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PART B, VOLUME 1, CHAPTER 8 MICROBIALITES

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INTRODUCTION

Microbially induced, lithified structures known as microbialites are both geologically and biologically significant, forming extensive sedimentary, geochemical, and microbiological records in modern and ancient environments. Depositional settings range from deep ocean hydrocarbon seeps, hydrothermal vents, and whale falls, to cool water carbonate banks—abundant occurrences within peritidal zones and, finally, to non-marine environments such as lakes, rivers, and springs. More than three billion years of Earth's biosphere is primarily recorded within microbialites, including the oldest macrofossils on the planet (Walter, Buick, & Dunlop, 1980; van Kranendonk, Webb, & Kamber, 2003; van Kranendonk, 2006). Even with diminished diversity and abundance during the Phanerozoic, periodic microbialite resurgences after mass extinctions are used as indicators for relative environmental recovery (Mata & Bottjer, 2012). Microbialites are also targeted by astrobiology studies for their ability to form in harsh environments and their capacity to preserve specific biosignatures (Corsetti & Storrie-Lombardi, 2003; Shapiro, 2004a; Ibarra & Corsetti, 2016). Yet, despite the broad scientific significance of microbialites, many authors note a lack of consistent terminology (Riding, 1999), while others address the challenges of differentiating microbialites from numerous abiogenic sedimentary deposits (Buick, Dunlop, & Groves, 1981; Grotzinger & Rothman, 1996; Grotzinger & Knoll, 1999; Awramik & Grey, 2005).

This chapter aims to provide the reader with a basic working guide for field and laboratory descriptions of microbialites, and to synthesize the various terminologies present in the literature. As a guide, this contribution is meant to complement the various review articles that focus more specifically on the fossil record of microbialites (Hofmann, 1973; Awramik & Riding, 1988; Awramik, 1991; Hofmann, 2000; Rowland & Shapiro, 2002; Riding, 2011, and references therein). For example, Flügel (2004) provided an excellent analysis of microbialite as a carbonate lithologic unit with much discussion on genesis, diagenesis, and terminology. There have also been significant contributions from non-English literature, primarily by Russian workers (e.g., Maslov, 1960; Krylov, 1963; Raaben, 1991) in addition to other international researchers, including the earliest description of stromatolites (Kalkowsky, 1908). The diversity of unique microbialite textures has produced many study-specific nomenclatures in the primary literature, and increases the difficulty of succinct review. Instead, this chapter synthesizes key features of previously published guides over multiple decades of microbialite research. Nomenclature that has gained acceptance by extensive utilization in the literature is given preference here, with references provided for more detailed discussions beyond the scope of this review.

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HISTORICAL PERSPECTIVE AND WORKING DEFINITION OF THE TERM MICROBIALITE

The word microbialite was introduced by Burne and Moore (1987) as a general term for sedimentary deposits created by the actions of microorganisms (see historical discussion in Riding, 2011). Current researchers employ the term for microbially induced deposits in general, or when specific discrimination of stromatolitic, thrombolitic, or other textures is untenable. An alternative spelling, microbolite (Riding, 1991), while perhaps more accurate, has not gained traction in the literature. In contrast to microbialites, microbial mats (often shortened to mats) are unlithified, macroscopic microbial communities in modern environments, often divided into layers with distinct microbial metabolisms. Special care should be taken to use the terms microbialite and microbial mat only for lithified and unlithified communities respectively, especially in modern and Holocene locations where both structures may be present.

Microbial activity preserved in the sedimentary record includes 1) mineral precipitation within mats due to the physico-chemical properties of microbial communities, and 2) the trapping and binding of detrital grains on and within mat layers (Awramik, Margulis, & Barghoorn, 1976; Burne & Moore, 1987; Noffke & Awarmik, 2013). Microbial deposits predominantly formed by trapping, binding, and stabilization of detrital grains are prevalent in siliciclastic environments and have distinct nomenclatures described in greater detail elsewhere in this volume. Microbialites described in this chapter are primarily formed via mineralization of mat textures, though detrital grains are often important components. The vast majority of microbialites are composed of calcium carbonate, though many examples have been described composed of primary opaline silica, oxides, sulfides, phosphates, and other minerals (Walter, Bauld, & Brock, 1972; Wallace, Keays, & Gostin, 1991; Martín-Algarra & Sánchez-Navas, 1994; Berelson & others, 2011). While individual microbes are very rarely preserved within microbialites, specific features in macro- and microscopic textures indicate origination via microbial activity, as opposed to abiogenic sedimentation or precipitation. When microfossils are preserved, the lithified microbialite structure on a microscopic scale may be largely composed of permineralized skeletons or mineralized molds.

