Stromatolites: Biogenicity, Biosignatures, and Bioconfusion

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ABSTRACT

Stromatolites represent a multifarious system of nested, physically, chemically, and biologically influenced components that range in scale from microscopic to macroscopic. These components can include microorganisms, organic compounds of microorganisms, sediment grains, precipitated sediment, sedimentary textures (fabrics), microstructure, laminae, domes, columns, branched columns, and cones. Millimeter to meter scale edifices (stromatolites) are the result. Stromatolites once played a significant role in establishing life's presence on the early Earth, but now a shift away from reliance on stromatolites is occurring. There is a perception that Archean stromatolite-like structures have low reliability to signal life. This is likely due to (1) no unified theory on stromatolite morphogenesis, (2) no valid or appropriate modern analog to use in the interpretation of Archean stromatolites, and (3) disagreement on how to define the word stromatolite. No single feature or line of evidence has yet been found that can unequivocally indicate a biogenic nature for a stromatolite. However, a range of features and their combinations that are well documented for the vast majority of fossil stromatolites and are found in some living stromatolites, are difficult, if not impossible, to account for by inorganic processes. Morphology remains a valid criterion to indicate biogenicity.

Keywords: stromatolites, biogenicity, abiogenic, Archean

1. INTRODUCTION

As the sedimentary layers of Earth's history are peeled away and Archean rocks (older than >2.5 Ga) are exposed, the record of sedimentary rocks becomes sparse and the evidence for life becomes meager and difficult to read. The stakes also get higher. Establishing the early records of life on Earth and its nature have profound implications for models on the origin of life, the early evolution of life, the Archean Earth system, and astrobiology. Evidence for the detection of early life falls into three main categories: chemical signatures, microfossils, and stromatolites. Such evidence is rarely questioned when found in Proterozoic (2.5 to 0.542 Ga) or Phanerozoic (0.542 Ga to present) rocks, but comes under intense scrutiny when reported from Archean rocks (pre-2.5 Ga) and in particular from the Early Archean (pre-3.0 Ga). This is not inappropriate because the intellectual stakes are so high. However, it appears that the extensive experience and the lessons learned from the study of Proterozoic and younger records of life, and from modern analogs do not seem to diminish the views of the overly critical. Although claims are often made that imply significant differences between Proterozoic and Archean examples[1], any such differences appear to be minor and have been poorly documented. There is evidence that demonstrates that this is not the case where the structures observed are essentially similar to younger ones and similar processes likely were instrumental in their formation [2].

Living stromatolites are organosedimentary structures produced by the trapping, binding, and precipitation of sediments under the influence of microorganisms. Today they are found in a variety of environments (shallow marine, lakes, streams, springs). The structures produced by this microbial activity have a wide variety of shapes, the commonest of which include wavy lamination, domes, columns, branched columns, and cones. They can be millimeters to decimeters in size. Fossil counterparts showing similar features are readily recognized in the field. The oldest structures that show comparable characteristics are from the

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3490 Ma Dresser Formation in the Warrawoona Group in Western Australia[3]. Better preserved structures have been reported from the 3458-3426 Ma Strelley Pool Chert, Kelley Group, also in the Pilbara region of Western Australia[2, 4]. Other Archean occurrences are known[5, 6], but it was during the Proterozoic (2500 to 542 Ma) that the greatest abundance and diversity was present[7]. The Phanerozoic (<542 Ma) record is still significant, but reduced in abundance and diversity. Although the fossil structures are easily recognized in the field and have many characteristics of living stromatolites, questions have been raised as to whether the structures seen are the products of microbially influenced sedimentary processes (biogenic), or were formed without biotic mediation (abiogenic). This argument has been raised to such a high level, that stromatolites are now a poor stepchild in the pecking order of reliable signals to establish the early evidence of life. What is it about an Archean stromatolite that reduces its reliability as an indicator of the existence of life? Why are many researchers willing to accept Phanerozoic and Proterozoic structures as biogenic, but draw the line at Archean ones? Why should chemical signatures (isotopes and biomarkers) and microbial fossils present information that is more reliable?

The perception that Archean stromatolite-like structures have a low reliability quotient can be attributed to a few critical issues: (1) there is no unified theory on stromatolite morphogenesis, (2) there is no valid or appropriate modern analog to use in the interpretation of pre-Phanerozoic stromatolites, and (3) the definition of the word stromatolite is contentious.

