Stromatolites, so what?! A tribute to Robert N. Ginsburg

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Abstract
In tribute to Dr. Robert N. Ginsburg (1925–2017), we examine his 1991 seminal paper *Controversies about Stromatolites: Vices and Virtues*, which summarized current ideas about stromatolites including controversies of definition, whether ancient stromatolites should be interpreted as sedimentary structures and mechanisms of carbonate fixation. The accepted model of stromatolite morphogenesis in 1991 was that biology controls microscale internal structure whereas environment controls macroscale morphology. Ginsburg, however, predicted that biology and environmental influences on stromatolite growth were closely coupled at macro, meso and micro scales. Recent research in Hamelin Pool and the Bahamas has advanced our understanding of the inherent duality of stromatolites and associated controversies. These studies suggest that at the macroscale, when physical forces are strong, the environment is the main control on the morphology; however, when physical forces are weak, biological communities become the main drivers of morphology. Therefore, stromatolites can be considered both as fossils and as sedimentary structures dependent on the energy in the environment of deposition. At the mesoscale, as predicted by Trompette, stromatolite fabrics are influenced equally by environment and biology. As the degree of lamination is often unknown or heterogeneous, a generic genetic term such as ‘microbialite’ is considered the most appropriate terminology for structures of probable microbial origin. At the microscale, stromatolite microfabrics reflect environmentally driven cycling of microbial communities, reflecting both biology and environment. With respect to carbonate fixation, research on modern stromatolites provides a model for biofilm precipitation of micritic laminae lacking microfossils in ancient stromatolites. As pointed out by Ginsburg, the inherent duality of environmental and biological controls of morphogenesis at all scales is at the root of many long-standing controversies. Recent investigations corroborate the foresight of Ginsburg nearly 30 years ago, further confirming well-preserved stromatolites can provide insight into both biology and environmental factors in ancient ecosystems.

Keywords
Duality, microbialites, microfabrics, morphology, stromatolites
1 | INTRODUCTION

Dr. Robert N. Ginsburg (1925–2017) had a life-long love affair with stromatolites. As a pioneer in comparative sedimentology, Bob applied a comparative approach to stromatolite formation. In 1964, he co-authored a seminal paper, *Classification and Environmental Significance of Algal Stromatolites*, with Brian Logan and Robert Rezak on the environmental controls of stromatolitic structures using modern examples (e.g. Shark Bay) to help interpret ancient structures (Logan, Rezak & Ginsburg, 1964). In 1968, Ginsburg organized an international conference on stromatolites (Hoffman, 2019). In 1991, he published another paper, *Controversies about Stromatolites: Vices and Virtues*, which summarized the current ideas about stromatolites stating, ‘Almost everything about stromatolites has been, and remains to varying degrees, controversial. Have these controversies influenced research and thinking about these laminated structures that play such a prominent role in earth history? To seek answers to this question, it is necessary to examine some of the controversies and try to gauge their vices and virtues…’ (Ginsburg, 1991). These ideas never left the forefront of his mind and in 2011, at the Gordon Research Conference on Geobiology in Ventura, California, Bob led a breakout group in a round table discussion on stromatolite controversies.

Ginsburg attributed the controversies regarding stromatolite formation in part to differences between modern and ancient examples and opposing philosophies among researchers but mostly to the inherent duality of stromatolites and disagreements regarding the competing roles of nature (biology) versus nurture (environment) in controlling stromatolite formation. The problem or the ‘vice’ of arguments regarding stromatolite formation was that polarization of opinion regarding duality detracted from resolving the issues. The benefit, or the ‘virtue’, was that the inherent duality of the stromatolite was emphasized. In a prophetic statement, Ginsburg (1991) suggested that ‘future efforts may well reveal that these two processes (biology and environmental influences on stromatolite growth) are closely coupled at all scales.’ Nearly 30 years after the publication of his 1991 manuscript, we can corroborate his foresight by looking at new insights made in the last three decades of research on modern and ancient stromatolites in both Hamelin Pool, Shark Bay and in the Bahamas.

