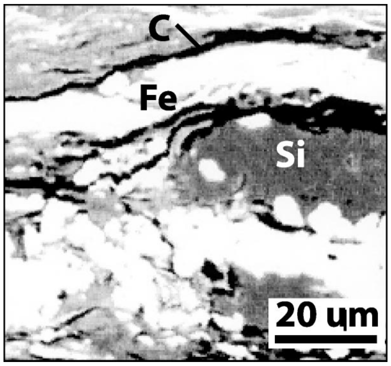

Figure 4. Elemental composition and abundances, mat fabrics. Inner parts of filaments are composed of iron oxides (Fe), whereas their outer walls are lined by carbon (C). Isotope composition of insoluble organic residue was determined as $\delta^{13}C = -24.2‰ \pm 0.5‰$. This value is typical of insoluble organic matter from Archean sedimentary rocks and is consistent with biological origin. Chert particles (Si) may indicate local enrichment of oxygen released during degradation of organic material of microorganisms.

reveal their three-dimensional preservation. The bent and intertwined microstructures are estimated to be ~200–300 μm long and 5–20 μm thick. Quantitative analyses and mapping of elemental composition and abundances show that the inner parts of the filament-like microstructures are composed of hematite and a ferric oxide-hydroxide (probably goethite), whereas their outer walls are lined by carbon (Fig. 4). The isotopic composition of the insoluble organic residue from these laminae is $\delta^{13}C = -24.2‰ \pm 0.5‰$. The filament-like microstructures have entangled mineral grains including quartz and irregularly shaped particles of chert. Zircon and rutile are also present in high concentrations.

EVIDENCE FOR MICROBIAL MATS

The paleoenvironmental setting and the taphonomy of wrinkle structures of the Mozaan Group, as well as their internal textures, support a microbial mat origin. Similar mats have been described from Neoproterozoic and Phanerozoic siliciclastic shelf environments (Noffke, 2000; Noffke et al., 2002).

The wrinkle structures occur in a sedimentary facies that has been shown to be essential to the development and preservation of microbial mats in such environments (Noffke, 2000; Noffke et al., 2002). (1) The associated physical sedimentary structures (such as ripple marks) record a moderate erosive-flow regime. (2) The wrinkle structures occur on beds of well-sorted, clean (translucent) quartz grains. (3) The alternating bedding of fine-grained sandstone beds (2–20 cm thick) with siltstone layers mirrors the characteristic taphonomic path of wrinkle structures. This taphonomic path leads to the preservation of sediment-stabilizing microbial mats (Noffke et al., 2002). The exclusive role of microbial mats in the stabilizing of pure sands was discussed by Gehling (1999).

In thin sections through the wrinkle structures, the lengths and widths of the filament-like microstructures mimic those of the trichomes of modern photoautotrophic cyanobacteria, sulfur-oxidizing proteobacteria, or chloroflexi (Boone et al., 2001).

The filaments are preserved in three dimensions and show no flattening by postdepositional pressure (Fig. 3). This preservation style may show that the filaments were embedded in a matrix rich in EPS that protected the microbes against postburial collapse. Other evidence for EPS in the ancient microbial mats includes the pores within the sandy layers between the mat laminae (Fig. 2B). Such pores are termed fenestral fabrics and are typical phenomena associated with microbial mats, both modern and ancient, that effectively seal the sedimentary surface by their EPS (Gerdes et al., 2000). Increasing gas pressure caused intrasedimentary hollows that were filled in by secondary chert during early diagenesis.

The organic carbon probably lines the former cell walls of the trichomes. The cell walls appear to have been more resistant to decomposition than the fluid-rich inner parts of the trichomes, which are now replaced by the ferric iron minerals hematite and goethite (Fig. 4). Similar selective lithification of bacterial cell parts and sheaths has been investigated in other studies (Knoll and Barghoorn, 1977; Gerdes et al., 2000). Whether these ferric iron minerals are primary or are weathered iron sulfides remains unresolved.

The isotopic composition ($\delta^{13}C = -24.2‰ \pm 0.5‰$) of the insoluble organic residue from the sandstone is typical of insoluble organic matter from Mesoarchean sedimentary rocks and is consistent with a biological origin (Schidlowski et al., 1983). This value contrasts, for example, with the isotopically heavier range ($-10‰ < \delta^{13}C < 0‰$) of Archean inorganic vein graphite (Schidlowski et al., 1983). Similarly, the isotopic values of our insoluble, kerogenous material are significantly lighter than the heterogeneous graphitic material ($-18 < \delta^{13}C < 2‰$) from the Isua supracrustal belt (Van Zullen et al., 2002). Note that whereas Sherwood Lollar et al. (1993, 2002) reported $\delta^{13}C$ values showing great depletions of ^{13}C ($\delta^{13}C = -22‰$ to $-57‰$) for abiotic methane and its C_2 to C_4 Fischer-Tropsch reaction products, similar depletions have, to our knowledge, not been reported for unambiguously abiogenic kerogen-like material.