Despite differences of opinion on definitions, the lack of an appropriate modern analog, and no unified theory on stromatolite morphogenesis, there are a number of features in stromatolite-like structures that provide consistent and reasonably reliable signals that biological processes were involved in their formation. "Andy Knoll's Law" states: A good biomarker is something that is *difficult* to make through inorganic processes[8]. No single feature or line of evidence has yet been established that can be used to determine unequivocally the biogenic nature of a stromatolite. However, a range of features and their combinations, well documented for the vast majority of fossil stromatolites are difficult, if not impossible, to account for by inorganic processes. Therefore, using Knoll's Law, these features qualify as good biosignatures. Moreover, it is the combination of features that is critical in trying to identify a biogenic origin for stromatolite-like structures. It may be possible to produce a single feature of a stromatolite-like structure by physical or chemical means, but it is extremely difficult, if not impossible, to produce a structure that has a complete suite of all the features commonly present in stromatolites by any process that excludes some degree of biological activity or influence. It is not the intent of this paper to elaborate in detail on the morphological features and other attributes that can be used to assist in recognizing a biogenic stromatolite. Much of this has been done by others[2, 9, 10]. This paper articulates the debate on biogenic versus abiogenic stromatolites and advocates an approach.

2. Definition and Nature of Stromatolites

The German term "Stromatolith" was coined by Ernst Kalkowsky in 1908[11] from the Greek words *stroma,* meaning bed, mattress or layer; and *lithos*, meaning stone. The name was in reference to masses of laminated limestone in the non-marine Lower Triassic Buntsandstein in the Harz Mountains of Germany. According to Krumbein[12], p. 499, Kalkowsky stated "stromatolites are organogenic, laminated, calcareous rock structures, the origin of which is clearly related to microscopic life, which in itself must not be fossilised." Kalkowsky attributed the formation of these structures to lower plants, mosses, and cyanobacteria[13]. The term appears to have found little use initially, although it was mentioned in such papers as Linck[14]. It may have been Holtedahl[15] who first used the English equivalent of the word (stromatolite). Pia[16] popularized the term in 1927 as a type of fossil produced by the calcium carbonate precipitation of cyanobacteria ("Stromatolithi"). A conclusion that such structures were built by cyanobacteria was reached a few years earlier by Walcott[17] in 1914; however, he did not use the term stromatolith and apparently wasn't aware of Kalkowsky's contribution.

Today, there is still no generally accepted definition of stromatolite. A number of papers have gone to great lengths to address the definition of the word and to explore its meaning[12, 13, 18-21]. The major disagreement is whether the term should be descriptive or genetic. Are stromatolites fossils or do they represent sedimentary structures? An often-used descriptive definition was proposed by Semikhatov and others[19] on

p. 993: "an attached, laminated, lithified sedimentary growth structure, accretionary away from a point or limited surface of initiation." A genetic definition proposed by Awramik and Margulis (in Walter[22], p. 1) and widely used is "organosedimentary structure produced by sediment trapping, binding, and/or precipitation as a result of the growth and metabolic activity of micro-organisms, principally cyanophytes [cyanobacteria]." The issue was further complicated by the introduction of the term "microbialite" by Burne and Moore[23]. Although they acknowledged the genetic and descriptive positions, they proposed that stromatolites be included as a type of microbialite that has lamination. They thus reserved the term for a structure with some component of biogenic origin. They defined microbialite on pages 241-242[23] as "organosedimentary deposits that have accreted as a result of benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation." Using the Burne and Moore definition of microbialite, the term stromatolite (together with thrombolite, and the less common dendrolite and leiolite) becomes a subset of microbialite.

Much has been written about the error of using stromatolite as a genetic definition, but many other commonly used terms are of genetic origin and do not provoke such antagonism. Acceptable genetic terms in use in the literature include: aeolianite, debrite, evaporite, geyserite, hemipelagite, kaolinite, oolite, pisolite, radiolarite, rhythmite, tempestite, and turbidite. Why should the term stromatolite be regarded as anything different? The name was intended to imply biogenicity, and it should not be ruled out just because it is a genetic term. By its original definition and its subsequent usage, the term indicates that the structure has a biogenic origin.

There is a current trend, however, to use stromatolite as a purely descriptive term, in the sense of Semikhatov and others [19] implying any laminated structure with a positive relief. This is a corruption of the original intention and has resulted in the use of terminology such as abiogenic stromatolite. Hofmann [24] introduced useful terminology for dealing with problematic pre-Phanerozoic structures that might, or might not, be biogenic. He used fossil, pseudofossil, and dubiofossil. A parallel terminology can be applied to stromatolites. A structure of biogenic origin is a stromatolite. A structure of abiogenic origin is a pseudostromatolite if it resembles a stromatolite. A structure resembling a stromatolite, but of uncertain origin is a dubiostromatolite. Adoption of this terminology permits the discussion to be simplified and focuses debate on the more important issues of (1) which characteristic features of stromatolites, pseudostromatolites, and dubiostromatolites are common to all three types (which is why it is hard, but not impossible, to distinguish between them), (2) which features are most likely to be different in each category, and consequently (3) which features are useful for distinguishing biogenic from abiogenic structures.