In this paper, we (1) give a brief overview of stromatolites through time, (2) summarize the controversies defined by Ginsburg (1991), (3) show how research on modern stromatolites in the past 30 years sheds light on those controversies, verifying Bob’s (1991) prediction regarding the closely coupled roles of biology and the environment in stromatolite morphogenesis and (4) consider Bob’s epic question of ‘So What?’. The paper stands as a tribute to Dr. Robert N. Ginsburg for his major impact on stromatolite research and carbonate sedimentology and acknowledge Bob for encouraging his many students and colleagues to think creatively, ‘while you are resting’.

2 | STROMATOLITES THROUGH TIME

Reef complexes known as stromatolites, built by benthic microbial communities, dominated the fossil record for over 80% of Earth history and are the first fossil record of macroscopic life (Allwood, Walter, Kamber, Marshall, & Burch, 2006; Awramik, 1992; Hofmann, Grey, Hickman, & Thorpe, 1999; Lowe, 1980; Nutman, Bennett, Friend, Kranendonk, & Chivas, 2016; Walter, Buick, & Dunlop, 1980). Well-preserved ancient stromatolites provide a window into ancient life (Grotzinger & Knoll, 1999). Stromatolites form when layers of bacterial mat grow sequentially on top of one another and lithify to form a three-dimensional rock framework. This framework forms by microbial trapping and binding of detrital sediment and/or mineral precipitation and is further strengthened by diagenesis and continued cementation through time (Awramik, 1984; Awramik, Margulis, & Barghoorn, 1976; Burne & Moore, 1987). These processes produce distinct build-ups that have relief above the seafloor (Playford et al., 2013).

A major decline in stromatolitic diversity is evident in the fossil record from 1 Ba to 540 Ma, reflecting evolution of higher animals and plants that were able to outcompete the stromatolite-building microbial communities (Awramik, 1971; Fischer, 1965; Garrett, 1970; Monty, 1973; Walter & Heys, 1985). As such, modern stromatolites are scarce worldwide. Two of the best-known assemblages of modern stromatolites are the marine systems in Shark Bay, Western Australia and the Bahamas. Stromatolites in Hamelin Pool, Shark Bay, were discovered by Phil Playford in 1954, who identified them as ‘algal mounds’, built by blue-green algae (now known as cyanobacteria) and later identified as stromatolites in 1956 by Richard Chase, drawing on knowledge from examples in the rock record (Playford & Cockbain, 1976). Bahamian stromatolites were discovered in the 1980s by Jeff Dravis who described small shallow subtidal structures in the Schooner Cays on the margin of Exuma Sound (Dravis, 1983) and Bob Dill who reported massive subtidal structures in the vicinity of Lee Stocking Island (Dill, Shinn, Jones, Kelly, & Steinen, 1986); they were then mapped at numerous locations throughout the Exuma Cays by Reid, Macintyre, Steneck, Browne, and Miller (1995). Additionally, less extensive stromatolitic assemblages have been discovered throughout the world in freshwater, brackish water, saline and highly alkaline lakes (Cohen, Talbot, Awramik, Dettman, & Abell, 1997; Defarge, Trichet, & Cou, 1994; Desnues et al., 2008; Farías et al., 2014; Farías, Poiré, Arrouy, & Albarracin,
3 | STROMATOLITE CONTROVERSIES

Stromatolites have been a subject of controversy since they were first described over a 100 years ago. Three controversies highlighted by Ginsburg (1991) are summarized below.

