

STROMATOLITES IN PRECAMBRIAN CARBONATES: Evolutionary Mileposts or Environmental Dipsticks?

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ABSTRACT

Stromatolites are attached, lithified sedimentary growth structures, accretionary away from a point or limited surface of initiation. Though the accretion process is commonly regarded to result from the sediment trapping or precipitation-inducing activities of microbial mats, little evidence of this process is preserved in most Precambrian stromatolites. The successful study and interpretation of stromatolites requires a process-based approach, oriented toward deconvolving the replacement textures of ancient stromatolites. The effects of diagenetic recrystallization first must be accounted for, followed by analysis of lamination textures and deduction of possible accretion mechanisms. Accretion hypotheses can be tested using numerical simulations based on modern stromatolite growth processes. Application of this approach has shown that stromatolites were originally formed largely through in situ precipitation of laminae during Archean and older Proterozoic times, but that younger Proterozoic stromatolites grew largely through the accretion of carbonate sediments, most likely through the physical process of microbial trapping and binding. This trend most likely reflects long-term evolution of the earth's environment rather than microbial communities.

“If you can look into the seeds of time and say which grain will grow and which will not, speak then to me.”

Macbeth, Act I, Scene III

INTRODUCTION

Stromatolites are among the most widespread and easily recognized components of Precambrian carbonate platforms. In terms of shape, stromatolites range from morphologically simple domes and cones to more complexly branched columnar structures (Figure 1). Stromatolitic facies characteristically range from thin sheets and lenses to major formation scale units that extend for hundreds of meters vertically and hundreds of kilometers laterally. Stromatolites commonly are interpreted to have formed in a spectrum of shallow-water environments, although available data occasionally suggest deeper-water settings. We know how stromatolites look and where they occur. However, despite almost 100 years of research, including the collection of taxonomic, micropaleontologic, and sedimentologic data, the origin and significance of these distinctive structures is still disputed. Several factors help to sustain this controversy: the routine use and acceptance of genetic rather than descriptive definitions; potential overemphasis on modern “analogs” that may have limited relevance for the interpretation of Precambrian structures—and which often are poorly understood themselves; too little emphasis on experimental and theoretical studies of stromatolite morphogenesis; and neglect of broader paleobiological and geological records that provide a necessary context for historical interpretation.

Our objective is to provide a framework for assessing the relative roles of different biologic and abiologic processes in stromatolite accretion. We adopt the nongenetic definition of stromatolites recommended by Semikhatov et al (1979), which states that a stromatolite is “. . . an attached, laminated, lithified sedimentary growth structure, accretionary away from a point or limited surface of initiation.” This definition provides a concise statement of the basic geometric and textural properties of all stromatolites while also allowing for multiple or even indeterminate origins. Accepting this as a general definition makes it possible to evaluate objectively the various processes that may influence stromatolite development. A few specific but critical issues are chosen for discussion, with emphasis on processes that lead to the macroscopic forms recognizable in the field. We specifically address the roles of microbial, physical, and chemical processes in the development of stromatolite laminae and textures, and we consider how these processes collectively determine stromatolite morphology. At the heart of this discussion is the observation that stromatolite morphologies and textures change through time. Can we understand enough about the genesis of these structures to interpret secular variation in terms of evolutionary and/or environmental change?

Definitions

Probably the most potent source of controversy concerning the origin and broader significance of stromatolites lies in the implication of knowledge

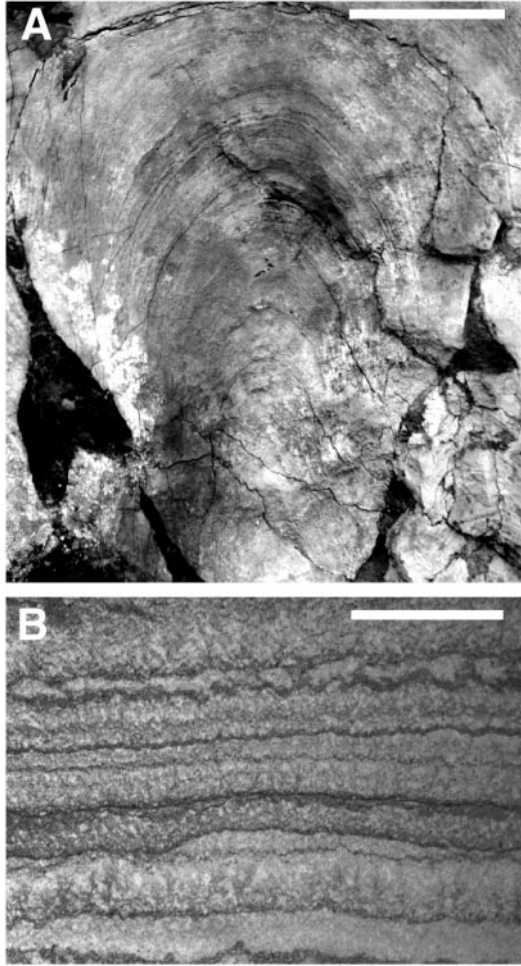


Figure 1 (a) Representative columnar stromatolite showing well-developed lamination that defines an upward-widening morphology during growth. Mesoproterozoic Debengda Formation, Olenek Uplift, Siberia. Scale bar is 5 cm. (b) Thin-section photomicrograph of representative stromatolite lamination, defined by alternations in finer, more clay-rich laminae (*dark layers*), and coarser laminae with internally mottled, possibly peloidal texture (*light layers*). Note the lack of preserved microfossils or filament molds. Paleoproterozoic Hearne Formation, Athapuscow Basin, northwest Canada. Scale bar is 2 mm.

inherent in genetic definitions of these features. This problem is immediately apparent in a consideration of Kalkowsky's original definition (Kalkowsky 1908): stromatolites are "organogenic, laminated calcareous rock structures, the origin of which is clearly related to microscopic life, which in itself must not be fossilized" (translated in Krumbein 1983). This seemingly paradoxical definition requires that microbial influence be interpretable from features of lamination and texture in the absence of direct paleontological evidence for mat organisms.

The controversy has changed little since Kalkowsky's day. A more recent and widely accepted definition indicates that "Stromatolites are organosedimentary structures produced by sediment trapping, binding and/or precipitation as a result of the growth and metabolic activity of micro-organisms, principally cyanophytes" (Walter 1976b). Injecting such a strong component of genesis into these definitions, without providing a clear basis for how biogenicity is to be demonstrated without recourse to direct observation of fossils, can retard useful description and attention to potentially important details. The point is not that this interpretation of ancient stromatolites is necessarily wrong—in many instances it is very likely correct—but, in assuming a set of accretionary processes, scientists have avoided developing specific process models that accurately describe stromatolite accretion dynamics. Such models might routinely predict the relative or even absolute contributions of biologic, physical, and chemical effects.

There are indeed some spectacular examples of stromatolites in which well-preserved microfossils document the specific roles of mat-building populations (Golubic & Hofmann 1976), but despite the attention that stromatolites have received since the discovery of microfossils in Precambrian sedimentary rocks more than 40 years ago, it is probably conservative to estimate that less than 1 percent of all stromatolites ever described have a fossilized microbiota associated with them. Note, as well, that the mere presence of fossils within ancient stromatolites does not demonstrate that these structures accreted as a direct result of microbial mat activities—just as the presence of skeletons in the La Brea tar pits does not obligate us to conclude that mammals secreted the tar. Preserved microfossils could simply have been trapped in accreting carbonates, either as plankton that settled out of the water column or as benthos that colonized surfaces between episodes of accretion. To sustain genetic definitions, one must be able to demonstrate via observations of the density and orientation of preserved populations that mat organisms trapped and bound or precipitated stromatolitic laminae. In the absence of such evidence, the role of biology in stromatolite accretion must be inferred by indirect methods. Insofar as laminated carbonates can accrete via processes other than those associated with mat biology, care must be taken in the interpretation of such morphological or textural observations. This suggests that Kalkowsky's

insight of nearly a century ago should be regarded not as fact but as a working hypothesis. At a level of detail where stromatolitic morphologies and microstructures might be used to illuminate Earth history, we still have a great deal to learn.

There is much to be gained in stating our ignorance. Our biggest loss might be the proposed utility of stromatolites in providing a proxy record for the antiquity of life on earth. This loss would be small, however, because in recent years stromatolites have been eclipsed by the more compelling records of fossil microorganisms in (nonstromatolitic) early Archean rocks (Schopf 1992, Schopf & Packer 1987) and by the carbon-isotopic composition of Archean organic matter, which shows high fractionation consistent with photosynthesis (Hayes 1983, Strauss et al 1992). The future value of stromatolite research lies more in the potential of stromatolites to provide a basis for reconstructing ancient environments and to help us understand how benthic microbial communities interacted with these environments. This must necessarily involve a process-oriented approach to stromatolite morphogenesis in which the correct interpretation of carbonate recrystallization textures is as important as understanding microbial diversity in modern mats. The goal is to build an understanding of stromatolite development that stems not from definitional assertion but from rigorous, quantitative analyses of stromatolite form and lamina texture, including the deconvolution of diagenetic overprints to reveal primary textures diagnostic of specific microbial and sedimentary processes. Critical questions, which get at the core of texture and morphologic development, can then be addressed. For example, over what length and timescales do biological, physical, and chemical processes operate? Do any of these processes—which might be critical at microscopic scales—remain sensitive at larger scales? If not, at what scale does the transition in process response take place? Questions like these must be answered before we have a real understanding of what, for example, some fundamental property such as stromatolite shape signifies.

LAMINATION AND TEXTURE—STROMATOLITE BUILDING BLOCKS

Background

The most conspicuous feature of stromatolites is their lamination (Figure 1). Lamination at any scale in sedimentary rocks is a manifestation of the discontinuous nature of sedimentation itself (Sadler 1981), and stromatolites are no exception. Individual laminae are the building blocks of stromatolites and therefore comprise a time series of progressive, albeit incremental accretion. The morphology of any stromatolite is a function of how lamina shape, particularly its relief, evolves in time. Topographic anomalies that are reinforced in

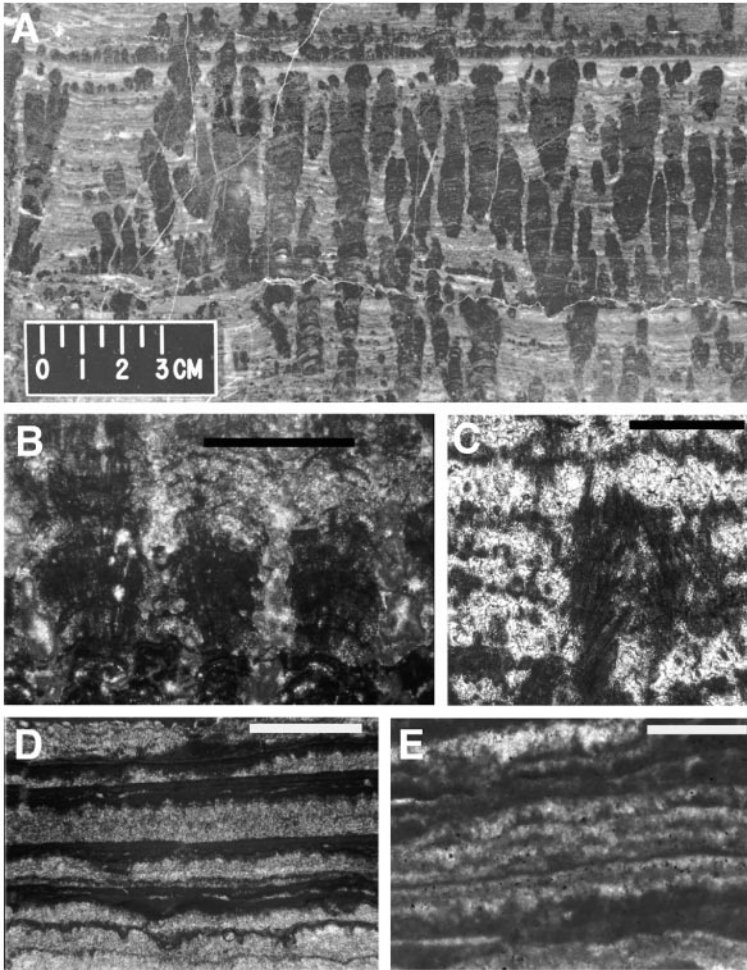
time give rise to greater relief for successive laminae, those that are stabilized give rise to greater inheritance of shape for successive laminae, and those that are damped result in diminished relief.