3. Modern Analogs

Geology and paleontology rely a great deal on modern analogs to interpret ancient examples. There are many modern analogs for ancient stromatolites. The most influential modern analog is the occurrence of columnar stromatolites forming in intertidal to very shallow subtidal regions of Hamelin Pool, Shark Bay, Western Australia[25, 26]. Although there were other marine examples known by the time the Shark Bay examples were published[27], Shark Bay provided the much-needed modern analog in terms of size. The Shark Bay columns are decimeters in size, like many columns found in the Proterozoic. Meter-size columns were also discovered growing in 10 meters of water off Lee Stocking Island, Bahamas[28]. But, Lee Stocking Island and Shark Bay do not serve very well as analogs to pre-Phanerozoic stromatolites. These stromatolites are coarse-grained (sand size) while almost all pre-Phanerozoic stromatolites are composed of very fine grained material (micrite)[20]. In addition, there are many shapes in the Proterozoic that lack modern analogs. Living stromatolites are also found forming in coastal lagoons/lakes[29], inland lakes[30], hot springs[22], and streams[31]. None of these or any of the other occurrences of actively forming stromatolites serves as an all-purpose model to understand the morphogenesis of stromatolites in the pre-Phanerozoic.

4. The Quest for Unambiguous Evidence for Biogenicity

The emergent field of astrobiology has sharpened concerns about the recognition of life and intensified demands for unambiguous evidence of life's presence on the early Earth. The quest for unmistakable biosignatures was elevated a few years ago with a paper by Brasier and others[32] that questioned evidence for microbial fossils and even stromatolites in Early Archean deposits of Western Australia. This has led to a flurry of papers taking various positions on the nature and reliability of evidence[33]. Proposals on the evaluation of evidence have been made to supplement or even supplant some of the pioneering work of Cloud[34, 35] and Schopf[36, 37].

Brasier and others[1] proposed on page 147 a null hypothesis for approaching the biogenicity problem: "very ancient/alien microfossil-like structures (or stromatolites or geochemical and isotopic signals older than c. 3.0 Ga) should not be accepted as being of biological origin until possibilities of their non-biological original (*sic*) have been tested and can be falsified (see Brasier *et al.*, 2002[32])." This places the putative fossil on a cusp; in an 'either/or' situation. It also "requires astrobiologists to become acquainted with the geochemistry and morphospace of abiological phenomena that mimic the earliest life forms"[38]. If an abiological origin cannot be falsified, the structure should not be accepted as of biological origin. This sets lofty standards for the science of paleontology.

A more reasonable approach is "Knoll's Law," mentioned earlier: A good biomarker is something that is *difficult* to make through inorganic processes. This was later expanded to the Knoll criterion[39, 40]: "in the course of that exploration, you find a signal that is (a) not easily accounted for by physics and chemistry or (b) reminiscent of signals that are closely associated with biology on Earth, then you get excited. What will happen then, I can guarantee you, is that 100 enterprising scientists will go into the lab and see how, if at all, they can simulate what you see – without using biology." However, with regard to Earth, Knoll[39] comments that "nobody would waste their time doing these things because, on Earth, we know that there has been biology for most of the planet's history. Biology is everywhere. Biology is pre-eminent in the signals that it imparts to sedimentary rocks."

Paleontology is not physics. "Because initial conditions can never be known at the required level of accuracy, predictability is not obtainable"[41] and predictability is a significant component of physics. Initial conditions for times in the geological past are not well known, in particular for very old rocks. Paleontology, as an historical science, requires a different approach than physics. Predictability is greatly diminished and qualitative evidence commonly overwhelms quantitative evidence. A key to the success of paleontology stems from taking an actualistic approach: the comparison of a putative fossil with a living counterpart to help establish the biogenic nature of the fossil. This was elegantly done by Steno in 1667[42]. Paleontologists also compare the putative fossil with a more confidently known fossil from another formation and age. We stress the relative nature of the phrase "more confidently known," because evidence is often imperfect. Hence, its reliability and interpretation can be subjective. In order to deal with this dilemma in a systematic way, Cloud facilitated the development of degrees of confidence or a level of credibility approach[43, 44] that Schopf and others[45] expanded and presented in detail. Terms like "suggestive," "permissive," "presumptive," "persuasive," and "compelling" evidence are not unique to paleontological studies, but are also part of the fabric of science (e.g., see Wilson[46]. Here is a useful descending scale of credibility:

Compelling evidence: Abundant evidence that permits only one reasonable interpretation[45].

