The Meaning of Stromatolites

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Abstract

Stromatolites document microbial interactions with sediments and flowing water throughout recorded Earth history and have the potential to illuminate the long-term history of life and environments. Modern stromatolites, however, provide analogs to only a small subset of the structures preserved in Archean and Proterozoic carbonates. Thus, interpretations of secular trends in the shapes and textures of ancient columnar stromatolites require nonuniformitarian, scale-dependent models of microbial responses to nutrient availability, seawater chemistry, influx of sediment grains, shear, and burial. Models that integrate stromatolite scales, macroscopic organization, and shapes could also help test the biogenicity of the oldest stromatolites and other structures whose petrographic fabrics do not preserve direct evidence of microbial activity. An improved understanding of stromatolite morphogenesis in the presence of oxygenic and anoxygenic microbial mats may illuminate the diversity of microbial metabolisms that contributed to stromatolite growth in early oceans.

Why waste lines on Achille, a shade on the sea-floor? Because strong as self-healing coral, a quiet culture is branching from the white ribs of each ancestor, deeper than it seems on the surface; slowly but sure, it will change us with the fluent sculpture of Time, it will grip like the polyp, soldered by the slime....

—Derek Walcott, *Omeros*

1. INTRODUCTION

Strolling along the shore of any carbonate-depositing sea during the Archean and Proterozoic eons, one would expect to see stromatolites. As presumed indicators of physical and chemical interactions among microbial communities, water, and sediments, stromatolites stand as one of the oldest topics in geobiology (e.g., Kalkowsky 1908). Yet, to this day, the outstandingly long Archean and Proterozoic record of stromatolite accretion continues to invite questions about trends in carbonate precipitation, past biological processes and evolution, and the changing seascapes of carbonate reefs through time. Archean and Proterozoic stromatolites are both conspicuous and widespread, ranging in height from millimeters to tens of meters and extending laterally from small lenses to aggregates hundreds of kilometers wide. Stromatolite shapes vary from flat to domical, branched, or conical (**Figure 1**), but regardless of their shape, all stromatolites accrete upward by the addition of millimeter- or micrometer-scale laminae (Greek: *stromae*). Laminae of different colors, shapes, thicknesses, continuities, and compositions record changes in the local chemical, biological, or physical environment during the growth of individual stromatolites. Distinct changes also exist in stromatolite lamination, textures, and macroscopic shapes over geologic history, and these require explanation.

Over the past decade, process-oriented stromatolite research has brought new qualitative and quantitative insights to the table. Here, we review observational and experimental models of stromatolite morphogenesis, emphasizing those directly inspired by the Precambrian stromatolite record, and suggest experimental, observational, and theoretical approaches to the study of modern and ancient stromatolites. Navigating the space of rather simple stromatolite morphologies, we evaluate the ability of present models to integrate realistic biological, physical, and chemical processes and generate quantitative predictions. Ideally, these insights will complement, rather than simply mirror, those from well-preserved outcrops and thin sections and, thus, bolster environmental and ecological reconstructions based on the long and widespread stromatolite record.

2. WHY DO WE NEED A THEORY, WHEN THERE ARE MODERN ANALOGS?

Early in the modern history of stromatolite research, Russian scientists documented the immense morphological diversity and recurring pattern of stratigraphic distribution for stromatolites in Meso- and Neoproterozoic carbonates from Siberia and the Ural Mountains (for an English language review of this literature, see Walter 1976c). Morphologies and fabrics varied across

Figure 1

Archean and Proterozoic stromatolites. (*a*) Mesoproterozoic domal stromatolites, Bangemall Group, Australia. (*b*) Mesoproterozoic columnar stromatolites, Bil'yakh Group, Siberia. (*c*) Late Paleoproterozoic columnar precipitates, Duck Creek Formation, Australia. (*d*) Mesoproterozoic domal precipitated stromatolites, Narssârssuk Formation, Greenland. (*e*) Mesoproterozoic columnar stromatolites, Southern Ural Mountains, Russia. (*f*) Neoproterozoic stromatolites nucleated on cobbles, Upper Eleonore Bay Group, Greenland. (*g*) Neoproterozoic columnar stromatolites, Southern Ural Mountains, Russia. (*h*) Archean conoidal stromatolite, Warrawoona Group, Australia.
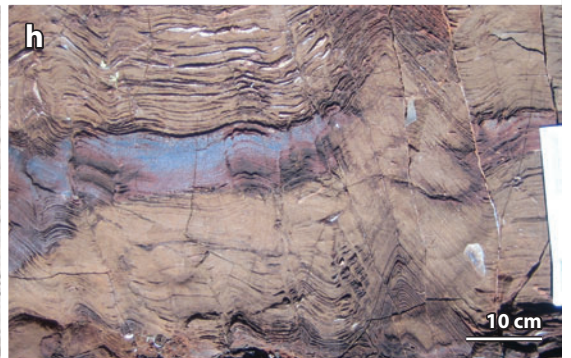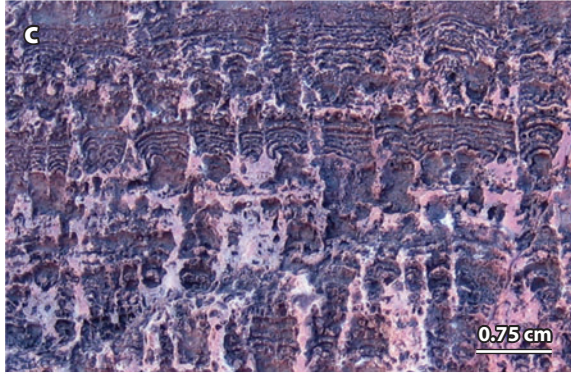
onshore–offshore gradients (e.g., Serebryakov 1976), as well as through time, a pattern interpreted by analogy to the Phanerozoic fossil record, in which evolution and environmental preference govern species distributions. Consequently, and by analogy to evolutionary changes recorded in younger rocks by fossils, temporal patterns in the abundance, morphology, and textures of stromatolites from the Archean to present were thought to reflect the evolution of stromatolite-forming microbial populations (Cloud & Semikhatov 1969). Similarly, the well-developed and widespread stromatolite reefs from the Late Archean and the Early Paleoproterozoic were suggested as evidence for the spread of oxygenic photosynthesis across marine platforms and shelves (DesMarais 2000).

Attractive as they may be, interpretations of stromatolites as evolutionary barometers rarely account for observed correlations between stromatolite forms of all ages and sedimentological and chemical parameters (e.g., Donaldson 1976, Hoffman 1976a, Beukes & Lowe 1989, Grotzinger 1989, Kah & Knoll 1996, Pope et al. 2000, Petrov & Semikhatov 2001, Altermann 2008, Kah et al. 2009). Therefore, regardless of whether stratigraphic trends in stromatolite morphology are properly viewed as biostratigraphic, stromatolites have a fascinating potential to tell us about environmental changes through Earth history (Grotzinger & Knoll 1999).

Modern microbes and microbialites provide essential tools in the interpretation of Precambrian stromatolites. Indeed, they underpin the widely quoted definition of a stromatolite as an "organosedimentary structure produced by sediment trapping, binding, and/or precipitation as a result of the growth and metabolic activity of micro-organisms, principally cyanophytes" (Awramik et al. 1976). The central assumption here is that biological activity mediates the incorporation of both major ingredients of any stromatolite: sediment grains and precipitated minerals. Were the morphological and textural similarities between ancient and modern stromatolites sufficient to allow one-to-one mapping of young on old, the present would offer a simple key to the past. Unfortunately, they are not.

A number of key observables from modern stromatolite-forming systems do not apply directly to the great majority of ancient stromatolites. Archean and Proterozoic stromatolites accreted across a range of marine environments where mats seldom, if ever, persist today. Furthermore, constraints on the Archean and Proterozoic seawater chemistry point to seas whose major element chemistry and redox profiles differed substantially from those of modern oceans. Finally, the ecology of stromatolite-forming microbial communities may have changed through time, particularly before the initial rise of atmospheric oxygen at ∼2.4 Ga and after the evolution of eukaryotic algae and animals. That being the case, we need to supplement observations with models capable of explaining more of the actual stromatolite record. Here, we outline some examples that inspire a nonuniformitarian stromatolite theory (Hofmann 1973), i.e., quantitative and process-oriented models of stromatolite morphogenesis, diagenesis, and biogenesis (Grotzinger & Knoll 1999) (see sidebar, Hans J. Hofmann).