3.1 | Controversy 1 – Definition

The first stromatolite controversy is the definition itself. In the Harz Mountains of Germany, Kalkowsky (1908) discovered a series of layered rocks in the fossil record that he proposed were of biological origin. Kalkowsky called these structures ‘stromaliths’ from the Greek ‘stroma’ meaning layered and ‘lithos’ meaning stone. The word stromatolite was subsequently used to describe ‘organogenic, laminated calcareous rock structures, the origin of which is clearly related to microscopic life which in itself must not be fossilized’ (Krumbein, 1983, p. 499). Since its inception, stromatolite has had a number of definitions. Awramik and Margulis (1974) and Walter (1976) broadened the Kalkowsky definition to encompass all microbial deposits, including laminated and unlaminated structures. Semikhatov, Gebelein, Cloud, Awramik, and Benmore (1979) circumvented the problem of identifying a biogenic origin for a fossil deposit by offering a descriptive definition for stromatolites, indicating that the fossil must be laminated but not necessarily organic; this is the most general definition and is practical for identifying structures in the field. Krumbein (1983) acknowledged the importance of laminated fabrics and input from microorganisms in concert with the surrounding environment in stromatolite formation and Schopf (1983) leaned even more towards genesis in his definition stating that the microorganisms forming stromatolites must be filamentous and photosynthetic. Burne and Moore (1987) coined an umbrella term, ‘microbialite’ to indicate structures with a biogenic origin and subdivided microbialites according to the degree of internal fabric laminated fabrics, thrombolites with clotted fabrics, dendrolites with dendritic or branching fabrics and leiolites with aphanitic fabrics. Based on Burne and Moore, stromatolites are commonly described as laminated organo-sedimentary structures produced by trapping and binding and/or precipitation of mineral matter resulting from the metabolic activities of microorganisms (combined from Awramik et al., 1976; Burne & Moore, 1987; Walter, 1976). As Ginsburg pointed out in 1991, stromatolite definitions run the gamut, capturing a purely descriptive definition at one end and an entirely genetic definition at the other.

3.2 | Controversy 2 – Fossils or Sedimentary Structures

The second stromatolite controversy involves controls of stromatolite morphogenesis, in particular the relative influences of biology versus environment in controlling growth at various scales. Are stromatolites biological fossils that can be used in biostratigraphy or are they sedimentary structures that can be used to interpret the environment of deposition? Ginsburg (1991) stated that the generally accepted theory was that of Trompette (1982): the environment acts as the main influence on stromatolite formation at the macroscale whereas the biology is the main influence at the microscale.

3.3 | Controversy 3 – carbonate fixation

The third stromatolite controversy highlighted by Ginsburg (1991) deals with stromatolite accretion, particularly the role of precipitation of cements versus trapping and binding of detrital grains. Ancient stromatolites have mainly fine-grained, micritic textures, resulting in a distinct textural difference with modern stromatolites, which are often sandy. This controversy raises several questions regarding the role of trapping and binding: What is the origin of the micrite in ancient stromatolites? Are micrite-sized grains trapped and bound or is the micrite precipitated in situ? What accounts for the larger grain size of modern stromatolites? As a result of the differences between modern and ancient stromatolite textures, a ‘gentleman's agreement’ definition was accepted, including accretion by both trapping and binding of detrital grains and microbially induced precipitation.

3.4 | A Ginsburgian perspective

As pointed out by Ginsburg (1991), the duality of environment and biology is inherent in all three of the controversies. In the next section, we will review how research on modern marine stromatolites in both Shark Bay and the Bahamas in the past three decades has advanced the understanding of this duality and the associated controversies.

4 | MODERN TAKE ON LONG-STANDING CONTROVERSIES

To follow up on Ginsburg’s prediction regarding the inherent duality of stromatolites at all scales, we will examine the roles of biology and environment in stromatolite morphogenesis at macro, meso and micro scales and consider the implications with respect to each of the controversies.
4.1 Macroscale – ‘Fossils or Sedimentary Structures’ Controversy

Macroscale morphogenesis of stromatolites refers to stromatolite morphology. Stromatolite formation at the macroscale is linked to the controversy of whether stromatolites are fossils or sedimentary structures. According to the Trompette (1982) model, stromatolite macroscale structure is dominantly influenced by the environment with relatively little biological influence (Figure 1). This would suggest that based on shape, stromatolites are sedimentary structures rather than fossils. New insight into controls of macroscale morphology and the controversy of fossils or sedimentary structures come from recent research in Hamelin Pool (Suosaari, Reid, Abreu Araujo, et al., 2016; Suosaari et al., 2019; Suosaari, Reid, Playford, et al., 2016).