Further refinement of microbialites is based on the mesostructure scale of observation (Fig. 1). Mesostructure refers to the millimeter to centimeter scale elements visible with the unaided eye or hand lens (Kennard & James, 1986). In contrast, microstructure encompasses all observations with a light or scanning electron microscope. The macrostructure refers to the larger association of mesostructural elements (Fig 2, Fig. 3). For instance, laminae (mesostructure) may be stacked to form a cylindrical column (macrostructure). Some authors employ a larger hierarchical stage, megastructure, to describe the bed or overall stratigraphy of the microbialite-bearing units (Kennard & James, 1986). The necessity of using several scales of description of microbialites is one of the distinguishing features of their taxonomy relative to other fossils (Awramik, 1991; Shapiro & Awramik, 2006). Importantly, microbialites are organosedimentary constructions, and all scales of structure need to be studied for both biogenic and sedimentologic signals. The next sections describe five major categories of microbialites based on mesostructure.

STROMATOLITES

Substrate-attached microbialites with laminated fabrics are defined as stromatolites, deriving from the word stromatolith in Kalkowsky (1908). More than a century of successive studies has produced various definitions of the term stromatolite, both genetic and purely descriptive, as recounted in detail by Riding (2000, 2008).

Many arguments center on the difficulty of directly identifying biogenicity in laminated deposits, which stems from 1) the removal of specific biosignatures by secondary alteration, and 2) the morphological similarity of laminated abiological structures to biogenic stromatolites (Grotzinger & Rothman, 1996; Grotzinger & Knoll, 1999). For simplicity, this chapter defines laminated microbialites as stromatolites, as opposed to abiogenic structures formed without the mediation of microbial communities. Recommended guides to stromatolite morphologies and textures include Logan, Rezak, & Ginsburg (1964); Walter (1976); Preiss (1976); Buick, Dunlop, and Groves (1981); Grey (1989); Riding (1999); and Shapiro (2007), to name a select few.

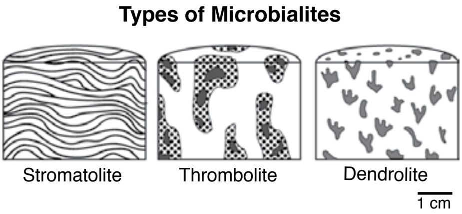

Fig. 1. Main groups of attached microbialites. The different groups are defined based on the mesostructure or constructional elements. Stromatolites are laminated, thrombolites are clotted, and dendrolites are composed of bushes (new).

On a macrostructural level, stromatolites vary from stratiform morphologies with low vertical relief, to simple columns, domes, and cones, to complex branching structures (Fig. 3). Furthermore, individual stromatolites can change morphologies with successive generations of laminae accretion. For example, slight irregularities of stratiform stromatolites can propagate into larger domes or cones with continued growth. A standard stromatolite classification scheme that accounts for vertical changes in structure is provided in Logan, Rezak, and Ginsburg (1964). Changes in stromatolite morphology can arise from shifting depositional environments, biological communities, hydrochemistry, or all of these factors over time. As previously mentioned, many stromatolite macrostructures resemble laminated textures formed by abiogenic mineral precipitation, especially less complex stratiform or domal morphologies (Grotzinger & Knoll, 1999). While branching and conical morphologies have been hypothesized in simulations of abiogenic mineral growth (Grotzinger & Knoll, 1999; Dupraz, Pattisina, & Verrecchia, 2006), such macrostructures have not been abiogenically replicated in physical experiments. One detailed method to study stromatolite macrostructure involves

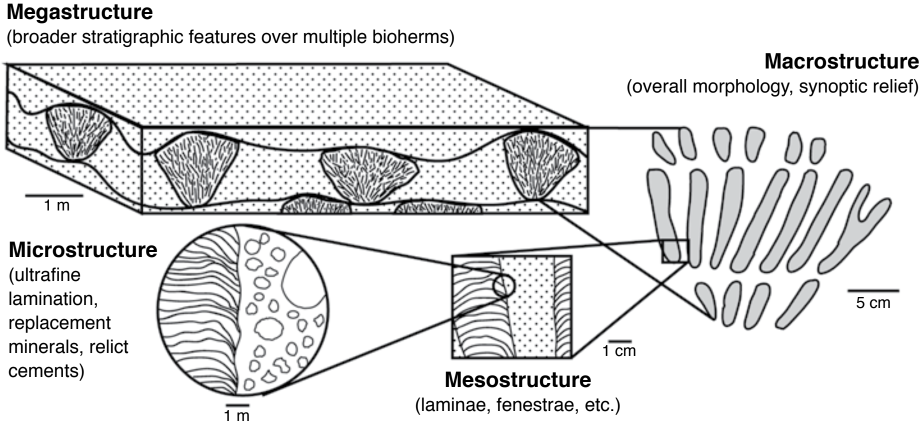

Fig. 2. Scales of observation of microbialites, tracing the various features of stromatolites from the megastructure through the microstructure (adapted from Shapiro & Awramik, 2006, fig. 2).