An interesting consequence of history, well discussed in Hoffman (1973), is that the first modern stromatolites to be studied carefully occurred entirely in freshwater environments and grew mostly through the precipitation of carbonate around algal or cyanobacterial filaments. On this basis, many geologists concluded that ancient stromatolites similarly grew through in situ precipitation and likely indicated freshwater to brackish environments (Bradley 1929, Eardley 1938, Walcott 1914). The subsequent discovery of microbial mats and columnar stromatolites growing in coastal marine environments primarily through microbial trapping and binding of carbonate mud and grains (Black 1933, Ginsburg & Lowenstam 1958, Logan 1961) caused a shift in interpretational emphasis: ancient stromatolites and stromatolitic facies came to be seen as products of the trapping and binding of loose sediment. Note that this interpretational shift did not stem from any new observations of the ancient stromatolites themselves. Rather, it grew from a new perception of what the most appropriate modern analog should be. Given that ancient stromatolites are generally associated with compelling evidence for growth in marine environments, it is understandable how nonmarine analogs could have been rejected in favor of marine analogs.

The logical prediction of this analogy is that ancient stromatolites should display lamination textures consistent with the trapping and binding of loose sediment. The lamination of ancient stromatolites is expressed as a physical attribute (Figure 1*b*), mostly related to variations in crystal size and orientation and to composition (Ca/Mg ratio, clay, silt, and organic content). Because the overwhelming majority of modern marine carbonates are precipitated as metastable

Figure 2 Examples of aggrading neomorphism in affecting stromatolite lamination textures in microdigitate-columnar and laminar-colliform stromatolites, Rocknest Formation, northwest Canada. (a) Polished slab showing microdigitate stromatolite columns and internal lamination. (b) Thin-section photomicrograph of three adjacent columns, showing crude lamination and palimpsest radial texture, interpreted to represent former fibers of aragonite now replaced by dolomite. Scale bar is 1 cm. (c) Same as in *b*, but texture now reflects aggrading neomorphism, which results in an increase in crystal size and loss of palimpsest fibrous texture except near center of photograph. Scale bar is 5 mm. (d) Thin-section photomicrograph of laminar-colliform stromatolites showing good preservation of lamination texture. Note that dark micritic layers infill rough microtopography on tops of lighter, more coarsely crystalline layers; light layers also have systematically smoother bases. Scale bar is 3 mm. (e) With aggrading neomorphism, the fabric in *d* is increasingly homogenized due to an increase in the crystal size of the darker, finer-grained layers, such that a distinction between the geometric attributes of the *dark* and *light layers* is no longer possible. Scale bar is 3 mm.

aragonite or high-Mg calcite (Bathurst 1975, Schroeder & Purser 1986), the occurrence of low-Mg calcite and dolomite in ancient stromatolites implies that at least some diagenesis of the laminae has occurred. Minimally, this would involve neomorphic inversion to more stable phases (Sandberg 1985), with associated grain size enlargement and, in former aragonite, loss of primary crystal orientation (Figure 2). More aggressive diagenetic regimes, especially dolomitization, can result in the loss of all primary variation in grain size and orientation (Sears & Lucia 1980, Zempolich et al 1988). In these instances, only a crude lamination is preserved, often expressed by traces of insoluble silt



and clay preserved along badly altered laminar surfaces (see Figure 4*d* in Sears & Lucia 1980).

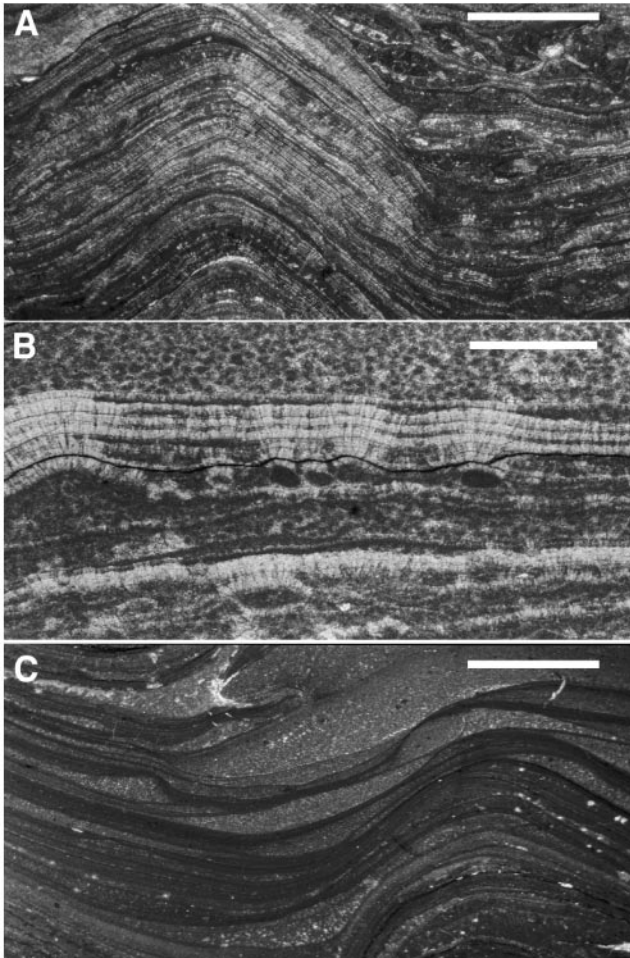
Many ancient stromatolites and stromatolitic facies, therefore, are sufficiently well recrystallized to preclude reconstruction of lamination processes. Fortunately, the record also includes numerous stromatolites that have suffered only minimal recrystallization so that primary textures are well preserved (Figure 3*a*, 3*b*, 3*c*), in some cases, with preservation of cyanobacterial filaments and molds (Figure 3*d*, 3*e*, 3*f*; see also Knoll & Semikhatov 1998, Semikhatov et al 1979, Walter et al 1988). In certain cases, fabrics are so well preserved that they imply neomorphic inversion of aragonite and high-Mg calcite directly to dolomite without a low-Mg calcite intermediary (Grotzinger & Read 1983). In rare instances, primary fabrics have been replaced by chert before neomorphic recrystallization, allowing clear distinctions to be made between laminae formed by sediment deposition, precipitation of sea-floor mineral crusts, and growth of microbial mats (Figure 4; see also Bartley et al 1999, Hofmann & Jackson 1987, Kah & Knoll 1996).

Much evidence has been supplied for the involvement of loose sediment in the formation of laminae (summarized in Semikhatov et al 1979); in contrast, the role of in situ precipitation has sometimes been viewed skeptically (e.g. Ginsburg 1991). Nonetheless, at least some ancient stromatolites were interpreted

Figure 3 Photomicrographs of stromatolite lamination textures, microbial filaments, and filament molds preserved in carbonate. (a) Small domal stromatolite with lamination defined by alternating layers of radiaxial dolomite, formed by in situ precipitation of calcite (replaced by dolomite). Note how some precipitated laminae pinch out in adjacent depression, filled by both precipitated laminae and peloidal grains. Paleoproterozoic Rocknest Formation, northwest Canada. Scale bar is 1.5 cm. (b) Stratiform stromatolite with lamination defined by alternating layers of radiaxial dolomite, formed by in situ precipitation of calcite (replaced by dolomite), and peloidal grainstone. Note how precipitation is localized on topographic highs formed by intraclasts and small peloid mounds. Mesoproterozoic Kyutingda Formation, Siberia. Scale bar is 450 μm . (c) Domal stromatolite with lamination defined by alternating micritic (*darker*) and microsparitic (*lighter*) layers. Lighter, microsparitic layers are highly discontinuous, consistent with an origin by sediment deposition. In contrast, darker layers are more continuous and organic rich and, through their draping, effectively bind sediment lenses in place. Mesoproterozoic Omachta Formation, Siberia. Scale bar is 20 mm. (d) Micrite-encrusted cyanobacterial filament sheaths. Note high abundance and recurrent position, both of which suggest preservation as a fossil mat. Neoproterozoic Ulukhan-Yuryakh Formation, Kolyma Massif, Russia. Scale bar is 500 μm . (e) Micrite-encrusted cyanobacterial filament sheaths. Note high abundance, and preservation of open framework created by intertwined filaments. Framework is lithified by drusy marine cement (*light gray, often lining filaments*), and residual pore space is filled by blocky spar (*bright white patches*). Texture is interpreted as a fossil mat, lithified before significant degradation of filaments. Neoproterozoic Chernya Rechka Formation, Igarka Uplift, Siberia. Scale bar is 500 μm . (f) Filament molds preserved in micritic stromatolite laminae. Stromatolites are completely enclosed in siliciclastic shales, thereby indicating in situ precipitation of micrite. Mesoproterozoic Svetli Formation, Uchuro-Maya Region, Siberia. Scale bar is 250 μm .

early on as the products of in situ precipitation, mostly on the grounds of indirect criteria that included fineness of lamination, oscillating Ca/Mg ratios between laminae, and bulk compositional differences between stromatolites and their enclosing sedimentary facies (Serebryakov & Semikhatov 1974). The last of these is perhaps most convincing, particularly where calcareous stromatolites are enclosed in entirely siliciclastic sediments (Figure 5; see also Hoffman 1976).

Petrographic studies of ancient stromatolites were slow to provide independent support for in situ precipitation models until criteria had been developed for the recognition of ancient cements based on distinctive crystallographic



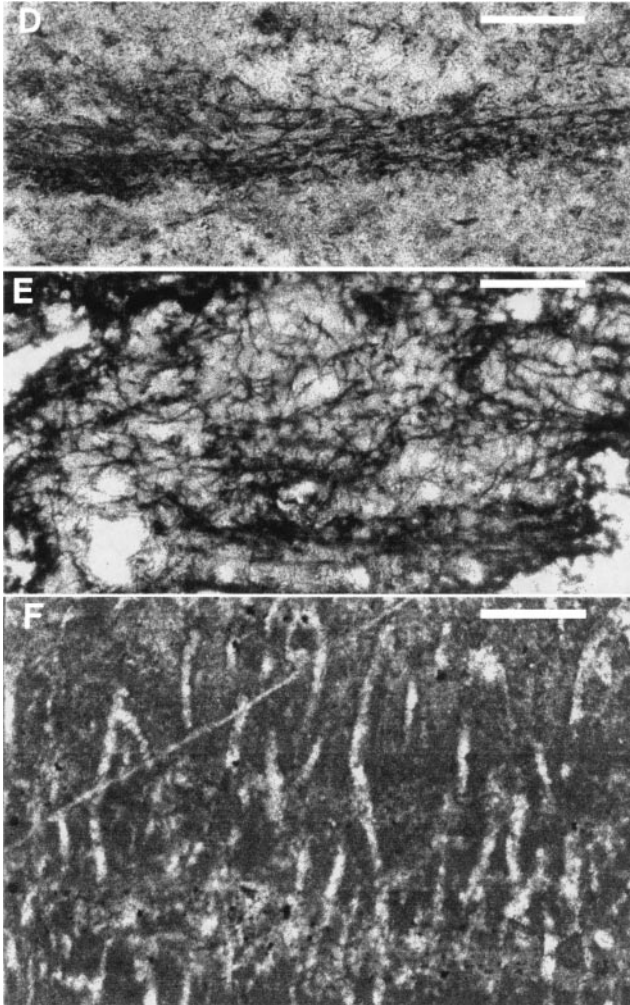


Figure 3 (Continued)

attributes. Based on recrystallization textures and analogy to Phanerozoic marine cements, it was argued that it was possible not only to recognize in situ precipitation in ancient stromatolites, but also to determine original mineralogy (Grotzinger 1986a, Grotzinger & Read 1983). Informative textures include radial fibrous (Figure 2b, 2c), radiaxial fibrous (Figure 3a, 3b), and fascicular optic calcite/dolomite (cf Kendall 1977, 1985; Kendall & Tucker 1973; Sandberg 1985). Strong support for this interpretation was provided by Hofmann and Jackson (1987), who discovered primary crystal textures that had been silicified

before neomorphic inversion or recrystallization to more stable mineral phases. Comparable textures have subsequently been observed in a number of other Precambrian stromatolites (Bartley et al 1999, Kah & Knoll 1996, Knoll & Semikhatov 1998, Sami & James 1996), mostly of Paleo- and Mesoproterozoic age (Figure 4c, 4d). Another mineral texture consistent with in situ mineral precipitation, herringbone calcite, commonly encrusts thin films of organic matter interpreted as former microbial mats (Sumner 1997, Sumner & Grotzinger 1996a). Finally, distinctive textures formed exclusively of micrite create encrusting, isopachous sheets as well as branching, micritic tufas, analogous to those forming in modern thermal pools (Figure 6; Pope & Grotzinger 1999).