FIGURE 1 Diagram illustrating the relative influences of environment and biology on stromatolite morphogenesis as proposed by Trompette (1985), with environment dominant at the macroscale and biology dominant at the microscale.

FIGURE 2 Location map showing Shark Bay, Western Australia. Hamelin Pool is the eastern embayment in Shark Bay and is home to the world’s most extensive and diverse assemblage of modern marine stromatolites, which are actively accreting along ~135 km of shoreline. Base map and inset source: SIO, NOAA, US Navy, NGA, GEBCO, Image Landsat/Copernicus.
Modern stromatolites in the restricted marine system in Hamelin Pool, Shark Bay (Figure 2), form the world’s most extensive and diverse system of active stromatolite accretion in a marine environment. Hamelin Pool, a unique embayment with unusual environmental parameters is located within the double-bay inlet system of Shark Bay, situated on Western Australia’s coastline about 800 km north of Perth. Extreme environmental parameters including hypersaline waters (average 66 psu), significant water temperature range (11–33°C at 2 m water depth) and broad tidal range largely driven by meteoric forces, restrict growth of most eukaryotic organisms (Suosaari, Reid, Abreu Araujo, et al., 2016; Suosaari, Reid, Playford, et al., 2016). This results in reduced grazing (sensu Garrett, 1970; Walter & Heys, 1985) and reduced competition for space (sensu Fischer, 1965). Together, the extreme extrinsic factors create a habitat capable of promoting extensive microbial growth.

Stromatolite research in Hamelin Pool over the last several decades (Bauld, 1984; Burne & Moore, 1987; Collins & Jahner, 2014; Golubic, 1985; Hoffman, 1976; Jahner & Collins, 2011, 2012, 2013; Logan, Hoffman, & Gebelein, 1974; Meischner, 1992; Playford, 1979, 1980, 1990; Playford & Cockbain, 1976; Playford et al., 2013; Reid, James, Macintyre, Dupraz, & Burne, 2003; and others) has generally been restricted to the classic locations of Flagpole Landing and Carbla Point (Figure 2). Extrapolation from these studies assumed that stromatolites around Hamelin Pool were similar to those at Flagpole and Carbla Point, with pustular mat stromatolites in the upper intertidal zone, smooth mat stromatolites in the mid-intertidal zone and colloform mat stromatolites in the sub-tidal zone. This tidal zone succession was assumed to be continuous around the pool, in a ‘ring around a bathtub’ scenario. More recent studies involving comprehensive data collection throughout Hamelin Pool (Suosaari et al., 2019; Suosaari, Reid, Playford, et al., 2016), revealed that Hamelin Pool stromatolites are highly variable in shape and size and that description of the structures by surface mat, while an indicator of location of the actively growing microbial mat within the tidal zone, does not capture the morphological heterogeneity of the stromatolites (Suosaari et al., 2019; Suosaari, Reid, Playford, et al., 2016). Moreover, a mapping approach based on stromatolite morphology in conjunction with lithofacies (Suosaari et al., 2019; Suosaari, Reid, Playford, et al., 2016) showed regional differences that led to the designation of distinct ‘stromatolite provinces’ around the margins of Hamelin Pool. This finding presented an ideal opportunity to explore controls of morphological diversity of stromatolites in a modern setting.

In the case of Hamelin Pool, morphological diversity can be correlated with physiographic gradients of the shelf margin, which can then be further linked with energy (Figure 3) (Suosaari et al., 2019). In particular, physiographic alteration of water flow appears to be important in determining stromatolite morphologies in high-energy environments (Suosaari et al., 2019). However, in depositional environments characterized by low gradients and low energy, biological controls appear to exert an overarching control on stromatolite morphology. With reduced energy in low-gradient environments, stromatolite build-ups may influence currents, with lower-level feedbacks leading to self-organizing patterns (sensu Camazine et al., 2003; Purkis, Koppel, & Burgess, 2016). In addition, low-gradient, low-energy environments in Hamelin Pool are characterized by extensive sheet-mat deposits that are un lithified to weakly lithified. In contrast, the higher energy environments of ramp settings are characterized by discrete, larger, taller and well-lithified structures. This suggests that lithification may be a mechanism used by the microbial community to prevent erosion and provide stabilization, enhancing the ability of the microbial community to persist in a high-energy environment (Suosaari et al., 2019). These coupled morphological and environmental observations (Suosaari, Reid, Abreu Araujo, et al., 2016) enabled a process-based link to be established between bathymetry, energy and microbial sedimentation in a well-constrained, modern environment. The recognition of both biological and environmental influences on macroscale stromatolite morphology in Hamelin Pool refines previous models of stromatolite morphogenesis (Suosaari et al., 2019). In contrast to the Trompette (1982) model, which suggests that macroscale morphology is dominantly controlled by environment, the new data from Hamelin highlight both environment and biology as important controls of macroscale morphology.