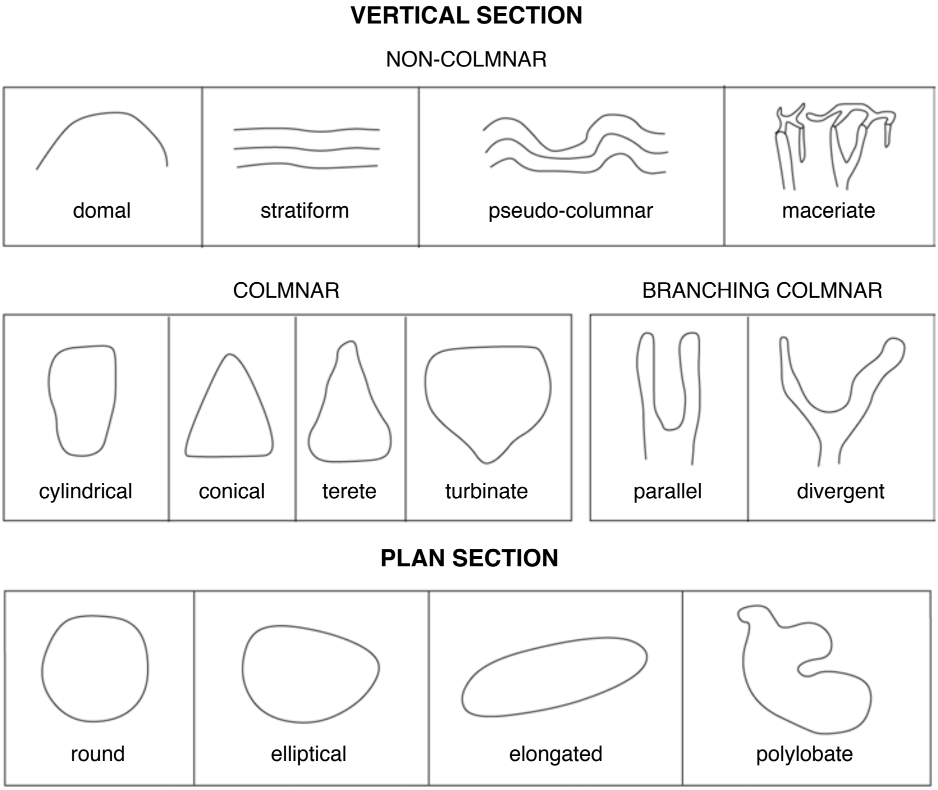

FIG. 3. Descriptive terminology as applied to the macrostructure of all microbialites (new).

serially sectioning samples so that true three-dimensional reconstruction can be quantitatively assessed (see discussion in Hofmann, 1973). A number of publications describe serial sectioning techniques (Krylov, 1963; Preiss, 1976), and the capabilities have been significantly enhanced with modern illustration computer programs. A critical aspect is recognizing that one or several two-dimensional planes are insufficient to truly understand the complexity of stromatolite structures.

As laminae are the defining mesoscale feature of stromatolites, special detail must be given to describing mesoscale textures. Laminae are often composed of light and dark couplets, with darker layers typically formed by finer-grained, less porous micrite or microspar in carbonates or microcrystalline quartz in cherts (Grotzinger & Knoll, 1999). Darker zones can also be attributed to higher concentrations of organic material or insoluble residue such as iron oxides. Lighter laminae are generally defined by higher amounts of cemented interstitial spaces, filled with spar in carbonates or macroquartz in cherts. Microfossils in well-preserved stromatolite laminae show different orientations of filamentous cells, with laminae-parallel filaments in dark layers and laminae-normal or vertical filaments in light layers (Gebelein, 1969; Walter, Bauld, & Brock, 1972; Golubic & Focke, 1978).

Key differences between stromatolites include laminae smoothness or waviness, thickness variation, nature of the laminae over the growth axis (apex), and nature of the laminae against the stromatolite margins (Fig. 4). For example, the height of a stromatolite at a single point in time (synoptical relief) can be established by measuring the vertical distance between the apex of a single layer and the same layer's intersection with the stromatolite margin. Another useful parameter when describing stromatolite textures is inheritance, or how well laminae inherit the shape of preceding layers. For example, a stromatolite that progresses upward from stratiform through domal to conical textures has low inheritance, as laminae over time do not resemble the shapes of lower layers. Conversely, a stromatolite that maintains consistent layer morphologies throughout the structure, whether flat, domal, or conical, has high inheritance.