The recognition of these textures makes it possible to recognize in situ precipitation textures in many other previously described stromatolites (e.g. Horodyski 1975, Walter et al 1988). Over the past decade it has become increasingly clear that in situ mineral precipitation is an important accretion mechanism in ancient stromatolites (Figures 2–6; see also Bartley et al 1999, Grotzinger 1986a, Grotzinger & Read 1983, Hofmann & Jackson 1987, Kah & Knoll 1996, Knoll & Semikhatov 1998, Pope & Grotzinger 1999). In some remarkably well-preserved stromatolites of late Archean age, it can be observed that the only components in the stromatolite structures were microbial mats, early marine cement, and later porosity-occluding burial cement—sedimentary particles are completely absent (Sumner 1997). Furthermore, it appears that the distribution of stromatolites with precipitated laminae is time-dependent; stromatolites with precipitated textures are common in Archean and Paleoproterozoic carbonates, decline through the Mesoproterozoic era, and are represented principally by encrusted filament textures in late Neoproterozoic marine successions (Grotzinger 1989, 1990, 1994; Grotzinger & Knoll 1995; Knoll & Semikhatov 1998).

Processes

A proper understanding of stromatolite morphogenesis must begin with an analysis of the processes that create lamination. In general, it is thought that there are a small number of essential processes that control lamina accretion, including growth of microbial mats, sedimentation, and precipitation of minerals (Monty 1973, Semikhatov et al 1979). It is useful to consider in more detail how each of these processes contributes to accretion of laminae. Although a thorough review of mat biochemistry, crystal chemistry, and sediment transport dynamics is beyond the scope of this article, our goal here is to touch on the main points that relate specifically to the growth of the macroscopic structures so commonly observed in the field.

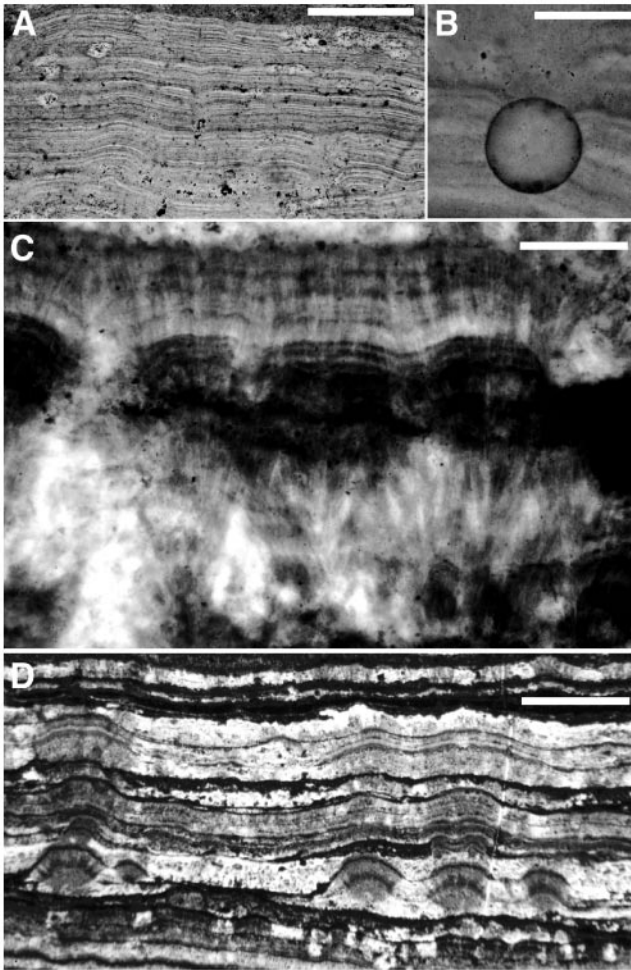
GROWTH AND DECAY OF MICROBIAL MATS The biological imprint on lamina texture is created through the orientation of filaments and unicells, the motility of major filamentous forms, and the adhesiveness and abundance of microbial

sheath material (Semikhatov et al 1979). It is important to distinguish between lamination in mats, which results from microbial-community stratification, and lamination in stromatolites, which results from the interaction of mats with depositing sediment and/or precipitating minerals—only the latter process creates stromatolites. Lamination in mats is driven by steep vertical gradients in light intensity and redox conditions that cause segregation of different microorganisms into layers that are generally less than a few millimeters thick (D'Amelio et al 1989, Revsbech et al 1983). Primary producers, usually filamentous cyanobacteria, form the top layer, which is supersaturated with oxygen and which effectively acts as a light filter, causing abrupt attenuation of the higher frequency end of the visible-light spectrum (Jorgensen & Des Marais 1988). Both oxygen and light decrease along sharp vertical gradients within the mat. If anoxic microenvironments form within the photic zone, a distinct layer of photosynthetic bacteria may develop beneath the cyanobacterial surface community. In any event, ambient oxygen levels commonly fall to zero near the base of the photic zone, providing microenvironments for bacterial heterotrophs that participate in the decomposition of the overlying mat via sulfate reduction and other metabolic processes (Canfield & Des Marais 1993). Thus, over relatively short vertical distances (less than a few millimeters), the mat biota are stratified into discrete communities with distinctive metabolic attributes. The daily cycle of light intensity may result in an oscillation of pore fluid composition between oxygen supersaturation and millimolar concentrations of sulfide (Canfield & Des Marais 1993).

Although relatively common in flat microbial laminites, preservation of fossil mat populations is rare in domal, coniform, and columnar stromatolites, and

Figure 4 Photomicrographs of stromatolite lamination textures and microfossils preserved in chert, Mesoproterozoic Kotuikan Formation, Siberia. See Bartley et al (1999) for further details. (a) Submillimeter-scale lamination in precipitated stratiform stromatolites. Early preservation in chert reveals near absence of organic matter and complete lack of fossil mats. Scale bar is 2 mm. (b) Well-preserved, uncompacted, coccoid microfossil (*Myxococcoides*) preserved in stratiform stromatolites shown in a. Note that the scale of laminations is markedly smaller than most microfossils. Scale bar is 50 μm . (c) Microdigitate stromatolites formed of radiating acicular crystals (interpreted as former aragonite) draped with organic-rich laminae. Each radiating crystal fan corresponds to a single column observed in outcrop, similar to that seen in Figure 2. Scale bar is 5 mm. (d) Radial crystal fans interlaminated with organic-rich layers (*dark layers*), interpreted as sapropels produced from decaying mats. *Light layers* are silicified clastic carbonates. Nucleation is inferred to have taken place at or just below the organic-rich sediment-water interface, perhaps triggered by sulfate-reducing heterotrophic bacteria. However, once established, fans produced a slightly positive topographic anomaly and thus sustained themselves despite occasional draping by subsequent mats. Note that *light layers* lap out against the margins of fans but occasionally smother them, forcing renucleation. Scale bar is 5 mm.

in no case has a multilayered community structure been observed. Generally, only thin films or disseminated sheets of organic matter remain, giving rise to justifiable uncertainty as to the source of the organic materials. Former mats are but one of several possibilities—an obvious alternative is the accumulation of plankton from the overlying water column. Assuming that organic films do represent the vestiges of former mats, their poor state of preservation commonly is attributed to homogenizing effects associated with diagenetic recrystallization (e.g. Ginsburg 1991, Semikhatov et al 1979). However, it is probably more closely related to the high rates at which cyanobacteria are decomposed by



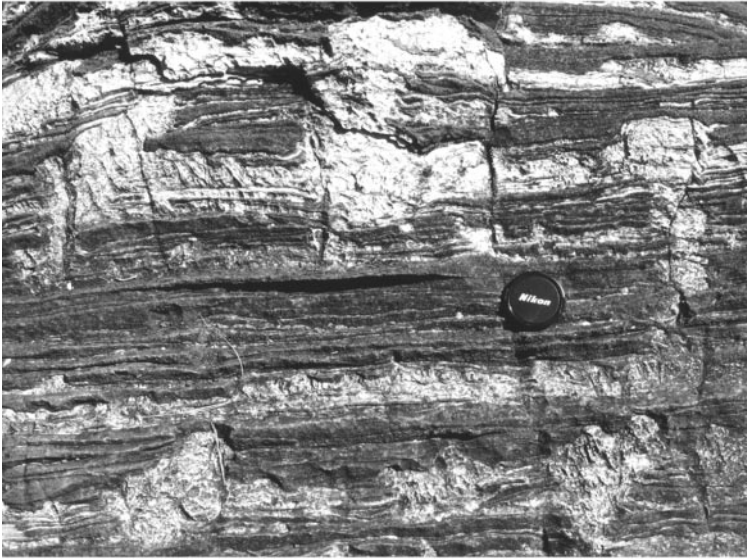


Figure 5 Stromatolites (light) within medium-grained to very-coarse-grained quartz sandstones (dark) of the Neoproterozoic Bildah Member where it overlies the Witvlei Arch, central Namibia. Carbonates also form uncommon thin beds, but only in close proximity to stromatolites. These observations are taken to indicate in situ precipitation of fine-grained carbonate. Lens cap is 6 cm.

heterotrophic bacteria within the lower layers of mats (Doemel & Brock 1977, Golubic 1991). Bartley (1996) has estimated that significant degradation of both cyanobacterial trichomes and sheaths can occur in a matter of days to weeks, greatly exceeding the rates at which diagenetic recrystallization occurs (more than 10 years) (Constanz 1986). This helps explain the general rarity of preservation of recognizable microfossils and mats in ancient stromatolites, except under conditions of extremely early lithification (Bartley et al 1999). Interestingly, the early lithification process may in part be aided by heterotrophic bacteria, which raise alkalinity in the course of degrading cyanobacterial sheaths (Canfield & Raiswell 1991) and therefore induce carbonate precipitation on sheath surfaces (Chafetz & Buczynski 1992). Some recent studies of well-preserved ancient stromatolites support a bacterial nucleation process in early carbonate precipitation (Knoll & Semikhatov 1998), whereas in other cases it appears that early marine cements preferentially avoided nucleation on mats (Sumner 1997). The summary point is that the lower, heterotrophic component of the mat has several roles in the development of stromatolitic lamination. It drives mat decay, while at the same time facilitating cementation that may lead to preservation of the upper, cyanobacterial component of the mat. Last,

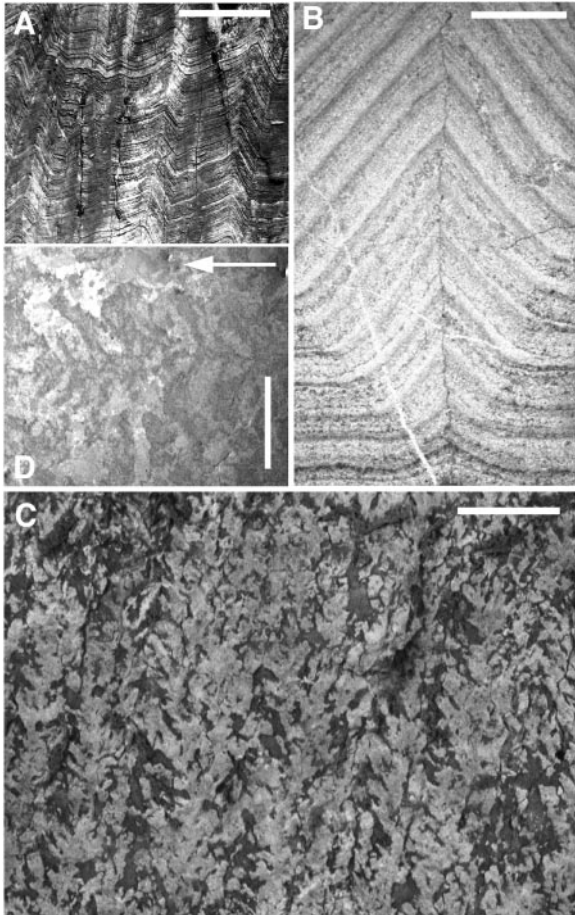


Figure 6 Micritic lamination textures formed by in situ precipitation, Paleoproterozoic Hearne Formation, northwest Canada. See Pope & Grotzinger (1999) for more details. (a) Outcrop photograph of very fine (submillimeter-scale), isopachous laminae defining laterally linked stromatolites. Scale bar is 10 cm. (b) Thin-section photomicrograph of lamination texture from stromatolites shown in a. Note extremely even, laterally continuous laminae with isopachous geometry. Isopachous geometry results from growth normal to the stromatolite surface, regardless of local curvature, typical of structures such as banded agates, which grow by in situ precipitation. Consequently, the stromatolite expands outwards (not just upwards) as it grows. Scale bar is 300 μm . (c) Outcrop photograph of dendritically branching tufa (light) which forms stratiform sheets on the scale of 1–2 cm. Branching structures are infilled with marine cement and micritic sediment. Scale bar is 5 mm. (d) Photomicrograph of a single dendrite structure with central thin stalk and numerous broad branches, both formed of micrite (dark). Lighter material is void-filling marine cement. Note arrow indicating growth orientation. Scale bar is 4 mm.

it generates high concentrations of dissolved sulfide that diffuse upward and stimulate mobility within the cyanobacterial layer.