Presumptive evidence: The preponderance of evidence suggests a most likely interpretation but for which less probable interpretations also merit consideration[45].

Permissive evidence: Evidence that seems consistent with at least two more or less equally tenable competing interpretations[45].

Suggestive evidence: Evidence that although weak, is at least consistent with the interpretation[43].

Missing evidence: There is no direct interpretable evidence to support the interpretation[45].

5. Criteria for Recognizing Biogenicity in Stromatolites

"Something that haunts geologists working on ancient stromatolites is the thought that they might not be biogenic at all."[47]. There have been several attempts to develop a comprehensive set of criteria that can be used to identify biogenicity in a stromatolite. Buick and others[9] presented the following on pages 165-167:

(1) the structures must occur in undoubted sedimentary or metasedimentary rocks; (2) it must be demonstrated that the structures are synsedimentary (formed at the same time the sediments constituting the bed were being deposited); (3) there should be a preponderance of convex-upward structures; (4) laminae should thicken over crests of flexures; (5) laminations should be wavy, wrinkled, and/or have several orders of curvature; (6) microfossils should be present in the structures; (7) changes in composition of microfossil assemblages should be accompanied by morphological changes of the stromatolite; and (8) microfossils must be organized in a manner indicating trapping, binding or precipitation of sediment by the organisms. These are exacting criteria and there are few stromatolites that would unambiguously meet all the criteria. Criteria (7) and (8) are dependent on criteria (6). In the fossil record, only a minute percentage of stromatolites contain microfossils. The structures originally defined as stromatolites[11] do not contain microfossils.

Walter[10], on page 190, proposed that a stromatolite must (1) be oriented in relation to sedimentary bedding in a way that demonstrably indicates that it formed synchronously with the bed in which it is found; (2) occur within a sedimentary facies in which the stromatolite can only be explained a primary sedimentary structure; (3) have a macromorphology consistent with a stromatolitic origin; (4) have a micromorphology (lamina shape and microstructure) consistent with a microbial origin, and (5) have a chemical composition consistent with an origin as a stromatolite.

More recently, Hofmann and others[2], page 1260, provided specific information with regard to biogenicity for 3.45 Ga coniform stromatolites from Western Australia, which are among the oldest known: (1) there is greater uniformity of laminae in the coniform structure compared to the layers/laminae in the intermound (inter-stromatolite) region that were subjected to more variable sedimentological/environmental conditions; (2) they are not the product of downward-directed slumping or sideways compression; (3) the continuity of laminae across different structures is difficult to attribute to chemical precipitation; (4) the arrangement and spacing of the coniform structures within sedimentary beds at specific stratigraphic levels indicate growth under uniform conditions within the basin for limited intervals of time; and (5) the slopes of the cones is higher than 40° (up to 75°) which is far greater than the angle of repose for loose sediment. The geological content of these structures is entirely consistent with them being biogenic. They formed in a near shore marine environment[2, 48].

There have been very few attempts so far to take a holistic approach in looking at Archean stromatolites. The focus has been mainly on gross morphology and commonly has concentrated on a single factor, rather than on the combination of characteristics. Recrystallization creates a major problem for the analysis of laminar details in both the Dresser Formation (oldest stromatolites) and Strelley Pool Chert (coniform) stromatolite-like structures, but there are some patchily preserved details that still require analysis.

Quantitative analyses of stromatolite morphology have been applied with two goals: (1) to provide for a more objective, quantitative (geometrical) description (for an example, see Hofmann[18]) and classification[49] of the stromatolite, and (2) as a tool to determine biogenicity[50]. Grotzinger and Rothman[50] made an important contribution in which they concluded the biogenicity of a stromatolite could be called into question through the combined use of self-affine fractal analysis (using the KPZ interface equation) and microscopic texture. This has resulted in a conclusion that if a supposed stromatolite's laminar geometry can be modeled following fractal geometry, the structure is likely abiogenic (see discussion in Ruiz and others[51]). Statements like this from Cocks[52] (page 352) have been made "Laminated structures known as stromatolites have been described from rocks as old as 3.4 Ga in Australia and South Africa; however, it appears that the earliest stromatolites were inorganic in origin." This was presumably influenced by such papers as Grotzinger and Rothman[50] and Brasier and others[32].