In addition, the high concentration of rutile and zircon within the mat fabrics is characteristic for baffling, trapping, and binding (Gerdes et al., 2000). Both photoautotrophic and chemotrophic bacterial mats are able to accumulate mineral grains through this behavior (Williams, 1984).

The irregularly shaped chert particles within the mat fabrics could have formed during the mineralization of organic material. This texture suggests the presence of oxygen, perhaps released during degradation of the organic material of the bacteria (Knoll, 1985; Gerdes et al., 2000; Noffke et al., 2003).

Taken together, these observations lead us to conclude that the wrinkle structures in the Mozaan Group quartzites are fossil microbial mats. In particular, the facies-related distribution of wrinkle structures, their internal textures recording the carpet-like network of filamentous microbiota, and their biogenic isotopic composition are not consistent with a tectonic origin.

MAT-CONSTRUCTING MICROORGANISMS

The question remains, which group of bacteria constructed the microbial mats? Benthic bacteria in marine habitats that form filaments of sizes comparable to those detected in the Mozaan sandstones include cyanobacteria (e.g., family Oscillatoriaceae) and the sulfur-oxidizing proteobacteria (e.g., genus *Beggiatoa*) (Holt et al., 1994; Boone et al., 2001).

The wrinkle structures show that the microorganisms effectively biostabilized their substrata even in moderate-flow regimes. In modern environments, only bacterial mats constructed either by sulfur-oxidizing *Beggiatoa* or by filamentous cyanobacteria (Oscillatoriaceae) are able to biostabilize sediments so significantly (Williams, 1984; Paterson, 1997; Noffke and Krumbein, 1999).

In addition, the hydrodynamic conditions represented by the Mozaan Group quartzites were too calm to erode the coherent microbial mats, but too agitated to prevent deposition of suspended fine-grained silt. A drape of fine-grained sediments would have blocked solar radiation and caused the death of any light-sensitive microbiota (Noffke et al., 2002). These reasons would favor photoautotrophic cyanobacteria, but would not necessarily exclude sulfur-oxidizing proteobacteria. The latter are chemotrophic and can colonize in deeper water than photoautotrophic bacterial groups (Williams, 1984; Boone et al., 2001); however, the wrinkle structures seem not to be found in marine paleoenvironments deeper than shallow shelf, i.e., in the Mozaan Group or in rocks of younger Earth ages (contributions in Hagadorn et al., 1999; Noffke et al., 2002). This situation would not be the case if the mat constructors had been independent of light. Furthermore, the existence of former sulfur-oxidizing proteobacteria such as *Beggiatoa* would hint to the presence of free oxygen, because these bacteria exclusively occur at the chemical boundary between anoxic sediments (where sulfur-reducing bacteria produce H_2S) and an oxic water column or sediment layer (Williams, 1984; Holt et al., 1994). In consequence, an occurrence of sulfur-oxidizing bacteria could imply a coexistence of oxygenic, photoautotrophic (?cyano-) bacteria.

Other filament-forming bacteria are chloroflexi and flexibacteria. *Chloroflexus*-like organisms have been reported from marine microbial mats, but their classification as chloroflexi seems to be questionable (Boone et al., 2001). Flexibacteria are regarded as chloroflexi without bacteriochlorophyll. Today they occur in freshwater, where they form filamentous morphologies only during their early growth stages. Mats constructed by these bacteria are unknown, and the nonmobile trichomes would not be able to cope with the extreme conditions of siliciclastic marine environments (Holt et al., 1994; Boone et al., 2001).

Because Beukes and Lowe (1989) regarded the stromatolites detected in carbonate parts of the Pongola Supergroup as induced by benthic cyanobacteria, the occurrence of this microbial group in siliciclastic paleoenvironments of same ages would not be a surprise. Beukes (1996) described similar phenomena from the contemporaneous Witwatersrand Supergroup.

The microbially induced sedimentary structures of the Mesoarchean Mozaan Group point to the oldest known occurrences of microbial mats in siliclastic marine settings. Whether the ancient mat constructors were cyanobacteria remains for future studies to show.

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