MICROBIAL RESPONSE TO SEDIMENT FLUX The upper, cyanobacterial layer within a mat affects the development of stromatolitic layering and lamina growth in several important ways. As a prime example, this is where the physical activity is concentrated that results in the process known as "trapping and binding." Loose sediment deposited on the upper surface of the mat is tethered in place by the upward propagation of cyanobacterial sheaths through the sediment layer (Gebelein 1974). Surprisingly, since the rediscovery of the trapping-and-binding effect almost 40 years ago (Ginsburg & Lowenstam 1958, Logan 1961), there has been limited progress in elaborating the actual mechanics by which variable sediment flux and microbial response combine to produce stromatolite accretion. It is readily apparent that, physically, the microbiota must compete with the influx of sedimentary detritus to populate the depositional interface at densities sufficient to maintain a coherent mat. Under conditions of relatively small sediment influx, all constituents of the mat community are capable of rising through a given sediment layer (Des Marais 1995). Primary producers are displaced first, followed by an assemblage of anaerobic photobacteria and heterotrophs (Golubic 1991). If a higher sedimentation rate is sustained, the proportion of filamentous cyanobacteria in mats increases relative to coccoid forms, because the gliding motility of filamentous forms provides a selective advantage (Des Marais 1995). Logically, as the sedimentation rate increases past some (currently unknown) critical value, the sediment-stabilizing effect should drop off dramatically because sediment accumulation simply outpaces the maximum possible microbial response. The key point is that in natural systems there will be specific response times and scales for both microbial and sedimentation processes, and the growth of stromatolites will clearly be sensitive to how these processes balance. The end-member products of these interactions are clear (Monty 1976). In the absence of sedimentation, mats will decay and stromatolites will not be formed due to a lack of building material. On the other hand, stromatolites will not develop in the presence of critically high sediment fluxes because mat growth is not sustainable. This critical point will vary as a function of the biology of mat-building populations.

We consider a proper evaluation of the temporal and spatial scaling of these processes to be critical to the understanding of stromatolite morphogenesis. Additional studies of modern and experimental depositional systems are essential to address this problem because of the importance of quantifying sediment fluxes and mat growth rates. At this point, significant advances have been made in evaluating the temporal and spatial scales of biogeochemical cycling of elements in mats as it relates to mat layering, although these efforts have taken

place at sites with little or no sedimentation (see summary in Des Marais 1995). On the other hand, recent work directed at understanding sediment accretion processes in regions where sediments significantly interact with mats has generated new information on the growth history of stromatolites, but not on the specific processes that lead to the accretion of sediment in the mats (Dill et al 1986, Dravis 1983, Macintyre et al 1996). Somewhat ironically, in the attempt to evaluate sediment accretion processes that take place on timescales of hours, days, and years, most studies of "modern" stromatolites have focused on the Holocene history and stratigraphy of stromatolitic facies. These studies seldom address sediment–mat interactions, in which microbial responses to sedimentation events might be monitored. For example, what is the minimum thickness of a layer of sediment that is required to smother and extinguish growth of an existing mat, so that it must recolonize? Alternatively, how frequently do tolerably thin layers have to be deposited before their integrated effect similarly results in termination of mat growth? Is either of these effects dependent on sediment grain size? How do these effects scale as a function of mat community structure? Only after these processes are fully characterized will it become possible to understand the significance of lamination in Holocene stromatolites formed by trapping and binding and, by extension, their equivalents in the more distant past.

EARLY LITHIFICATION A point on which all students of stromatolites seem to agree is that microbial mats and their associated sediments must be lithified early to be preserved in the record as stromatolites. Precisely when this happens and by exactly what mechanism are vigorously debated for both modern and ancient stromatolites. In modern (Holocene) stromatolites, it is clear that lithification occurs within a few centimeters of the depositional interface by the precipitation of aragonitic and high-Mg calcitic fibrous and micritic cements to form hard, current-resistant structures (Dill et al 1986, Dravis 1983, Logan 1961, Logan et al 1974, Macintyre et al 1996, Monty 1976). The case is clear cut because the stromatolites are obviously hard and primary marine cements can be observed petrographically to fill voids and cement particles. In ancient stromatolites, however, diagenesis characteristically has erased most evidence for early, pore-filling cements, and arguments for early lithification were, thus, traditionally based on indirect criteria such as the growth of steep or even overhanging margins (Donaldson 1976), the ability to withstand strong currents (Hoffman 1974), the chemical purity of lamination (Serebryakov & Semikhatov 1974), and the ability to form reefal escarpments with up to hundreds of meters of relief (Grotzinger 1986b). As mentioned previously, more recent studies supply direct petrographic evidence not only for early lithification, but also for growth of encrusting marine cement directly on the growing

stromatolite, particularly for stromatolites of Mesoproterozoic and older ages (Bartley et al 1999, Grotzinger & Read 1983, Hofmann & Jackson 1987, Kah & Knoll 1996, Knoll & Semikhatov 1998, Pope & Grotzinger 1999, Sami & James 1996, Sumner 1997, Sumner & Grotzinger 1996a).

The processes of early lithification and growth of sea-floor crusts are poorly understood. Early lithified mats occur in modern marine and nonmarine environments and relate to calcification of the sheaths of primary, filamentous cyanobacteria which often form upward-divergent radially arranged bundles (Monty 1967, 1976). Consequently, when certain Precambrian stromatolites were discovered to contain laminae with palimpsest radial fabrics, these were attributed to the former growth of calcifying cyanobacteria (e.g. Bertrand-Sarfati 1976, Grey 1984, Walter et al 1988). However, subsequent detailed examination of petrographic textures revealed that these textures were more consistent with recrystallization of former radially arranged crystals than the micritic sheath coatings of cyanobacteria (Fairchild et al 1990, Grotzinger 1986a, Grotzinger & Read 1983, Hofmann & Jackson 1987). These observations favored a non-cyanobacterial interpretation, at least in accounting for both the domal morphology of related microdigitate or "asperiform" stromatolites and the development of an initially macrocrystalline (as opposed to micritic) texture. Of course, this interpretation does not deny a role for biologic processes in crystal nucleation. For example, it recently has been observed in some stromatolites that crystals were nucleated on mats only after the mats had decayed to thin organic laminae. This supports the hypothesis that heterotrophic bacteria played a role in nucleation of the crystal bundles (Bartley et al 1999, Knoll & Semikhatov 1998). Although they allow for the potential role of bacteria in catalyzing precipitation, these studies provide no evidence for cyanobacterial calcification of sheaths (cf Riding 1982). A number of studies of ancient stromatolites now indicate that early lithification of mats was simply a process of entombing microbes and mats within sheets and botryoids of marine cement. Cyanobacterial processes exerted little or no control over the morphology of crystal bundles; at best, heterotrophic bacteria may have helped trigger crystal nucleation. Even when Proterozoic stromatolites contain cyanobacterial sheaths preserved by carbonate encrustation, there is no direct evidence that precipitation was driven by cyanobacterial rather than heterotrophic bacterial metabolism (Knoll et al 1993, Knoll & Semikhatov 1998). Consistent with this, Chafetz & Bucyzinski (1992) succeeded in inducing the calcification of cyanobacterial sheaths in seawater only when experimental conditions included dead cyanobacteria and living heterotrophic bacteria.

Whatever the role of bacteria in aiding or impeding (Golubic 1991) carbonate precipitation and the genesis of crystalline crusts, it is clear that these crusts decline in importance through Proterozoic time (Grotzinger 1989, 1990, 1994;

Grotzinger & Kasting 1993; Grotzinger & Knoll 1995). This decline likely relates to a corresponding decrease in the calcium carbonate saturation of surface seawater, discussed in more detail below.

ARE STROMATOLITES JUST HARD GROUNDS? We close this section with one final point that addresses the importance of early lithification. An obvious but little discussed fact concerning the distribution of stromatolites is how profoundly biased they are toward formation in carbonate and, to a much lesser extent, other chemical sediments precipitated from seawater (iron, manganese, and phosphate, for example). Despite being the most common rock types in the sedimentary geologic record (Ronov 1968), siliciclastic sandstones and shales do not contain stromatolites made of sandstone or shale. If stromatolites are present their laminae are composed mainly of marly carbonate (Hoffman 1976, Serebryakov & Semikhatov 1974). Curiously, siliciclastic sediments are not devoid of features that suggest the former presence of mats (Hagadorn & Bottjer 1997, Pflueger 1997, Schieber 1986), the mats just simply didn't form stromatolites. Put another way, biology is ubiquitous and appears to have been so for more than three billion years; stromatolites are not. Therefore, stromatolite accretion requires conditions beyond those necessary for the establishment of microbial mats. Siliciclastic settings share many features in common with carbonate environments: they support well developed, ecologically diverse mats; they contain abundant grains of suitable size for trapping and binding; and they exhibit features such as shallow water depth, a spectrum of wave energies and salinities, and adequate nutrient supply known to be correlated with stromatolite development on carbonate platforms. One potential difference may be the degree of light penetration in the more turbid water column of siliciclastic settings, but this should place shallower limits on the depths at which photosynthetic mats could exist, rather than act as a fundamental barrier to mats being established within shallow-water settings. Another factor might be higher sediment mobility in siliciclastic settings, but stromatolites grow well in many modern carbonate environments with moderate to high sediment transport rates (Dill et al 1986, Macintyre et al 1996).

In our view, the fundamental difference is in the relative timing of early lithification. Trapping and binding by mats is insufficient to permanently stabilize sedimentary particles against currents and other destructive environmental processes (papers in Krumbein et al 1994) unless the particles are lithified very early with marine cement. The key is to recognize that this process is kinetically regulated and is therefore dependent on several factors besides the saturation of calcium carbonate in pore fluids. For the most part, the upper layer of the modern oceans is oversaturated with calcite and aragonite, regardless of latitude and whether siliciclastic or carbonate sediments are being deposited (Broecker

& Peng 1982, Broecker & Takahashi 1978, Li et al 1969). Similarly, microbial communities that might help catalyze carbonate precipitation (photoautotrophs and sulfate-reducing bacteria) are also ubiquitous in mats of all settings (Des Marais 1995, Golubic 1991). These important factors appear to be constant for both carbonate and siliciclastic settings. However, the suitability of substrate for catalyzing calcium carbonate precipitation is far greater for calcium carbonate versus quartz or clay. Therefore, the preference of mineral overgrowths for preexisting crystals will systematically select for early lithification of stromatolites made of carbonate grains rather than other sedimentary minerals. Viewed in this manner, the weight of the evidence argues strongly that crystal chemistry may have as much to do with the preservation of stromatolites as microbial processes have to do with forming them. Stromatolites are just another form of hard ground. For stromatolites formed by trapping and binding loose sediment, where biology begins and ends is comparatively easy to interpret. Without an active mat, sediments would not have accreted to form a topographic anomaly on the sea floor, whereas without grains of the correct composition, the structure would not have been lithified early and therefore preserved in the record. However, for stromatolites formed by mineral precipitation the problem of distinguishing uniquely biogenic and abiogenic processes becomes more difficult simply because the process of mineral precipitation can be dependent on only chemical processes. In the next section of this paper, we explore how the three lamina-forming processes (mat growth, sediment deposition, and mineral precipitation) interact to form stromatolites and their diverse morphologies.

STROMATOLITE MORPHOGENESIS

Background

In addition to lamination, the other distinguishing feature of stromatolites is their shape. A typical stromatolite is made up of numerous successive laminae that stack on top of each other to form domal, coniform, columnar, or branching columnar structures. Although laminae generally describe upwardly convex structures, they can also form upwardly concave or discrete conical structures. In general, it is thought that there is a broad but gradational variation in the forms of stromatolites encompassing several major morphological motifs (Semikhatov et al 1979). It has long been observed that stromatolite morphology varies as a function of facies. Thus there is broad agreement that physical environment plays a role in the generation of shape (papers in Walter 1976b).