HANS J. HOFMANN

Hans J. Hofmann (1936–2010) spent an academic lifetime investigating Precambrian fossils and stromatolites, their relationships to sedimentary environments, and their use in stratigraphic correlation. Hans was an early advocate of the quantitative approach in stromatolitology and the quantitative description of the stromatolite form. He received his doctorate from McGill University in 1962 and taught at the University of Cincinnati, McMaster University, Université de Montréal, and McGill University. Hans also worked as a Precambrian paleontologist at the Geological Survey of Canada in Ottawa, where many of his fossil finds, including stromatolites, are reposited.

3. PRINCIPLES AND THEORY OF STROMATOLITE GROWTH

3.1. Past and Present Shapes, Sizes, and Textures of Stromatolites

Even casual inspection of any Archean or Proterozoic carbonate platform reveals that modern marine stromatolites display only a subset of the shapes and sizes of stromatolites in the rock record. For example, most columnar stromatolites in marine rocks deposited through geologic history have smaller diameters than their modern marine counterparts (Raaben 2005, 2006) (**Figures 1** and **2**). In fact, more than half of all columnar stromatolites in the rock record, including most Phanerozoic samples, have diameters smaller than 5 cm, and only 5% of all stromatolites have diameters larger than 30 cm (**Figure 2**). In contrast, the diameters of most modern marine stromatolites exceed 20 cm. Many Proterozoic and some Late Archean stromatolites (e.g., Srinivasan et al. 1989) also branch (**Figure 1**), but branching is very uncommon in modern marine stromatolites, as are conical forms (**Figure 2c,d**).
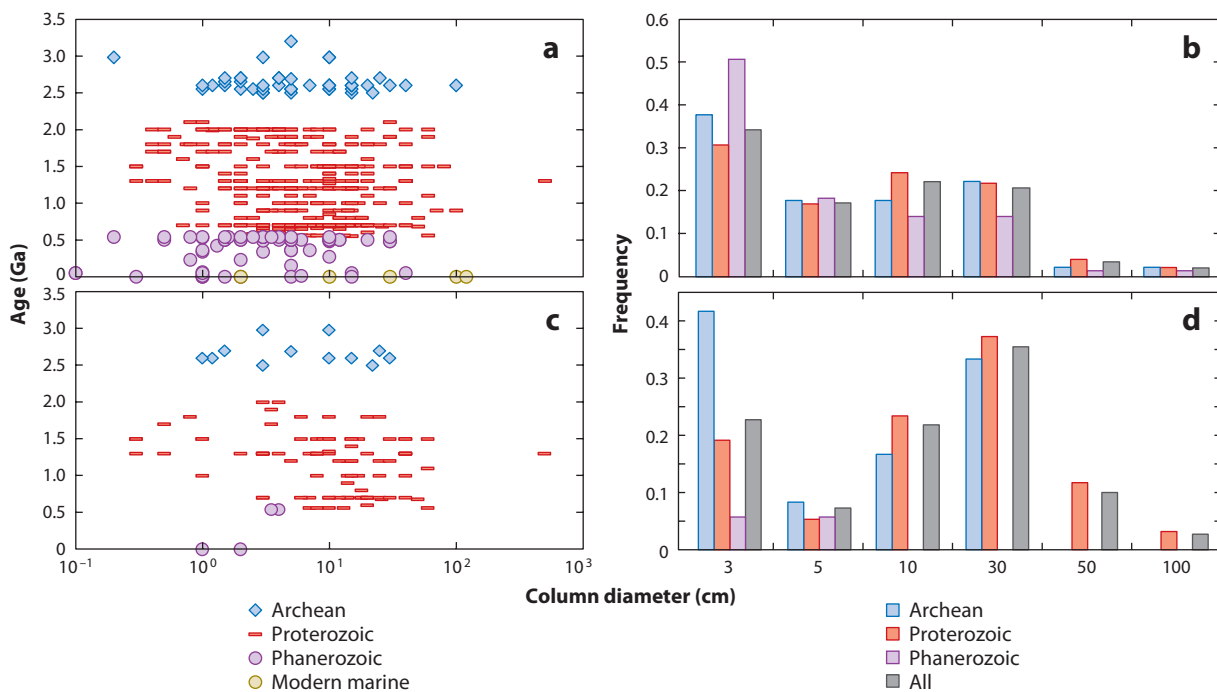
Figure 2

Temporal distribution of maximum diameters of columnar stromatolites. (*a*) Diameters of columnar stromatolites: Archean (*blue diamonds*), Proterozoic (*red bars*), Phanerozoic (*purple circles*), and modern marine stromatolites (*brown circles*). (*b*) Frequency distribution of maximum column diameters: Archean stromatolites (*blue bars*; $n = 45$), Proterozoic stromatolites (*red bars*; $n = 372$), Phanerozoic stromatolites (*purple bars*; $n = 72$), all stromatolites (*gray bars*). (*c*) Diameters of conical stromatolites, with symbols labeled as in panel *a*. (*d*) Frequency distribution of maximum cone diameters (labeled as in panel *b*). The distribution of diameters of Phanerozoic stromatolites is statistically different from that of all Proterozoic stromatolites (Smirnov-Kolmogorov test: $D = 0.21$, $D_{critical} = 0.16$, $p = 0.98$; Wilcoxon-Mann-Whitney two-sample rank test: $z = 3.8$, two-tailed $p < 0.05$) but similar to the distribution of Paleoproterozoic stromatolites alone ($n = 89$; Smirnov-Kolmogorov test: $D = 0.073$, $D_{critical} = 0.193$, $p = 0.98$). The size distribution of Archean stromatolites is similar to that of Proterozoic stromatolites (Smirnov-Kolmogorov test: $D = 0.08$, $D_{critical} = 0.19$, $p = 0.95$; Wilcoxon-Mann-Whitney two-sample rank test: $z = 0.41$, two-tailed $p < 0.05$).

Hofmann (1976) pioneered morphospace quantification of Precambrian stromatolites. Compilations of stromatolite diversity (best viewed qualitatively as indications of morphological variability) suggest a maximum ca. 1200–900 Mya, with declining morphospace occupation thereafter (e.g., Walter & Heys 1985, Awramik 1992, Semikhatov & Raaben 1996). Renewed emphasis on the quantification of form and the sequential occupation of multidimensional morphospace through time could provide an improved view of the ways that stromatolite form varied through Earth history. Similarly, linking stromatolite form to stratigraphic occurrences (as in the Paleobiology Database, **http://paleodb.org**) could normalize stratigraphic data for statistical analyses.

Lower observed morphospace occupation in older intervals may simply reflect a decreasing inventory of carbonate rocks as we descend more deeply into early Earth history. Morphospace decline toward the present, however, is associated with the restriction or elimination of morphological classes, requiring explanation beyond record failure. For example, microdigitate structures decline in abundance throughout the Proterozoic and no longer occur by the later Neoproterozoic (Grotzinger & Knoll 1999). Similarly, *Conophyton* is rare or absent after the earliest Neoproterozoic (**Figure 2c**), as is the related, more complex form *Jacutophyton*, best interpreted as the morphogenetic consequence of regression that introduces cones into a sedimentary regime prone to the accretion of columnar stromatolites (Kah et al. 2009). Major changes through time that may have affected stromatolite growth include the evolution of modern photosynthetic eukaryotes (Feldmann & McKenzie 1998), grazing animals, and benthic invertebrates that commandeer space on the shallow seafloor (Garrett 1970, Walter & Heys 1985, Garcia-Pichel et al. 2004), as well as an increase in oxygen availability in the oceans and a decline in the saturation state of seawater with respect to calcium carbonate minerals (Grotzinger 1990).