In well-preserved carbonates, the laminar mesostructure can also help distinguish biogenic stromatolites from abiogenic precipitates (Grotzinger & Knoll, 1999). Laminae formed within microbial mats are typically composed of micrite or microspar and have irregular, wavy laminae resulting in low inheritance. In contrast, many laminated abiogenic carbonates are comprised of bladed or acicular needles, maintaining isopachous thicknesses across the stromatolite and extremely high inheritance. While there are exceptions to these trends, a meaningful assessment of biogenicity cannot be accomplished without first analyzing laminae petrography. For example, several lacustrine stromatolites exhibit both styles of lamination, alternating between irregular micritic layers and isopachous bladed fabrics, and have been correlated with changes in lake environments (Frantz & others, 2014; Fedorchuk & others, 2016)

Microstructural attributes vary widely between stromatolites (Fig. 5). The variety of textures observed is due to both depositional heterogeneity and subsequent diagenesis. Original fabrics include detrital grains (micrite, silt to fine sediment, coated grains, skeletal fragments), organic films, and various cements (isopachous rims, bladed fringes, botryoids, etc.). Among the many potential microscopic features within stromatolites, several diagnostic textures can help increase the confidence of stromatolite biogenicity (Buick, Dunlop, & Groves, 1981; Grotzinger & Knoll,

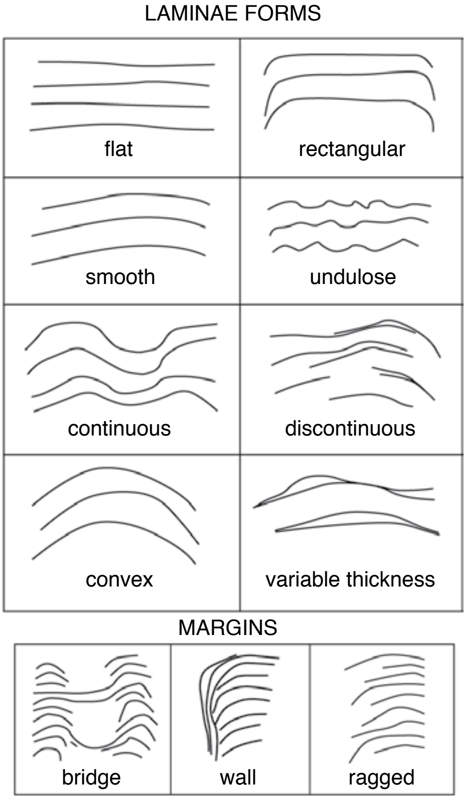

Fig. 4. Descriptive terminology as applied to the mesostructure of stromatolites (new).

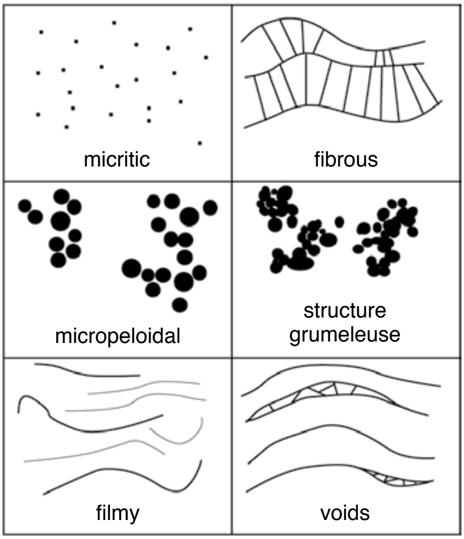

Fig. 5. Descriptive terminology as applied to the microstructure of all microbialites.

1999). Some Phanerozoic stromatolites preserve microfossils as carbonate permineralized sheaths, such as the filamentous morphotype *Girvanella* (Nicholson & Everidge, 1878), but these are relatively uncommon. Rounded fenestrae, which do not crosscut primary stromatolite textures, represent the preservation of former void spaces within microbial mats, which can be produced either by metabolic gas production or by natural irregularities in microbial mat textures (Sumner, 2000; Bosak & others, 2009, 2010; Mata & others, 2012; Wilmeth & others, 2019). Finally, the presence of detrital grains on sloped laminae that exceed the angle of repose indicate the presence of adhesive microbial mats rather than pure mineral precipitates (Bailey & others, 2009; Tice, 2009; Frantz, Petryshyn, & Corsetti, 2015).

Early diagenesis in carbonates often leads to both micritization and aggrading neomorphic spar, obscuring original textures. Additionally, many stromatolites show destructive replacement of primary fabrics by mosaic dolomite. In some cases, placing a white card underneath a thin section increases the potential to view original textures on a microscope stage (Folk, 1987). Examples show that dolomitization is fabric selective, even down to individual laminae (Glumac & Walker, 1997; Riding, 2008). Dolomitization can be accentuated by staining with Alizarin Red to differentiate calcite (stained) from dolomite (unstained). Regardless of the preservation, describing stromatolite microstructure is critical when possible, noting presence or absence of microfossils, and any variation in mineralogy.