At the level of process, however, there is no such guiding consensus, severely limiting our ability to understand either paleoenvironmental or stratigraphic

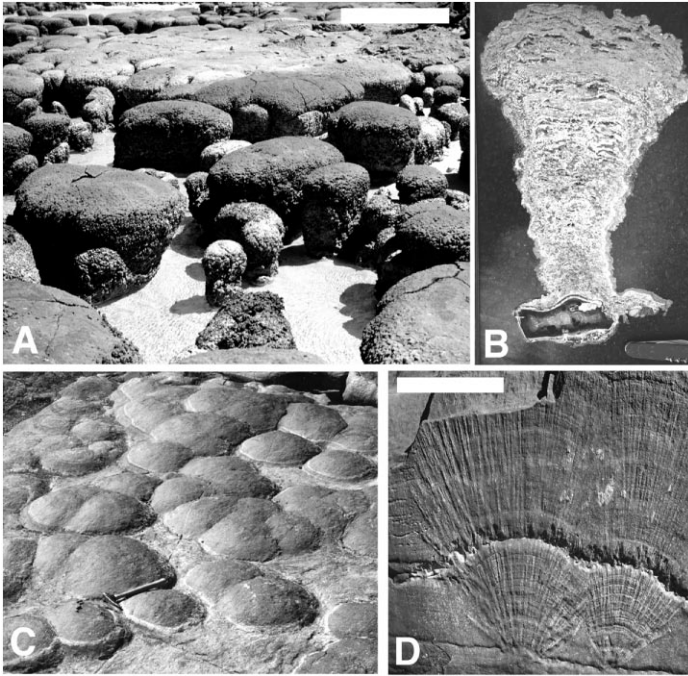


Figure 7 Stromatolites with similar shape but different origins. (a) Modern domal to columnar stromatolites from Shark Bay, Western Australia. Scale bar is 40 cm. (b) Stromatolites are formed by trapping, binding, and early lithification of loose carbonate sediment to form crude lamination. Knife is 7.5 cm long. (c) Domal stromatolites preserved in Neoproterozoic Campbellrand Subgroup, South Africa. Hammer is 35 cm long. (d) Stromatolites are formed by growth of crystal fans that trap sediment as it settles into the interstices of growing crystals. This produces a faint but relatively fine lamination along which preferential weathering has exposed domal shapes whose radii of curvature correspond to that of each radiating crystal fan. Scale bar is 20 cm.

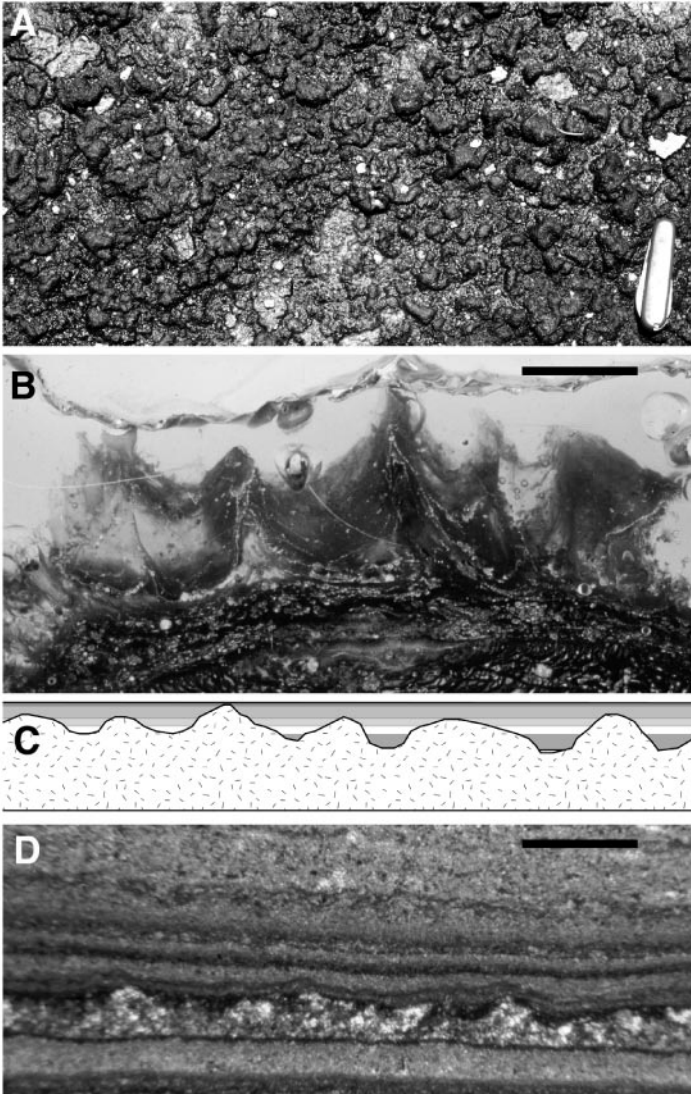
variations in stromatolite form. As Hofmann (1987) stated, “. . . we still have no stromatolite theory, no model that shows which attributes changed in what way through time.” Without a viable theory we are always at risk of misinterpreting the genetic significance of growth form. This is well illustrated in Figure 7, where it is obvious that the present is not the key to the past—modern domal and columnar structures formed by microbial mats (Figure 7a, 7b) are mimicked by Neoproterozoic domal structures formed by radiating crystal fans of calcitized aragonite (Figure 7c, 7d). Clearly, two very different sets of processes have acted over time to produce nearly identical structures. What is missing is a model in which lamina-scale morphology can be related to macromorphology through iteration of specific biological, physical, and chemical processes.

Accretion Mechanisms

One can easily list numerous factors that might influence stromatolite development, including light intensity, salinity, nutrient supply, current velocity, sediment grain size distribution, mat community diversity, and carbonate saturation, to name a few. In detail, stromatolite growth is dependent on many processes that are complexly interrelated. Not only are the processes mechanistically complex, but they evolve over long timescales that are difficult to reproduce experimentally or monitor in the field. Given these difficulties, our initial goal should be to construct a simple model of this complex system. Even this will be a difficult task, in need of studies that can serve to calibrate important model parameters (e.g. Jorgensen & Des Marais 1988, 1990). In principle, growth of stromatolites can be described as a simple system, depending only on three fundamental processes: growth and degradation of a microbial mat or biofilm, deposition of sediment, and precipitation of minerals. Interactions among these end-member processes should account for the bulk of stromatolites in the record.

As mentioned earlier, stromatolite growth depends on the iterative process of upward growth by mats or sea-floor crusts alternating with periods of sediment deposition. In addition, these processes must be balanced such that sediment does not overwhelm mats or crusts. On further inspection, an additional but critically important attribute of the iterative process is revealed. The growth of mats tends to produce an irregular, relatively rough surface, whereas the settling of sediment tends to create a smoother surface by filling in the microtopography of the underlying mat (Figure 8). The surface roughness of mats will vary depending on community. Gebelein (1974) notes that "Mats that have very smooth surfaces and little or no micro-relief are usually created by

Figure 8 Development of surface roughness in microbial mats and the consequences of sedimentation. (a) Irregular, mamillate growth surface produced by chroococcalean mat, Shark Bay, Western Australia. Knife is 7.5 cm long. (b) Tufted mat produced by *Phormidium*, Lake Hoare, Antarctica. Although these mats are often suggested as morphologic analogs of coniform stromatolites (e.g. Parker 1981), we note that the tufted morphology in this case is not preserved at depth in the mat due to rapid decay in the absence of early mineralization. (c) Cartoon illustrating how a building mat may interact with depositing sediment. If the sediment is thin and capable of spreading laterally, it will fill depressions, such as for the basal darker layer. Smothering of the mat in depressions may lead to fragmentation of the growing mat, resulting in growth of columns. However, if the sediment layer thickness is too great, as shown here, then the entire mat may be covered leading to damping of topography and forcing mat growth to start again. (d) Possible fossil mat (*light layer*), showing flat base and mamillate top, smothered by several successive layers of clastic carbonate. Note that the first set of laminae drape the growth topography, but the third layer infills depressions and thereby "resets" the growing interface back to a flat condition. Mesoproterozoic Omachta Formation, Siberia. Scale bar is 300 μm . Photograph courtesy of M Semikhatov.



oscillatoriacean algae, which have thin sheaths. Mats that have a tufted or crenulated surface are created by oscillatoriaceans, which have thick mucilaginous sheaths [Figure 8*b*]. Mats that have an irregular, mamillate surface texture are created by chroococcalean algae, mainly of the family Entophysalidaceae" (Figure 8*a*). Therefore, over many iterations the surface roughness of a growing stromatolite may be enhanced or suppressed depending on the competitive processes of surface roughening by mats and surface smoothing through sedimentation (Figure 8*c*, 8*d*). Precipitation may preserve or dampen surface roughness depending on whether mineral emplacement occurs before or after significant mat decay. As used here, the "surface roughness" (or width, w) of any depositional (or erosional) interface is defined (Barabasi & Stanley 1995) as the root-mean-square fluctuation in the height of the interface

$$w(L, t) \equiv \sqrt{\frac{1}{L} \sum_{i=1}^L [h(i, t) - \bar{h}(t)]^2} \quad (1)$$

where L is the length of the interface, h is the interface height for any position along L , t is time, and i is an index. By definition, growth starts from a horizontal line; the interface is initially a simple straight line. As deposition occurs, peaks and valleys form and the interface gradually roughens. This quantity is easily measured and could potentially reveal a great deal about both mat biology and community structure, as well as the relative proportions of mat growth and sedimentation.

Unfortunately, even though it has been recognized for decades that mats have variable surface roughness in a qualitative sense, this attribute has never been quantified. In future studies of modern mats it would be sensible to measure, particularly where sedimentation also occurs. Here's why: theory, experiments, and observations in nature of dynamically evolving interfaces over the last 15 years have placed important constraints on the possible range of growth mechanisms for both microbial and abiotic systems. In almost all of these studies, the most commonly measured feature is the roughness of the interface, which is used as a basis for deduction of dynamical process and for taxonomic assignment to model class. It is worthwhile to review some of these advances and how they may relate to growth and interpretation of stromatolites. Studies of interface dynamics may possibly lead to a "stromatolite theory" of the sort envisioned by Hofmann (1987).

INTERFACE DYNAMICS AND STROMATOLITES The texture, particularly the roughness, of any depositional surface (interface) is subject to certain force balances and the presence of noise or randomness. In general, and regardless of whether growth is abiologic or solely microbial, there are two end-member

models that control the morphology of an accretionary interface. These different models feature local versus nonlocal growth processes. When interface growth is controlled by local growth processes, the rate of growth is dependent only on the local properties of the interface, such as height of the interface and its nearest neighbors (e.g. Kardar et al 1986). Local growth models are consistent with accretion under equilibrium conditions, with “particles” (ions, sediment, or cells) rejecting attachment sites of the growing object until the most stable configuration is established. For growth by local processes, interface morphologies may be smooth or irregular, but always relatively compact (Figure 9a), whereas nonlocal processes lead to steady-state morphologies that are usually highly ramified, featuring columnar to dendritic branching patterns (Figure 9b).

A widely applied local growth model is represented by the KPZ equation (Kardar et al 1986), whose relevance to understanding stromatolite growth has been recently evaluated (Grotzinger & Rothman 1996). In that study, the following four mechanisms were considered important in controlling stromatolite growth: (a) fallout of suspended sediment; (b) diffusive smoothing of the settled sediment (i.e., sediment fills in depressions in underlying microtopography and moves downhill at a rate proportional to slope); (c) surface-normal mineral precipitation or mat growth, and (d) uncorrelated random noise representative of surface heterogeneity and environmental fluctuations. Under these circumstances, the KPZ equation can be slightly modified (Grotzinger & Rothman 1996) to predict a growth rate ($\partial h/\partial t$) for the stromatolite by

$$\frac{\partial h}{\partial t} = v_s + \kappa \nabla^2 h + v_p \sqrt{1 + (\nabla h)^2} + \eta(x, t) \quad (2)$$

where v_s is the time-averaged rate of sedimentation, κ is an effective diffusion coefficient, v_p is the time-averaged rate of surface-normal precipitation, and η is uncorrelated random noise with zero mean and variance η_0^2 . The square-root factor is a geometric correction that acts to project the surface-normal growth along the h -axis. The smoothing represented by the second term of Equation 2 is equally representative of surface tension and diffusion. The net effect of these two processes is represented in the single coefficient κ . The validity of the KPZ equation and therefore the process of local growth in accounting for growth of these stromatolites were tested and tentatively confirmed by calculating the surface roughness of several stromatolitic laminae and comparing the obtained scaling exponent (and fractal dimension) to that predicted by the KPZ theory (Grotzinger & Rothman 1996). This growth model predicts smoothing and broadening of domes with time because particles (ions, nutrients, and sediment) that arrive at the surface have an equal probability of attaching to all sites, including those on the sides of bump in addition to the tops of bumps or the