3.2. Soldering by Slime

Even the earliest descriptions of modern marine stromatolites (**Figure 3b,d**) note the trapping-and-binding of carbonate sand grains by sticky microbial mat communities (e.g., Black 1933, Ginsburg & Lowenstam 1958). Accretion of these structures depends on a fine balance between the supply of sediment, mat destruction by shear and abrasion (the very environmental forces delivering the sediment; Logan 1961, Gebelein 1969, Logan et al. 1974, Hoffman 1976b, Andres & Reid 2006, Eckman et al. 2008), and microbially influenced cementation of grains into cohesive, lithified structures able to withstand turbulent shear (e.g., Reid et al. 2000, 2003). This favorable conspiracy of biological, hydrodynamic, and sedimentological conditions occurs only rarely in modern marine environments.

Trapped-and-bound grains in the laminae of Phanerozoic marine stromatolites commonly exceed ∼0.1 mm in diameter (e.g., Gebelein 1969, Riding et al. 1991). This happens even though microbial mats selectively trap smaller sediment grains (e.g., Gebelein 1969). Similarly large grains are found only occasionally in Proterozoic columnar stromatolites (Awramik & Riding 1988). This cannot be explained by the shortage of large grains in the Proterozoic, as ooids, peloids, and clasts are commonly present in intercolumnar spaces and nearby areas devoid of stromatolites (e.g., Hoffman 1976a, Beukes 1987, Pelechaty & Grotzinger 1989, Knoll & Swett 1990, Petrov & Semikhatov 2001). Instead, large grains do not seem to have been a major component of the suspended and subsequently trapped sediment in many stromatolite-forming environments. According to the scaling relationship between turbulent energy and the median size of suspended grains (Soulsby 1997), the tops of many ancient stromatolites accreted in areas of lower average turbulent shear than they do today. The seemingly larger resistance of modern mats to shear may owe something to the ubiquity of diatoms (Awramik & Riding 1988),
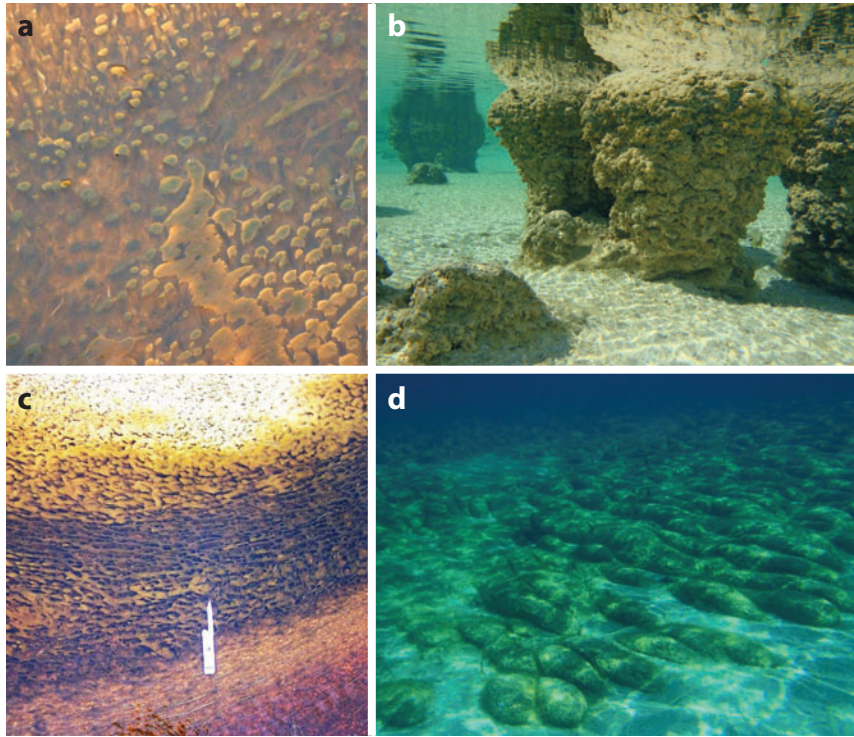
Figure 3

Stromatolite shape as a function of hydrodynamic and sedimentological parameters. (*a*) Stromatolite columns with centimeter-scale diameters in a shallow, quiet pool of modern hot springs. Sediment around columns is absent. (*b*) Large, ~0.5-m-diameter columns of modern marine stromatolites in Shark Bay, Western Australia. Stromatolites and the areas between columns contain sand grain–sized carbonate particles. (*c*) Elongated centimeter-wide columns in channels characterized by stronger flow in modern hot springs. Knife for scale. (*d*) Elongated columns in areas with stronger flow in Shark Bay, Western Australia. In panels *b* and *c*, the elongation follows the direction of the current.

as well as to the distribution of microbial mats over a broader environmental range in earlier oceans.

3.3. Sculpting by Shear

Interactions between microbial mats and local hydrodynamic conditions contribute to columnar morphology, defined both by the topographic highs of the microbialites, stabilized by microbes, and by "negative" intercolumnar spaces susceptible to erosion (Logan 1961) (**Figure 1**). Patterns sculpted by microbial stabilization and scour occur in modern intertidal siliciclastic mudflats as ~1-m-wide, exposed ridges colonized by diatoms and separated by sediment- and water-filled troughs. Where currents are weaker, the ridge/trough patterns occasionally give way to regularly spaced, round ~1-m-wide hummocks surrounded by water-filled hollows (de Brouwer et al. 2000). The elongated shapes can be appreciated by considering the runnels as conduits for sediment-laden water and the exposed, diatom-colonized ridges as areas of reduced scour and increased sediment stabilization. It is less clear how weaker but directional water flow driven by tidal currents

gives rise to the rounded hummocks. A recent model suggests that both patterns emerge from the interactions among water flow, biological stabilization of sediment, sediment deposition, and importantly, erosion (Weerman et al. 2010).

Similar patterns occur in modern peritidal microbialites, whose top surfaces are scour-free during episodic exposure and covered by indurated and often desiccated microbial mats, but where submerged intercolumnar spaces experience continual scour and remain mat-free (Logan 1961). The similarity between modern subtidal and intertidal stromatolites (**Figure 3**) identifies erosion as a stronger influence on the development and persistence of elongated and hummocky patterns than episodic emergence. In modern hot springs, small columnar stromatolites form in side ponds, characterized by low to negligible flow, whereas elongated ridges form in channels, where the flow is stronger (e.g., **Figure 3**), but these structures are two orders of magnitude smaller than modern marine stromatolites. Different morphogenetic mechanisms may be at work here: Instead of sediment scour and laminar accretion by microbial trapping and binding, millimeter- and centimeter-scale forms in hot springs may self-organize due to biological competition for resources in the presence or absence of flow (Petroff et al. 2010).

Scour by moving sediments prevents mat growth between individual stromatolite columns and may be the source of stromatolite fragments and larger grains commonly reported in spaces between columns. Columnar stromatolites also may owe their characteristic convex-upward shape, at least in part, to the reduced abrasion on topographic highs. On topographic highs, mats experience (and trap) a maximal fallout of fine, suspended sediment (e.g., Hand & Bartberger 1988) but are less commonly exposed to the traction carpet of larger, saltating grains. This is readily apparent in laboratory experiments. When >1-mm-thick mats composed of filamentous cyanobacteria are exposed to horizontal sediment transport across their surface in excess of ~0.01–0.03 $g\,cm^{-1}\,h^{-1}$, only mats on rock fragments and in some protected areas persist in the face of destruction (**Figure 4**).

The abradability of microbial mats should change as a function of mat ecology and growth conditions, as well as of the timing of cementation. The cohesive shear strength of modern mats is typically measured in diatom-rich, siliciclastic environments, often using methods that measure the resistance of a mat to vertical impact, and not to abrasion by the horizontal flow of fluids and sediments (reviewed in Le Hir et al. 2007). Abradability, rather than cohesive shear strength, may serve as a better indicator of a mat's ability to withstand erosion at various rates of sediment transport, stabilize sediments, and promote sustained growth of topographic highs during the "average" conditions rather than in the rare extreme events. To the extent that this is the case, it helps explain the observed correlation between stromatolite shape and clastic sediments in ancient bioherms (**Figure 1f**).