ONCOIDS

Oncoids are laminated microbialites that form unattached grains (Heim, 1916; Pia, 1927), in contrast to stromatolites attached to benthic substrates. Oncoids are typically spherical to ellipsoidal in shape, with variably smooth, pustular, or lobate surfaces (Fig. 6) resulting from patterns of primary precipitation and mechanical weathering. Most oncoids are composed of calcium carbonate, with some siliceous examples surrounding hot springs (Jones & Renaut, 1997; Jones, Renaut, & Rosen, 1999; Konhauser & others, 2001), and several phosphatic and oxide-rich samples in ancient lithologies (Krajewski, 1983; Schaefer, Gutzmer, & Beukes, 2001; Gradziński & others, 2004; Sallstedt & others, 2018). A detailed review of oncoid terminology and sedimentology, including comparisons with other coated grains, can be found in Flügel (2010).

Internal oncoid mesostructure consists of a nucleus surrounded by a cortex of variously concentric laminae. Nuclei vary depending on depositional environment, and include clastic grains, fossils, or reworked chemical sediments, such as surrounding carbonates or cherts. Nuclei are sometimes absent from samples, depending on diagenetic alteration, the angle of dissection, or an initial particle that was soft and/or featureless (Flügel, 2010). Cortices contain micritic or fine-grained laminae, which vary in thickness and concentricity, in contrast to grains such as ooids and pisoids, which contain radially fibrous, highly concentric laminae. Variable thicknesses of oncoid laminae typically result in low inheritance, leading to asymmetrical shapes including small domes and even cones (Logan, Rezak, & Ginsburg, 1964; Wilmeth & others, 2015). Logan, Rezak, and Ginsburg, (1964) included a classification scheme for oncoid morphologies in addition to stromatolite textures. Oncoid laminae are similar in microstructure to biogenic stromatolites, including light and dark couplets, variously oriented microfossils, and rounded fenestrae (Peryt, 1981; Flügel, 2010; Wilmeth & others, 2015; Sallstedt & others, 2018). Microfossils are often present as filamentous permineralized sheaths, usually described as the morphotype *Girvanella* (Peryt, 1981; Riding, 1983).

The unattached nature of oncoids, unique among microbialites, provides useful insights into paleoenvironment. An oncoid-rich facies is called an oncolite, as opposed to singular oncoid grains. Oncolites can be described in a similar manner to other grain-dominated facies in terms of sorting, roundness, and grain vs. matrix support. Oncoids and oncolites provide evidence for agitated environments, requiring frequent exposure of fresh surfaces for microbial colonies to grow and eventually mineralize (Dahanayake, 1977; Ratcliffe, 1988). As oncoids grow larger, layers often become increasingly asymmetrical due to longer periods of quiescence (Wright, 1983; Smith & Mason, 1991; Shapiro, Fricke, & Fox, 2009; Wilmeth & others, 2015). Oncoids that become too large for continued agitation often become the stable base for subsequent stromatolite nucleation (Martín-Algarra & Vera, 1994; Burne & Moore, 1987).

THROMBOLITE

Thrombolites are clotted microbialites (Aitken, 1967). Although the term is nongenetic, the study of thrombolites has shown that clotted fabrics are largely constructional and not merely secondarily altered stromatolitic textures. Shapiro (2000) addressed the terminological confusion of thrombolites, further elaborated upon by Shapiro and Awramik (2006). Because thrombolites lack laminae as a mesostructural fabric, synoptic relief is more difficult to assess. However, column margins and their relationship with surrounding sediments can still hold clues to syndepositional relief, with margins varying between smooth, invaginated, wrinkled, or lobate morphologies. If margin walls are not smooth, it is important to recognize whether surrounding sediments interfinger (low synoptic relief) or truncate against the margin (potentially higher synoptic relief).

The mesostructure of thrombolites is dominated by mesoclots separated by either cements or sediment (Kennard & James, 1986). Mesoclots are millimeter to centimeter scale zones of variable texture seen on both plan and longitudinal sections. Petrographic analysis of the mesoclots show them to be composed of a variety of elements, including coccoid calcimicrobes (Kennard & James, 1986), botryoidal calcimicrobes (Latham & Riding, 1990), filamentous calcimicrobes (Moore & Byrne, 1994), algal-foraminiferal colonies (Toomey & Cys, 1979), dense micrite (Glumac & Walker, 1997), and peloids (Pratt & James, 1982). The distribution of mesoclots across two-dimensional thrombolitic surfaces imparts a clotted composition (see Fig. 7 for a compendium of the more common mesoclot forms as described in the literature).

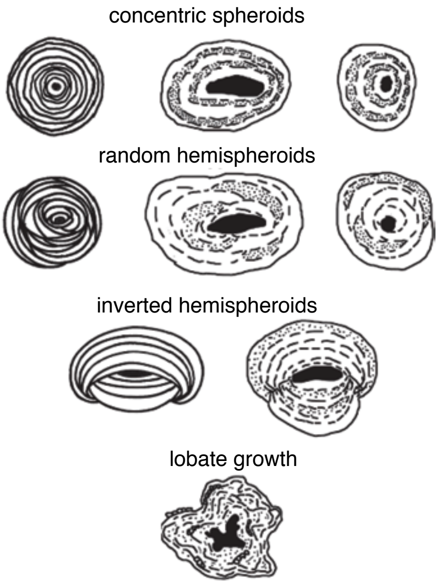

Fig. 6. Descriptive terminology as applied to the macrostructure of all oncoids (adapted from **Logan, 1964**, as presented in Flüge, 2010).