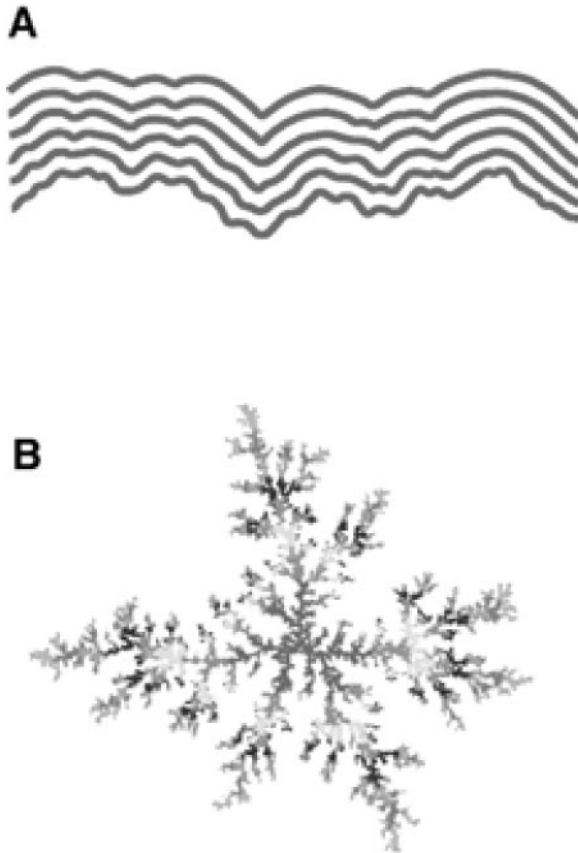


Figure 9 Local versus nonlocal growth models. (a) Local growth predicted by KPZ model, in which an initial surface with arbitrary roughness grows through time. Because of the strong influence of surface-normal growth, irregularities in the topography merge, resulting in selection of progressively fewer, progressively wider domes through time. Growing structures are relatively compact. Modified after Kardar et al (1986). (b) Nonlocal growth created by diffusion-limited aggregation. Growth begins at center as a result of accretion of particles undergoing random walks, which simulates the diffusive process. All particles stick on reaching the growth surface. Once a protruding branch develops, the probability of a random walker making it to an attachment site located near the branch point is dramatically reduced. This condition amplifies in time, resulting in preferential growth of tips over depressions and generation of a high degree of branching. Common shades of gray record equivalent times of growth. Model algorithm based on Witten & Sander (1983) and executed courtesy of K Chan.

depression between bumps. Thus, lateral growth may be as important as upward growth (Figure 9a). An initially rough surface grows with constant velocity normal to all local surfaces, and with time larger domes overtake smaller domes leading to a smoother interface with fewer broader domes, when compared to the initial condition (Figure 9a). Growth of this type may characterize many Precambrian stromatolites and also describes the geometry of layering in the walls of agates, botryoidal mineral clusters, travertines, and at least certain types of stromatolites, in a quantitative manner where seafloor precipitation is thought to have been important. For example, stromatolites formed immediately before precipitation of some of the world's largest evaporite deposits are characterized by fine, isopachous lamination, and internal textures consistent with in situ precipitation (Pope et al 1999).

In contrast, for other systems a number of nonlocal effects contribute to interface morphology and growth velocity, the most important of which is the presence of a diffusing field, which may reflect pressure, electric potential, temperature, and chemical or nutrient concentration (e.g. Witten & Sander 1983). For these models, growth rate ($\partial h/\partial t$) is simply related to a diffusion process and is given by

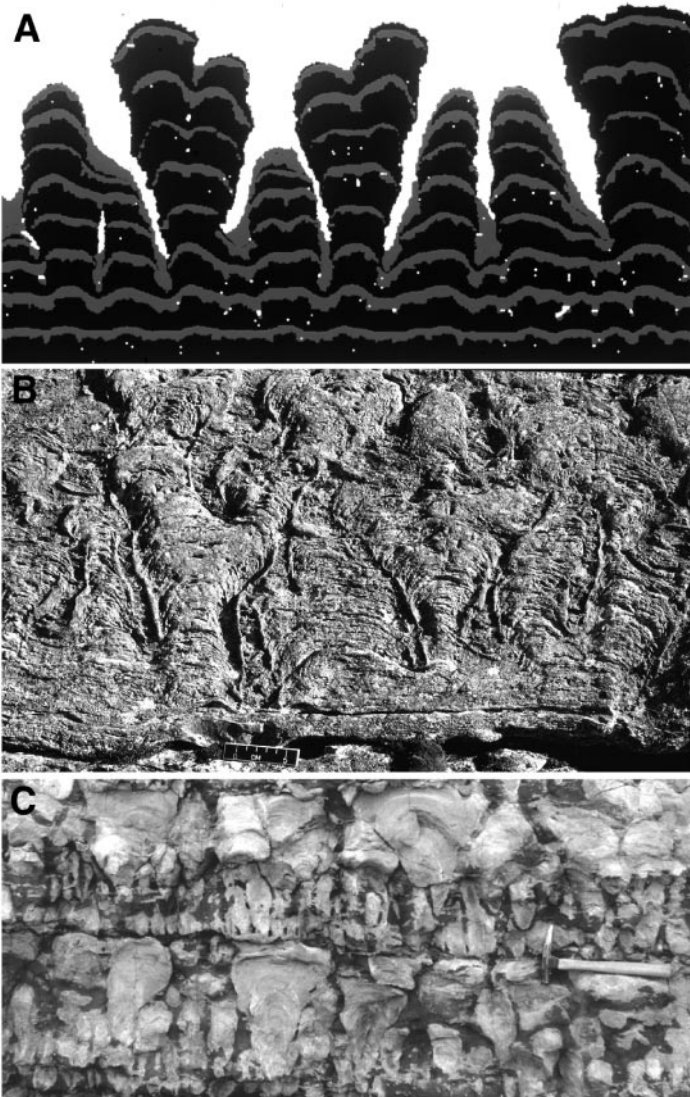
$$\frac{\partial h}{\partial t} \propto \frac{\partial c}{\partial t} = D \frac{\partial^2 c}{\partial z^2} \quad (3)$$

where D is the diffusion constant, h is the height of the interface, z is the vertical position in the overlying water column, c is the concentration of diffusing ions or nutrients, and t is time. This equation states that the increase (or decrease) in the growth rate of the interface in time is proportional to the increase (or decrease) of the concentration of diffusing ions or nutrients in time. In turn, the time rate of change in concentration is directly related to the gradients in concentration scaled by a diffusion constant. Basically, growth is fastest where concentration gradients are steepest. Nonlocal growth models are consistent with accretion under nonequilibrium conditions such that particles are accreted to the first site of attachment they encounter, and attachment sites that project farther into the diffusing field have a higher probability of being selected. The most common model used to account for dendritic growth, biologic or abiotic, is known as diffusion limited aggregation, or DLA (Witten & Sander 1983). As the name of the model implies, aggregation in DLA is controlled by the dynamics of diffusion away from the interface, rather than the kinetics of reaction at the interface—the essential difference between nonlocal and local growth dynamics. The key premise of the DLA model is that particles (ions, nutrients, and sediment) arrive at the site of deposition through a random walk that simulates Brownian motion (diffusion). Particles are successively released, each undergoing a random path, until a macroscopic cluster is formed

(Figure 9*b*). Numerical models have shown that the dendritic structures that are formed by DLA have fractal geometry, and experiments in both biological and abiotic systems have confirmed the essential role of diffusion in controlling the geometry. The complex branching of the dendritic structures best illustrates the nonlocality of the DLA model. As branches begin to develop, they create a screening effect, which makes it increasingly improbable (exponentially so) that new particles will ever find their way into the depressions between branches (Figure 9*b*). Thus, no matter what may occur at the interface itself, the growth process is fundamentally controlled through effects away from the interface (i.e. nonlocal effects), in this case diffusion of particles in a potential field. Furthermore, the growth rate at any given point depends on the entire geometry of the growing structure, not only on the local morphology.

Initial studies of the DLA model strongly suggest that it is also applicable to understanding the growth of certain stromatolites (Chan & Grotzinger, unpublished observations). Whereas DLA by itself predicts highly branched, dendritic structures, in the presence of incremental sedimentation events a simple model predicts many of the domal-, columnar-, and branching-columnar-stromatolite morphologies that are observed in the record (Figure 10*a*). In this model, an episode of upward growth by randomly attaching particles is taken to simulate growth of either mats or crystals and is followed by an episode of sediment settling in which the sediment is allowed to settle preferentially well into the microdepressions formed in the underlying mat or crystal layer. If thick enough and/or diffusive enough, the sediment may damp all of the initial topography created by the underlying layer. However, if antecedent topography remains, the next iteration of mat/crystal growth will result in preferential accretion on those topographic highs. The next layer of sediment now has a tougher

Figure 10 Stromatolite growth model of Chan & Grotzinger (unpublished observations) and comparison to ancient stromatolites. (a) Growth model based on diffusion-limited aggregation and episodic sedimentation. Initially the interface is allowed to grow through diffusion-limited aggregation, which simulates the growth of either microbial mats or precipitating minerals (*dark layers*). After some time, the interface has become rough, and sediment is allowed to settle down onto the rough surface (*light layers*). It is assigned a lateral mobility and therefore can migrate into depressions; in doing so it partially damps the preexisting topography. However, this process is incomplete, so the next interval of upward growth builds selectively on the remnant highs, reinforcing their topography. As long as the thickness of sedimentation events does not exceed some critical value, the growing interface eventually will produce branched columnar structures, similar to certain ancient stromatolites. Note that, in the late stages of growth, depressions are filled only by sediment. (b) Branching columnar stromatolites of the Paleoproterozoic Talthelei Formation, northwest Canada, showing strong similarity to model results. (c) Columnar stromatolites from Mesoproterozoic Debengda Formation, Siberia, also showing strong similarity to model results. See text for further discussion.



task to fill depressions, giving rise in the next iteration of mat/crystal growth to an even higher preference for growth on highs. This is the particular feature of DLA models, that small perturbations can be amplified in time to become dominant features of the structure itself. In this manner, no special conditions may be required to generate columns and branching columns in stromatolites—only time and the positive reinforcement of randomly produced protuberances. This type of growth may help account for the diversity of branched columnar stromatolites, which are common in the geologic record (compare Figure 10a with Figure 10b and 10c).

The fundamental point to be made is that growth of morphologically complex stromatolites is possible only within a fairly narrow range of environmental conditions, where mat growth, sediment flux, and mineral precipitation rates all optimally coincide (Chan and Grotzinger, unpublished observations). Sediment accumulation rates that are either too high or too low tend to force growth of stratiform stromatolites. Where too high, mats and/or precipitating crystals are blanketed in sediment, terminating stromatolite growth. At the other extreme, where sedimentation rates are too low, mats will decay before sediments can be bound into place to build larger structures.

Stromatolites formed by laminae precipitated in situ reflect a considerably different range of environmental conditions. Again, if the stromatolite is exposed to critically high sedimentation rates, growth will be terminated. However, the effect of negligible sedimentation rates is less severe because upward growth can be sustained by either early lithification of mats (preventing their decay and collapse of relief) or simply through crystal growth in the absence of mats. Consequently, development of precipitated stromatolites is predicted at sites where sedimentation rates are low, consistent with field data that indicate restricted peritidal settings for many such stromatolites (Bartley et al 1999, Grotzinger 1989, Kah & Knoll 1996).

Branching in stromatolites is apparently favored when topographic low points are preferentially filled, leaving high points as selected sites for continued growth (Figure 10). Although the temporal and spatial scales over which small topographic anomalies are amplified to generate branched, columnar structures may be dependent on the specific mat-building communities and/or precipitating minerals, from a dimensionless viewpoint the fundamental parameters are revealed as the mat/crystal growth rate and sedimentation rate, whose balance regulates both the onset and termination of branching and whose ultimate control is essentially environmental.

Conoform stromatolites appear to constitute a special case. Consistent with the empirical observations of Walter (1976a) of conoform stromatolites in silica-charged thermal pools at Yellowstone Park, K Chan & JP Grotzinger's unpublished observations suggest that both highly motile mat builders and penecontemporaneous mineral precipitation are required to generate and sustain

these distinctive structures. Motile cyanobacterial filaments aggregate to form vertical tufts on mat surfaces, and these provide the template for conical accretion. However, unless the tufts are lithified early, their distinctive morphology can be lost quickly (see Figure 8*b*). Although filament tufts characterize mats found in a variety of environmental settings and presumably have done so for 2000 Ma or more, preserved vertical filament tufts are characteristic only of Mesoproterozoic and older successions (Kah 1997, Knoll & Sergeev 1995) more or less coincident with the stratigraphic distribution of conical stromatolites (Walter & Heys 1985). It is intriguing that the Miocene coniform stromatolites described recently by Feldmann and McKenzie (1997) are part of a transitional, evaporite-related facies assemblage formed when seawater may have strongly favored early lithification of mats.