3.4. Cementing in Place

Mineral precipitation transforms stromatolites from temporarily consolidated piles of sediment into structures that persist over geologic timescales. Archean and Proterozoic stromatolites can contain exquisite textures preserved by the micritization of primary mat builders and early lithification of pore spaces (e.g., Komar et al. 1965, Grey 1994, Sumner 1997, Knoll & Semikhatov 1998, Seong-Joo & Golubic 1999, Cao & Yin 2011, Mata et al. 2012). The closest modern analogs of these textures are found in nonmarine stromatolites (e.g., Arp et al. 1998, 1999) and are commonly preserved by the micritization of cyanobacterial sheaths (Golubic et al. 2000, Riding 2000). It is thus tempting (and often justified) to view stromatolite laminae as products of the encrustation and permineralization of microbial mats and their constituent cyanobacteria. A biological contribution to the lamination of old stromatolites can be confirmed in rare instances when populations of mat-building microorganisms are preserved within laminae as alternating
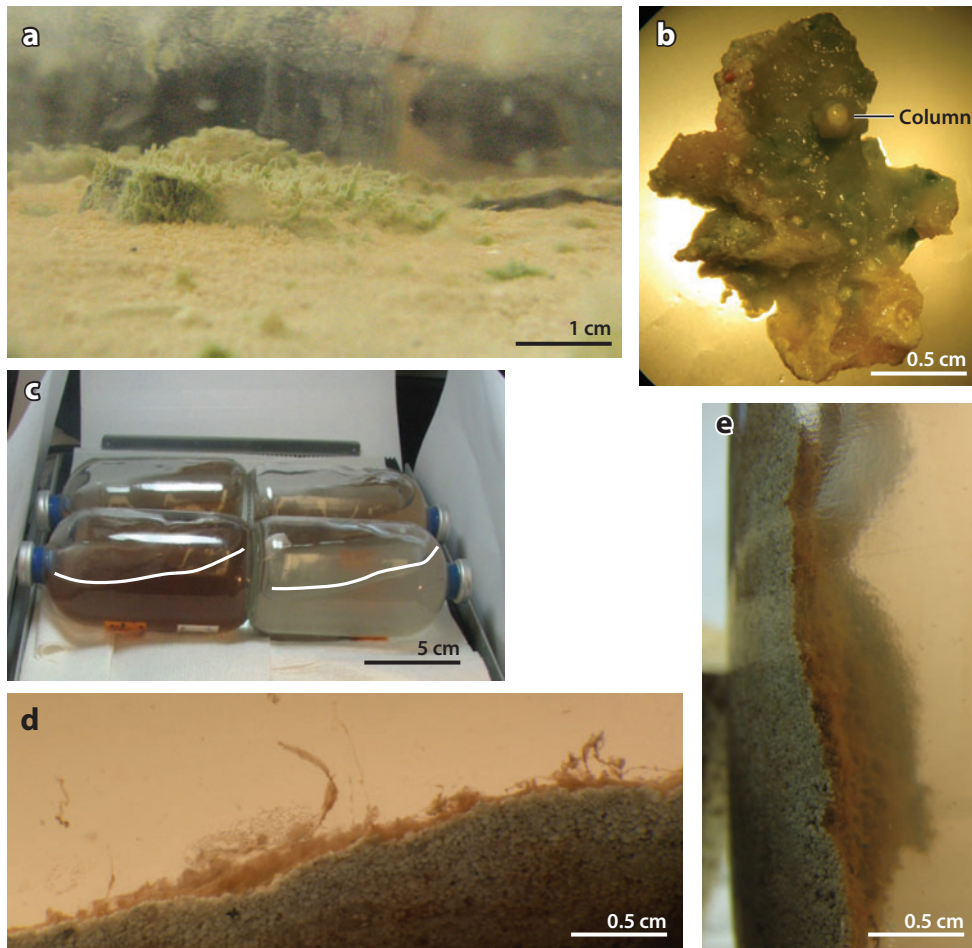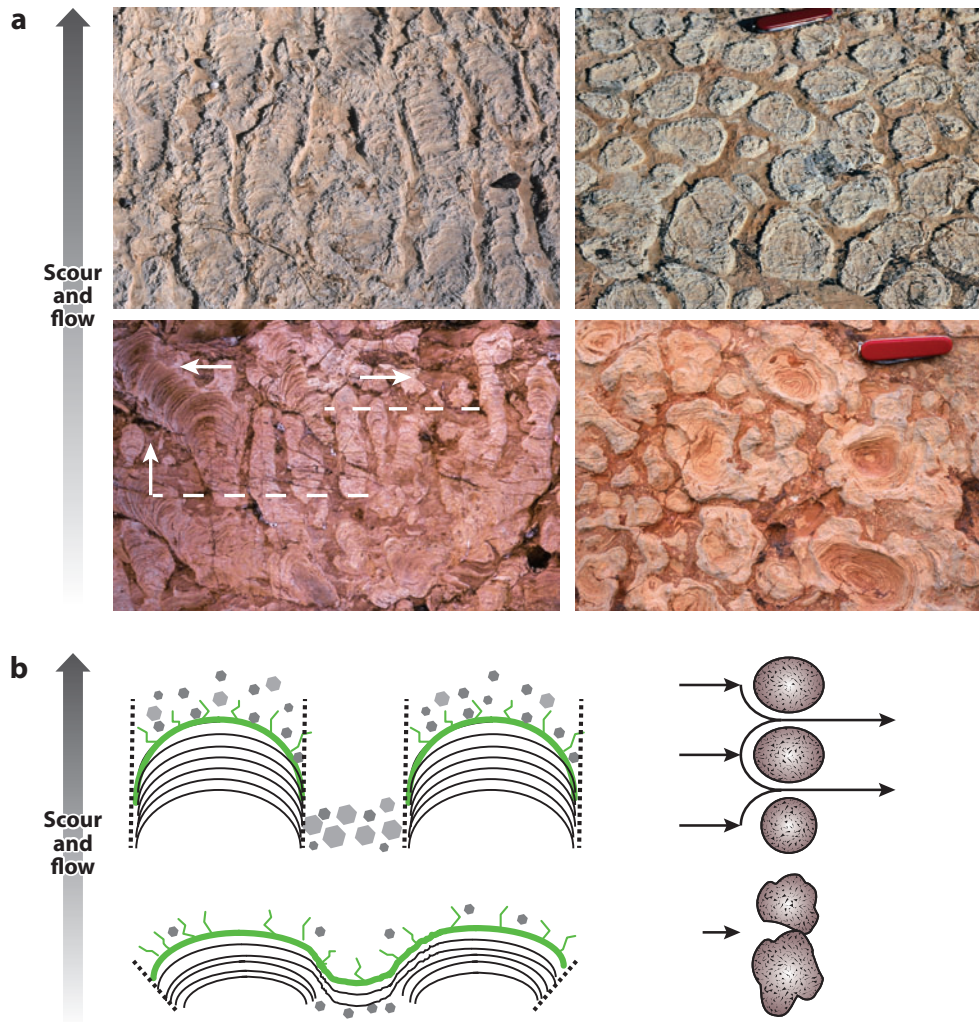
Figure 4

Mats growing in the presence of moving sediment grains. (*a*) Tufted cyanobacterial biofilms (*green*) colonizing the top and the side of the rock in an agitated culture. Biofilms colonize carbonate sand before the onset of agitation but are broken up and suspended afterward, except in the few protected areas (see panel *b*). The solution is cloudy because of the fine, suspended carbonate sediment. (*b*) Gelatinous cyanobacterial biofilm with a small column. (*c*) Shaken cultures of anoxygenic photosynthetic microbial communities grown on carbonate sand in the presence of 1.5 mM sulfate and <0.5 mM sulfide. The surface of each shaken liquid is highlighted by a white line. (*d*, *e*) Thick, tufted, and stringy anoxygenic photosynthetic mats grown in the presence of sediment and flow. These mats can prevent the rolling of sediment when bottles are placed vertically instead of horizontally.

vertical and horizontal, bundled or tufted filaments (e.g., Schopf & Sovietov 1976, Green et al. 1989, Knoll et al. 1991, Cao & Yin 2011) or when the laminae contain unambiguously trapped and bound sediment grains (e.g., Knoll & Semikhatov 1998). The uneven temporal distribution of these fabrics (Knoll et al. 1993) once again suggests that patterns of penecontemporaneous mineral precipitation have, themselves, varied through geologic history.