The term mesoclot was first proposed by Kennard and James (1986) as an emendation for Aitken's (1967) clots, as the latter term was ambiguous and could be mistaken for submillimeter-size clotted microstructures. Other terms employed include fenestrae (Pratt & James, 1982) or thromboids (Kennard, 1994) (see review in Shapiro, 2000). Thromboid is unacceptable because the term is confusing when considering the present non-parallel usage of stromatoid and the multiple, conflicting definitions in the literature. The term fenestrae is not appropriate because it refers to a former void within a rock (Bates & Jackson, 1987) and

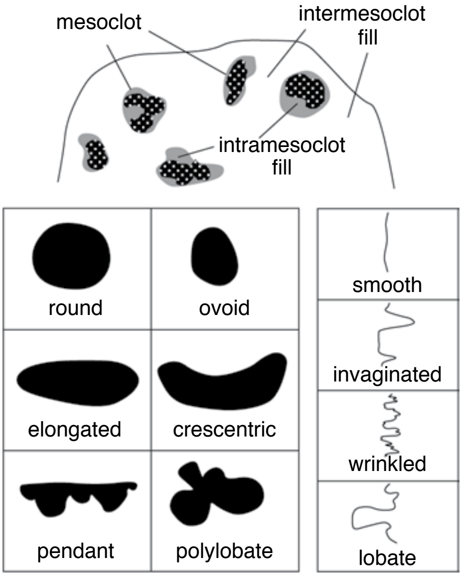

FIG. 7. Descriptive terminology as applied to the mesostructure of thrombolites (new).

not all mesoclots were open spaces. As with stromatolite laminae, the morphology and texture of the mesoclots are referred to as the fabric of a thrombolite. Microscopic features of the mesoclots should be described under microstructure. Using the terms macroclots or microclots is not advised, as this will only exacerbate confusion.

The three-dimensional morphology of a mesoclot is referred to as the mesoclot shape. There has not been a quantification scheme proposed for the study of mesoclots; the method of geometric study is left up to the discretion of the researcher, with the hopes that clear explanations are given. As with stromatolites, mesostructural aspects of thrombolites are best studied in three-dimensional preparations as their typically polymorphic shapes may present a variety of patterns on two-dimensional surfaces (SHAPIRO & AWRAMIK, 2006). Qualitative description of two-dimensional surfaces are still of great use for field and comparative study and should also be undertaken. To date, most studies have featured longitudinal sections, or mesoclot profiles (e.g., AITKEN & NARBONNE, 1989; KENNARD, 1994). However, much information can be gleaned from plan-view sections, or mesoclot outlines. It is good practice to trace the mesoclots physically or digitally to demonstrate clear shapes, and then present patterns in a simple, two-tone scheme. Instead of using vague terms such as irregular or globular, measurements should be made of mesoclot height, length, and width, citing the orientation of the viewing plane relative to the growth axis of the thrombolite. Mention should be made if the mesoclot dimensions vary in different spots within one thrombolite, particularly from the base toward the top of the structure or from the margins toward the center.

The spatial relations of mesoclots can be isolated, interconnected, or coalesced (KENNARD & JAMES, 1986; SHAPIRO & AWRAMIK, 2006). The degree of coalescence can further be qualified as slightly coalesced or highly coalesced. In turn, mesoclots can be arranged in parallel to subparallel patterns within the thrombolite, presenting a horizontal, radial, or vertical mesostructure. Mention should be made of the amount of mesoclots (as percent abundance) within thrombolites. In addition to mesoclots, the mesostructural analysis should also include descriptions of any voids, inter-mesoclot fill, calcimicrobes, and metazoans. Laminae are extremely rare, but if present should be described following the guidelines set forth for stromatolitic mesostructure. Care should be taken to note the relationship of the laminae to the mesoclots, whether gradational, alternating, or adjacent.

It is common for mesoclots in localized portions or in the entire thrombolite to be oriented in a regular pattern. Although much of the existing literature describes the orientation of thrombolite columns (macrostructure)—often misidentifying the elements as clots or thromboids (see RIDING, 2011)—the terms here are still applicable to mesoclot orientation. Orientations of the columns should be described under macrostructure. For example, SHAPIRO and AWRAMIK (2006) presented a variety of plan-view shapes of arabesque columns (maceriae) that are macrostructural, as opposed to the mesoclots that comprise the mesostructure of maceriae.