BIOGENIC VERSUS ABIOGENIC GROWTH Although the biogenicity of stromatolites is seldom questioned outside of the hallways of academia, we tend to agree with Hoffman (1973) that "Something that haunts geologists working on ancient stromatolites is the thought that they might not be biogenic at all." Twenty-five years after its publication, we can profitably rephrase this statement as a question: how can we recognize biogenic stromatolites based on their morphology? The curious aspect of both local and nonlocal models is that examples of each can be found for microbial systems (compare Matsushita & Fujikawa 1990 with Ben-Jacob et al 1994), as well as purely abiotic systems (compare Kardar et al 1986 with Matsushita et al 1985) that have qualitatively identical appearances and often quantitatively similar scaling relationships (see summary in Barabasi & Stanley 1995). This similarity may be frustrating in the attempt to use the morphology of depositional surfaces as a parameter to ascertain the biogenicity of stromatolites (cf Grotzinger & Rothman 1996). On the other hand, it is fascinating in that it implies that microbial populations may behave almost atomistically in their self organization to form clusters, biofilms, and mats. The physical basis and rationale for this kind of microbial organization is well explained in Berg (1983).

Understanding, through the use of simple process models, that stromatolite growth may result from the competitive interaction of upward growth and surface roughness forced by mats and damping of surface relief by sediment settling, it becomes easy to see how the growth of abiotic marine crusts might substitute for mats and create the same end result. The good news is that we may now have a theory that can account for the growth of a remarkable range of stromatolites, but the bad news is that this theory predicts that we can no longer accept only morphological descriptions of stromatolites as evidence of their biogenicity. This does not mean that stromatolites may not have grown in the presence of biogenic influences; it means that morphology may well be a non-unique parameter—a point made clear by Grotzinger & Rothman (1996)

but easily misunderstood. Biogenicity cannot be easily demonstrated by relationships observed at the outcrop scale; it is essential to examine lamination textures petrographically and demonstrate the presence of textures uniquely attributable to the presence of microbial mats or biofilms (Cady & Farmer 1996, Knoll & Semikhatov 1998). However, for many stromatolites this may not be possible due to an indecipherable level of diagenetic recrystallization.

After almost a hundred years of debate, it seems obvious that there is still a fundamental lack of agreement over where the roles of biology begin and end in many stromatolites, modern as well as ancient. Now, at least we may know why this controversy has been so long lived. As individual cells, microbes may react in similar fashion to many of the same influences that stimulate abiotic growth or vice versa. Consequently, we choose to reinforce the many valid points made by Semikhatov et al (1979) in formulating their definition. This definition specifies the principal textural and morphological attributes that make their identification in the field easy, but it does not make assumptions about their origin. Doing so allows for laboratory-based investigations that may reveal whether a given stromatolite is largely biogenic or abiogenic. If biogenic, it allows for the fact that it may be principally of bacterial or algal, as opposed to cyanobacterial, origin.

STROMATOLITE DIVERSITY—TRENDS AND SIGNIFICANCE

Background

In fairness to the many studies of Proterozoic stromatolites, the fundamental question of biogenicity is most critical in older Proterozoic and Archean (and, potentially, Martian) stromatolites. However, there is a second set of biological questions that is highly relevant to research on Proterozoic stromatolites. If we accept that most Proterozoic stromatolites accreted under the influence of microbial mats, can we assume further that the biological influence on accretion is so pervasive that specific stromatolites can be used as proxies for discrete microbial communities? Can we further view observed secular variations in stromatolite form and microstructure as the preserved record of microbial evolution?

In widespread, if long debated, practice, stromatolites have been classified by a quasi-Linnean system in which groups and forms—analogueous to the genera and species of Linnean hierarchy—are recognized by the reconstructed shapes of columns, branching patterns, and lamination textures. The shorthand provided by this classification system has undeniably contributed to the important observation that at least some stromatolite morphologies and microstructures have distributions that are limited in time and space (summarized in Semikhatov

1991). It has also spawned a cottage industry in the analysis of stromatolitic diversity through time (Figure 11). Of course, the utility of such compilations depends greatly on the discreteness of the entities formally recognized as groups and forms.

Awramik (1971) was the first to compile Proterozoic stromatolite diversity data (Figure 11*a*). He recorded an increasing diversity of columnar forms through the Proterozoic Eon that culminated in a Neoproterozoic peak followed by a sharp decline in the latest Proterozoic and Early Cambrian. Awramik attributed this drop to the radiation of animals capable of disrupting mats by grazing and burrowing and outcompeting mat populations for space on the shallow seafloor; Garrett (1970) had earlier attributed the ecological restriction of modern mat populations to similar processes. Awramik (1971) did not take into consideration the unequal time intervals under consideration or the unequal representation of carbonate rocks in these time blocks, but his general conclusions have by and large been confirmed by subsequent analyses.

In 1985, Walter & Heys (1985) revisited the problem, using a much expanded database (Figure 11*b*). They explicitly addressed the issues of time and sampling, showing how various efforts to correct for these influenced diversity trends. Walter & Heys (1985) also added a parameter, “abundance,” and defined it as the number of occurrences of individual forms in different basins, summed over the total number of forms documented for each time interval. Used this way, “abundance” does not have the meaning ascribed to it by ecologists. Rather, the term carries biogeographic (and both taxonomic and sampling) implications. Walter & Heys’ (1985) summary diagram shows a broad diversity plateau that extends across the Meso- and Neoproterozoic Eras, followed by a decline comparable to that noted by Awramik (1971). Interestingly, Walter & Heys (1985) also plotted the diversity of conoform stromatolites separately and showed that such forms peaked in diversity during the Mesoproterozoic Era—with the unstated but necessary consequence that the diversity of columnar stromatolites was highest in the early Neoproterozoic, as claimed by Awramik (1971). Walter & Heys (1985) further suggested that overall stromatolitic diversity began to decline midway through the Neoproterozoic Era—perhaps 700 to 800 Ma—and hypothesized that this reflects the initial diversification of animals, as yet unrecorded by metazoan fossils or trace fossils. The Late Riphean interval (circa 1000 to 600 Ma) is not subdivided in their dataset, and so support for this conjecture cannot be drawn from their analysis. Further work by Awramik (1991, 1992) showed overall diversity trends (Figure 11*c*) comparable to those reported by Walter & Heys (1985).

The most comprehensive (and recent) attempt to interpret stromatolite diversity through time is that of Semikhatov & Raaben (Figure 11*d*; Semikhatov & Raaben 1993, 1994, 1996; Raaben & Semikhatov 1996). In this work, the

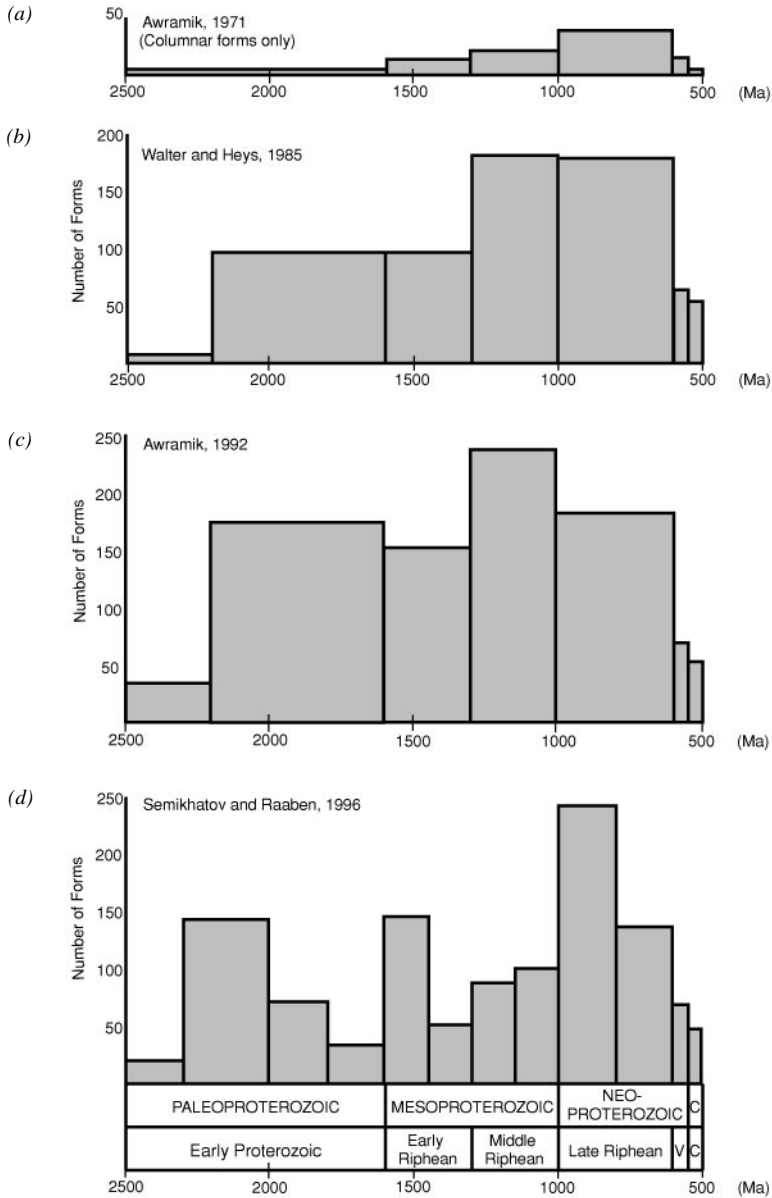


Figure 11 Four attempts to characterize the diversity history of stromatolites. Stratigraphic divisions reflect standard international usage (*upper bar*) and Russian stratigraphic scheme used in published compilations (*lower bar*). V, Vendian; C, Cambrian.

stratigraphic intervals used in previous studies were subdivided, and data were presented for both individual geographic regions and all major morphological classes of stromatolites. The effects of carbonate distribution are clearly seen in comparisons among continents, as are the influences of taxonomic practice (the three prominent peaks in their global diversity compilation correspond to peaks in the histograms presented for China). With this in mind, it is interesting to note that Raaben & Semikhatov (1996) support the hypothesis that stromatolite diversity began its decline within the early Neoproterozoic Era. Further, Semikhatov & Raaben (1996) confirmed earlier conclusions (e.g. Grey & Thorne 1985, Grotzinger 1989) that the microdigitate stromatolites considered by most workers to be pure precipitate structures are abundant in Paleoproterozoic carbonates, but rare thereafter. While acknowledging the potential role of animals in stromatolite decline, Semikhatov & Raaben stressed the roles of algal evolution and changing ocean chemistry.

Taken together these studies suggest that stromatolites are prominent features of carbonates throughout the Proterozoic, but are less common in later Neoproterozoic successions than earlier and much less common after the initial radiation of macroscopic animals. The initial decline in stromatolite abundance correlates in time with diversification of seaweeds capable of outcompeting microbial mats for space on the sea floor (Fischer 1965, Knoll & Swett 1990, Monty 1973). As well, it corresponds to a time of change in the chemistry of seawater and carbonate production (Grotzinger 1990, Semikhatov & Raaben 1996). The end-Proterozoic decline in stromatolites is accepted by most authors as a reflection of grazing and competition for space by metazoans (Awramik 1971, Garrett 1970, Walter & Heys 1985).

Further interpretation of these diagrams requires that we know what a stromatolite taxon is. Most biologists accept that species are discrete evolutionary units, with genera being more arbitrary groupings of closely related species. Species and genera are both components of a larger taxonomic hierarchy justified by evolutionary process. The information content of a stromatolitic form or group is less clear. It certainly denotes a shape or range in shape and may also be associated with a particular microstructure or limited range of petrographic textures; however, unlike the taxonomic hierarchy in biology, this classification scheme for stromatolites is not (or, at least, not yet) underpinned by process models that inform morphological interpretation.

There is broad agreement that stromatolite morphology reflects influences of environment as well as biology. Thus, unless we know what component of morphology is contributed by specific microbial associations, it is impossible to equate diversity of form with biological diversity of mat builders. Lamination texture is more commonly interpreted as a direct reflection of constituent mat builders, but as Knoll & Semikhatov (1998) have demonstrated, a single

mat community can give rise to several distinct lamination textures depending on the relative timing of organic decay and carbonate precipitation. Textures in many stromatolites are principally the products of carbonate precipitation and diagenesis, obscuring mat community influence. Thus, whether defined by morphology or microstructure, stromatolite names do not provide a quantitatively reliable proxy for microbial diversity.

Analysis of diversity trends in stromatolites was inspired by studies of animal diversity through Phanerozoic time, and continuing research on secular variation in stromatolites might well borrow another approach from invertebrate paleontology. In efforts to move beyond taxon counting, paleontologists (e.g. Foote 1997) have turned to morphospace studies in which the shapes of fossils are quantified and displayed within a multidimensional space defined morphometrically. Such an approach has been slow to catch on in studies of stromatolites, with notable exceptions (Banerjee & Chopra 1986; Hofmann 1976, 1994; Zhang & Hofmann 1982). However, a weakness of some such studies is that the developmental (i.e., process) basis for interpreting position within the morphological space is unknown. Fortunately, morphospace studies of stromatolite form can potentially be integrated with process models (Grotzinger & Rothman 1996), enabling research to move beyond debate over taxa and their meaning. Given the possibility of defining and measuring dozens of attributes (Hofmann 1994), it is essential to identify which of these might reflect variability in the fundamental parameters controlling growth and, thus, form (Grotzinger & Rothman 1996; K Chan & JP Grotzinger, unpublished results).