In the past decade, studies of mineral precipitation have shifted focus from the encrustation of cyanobacterial filaments (reviewed in Riding 2000) to micritization driven by organic decay

Figure 5

(*a*) Photographs of vertical and top sections of stromatolites from the upper (regular) and lower (irregular) part of the same biostrome from the 750–800-Ma-old Upper Eleonore Bay Group, East Greenland. (*b*) Diagram of morphogenetic model. Vertical and horizontal arrows in the bottom row of panel *a* indicate, respectively, temporal and spatial records of increasing scour and shear. These variations suggest that we must be alert to factors that vary in space as well as in time. Strong flow and scour by the traction carpet between columns stabilize column diameters and increase synoptic relief. Laminae contain smaller trapped-and-bound grains and precipitates, but larger grains can be transported in the traction carpet. Weakening flow and scour enable the growth of intercolumnar bridges, reduce the synoptic relief, and lead to the formation of domal, upward-coarsening, and merging structures with irregular cross sections. Stromatolite columns interact with the flow, with the magnitude of the flow indicated by the length of the arrows. These interactions and the resulting scour and shear depend on column diameters and initial spacings (e.g., Vandenbruwaene et al. 2011).

within the extracellular matrix (reviewed by Dupraz & Visscher 2005, Decho 2010). The latter process produces and preserves finer micritic laminae, principally in zones of intense sulfate reduction, where photosynthetic laminae are degraded or absent (Visscher et al. 2000, Reid et al. 2003, van Lith et al. 2003, Dupraz et al. 2004, Gautret et al. 2004, Bontognali et al. 2010). The preservation of finer biological fabrics in ancient stromatolites (**Figure 5**) suggests different biogeochemical

dynamics at work, even though the micritization of the past biological laminae did involve organic decay (Knoll & Semikhatov 1998). Mounting geochemical evidence indicates that sulfate and oxygen, major drivers of $CaCO_3$ precipitation and dissolution in modern lithifying mats, were less available before the Neoproterozoic Era (e.g., Canfield 2004). At the same time, the concentration of CO_2 would have been higher in the past (Pierrehumbert et al. 2011). These chemical differences would have reduced the metabolic influence of sulfate reduction (Bosak & Newman 2003) on mineral precipitation, also reducing carbonate dissolution in zones of aerobic organic degradation and sulfide oxidation. Given that carbonate dissolution and recrystallization contribute to the formation of coarser, clotted textures in modern stromatolites (Planavsky & Ginsburg 2009), finer textures would be expected under conditions that do not favor dissolution. Thus, changes in the textures and the taphonomy of Neoproterozoic carbonate-depositing environments (Knoll & Swett 1990) may be related to global redox changes, as seen in other lithologies (Canfield et al. 2008, Li et al. 2010).

In modern photic marine environments, microbially mediated lithification occurs in the presence of high concentrations of oxygen, sulfate, and frequently, sulfide. Laboratory experiments can expand the chemical space of stromatolite lithification toward more Archean- and Proterozoic-like conditions by investigating microbial mats fueled by sulfur- (Bosak et al. 2007, Warthmann et al. 2011) (**Figure 4**), H_2-, or iron-based anoxygenic photosynthesis; lithification in solutions designed to mimic metabolisms in and the chemical composition of seawater in the past (Bosak & Newman 2003, 2005; Bosak et al. 2007; Warthmann et al. 2011); and lithification in the presence of higher concentrations of silica and ferrous iron.

3.5. Theory of Stromatolite Growth and Form

One of the most poorly understood aspects of stromatolite morphogenesis is the translation of microscopic laminae into macroscopic shapes over long timescales. Macroscopic stromatolites take a long time to grow under realistic conditions (years to hundreds or thousands of years), outlasting those who study these structures. Theoretical approaches can circumvent this issue by enabling quantitative reconstructions of growth processes from actual rocks. Because any mathematization of the complex physical, biological, chemical, and environmental processes shaping stromatolites is rife with simplifying assumptions and approximations, it is sensible to ask what these models add that is not readily obvious in the field and in thin sections of well-preserved stromatolites. At their most informative, mathematical models of stromatolites arise from explicit considerations of physical, biological, and chemical processes and offer a threefold contribution to our understanding of life on the ancient Earth. First, they enable us to infer physical attributes of ancient microbial mats that can be compared with modern examples. Second, they provide quantitative tests of stromatolite growth mechanisms. Third, they identify the dynamics that produce different stromatolite forms and organize fields of stromatolites.

3.5.1. Principles of mathematical models. All present mathematical models of stromatolite morphogenesis ask a similar question: How do the accretion of minerals, the accumulation of sediment, and biological processes lead to the observable shapes of stromatolites? In general, the accretion rate of any particular point on a stromatolite depends on chemical (e.g., mineral precipitation), environmental (e.g., sedimentation, wave motion), and/or biological processes (e.g., phototaxis, growth, production of biopolymers).

When processes that build laminae occur on scales much smaller than that of the stromatolite, local models that consider only events immediately around the point of interest describe the growth dynamics. Present local models of stromatolite growth (Grotzinger & Rothman 1996;

Batchelor et al. 2000, 2004, 2005; Cuerno et al. 2011) focus on four basic processes: vertical growth, growth normal to the surface, diffusive smoothing, and random noise. These models are expressed as a modified Kardar-Parisi-Zhang (KPZ) equation (Kardar et al. 1986) for the height h of the stromatolite above some reference point. h changes according to the equation

$$\frac{\partial h}{\partial t} = v_0 + \lambda\sqrt{1 + (\nabla h)^2} + \nu\nabla^2 h + \eta(x, t). \tag{1}$$

The first term on the right-hand side of the equation says that, regardless of the local shape of the stromatolite, everything grows upward at a constant velocity v_0. This process is attributed either to the accumulation of sediment (Grotzinger & Rothman 1996) or the behavior of bacteria in the overlying mat (Batchelor et al. 2004). The second term describes the velocity of interface growth in the normal direction, where the coefficient λ indicates the importance of mineral precipitation. The third term states that topographic highs tend to erode, whereas lows tend to be filled in; the magnitude of coefficient ν determines the importance of this process. The final term, $\eta(x, t)$, is a random function of time that describes the stochastic deposition and erosion of material. Present KPZ models focus on the steady-state dynamics of stromatolite growth, identifying large-scale abiotic shapes that are consistent with the statistical steady-state shape predicted by the KPZ equation (Grotzinger & Rothman 1996). The KPZ model also predicts changes in the thickness of laminae in different regions of some stromatolites that, given certain initial conditions and the absence of random forcing, generate shapes quite similar to conical and domal stromatolites (Batchelor et al. 2004, 2005). Importantly, the KPZ equation also predicts that the shape of an initially flat stromatolite will become rougher as the structure grows (Kardar et al. 1986). Future work may compare the predictions of these models to the growth of lamina under changing conditions and ask why many stromatolites do not coarsen as they grow upward (i.e., they do not conform to the simple predictions of the KPZ equation).

Even if a model, whose individual terms (Equation 1) are invested with a physical meaning a posteriori, produces shapes that resemble stromatolites, how does one infer specific biological and geological processes from the general processes of surface-normal and vertical growth with diffusion and noise? The KPZ equation (Equation 1) describes a wide class of local interface growth equations ranging from the growth of snow banks and brains to the deposition of thin films and the propagation of light through random media and drying films (Barabási & Stanley 1995). In the KPZ equation, a snow bank and a stromatolite differ only in the interpretation of coefficients. Therefore, models based on the KPZ equation that predict stromatolite growth and form should always consider the realistic scales, as well as the stratigraphic, sedimentological, geochemical, and mineralogical context of real stromatolites.