DENDROLITES

Dendrolites are neither laminated nor clotted but are composed of branching millimeter-scale bushes (Riding, 1991). The bushes are inferred to be organic in origin, though the exact nature of the biota necessary for the construction is not known. In many structures, bushes can be identified to [inferred genera of] calcimicrobes such as Epiphyton (Bornemann, 1886), *Renalcis* (Vologdin 1932), *Gordonophyton* (Korde, 1973), or *Angusticellularia* (Vologdin, 1962)(Rowland & Shapiro, 2002). The term dendrolite should not be utilized for structures that display branching crystalline growth, which can be easily recognized by clear crystal boundaries and more regular arrangement of the branches (Shapiro, 2004b). Thrombolites and dendrolites may represent end members of a continuum of diagenetic alteration, in which dendrolite bushes recrystallize to amorphic micrite that may then be considered a thrombolitic mesoclot (Riding, 1991).

Dendrolites occur as meter-scale domes, tabular biostromes, and centimeter-scale crusts. It may also be most accurate to refer to the microbial frameworks within archeocyath and lithistid reefs as dendrolite though the term has not been used in that regard. Dendrolites are distinctive but are found alongside and even interfingering with thrombolites and stromatolites. To date, there are few described dendrolites in the literature, though it is likely that some published accounts of thrombolites should more accurately be termed dendrolites. The original papers discussing dendrolites (Riding, 1991; Riding & Zhuravlev, 1995; Turner, James, & Narbonne, 2000; Shapiro & Rigby, 2004) did not propose a formal definition of dendrolite morphology. Recently, Howell, Woo, and Chough (2011) in a study of three-dimensional dendrolite reconstruction, proposed terminology for the dendrolite elements. Figure 8 provides a model that merges the suggestions of that paper with published accounts of other occurrences, including Cambrian and Devonian samples (Riding & Zhuravlev, 1995; Turner, James, & Narbonne, 2000; Kruse & Zhuravlev, 2008). Howell, Woo, and Chough (2011) suggested several tiers of mesostructure based on growth structure of the dendroids, which may prove to be a valuable level of differentiation in future studies.

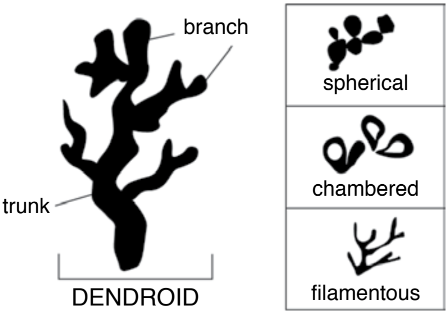

Fig. 8. Descriptive terminology as applied to the mesostructure of dendrolites (new).

LEIOLITES

Braga, Martin, and Riding, 1995 suggested the term leiolite to encompass microbial constructions that lack diagnostic mesoscale structure. While there are many pathways to create massive structure (e.g., irregular accretion of microspar, extensive boring or bioturbation, or burial dolomitization) the term leiolite is valuable as it is non-genetic and does not presume a prior mesostructure. If, however, the microbialite can be shown to have originally been laminated, clotted, or dendrolitic, the pre-alteration terminology should be utilized. It may be possible to recognize pre-alteration original fabrics in dolomitized leiolites using the white card technique of Folk (1987). Leiolites have not received the same amount of descriptive study as other microbialites, though a further short review can be found in Riding (2000).

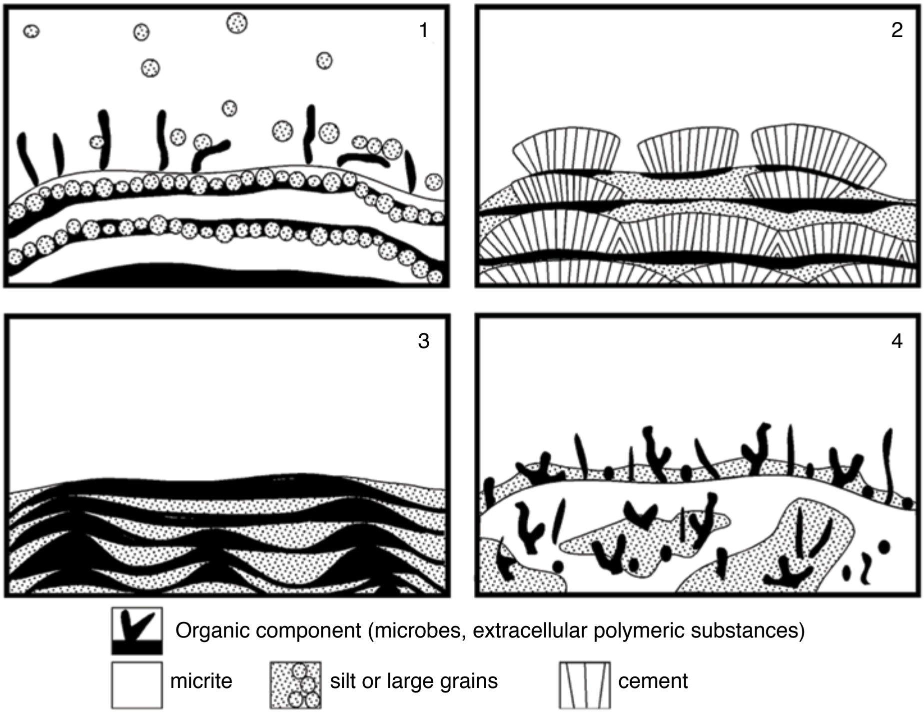

FIG. 9. Models of formation of microbialites. *1,* Trapping and binding of particles; *2,* precipitation of cement layers; *3,* entombing of sediments by mats or extracellular polymeric substances; *4,* skeletal algae or metazoans (adapted from Shapiro, 2007, fig. 3).