With respect to the ‘Fossils or Sedimentary Structures’ controversy, results from these recent studies in Hamelin Pool (Suosaari et al., 2019) indicate that stromatolites can act either as fossils or as sedimentary structures, depending on the environment. When physical forces are strong, the environment is the main control on the morphology of the structures and the stromatolite acts as a sedimentary structure. However, when physical forces are weak, that is, no strong currents or steep bathymetric profiles, the biological communities may become the main drivers of the morphology and the stromatolite acts as a fossil (Suosaari et al., 2019). Therefore, at the macroscale, Ginsburg’s (1991) prediction holds true: biology and environmental influences on stromatolite growth are closely coupled.

4.2 | Mesoscale – ‘‘Definition’’ Controversy

Mesoscale morphogenesis of stromatolites refers to the creation of internal fabrics and involves the presence or absence of lamination as well as genesis; these concepts are inherently linked to Ginsburg’s (1991) ‘definition’ controversy. To investigate stromatolite morphogenesis at the mesoscale, we will again draw upon recent research in Hamelin Pool (Suosaari, Reid, Abreu Araujo, et al., 2016; Suosaari et al., 2019).
According to the Trompette (1982) model, mesoscale fabrics should be influenced equally by environment and biology. This dual influence is supported by current research in Hamelin Pool (Suosaari et al., 2019; Suosaari, Reid, Playford, et al., 2016).

Observations of 45 stromatolites from Hamelin Pool that were sampled, slabbed and polished between 2012 and 2014 showed that their internal fabrics are heterogeneous (Suosaari, Reid, Playford, et al., 2016), often being highly variable in degree of lamination. As these internal fabrics reflect former surface mats and surface mats reflect their position in a tidal zone (Jahnert & Collins, 2012; Playford, 1990; Suosaari, Reid, Playford, et al., 2016), the changes in fabric are thought to correspond to changes in water depth. Therefore, at the mesoscale, in agreement with the Trompette (1982) model (Figure 1), biology and environment are both important in controlling fabric.

In relating mesofabric to the controversy about definition, recent research does little to settle questions of whether or not lamination and/or genesis should be included. In many modern examples, however, microbial influence is obvious but the degree of lamination is unknown until the sample is sliced open. Therefore, from our point of view, the generic genetic term ‘microbialite’ is the most appropriate term for modern structures likely to be microbial. However, as a single term or definition is unlikely to fit all circumstances, the simple solution is to simply define terms being used. For example, in the case of Hamelin Pool research, we state that the term ‘stromatolite’ is used ‘for all organo-sedimentary build-ups formed by the sediment trapping, binding and/or carbonate precipitating activities of microorganisms regardless of degree of