A second class of models describes stromatolite growth through nonlocal processes. Consider a sand grain that is being swept chaotically around a stromatolite by flowing water. When the grain strikes the structure, it can become stuck in the mat and contribute to the growth of the stromatolite. If sediment grains rarely reach the bottom of deep crevices without first hitting a sticky wall and becoming trapped, topographic highs will grow at the expense of topographic lows, commonly giving rise to branching morphologies. This model is nonlocal: To know how fast a particular part of the stromatolite grows, one must know where this part is located. The mathematical description of this process is called diffusion-limited aggregation (DLA; Witten & Sander 1981) because an aggregate grows in response to a diffusing resource. In the context of stromatolites, the diffusing resource can be either a nutrient required for the growth of the microbial mat or, as above, mineral grains or ions that become incorporated into the stromatolite (Verrecchia 1996, Grotzinger & Knoll 1999). Additionally, one can consider more elaborate descriptions of how diffusing particles become trapped at topographic highs and lows (Dupraz et al. 2006). Although DLA models can

generate branching forms that resemble stromatolites (Verrecchia 1996, Grotzinger & Knoll 1999, Dupraz et al. 2006), they are yet to be used in quantitative, scale-dependent comparisons to field observations. This matters, because similarly shaped stromatolites can differ in scale by more than two orders of magnitude and can grow under different sedimentological, chemical, and biological regimes. For example, both submillimeter- to centimeter-scale precipitated stromatolites (e.g., Maliva et al. 2000, Jones & Renaut 2003) and decimeter-scale stromatolites that accrete in turbulent environments can be columnar and branched (**Figure 1**).

Future models of stromatolite morphogenesis should integrate realistic and measurable sedimentological parameters and attempt to explain various observables from the record: relationships among the spacing, sizes, and shapes of stromatolite columns; the synoptic relief of individual stromatolite laminae; the branching frequency of columnar stromatolites; the initiation of growth around topographic highs; and interactions of mats with grains of different sizes.

Given that many columnar stromatolites are not branched or branch rarely (**Figure 5**), whereas DLA models generate branching structures almost too readily, some form-stabilizing mechanisms must be at play in the real world. Biology may be key to the stabilization of decimeter- to meter-scale columnar stromatolites (**Figure 5**) because abiotic three-dimensional bedforms are unstable in oscillatory flow (e.g., O'Donoghue & Clubb 2001 and references therein) and upward-coarsening noncolumnar precipitates (Grotzinger & Rothman 1996) or submillimeter- to centimeter-scale dendrites (e.g., Walter 1976b, Maliva et al. 2000, Jones & Renaut 2003) grow when diffusion limitation, evaporation, and splashing overwhelm biological controls on mineral precipitation. In the absence of scour, cementation and trapping-and-binding can proceed at a similar pace in all directions but downward, leading to upward-coarsening stromatolite columns and domes (**Figure 5**) such as decimeter-scale microbial biscuits (e.g., Gebelein 1969) and domal or cauliflower-like microbialites from shallow, hypersaline environments (e.g., Burne & Moore 1987, Srivastava 1999). The stabilization of stromatolite diameters against coarsening or branching also assumes that the delivery of sediment to stromatolite tops and the scour in intercolumnar areas are more or less constant (**Figure 5**). Much remains to be elucidated about three-dimensional bedform morphologies accreting in fine sediments in the presence of directional flow, so any such studies are certain to improve quantitative understanding of the characteristic shapes, sizes, spacings, and branching characteristics of Precambrian columnar stromatolites.

3.5.2. Scale-dependent models of stromatolite morphogenesis. Recent models of stromatolite morphogenesis seek to infer realistic physical or biological processes from stromatolite morphologies. Petroff et al. (2010) recognized biological competition for nutrients as a factor that sets the spacing among small stromatolites in hydrologically quiet environments where nutrients are delivered to the mat by diffusion (e.g., Jorgensen & DesMarais 1990). When the maximal extent of nutrient gradients is determined by the time during which a photosynthetic mat takes in nutrients from its surroundings, approximately centimeter-scale spacing between vertical structures should record the length of day (Petroff et al. 2010). This mechanism does not explain the size or the spacing between large Late Archean (Altermann 2008) and Proterozoic cones (**Figure 6**) that grew in subtidal environments where mixing would have destroyed strong diffusive gradients in the fluid.

Tice et al. (2011) focused attention on the mechanical properties of biofilms and proposed a coupling between biofilm growth and turbulent shear. Their analysis predicts better biofilm growth on topographic highs due both to a higher local supply of nutrients by turbulence and to the development of smoother biofilms in the presence of stronger shear (Tice et al. 2011). Our observations confirm a simple "the tall get taller" mechanism whereby hydrodynamic conditions promote faster mat growth on topographic highs (**Figure 4**), but they also indicate that this mechanism may owe more to the negative influence of scour by saltating sediment in the topographic
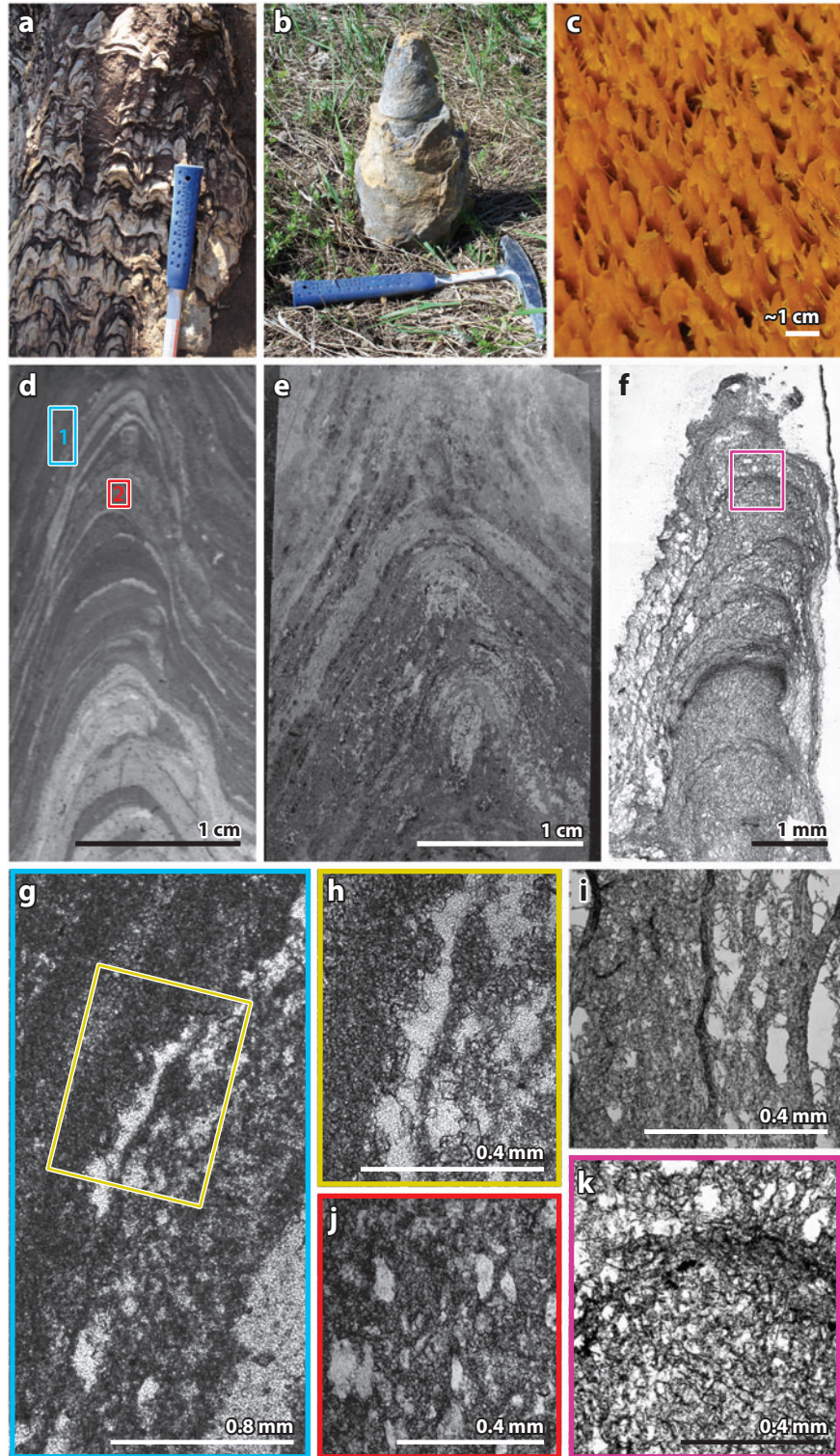
lows than to the positive influence of nutrients and shear at the topographic highs. Moreover, the frequent development of streamers in areas of strong flow (**Figure 4**) belies the simple prediction of smoother biofilms in areas of strong shear. The negative influence of scour is consistent with the nucleation of modern columnar stromatolites around hard or firm substrates but not on moving sands (Ginsburg & Planavsky 2008) (**Figure 1f**).