Diversity of Microbes Versus Diversity of Stromatolites

Secular variation in stromatolites has commonly been interpreted as a reflection of evolution within constituent mat communities. In part this stems from analogies to the Phanerozoic record, where biological evolution is a principal vector in the changing composition of sedimentary rocks. In part, evolutionary inferences also reflect the observation that the mat communities observed along environmental gradients in modern environments, like Shark Bay, Australia (Golubic 1991), vary systematically in both taxonomic composition and texture. The inference is that since microstructure relates closely to taxonomic composition, stratigraphic changes in microstructure relate to evolutionary changes in mat communities. Logically, however, this inference is questionable. Observations of modern systems show that mat communities and microstructures vary as a function of environment, so stratigraphic changes could equally well reflect changes through time of some environmental variable, especially the chemistry of carbonate precipitation and diagenesis.

We can approach this question another way. Given that Proterozoic cherts and shales preserve a good record of ancient biology, do observed changes

in stromatolite form or microstructure correlate with independently observed changes in biological diversity? This exercise is straightforward in principle—less so in practice. First of all, the most conspicuous changes in Proterozoic biological diversity are seen in nonstromatolitic fossils. Acritarchs (single-celled protists) and seaweeds document a major radiation of eukaryotic organisms beginning 1200–1000 Ma (Knoll 1992). It is conceivable that the influx of eukaryotes into mat communities might have affected stromatolite morphology, microstructure, or both. However, as better data become available, the stratigraphic correspondence between paleontologically inferred evolutionary radiations and changes in stromatolite morphology and microstructure is weakening (e.g. Xiao et al 1997).

Cyanobacteria have a rich fossil record that extends throughout the Proterozoic, and heroic attempts have been made to track their diversity through time (Schopf 1992). It is clear, however, that compiled diversity strongly reflects sampling and provides only limited insight into the details of cyanobacterial evolution. What we do know is that by the time that abundant and widespread cyanobacteria are first found in the fossil record (circa 2100 Ma), all major clades within this group had already diverged from one another (Golubic et al 1995). The second observation of relevance is that Proterozoic cyanobacteria that are morphologically and developmentally distinctive tend to have paleoenvironmental distributions closely approximating those of their modern equivalents (Knoll & Golubic 1992). This suggests that Proterozoic cyanobacteria were physiologically as well as morphologically comparable to their living descendants. In light of this evolutionary conservatism it is notable that silicified cyanobacterial assemblages actually change in composition near the Mesoproterozoic-Neoproterozoic boundary (Kah & Knoll 1996, Knoll & Sergeev 1995). They do so, however, because of a change in the nature of carbonate substrates in coastal marine environments (Kah & Knoll 1996). Thus, even the observation that cyanobacterial representation in the fossil record changes through time can be traced to environmental rather than evolutionary causes. In any event, the cyanobacteria best represented in Proterozoic cherts come from peritidal laminites and not the domal, coniform, and branching columnar stromatolites that contribute to diversity curves.

In summary, any relationship between microbial evolution and stromatolite distributions in the Proterozoic record is indirect and difficult or impossible to substantiate based on known fossils. To the extent that evolution played an important role in influencing the Proterozoic stromatolite record, it may have done so through the effects of seaweeds and, later, animals in restricting the environmental distribution of stromatolite-building mat communities (Knoll & Semikhatov 1998). Certainly, the initial Neoproterozoic decline in stromatolites corresponds in time with the independently observed radiation of seaweeds

(Knoll 1994, Knoll & Golubic 1992). A role for micrometazoans in this initial decline is more speculative, but the Ediacaran and Cambrian radiations of large animals undoubtedly contributed to the further, terminal Proterozoic–Cambrian decline of stromatolites (Awramik 1971). Additional support for the role of algae and animals in limiting stromatolite-building mat communities to restricted coastal environments comes from carbonates deposited in the immediate aftermath of mass extinctions. When algal and animal biomass is low, stromatolites show a transient reprise in abundance and environmental distribution (Schubert & Bottjer 1992).

One potential example of microbialite response to evolutionary events within the microbenthos is provided by thrombolites—microbialites characterized by a clotted rather than laminated microstructure (Kennard & James 1986). Based on the observed link between clotted textures in modern Bahamian microbialites and green algal microbenthos, it can reasonably be hypothesized that the latest Proterozoic expansion of thrombolites reflects aspects of chrolophyte evolution (Feldmann & McKenzie 1998).

Stromatolite Diversity as a Record of Environmental Change

If the diverse patterns of form and lamination texture in Proterozoic laminates are not a record of microbial evolution, what do they signify? As discussed, accretion of sediments and/or cement crusts to form primary stromatolitic lamination results from biological, chemical, and physical processes at the sediment-water interface. However, the lamination expressed in ancient stromatolites also reflects the postdepositional processes of mat degradation and diagenetic recrystallization of metastable mineral phases. To a lesser or greater degree, primary lamination is variably modified to form a secondary lamination, and the range of textures observed in ancient stromatolites must surely reflect this spectrum. Recent research strongly suggests that stromatolite diversity, as recorded in the variability of these lamination textures, reflects closure of a primary facies and early diagenetic/taphonomic window at some point during Proterozoic time. For example, the radial fibrous textures of microdigitate stromatolites likely reflect the former presence of fibrous cement crusts (Grotzinger 1986a, Grotzinger & Read 1983, Hofmann & Jackson 1987); so-called “tussocky” texture is similarly reinterpreted as crusts of former acicular marine cements (Fairchild et al 1990; but see Bertrand-Sarfati & Pentecost 1992). It has been shown recently that several important stromatolite textures reflect variable degrees of mat degradation—the degree of preservation is closely correlated with the degree of early lithification—the sooner, the better (Bartley et al 1999, Kah & Knoll 1996, Knoll & Semikhatov 1998, Sumner 1997). If mats are not preserved, as is likely the case for most younger Proterozoic and Phanerozoic

stromatolites, then lamination textures should be significantly more limited in their diversity.

It is likely that the literature of stromatolitic microfabrics seriously underestimates the importance of precipitation in the formation of stromatolites. For example, Semikhatov et al (1979) state, "In interpreting microstructures it is, of course, essential that only recognizably primary or penecontemporaneous ones be utilized. Superimposed microstructures of later diagenetic and metamorphic origin, commonly revealed as acicular or radiating microcrystallites or other doubtfully primary micromorphologies, must be excluded." However, as is argued here, textures that were once thought be associated with recrystallization are now regarded as palimpsest relicts of primary textures, particularly acicular or radiating microcrystallites. Studies of early silicified textures have been extremely important in demonstrating the precipitated origin of certain stromatolites (Bartley et al 1999, Hofmann & Jackson 1987, Kah & Knoll 1996), but, because these are few in number, interpreting the vast majority of stromatolite lamination textures will come from analysis of carbonate recrystallization fabrics (e.g. Fairchild et al 1990, Grotzinger & Knoll 1995a, Grotzinger & Read 1983, Knoll & Semikhatov 1998, Sumner 1997). Future investigations of Proterozoic stromatolites will have to consider the wide variety of possible fabrics, and their origins, that are associated with neomorphically recrystallized marine sediments and cements.

The role of in situ precipitation in the development of stromatolitic lamination is interpreted here to be a time-dependent process, correlated with changes in the carbonate chemistry of seawater. The transition through time is ultimately interpreted to be partially responsible for the decline of Proterozoic stromatolites as a result of their reduced capacity to accrete sediment. According to previous interpretations, saturation is proposed to have been highest in the early Proterozoic, decreasing through the middle and late Proterozoic (Grotzinger 1989, 1994; Grotzinger & Kasting 1993; Sumner & Grotzinger 1996b). Late Proterozoic levels are interpreted to be somewhat higher than Phanerozoic levels (Fairchild 1991, 1993; Knoll & Swett 1990). An obvious implication of this model is that the decline in diversity of Proterozoic stromatolite textures could, in part, be related to a global reduction in carbonate saturation through time (Grotzinger 1990). It is revealing that the microdigitate stromatolites (tufas) decline at the end of the early Proterozoic (Grey & Thorne 1985, Grotzinger 1989), followed by the coniform stromatolites and *Omachtenia*-like forms, which decline at the end of the middle Proterozoic, before the decline of most other stromatolite taxa (Walter & Heys 1985). Of all the stromatolite groups, the mechanisms for growth of these three can be most obviously related to direct precipitation (Grotzinger 1986a, Grotzinger 1990, Knoll & Semikhatov 1998). Whereas the microdigitate stromatolites formed

on tidal flats, the coniform stromatolites are of subtidal origin. As carbonate saturation of seawater decreased through the Proterozoic, it can be expected that subtidal environments would have remained more productive, where a constant supply of calcium and bicarbonate was available.

Toward the end of Mesoproterozoic time, the abundance of textures associated with primary sea-floor encrustation and penecontemporaneous lithification of fossil mats declines sharply and so does the diversity of stromatolites. To a first-order approximation, this event signals the end of a period in Earth history when diverse stromatolite lamination textures could be developed owing to extremely early lithification, in many cases directly on the seafloor itself (Grotzinger 1990, Kah & Knoll 1996, Knoll & Semikhatov 1998). It is important that the decline of these textures also implies the loss of a powerful accretion mechanism for stromatolite growth, in that precipitation on the seafloor is extremely efficient (Grotzinger 1990). As discussed above, precipitation of carbonate on the sea-floor contributes directly to increasing local surface roughness and also accelerates the propagation of instabilities that may result in development of branching. In contrast, sedimentation either from suspension or by traction is a smoothing process that will contribute toward damping of small-scale surface irregularities. Consequently, branching stromatolites are predicted to occur more abundantly in regimes in which growth via sea-floor encrustation can occur. Thus, a decrease in stromatolite diversity, as measured either by stromatolite form or texture, is predicted if the time scale for early lithification is increased.

CONCLUSIONS

The Phanerozoic perspective on stromatolites is that they are unusual sedimentary features, commonly indicative of restricted environments or mass extinction. Rocks deposited during the first 85 percent of Earth history tell a different story, one in which stromatolites are the principal features of platform and shelf carbonates. We know that stromatolites generally reflect a spectrum of interactions among microbial-mat communities, sedimentation, and carbonate precipitation, but we remain in need of models and experiments that will enable us to deconvolve the sedimentary signals encrypted by each contributing process.

The common wisdom is that marine stromatolites result from the trapping and binding of micrite and calcisiltite by microbial-mat communities, and this does indeed provide the best explanation for a range of stromatolites seen in later Neoproterozoic successions. As we go back further in time, however, precipitated carbonates comprise a larger and larger proportion of the record, and the relationship between mat biology and lamination and microstructure

becomes more difficult to interpret with confidence. At the extreme, in Archean rocks and (potentially) in sediments on Mars or other planetary bodies, the role, if any, played by biology can be difficult to ascertain. At no time in the last 3.5 Ga has the Earth's surface been sterile, so all stromatolitic structures surely accreted in the presence of biology. The question, then, is not whether organisms were in site as stromatolites accreted, but what roles they played in development and how those roles can be understood from preserved morphology and microstructure. On a sterile Earth, carbonates would still be removed from seawater, and they would likely form precipitated laminates in coastal environments.

The conclusion that biology played a role in the accretion of most stromatolites does not equate to a statement that secular changes in stromatolite form or microstructure reflect changes in the mat-building biota. Testable hypotheses about the role of evolution in driving stromatolite stratigraphy require that one must articulate the features of stromatolites that most directly reflect biology, and explain how evolution can account for observed changes through time. To date, this has not been accomplished. Whether longstanding interpretations of stromatolites as "evolutionary mileposts" can be sustained will require quantitative studies of stromatolite morphologies, to search for forms that can be shown to be uniquely biologic, coupled with detailed analyses of microfabric in which the influences of precipitation and diagenesis have been removed.

In contrast, we can be relatively confident in our assessment of how environmental change has contributed to the stratigraphic distribution of stromatolitic forms and textures. Thus, a promising avenue for continued research lies in the use of Proterozoic stromatolites as "environmental dipsticks"—as sensitive proxies for the evolution of seawater. Changing ocean chemistry undoubtedly contributed to the observed stromatolite record. The outstanding question is whether environmental change can account for all of the stratigraphic variation observed by geologists.

Whatever the outcome of current debates, it is clear that, insofar as stromatolites represent a conspicuous sedimentary manifestation of interactions among physical and biological processes, they will remain principal foci of research in the emerging discipline of geobiology.

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