Other mathematical approaches for determining biogenicity include lossless compression[53], a different application of the KPZ interface equation[54, 55], and modeling using the SRK equation[56]. These examples have suggested that mathematical modeling of laminar geometry can be consistent with a biogenic interpretation. This has been elegantly supported by the work of Kaandorp and Kubler[57] on sessile organisms, including stromatolites. The physical and chemical properties manifest in the environment where a (a) single organism, (b) colony, and/or (c) microbial community grows will have influence on morphogenesis. It is unclear where the mathematical modeling approach to determine the biogenicity of stromatolites will lead.

Rather than focus on criteria suggesting a biogenic origin, Brasier and others[1, 38]looked at the problem from a different perspective: Can stromatolite-like structures be produced abiogenically? They[38] pointed out that observations within the literature indicate that they can. Therefore, they contended, it is necessary to characterize the mechanisms and falsify the abiogenic possibilities before acceptance of a biogenic origin. However, as a matter of course, most credible researchers spend a considerable amount of time considering alternative modes of genesis before reaching a conclusion that structures are stromatolites. This was certainly the case when Hofmann and others[2] examined the Kelly Group (formerly part of the Warrawoona Group) stromatolites. Numerous hypotheses for mechanical or chemical formation were considered and tested by examination of the structures in outcrop. Often these deliberations are not included in the final publication. Perhaps for examples younger than 3.0 Ga, such deliberations will be required in the future, raising the burden of proof. Moreover, at this point in time, it is far from clear that abiogenically generated structures resemble undoubtedly biogenic stromatolites more than superficially.

The black and white nature of the arguments proposed recently is clouding the actuality. Living stromatolites result from an integration of processes that can be depicted on a triangular diagram [6]. The problem facing most stromatolite researchers is not the black and white issue of whether a structure had a biogenic component, but where it plots in terms of the contribution made by physical, chemical, and biogenic processes. A structure that has some biogenic contribution is a stromatolite. A structure that is entirely physical, entirely chemical, or a combination of the two with no biogenic component is a pseudostromatolite. The task of the paleontologist is to determine from morphological and other forms of examination whether biogenic processes contributed or did not contribute to the formation of the structure.

6. Summary

The lack of a generally accepted definition of stromatolite has led to unfortunate confusion and some unintended consequences. Combined with the lack of an appropriate modern analog and no general 'theory' of stromatolite morphogenesis, it appears to the uninitiated that there is a lack of information and rigor in the study of stromatolites. A keyword search of *GeoRef* using "stromatolite*" produced 4796 entries on July 27, 2005 ("trilobite* produced 4817 entries). So there is a robust literature. The complicated nature of stromatolites also makes them seem inadequately understood. However, knowledge about distinctive shapes and features at the megascopic to microscopic level (complicated nature) of stromatolites and their restriction to certain intervals of geological time have led to their demonstrated use in biostratigraphy[58-60].

Stromatolites are viewed to represent a multifarious system of nested, physically, chemically, and biologically influenced components. These components can include microorganisms (from a few species to many species), organic compounds of the microorganisms, vital effects of the microorganisms, sediment grains, precipitated sediment (both biologically influenced and non-biologically precipitated), sedimentary textures/fabrics (microstructure), laminae (mesostructure), domes, columns, branched columns, and cones (macrostructure). The interactions of the physical, chemical, and biological components with sediment, both detrital and precipitated, result in the accumulation of material, micrometers to a few millimeters in scale, that accrete continuously, episodically, or periodically, to produce organosedimentary structures at the millimeter to meter scale. This process appeared early in the Archean, the oldest evidence is from the 3.49 Ga Dresser Formation (Warrawoona Group). Stromatolites diversified greatly and became abundant in the Proterozoic. Some of these, in particular from the Proterozoic, are morphologically unique and restricted in time.

Attempts to place what Wilson[46] on page 59 calls an "objective yardstick" for evidence and the degrees of acceptance of that evidence can result in a perverted conclusion. Rather than approach the problem in the more binary and seemingly objective approach that Brasier and others advocate (their null hypothesis), we suggest that the descending scale of credibility is better. This doesn't "throw out the baby with the bath water," which is critical when dealing with this subject. Morphology remains a valid test of biogenicity.

Unequivocal proof is something on which paleontology is largely moot. Compelling evidence, however, can be an obtainable goal, but lesser degrees of confidence are also constructive contributions.

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