4. BACK TO THE RECORD

4.1. Environmental Factors

Meter-scale, columnar and ridged, coarsely laminated stromatolites similar to modern marine stromatolites occur in marine intertidal and subtidal settings in a number of older Phanerozoic deposits (e.g., Logan 1961, Gebelein 1969, Riding et al. 1991, Eagan & Liddell 1997). Meter-scale examples of mound and channel topography and decimeter-scale, rounded, regularly spaced but more finely laminated domes and columns are also present in Proterozoic and some Late Archean stromatolite assemblages (e.g., Hoffman 1976a, Pelechaty & Grotzinger 1989, Altermann 2008). Only the elongated morphology is commonly used as an indicator of current direction (e.g., Logan et al. 1974, Cecile & Campbell 1978, Southgate 1989), but if the analogy with modern features is correct, directional flow can shape both elongated and rounded stromatolites.

Following the analogy with ripples, whose spacing scales with the square root of the energy of near-bed orbital waves (e.g., Wiberg & Harris 1994), lower energy near stromatolite tops, reduced turbulent shear at the surface of the stromatolite, and lower sediment transport between the columns should result in smaller stromatolite diameters and spacings. Thus, modern stromatolite-forming marine environments (e.g., Gebelein 1969, Eckman et al. 2008) do not offer direct analogs of the flow/scour/turbulence regimes that shaped the decimeter- and centimeter-scale columnar stromatolites common in Proterozoic carbonates (**Figure 2b**). That said, insights into how changes in flow or sedimentation influence the diameters and the branching of columnar stromatolites in any setting may refine our interpretation of the rock record (**Figure 5**).

A secular decrease in the maximum diameter of Proterozoic stromatolites has been attributed to evolutionary processes (Raaben 2006). In most cases, however, similar diameters of columnar stromatolites reflect similar morphogenetic processes, calling for an environmental lens through which to view the distribution of stromatolite sizes through time. If the record from any given time contains many carbonates and stromatolites from low-energy environments with shallow, highly oversaturated waters (e.g., Paleoproterozoic) or nonmarine environments where lithification is fast (e.g., Phanerozoic hot springs), small, digitate forms should be abundant. The diameter

←——————————————————————————————————————

Figure 6

Conical stromatolites. (*a*) Small, Archean conical stromatolites from the 2.98-Ga Pongola Supergroup, South Africa. (*b*) Conical stromatolite from the Mesoproterozoic Bakal Formation, Russia. The hammer in panels *a* and *b* is 30 cm long. (*c*) Small, modern conical stromatolites from Yellowstone National Park, western United States. (*d–f*) Vertical thin sections through the centers of the stromatolites shown in panels *a*, *b*, and *c*. Areas labeled 1 (*blue*) and 2 (*red*) in panel *d* are magnified in panels *g* and *j*, respectively. Dark laminae contain micritic and microsparitic dolomite; very bright areas are silicified. Area from the magenta rectangle in panel *f* is magnified in panel *k*. (*g*) Fine lamination and fenestrae on the side of the Archean stromatolite. (*h*) Magnified area from the yellow rectangle in panel *g*. (*i*) Laminae around oxygen bubbles on the sides of a modern cyanobacterial structure (Bosak et al. 2010). (*j*) Silicified fenestrae in the center of the Archean cone. (*k*) Fenestrae surrounded by cyanobacterial laminae in the center of a modern cone (*magenta rectangle* in panel *f*).

distributions of Paleoproterozoic and Phanerozoic columnar stromatolites are thus similar (**Figure 2**) in that both records include many very small, dendritic forms in which precipitation probably swamped any mat influence (e.g., Makarikhin & Kononova 1983, Ross & Donaldson 1989, Zhu & Chen 1992, Maliva et al. 2000, Jones & Renaut 2003). Few large forms will be preserved during times that do not favor lithification in deeper parts of carbonate shelves. For example, Neoproterozoic shifts in carbonate sedimentation from a preponderance of precipitates to mainly grainstone and micrite (Knoll & Swett 1990), compounded with the concurrent radiation of algae, may account for the rarity of large conical forms in the deeper parts of carbonate platforms younger than ~0.7 Ga (**Figure 2c**). Even though these large forms disappeared in the later Neoproterozoic (**Figure 2d**), fast lithification and microbial interactions with sediments enabled the growth of small columnar stromatolites in shallower parts of later Neoproterozoic carbonate platforms.

Conical stromatolites with fine micritic laminae (**Figure 6**) constitute a dynamically simple system because their formation does not rely on trapping-and-binding, scour, or shear. Today, millimeter- to decimeter-scale organic cones and pinnacles are shaped by cyanobacterial communities (e.g., Walter et al. 1976, Parker et al. 1981, Andersen et al. 2011, Bosak et al. 2012, Voorhies et al. 2012), but only in hot springs does rapid lithification preserve the fine internal textures and the macroscopic morphologies of these structures (Walter et al. 1976, Jones et al. 2002). The aggregation of photosynthetic microbes into modern conical stromatolites inspires interpretations of ancient cones as indicators of photosynthesis, phototaxis, and growth toward light (Walter et al. 1976, Awramik & Vanyo 1986). Yet, recent studies (Petroff et al. 2010, 2011; Shepard & Sumner 2010; Bosak et al. 2012; Sim et al. 2012) challenge the attractive simplicity of earlier hypotheses by showing that light may exert a smaller influence on the growth geometry of small, conical microbial aggregates than does competition for nutrients within the mat. The remarkable size differences between modern centimeter-tall cones from shallow ponds and large Proterozoic cones from deeper parts of carbonate shelves (**Figure 6**) also invite the question of whether all conical shapes reflect similar morphogenetic mechanisms. A recent model couples the shape and the thickness of precipitated stromatolite laminae to the geometry of the overlying mat by considering the formation of mineral laminae as a function of the diffusion of ions and molecules through the mat (A.P. Petroff, N.J. Beukes, D.H. Rothman & T. Bosak, unpublished data). According to this model, the principal factor responsible for the central thickening of the laminae and the resulting conical shape is the precipitation of mineral surfaces under a 0.1–1-cm-thick diffusive boundary. This process does not explicitly require that the diffusive boundary layer be biological, phototactic, or photosynthetic. Nonetheless, the persistence of the conical shape through many growth cycles, the rarity of branching, and the growth of large cones in settings with nonnegligible currents once again imply a strong stabilizing influence that probably required biology.

4.2. Archean Stromatolites

The forms of most Archean stromatolites are qualitatively similar to those of later stromatolites (Walter 1983, Hofmann 2000, Schopf 2006, Altermann 2008), and Archean stromatolite assemblages are subject to all interpretative challenges discussed above. Additional uncertainties concern the problematic distinction between biogenic and abiotic structures whose laminae accrete exclusively by mineral precipitation, and the reconstruction of biogenic Archean stromatolites that lack obvious modern chemical and ecological analogs.