FIGURE 3 Stromatolite morphogenesis at the macroscale. Idealized transects depicting bathymetry for 1,500 m from shore with characteristic structures around the margins of Hamelin Pool. A) Low-gradients coupled with low-energy settings are associated with sheet mats and elongate-clustered stromatolites that exhibit regular spatial patterns, possibly indicative of self-organization. B) Low-gradients coupled with high-energy settings resulting from strong winds are associated with seif stromatolites with pronounced directional bands. C) Medium-gradients coupled with medium-energy are associated with individual and merged stromatolites, often with thin basal necks. D) Medium-gradients coupled with high-energy where topography deflects currents are associated with elongate-nested stromatolites. E) High-gradients coupled with medium to high-energy are associated with individual and merged stromatolites in the intertidal and composite structures in the subtidal. Observations linking macro-scale structures to physiography in a modern microbial system help elucidate environment vs. biological influences in stromatolite morphogenesis: when physical forces are strong, the environment is the main control on the morphology of the structures; however, when physical forces are weak, biological communities may become the main drivers of the morphology. Illustrations by G. Suosaari.
lamination to be consistent with historical usage’ (Jahnert & Collins, 2011, 2012; Logan, Hoffman and Gebelein, 1974; Playford, 1990; Playford et al., 2013). Clarifying definitions reduces confusion regarding terminology without the need for consensus.

4.3 | Microscale – ‘Carbonate Fixation Controversy’

Stromatolite formation at the microscale is relevant to the controversy regarding carbonate fixation. To consider advances in the understanding of stromatolite accretion and controls of microscale morphogenesis, we will draw on work from the Research Initiative on Bahamian Stromatolites (RIBS). According to the Trompette (1982) model, stromatolite microscale should be dominantly influenced by biology, with relatively little environmental influence.

Unlike Hamelin Pool stromatolites, which form in a restricted hypersaline marine environment, Bahamian stromatolites form in open marine environments where eukaryotic growth is restricted by migrating sand waves (Andres & Reid, 2006; Andres, Reid, Bowlin, Gaspar, & Eisenhauer, 2009; Eckman et al., 2008; Perkins, Kromkamp, & Reid, 2007; Reid, Gaspar, Bowlin, Custals, & Andres, 2011). Stromatolites occur in subtidal tidal passes, subtidal sandy embayments and on intertidal beaches.

Geologists and microbiologists of the RIBS group conducted a detailed investigation into the origin of lamination in Bahamian stromatolites; a critical finding of which was that stromatolite microstructure is a fingerprint of the microbial community, meaning the subsurface microstructure represents communities that were formerly at the surface of the stromatolite (Reid et al., 2000). Prokaryotic microbes in the Bahamas are responsible for building sandy stromatolites with microfabrics characterized by millimetre-scale lamination. Lamination results from an alternation of three fabrics associated with cycling through three prokaryotic communities: filamentous cyanobacteria trap and bind sand grains; heterotrophic bacterial biofilm layers precipitate micritic horizons; and endolithic coccoid cyanobacteria produce fused grain layers that are heavily micritized and cemented at point-contacts (Reid et al., 2000). The micritic horizons in the Bahamian stromatolites, which are tens of microns thick and resemble micritic laminae in Precambrian stromatolites, are formed through heterotrophic decomposition of biofilm organic matter (Visscher, Reid, & Bebout, 2000).

To further explore the controls of microbial community cycling forming laminae in Bahamian stromatolites, the RIBS group monitored stromatolite growth continuously for 2 years at Highborne Cay (Figure 4). This study showed that microbial communities cycled as a result of

![Figure 4](image-url)
environmental pressures including water temperature, light, wind, burial, exposure and sand abrasion, often related to local storms (Bowlin et al., 2012; Reid, Gaspar, Bowlin, Custals, & Andres, 2011). For example, filamentous cyanobacteria responsible for trapping and binding cycled to biofilms responsible for the generation of micritic crusts associated with abrasion and high summer temperatures. Alternatively, if the structures were not covered by sediments for an extended period of time, they became covered in diatoms and formed unlaminated, un lithified layers (Figure 5) (Andres & Reid, 2006; Bowlin et al., 2012).

In contrast to the Trompette (1982) model which suggests that microstructures are dominated by biological factors and minimally influenced by the environment, Bahamian studies show that microfabrics reflect a cycling of microbial communities that is driven by environmental factors. Once again, the duality of stromatolites, with both biological and environmental controls is evident at the microscale. With respect to the controversy regarding mechanisms of stromatolite accretion, the Bahamian studies provide a model for precipitating micritic laminae in ancient microbial mats through heterotrophic degradation of biofilms. This model could explain a paucity of microfossils in the micrite of ancient stromatolites (Schopf, Kudryavtsev, Czaja, & Tripathi, 2007). Ongoing studies of rare earth elements in stromatolites may prove useful in discriminating precipitated micrite from trapped and bound fine-grained material (Corkeron, Webb, Moulds, & Grey, 2012).