The question of biogenicity is least academic in the case of the oldest, largely stratiform and laterally linked stromatolites from 3.43-Ga Strelley Pool Chert (SPC; Walter et al. 1980, Hofmann et al. 1999, Allwood et al. 2006). These laminated structures formed in largely evaporitic

settings (e.g., Lowe 1983), where the prevalence of precipitates, a key but not unique or diagnostic stromatolite-forming process (e.g., Hofmann & Jackson 1987, Lowe 1994, Grotzinger & Rothman 1996), and pervasive recrystallization hamper the recognition of former microbial presence. All-wood et al. (2006) attributed the morphological variation among SPC stromatolites to the paleoenvironmental responses of stromatolite-forming microbes. Such hypotheses could be bolstered by a quantitative understanding of stromatolite scales and shapes that can be produced in fast-lithifying environments in the presence of evaporation, waves, and currents. The strongest arguments favoring the biogenicity of the SPC stromatolites are large, elongated conical forms (Hofmann et al. 1999, Allwood et al. 2006) and petrographic textures similar to those found in Proterozoic stromatolites influenced by both precipitation and detrital influx (Allwood et al. 2009). Improved growth models of conical stromatolites (A.P. Petroff, N.J. Beukes, D.H. Rothman & T. Bosak, unpublished data) may help relate the geometry of the SPC cones to that of later, unambiguously biogenic cones in a quantitative fashion. The presence of organic laminae in some domal SPC stromatolites is consistent with the former microbial colonization of these structures (Allwood et al. 2009). Modern, analytical techniques with high spatial resolution can detect concentrated biogenic elements and primary minerals in stromatolites at a submicrometer scale (Lepot et al. 2008) and map them in the context of the stromatolite fabrics (Wacey 2010). These techniques can trace biogenic elements such as S and N in carbonaceous particles (Wacey 2010) in some but not most SPC forms. That said, the incorporation of biological materials into precipitating carbonates does not in and of itself demonstrate that microbial mats templated accreting laminae (Grotzinger & Knoll 1999). Roughly coeval, draped, contorted, rolled, pinched, or broken organic-rich remnants of formerly cohesive biofilms from 3.42-Ga nonstromatolitic cherts (Tice & Lowe 2004) provide independent evidence for the early microbial colonization of shallow-water environments. Yet, metabolisms present in these early communities and sedimentary environments are not well constrained.

Cyanobacteria construct textures in modern stromatolites (Golubic et al. 2000), and various lines of genomic and proteomic evidence point to the evolution of oxygenic photosynthesis as early as ∼3.0 Ga (e.g., David & Alm 2011). At best, microfossils provide limited support for the hypothesis that cyanobacterial evolution was a primary determinant of Precambrian trends in stromatolite morphogenesis (Grotzinger & Knoll 1999). Tice et al. (2011) use the inclinations of bent laminae and the failure angles of torn biofilms to infer an increase in the cohesive properties of fossil biofilms in the Late Archean, possibly driven by evolutionary change. These intriguing estimates do not consider the possibility that these biofilms were variably lithified, although the degree of lithification at the time of deformation may exert a larger influence on estimates of biofilm cohesion than any evolutionary trends. Laboratory observations show that anoxygenic and anaerobic mats grown in agitated solution can resist scour and shear much as oxygenic mats do (**Figure 4**).

Alternative indicators of oxygenic photosynthesis may be present in a Mesoarchean stromatolite assemblage from the 2.98-Ga Pongola Supergroup. This assemblage contains various columnar forms, including decimeter- and centimeter-scale cones that grew submerged on a rather shallow carbonate-precipitating platform (Beukes & Lowe 1989). The centimeter-scale spacings, sizes, and shapes of the smaller cones (**Figure 6**) are consistent with the growth of photosynthetic mats in hydrodynamically quiet solutions by mineral precipitation under a diffusive boundary (Petroff et al. 2010; A.P. Petroff, N.J. Beukes, D.H. Rothman & T. Bosak, unpublished data). The laminae of these small cones preserve textural evidence of microbial orientation, aggregation, and likely, growth around gas bubbles (**Figure 6**). Nearly identical textures are present in modern conical stromatolites, where cyanobacteria produce oxygen and grow around oxygen bubbles but are not reported in microbialites that form around other gas bubbles. Fenestrae in modern, permanently submerged, fast-lithifying cyanobacterial stromatolites are 0.05–0.2 mm wide and cluster regularly

with respect to the fine and uniform lamination (Bosak et al. 2009, 2010; Mata et al. 2012) but do not disrupt the primary fabrics, as would be expected from heterotrophic degradation. Modern cyanobacterial mats provide the only direct analog for this combination of stromatolite shape and texture. The only other plausible alternative is anoxygenic photosynthetic mats whose fine primary fabrics are not destroyed during the organic decay by methanogenesis, but modern, aphotic, methane-based carbonates are chimney-like; contain large, irregular fenestrae; and are only occasionally and irregularly laminated (e.g., Barbieri & Cavalazzi 2005). Therefore, these Archean stromatolites are likely to preserve textural evidence of early oxygenic photosynthesis (Bosak et al. 2009) (**Figure 6**). Such evidence hints at a delay of at least ~0.5 Ga between the evolution of cyanobacteria and the oxygenation of the atmosphere.

The more abundant Neoarchean stromatolite assemblages may contain additional records of Archean biological and geochemical transitions, as they sample a larger range of microbial interactions with sediments, encompass a greater diversity of forms (Walter 1983, Hofmann 2000, Schopf 2006, Altermann 2008), and include a number of columnar stromatolites with diameter distribution and geometries comparable to those of the Proterozoic stromatolites (**Figure 2**) and regularly spaced clumps whose formation in modern mats is linked to the presence of molecular oxygen (Sim et al. 2012). Curiously, the cuspate and fenestrate microbialites from the deeper parts of the Late Archean platforms (e.g., Sumner 1997, Murphy & Sumner 2008) lack younger analogs, offering a potential window into the irreversible quirks of the Archean biosphere. These microbialites contain beautifully preserved textures characterized by narrow central supports and numerous thin, draping, contorted, horizontal, and rolled-up laminae. The cuspate, concave-upward, vertical cross sections (e.g., Sumner 1997) record different morphogenetic mechanisms than some older and many younger conical stromatolites (A.P. Petroff, N.J. Beukes, D.H. Rothman & T. Bosak, unpublished data). The growth and the exquisite preservation of these microbialites may have required the presence of stratified and carbonate-, iron-, and sulfide-rich waters in the deeper photic zone of the Late Archean carbonate platforms (Ono et al. 2009).

5. CONCLUSIONS

Models provide our best prospect of bridging the still sizable gap between observation and experiments on modern mats and the geologic record of stromatolites. This bridge, in turn, will help us to address a number of key questions about Earth's evolutionary and environmental history.

At present, four evolutionary questions seem especially tractable. What morphological, textural, ultrastructural, or chemical measurements can be made that will unambiguously demonstrate (or refute) the biogenicity of the oldest stromatolites? Can stromatolite morphologies and textures resolve the thorny issue of when cyanobacteria (and, thus, oxygenic photosynthesis) emerged? Is there a meaningful relationship between stromatolite diversity and environmental change through time? And, related to this, can we demonstrate an evolutionary influence on secular changes in either macro- or microscale features of stromatolites through time, or does environmental influence swamp any evolutionary signal?

This last question, of course, can be rearranged to focus stromatolite models on physical environment, seawater composition, and redox profiles of basins and sediments. Can we understand the observed relationships between the geometries of fields of stromatolites and facies in terms of sedimentary processes and the changing composition of seawater (including redox conditions)?

Microbial mats, witness to so much of Earth history, have recorded our planetary past in the forms, textures, and distribution of stromatolites. A new generation of models holds the potential to provide the geobiological Rosetta Stone needed to interpret this remarkable record.

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