5 | SO WHAT?!

Recognition that both biological and environmental influences are important at macro, meso and micro scales of stromatolite morphogenesis in both Hamelin Pool and the Bahamas revises previous models. In particular, discussions in this paper provide new perspectives on the Trompette (1982) model, which suggested that biology controls microscale internal structure whereas environment controls macroscale morphology (Figure 6). Research in the past few decades in Hamelin Pool and the Bahamas confirms the prophetic nature of Ginsburg’s comment made nearly 30 years ago, revealing that biology and environmental influences on stromatolite growth are closely coupled at macro, meso and micro scales.

Understanding the dual nature of stromatolites, which reflects both biology and the environment at all scales, together with research results as discussed above provide
new perspectives on long-standing controversies. At the macroscale, stromatolites can be considered sedimentary structures that are dominantly shaped by the environment in high-energy environments. However, in low-energy environments, stromatolites act like fossils, with shapes that are largely controlled by biology. With respect to definition, the generic genetic term ‘microbialite’ is probably the most appropriate term for structures of probable microbial origin, when mesoscale structures such as internal lamination are unknown or heterogeneous. In all cases, terminology must be explained to avoid confusion. With respect to carbonate accretion, research on modern stromatolites provides a model for biofilm precipitation of micritic laminae lacking microfossils in ancient stromatolites and ongoing research involving rare earth elements may help to discriminate precipitated micrite from fine-grained material that is trapped and bound.

In summary, research in the past few decades highlights stromatolites as quintessential embodiments of geomicrobiological processes, representing an ecosystem in the palm of your hand. As the first fossil record of macroscopic life, which dominated the fossil record for over 80% of Earth history (Allwood et al., 2006; Awramik, 1992; Hofmann et al., 1999; Lowe, 1980; Nutman et al., 2016; Walter et al., 1980), stromatolites are indeed a significant part of Earth history. Confirmation of the Ginsburg (1991) prediction that stromatolites contain records of both biological and environmental influences at all scales is a further indication that well-preserved ancient stromatolites can provide a window into ancient ecosystems. The challenge of future research is to advance the Ginsburg Legacy and deconstruct the dual influences of biology and environment recorded in stromatolites for 3.5 billion years of Earth history.

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I completed my PhD at the University of Miami RSMAS and would consider myself an academic ‘grandchild’ of Robert Ginsburg, as Dr. Pamela Reid was my supervisor, who completed her PhD under Dr. Ginsburg. During my time at

FIGURE 6  Revised Trompette (1985) model of stromatolite morphogenesis showing biology and environmental influences on stromatolite growth are closely coupled at macro, meso and micro scales. Original Trompette (1985) model (A) shows biology controls microscale internal structure whereas environment controls macroscale morphology. Modifications based on recent research from Hamelin Pool, Shark Bay and the Bahamas have revised the model showing: (B) at the macroscale, stromatolites are dominantly shaped by the environment when influenced by high energy, however in low-energy environments, stromatolites are dominantly shaped by biology; (C) at the mesoscale, the dual influence predicted by Trompette (1985) is supported by current research, showing fabrics are influenced equally by environment and biology; and (D) at the microscale, microfabrics reflect a cycling of microbial communities that is driven by environmental factors.
RSMAS, I was lucky enough to have Dr. Ginsburg for one of his final classes, which included field trips to explore the Miami Oolite, Florida mudbanks and Florida Reef Tract. Dr. Ginsburg had a long relationship with stromatolites, as I hope I was able to convey in this manuscript and they were also the topic of my PhD research. His interest in the biological versus environmental influences on stromatolites had an unequivocal impact and influence on my own research interests. In this tribute to Dr. Ginsburg, I want to thank him for his vision and inspiration as I am honoured and proud to be part of his Legacy. – E. Suosaari.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

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