MODELS OF MICROBIALITE FORMATION

No single model of formation produces the variety of microbialites described above. The mineralization of a microbial mat is the final result of interplay between the physical sedimentary environment, surrounding chemical parameters (temperature, mineral saturation states), and biological processes within microbial communities themselves (Riding, 2000; Shapiro, 2007; Dupraz & others, 2009). In contrast, the shells and tests of organisms described in other volumes of the *Treatise,* while influenced by surrounding chemistry, are directly formed from the cellular activity of eukaryotes (Weiner & Dove, 2003). Microbialites can also be considered as trace fossils, recording the previous activity of localized microbial ecosystems, while only rarely preserving the organisms themselves (Shapiro, 2007). A further discussion on the differences between microbial and metazoan biomineralization, as well as modern processes of microbialite formation, is provided in Dupraz and others(2009).

Broadly speaking, there are four models that encompass microbialite formation, and any one deposit may show components of all four (Fig. 9). 1) The physical properties of microbial mats often result in the trapping and binding of sedimentary particles, either by filamentous cells or adhesive extracellular polymeric substances (EPS) produced by the mat (Gebelein, 1969; Riding, 1991; Frantz, Petryshyn, & Corsetti, 2015). Most Phanerozoic and many Proterozoic marine stromatolites preserve detrital material, with grains ranging from clay through sand-sized particles. Further cementation of the grains within mats may be accomplished below the accreting and stabilizing surface by heterotrophic bacteria and other biota. 2) Mineral precipitation within microbial mats is induced by elevated saturation states in surrounding waters, occurring both on cells and on organic compounds such as EPS (Arp, 2001; Arp, Reimer, & Reitner, 1999, 2004; Reid & others, 2000; Dupraz & Visscher, 2005; Braissant & others, 2007). Mineral saturation states can be altered by metabolic processes of living organisms, such as photosynthesis, respiration, or chemosynthesis (biologically induced mineralization; Dupraz & others, 2009). Alternatively, chemical changes in the surrounding environment can also force mineral precipitation, with mats serving as a nucleation site (biologically influenced mineralization; Dupraz & others, 2009). Many Archean and Paleoproterozoic stromatolites are composed of precipitated cement layers (Riding, 2008, 2011), though the role of diagenesis in promoting aggrading neomorphic spar must also be considered. 3) A third model, typified by the Omachta Formation of Siberia, comprises stromatolites that form not from trapping sediments but from microbial mats enclosing sediments that have already been deposited. This construction preserves signatures of mechanical deposition such as crossbeds and ripples (Knoll & Semikhatov, 1998). 4) A fourth model of formation recognizes the importance of skeletal algae, foraminifera, and invertebrates in comprising a significant component of Phanerozoic microbialites (Riding, 1977). There may be secular trends to both abundance and diversity of these skeletal microbialites related to evolutionary patterns of the constructors as well as ocean chemistry (Riding, 1977, 2011).

Important to note, the vast majority of described microbialites occur in carbonates and thus are susceptible to the myriad of diagenetic processes that affect all carbonate facies (Beukes, 1987; Burne & Moore, 1987; Planavsky & others, 2009; Pace & others, 2016). Such considerations include near-surface void cementation and dissolution in the phreatic and vadose zone, recrystallization or aggrading neomorphism in shallow burial conditions, and significant dissolution and reprecipitation under deeper burial conditions. Replacement by silica is common and can be either fabric retentive or destructive. Therefore, interpreting the model of formation of all microbialites must take into account the effects of secondary diagenesis.

MODERN STRUCTURES

Both microbial mats and subsequently mineralized microbialites are known from many different facies. Rather than attempt to provide a comprehensive list or to fit microbialites into generic facies models, this section will highlight unique attributes of several key modern environments.

Peritidal Open Marine and Reef

Some of the most well-studied modern microbialites are found in the intertidal embayment of Shark Bay, Western Australia (Logan, 1961; Hofmann, 1973; Chivas, Torgersen, & Polach, 1990; Reid & others, 2003) and unrestricted tidal channels of the Bahamas (Dravis, 1983; Dill & others, 1986; Shapiro & others, 1995; Andres & Reid, 2006; Planavsky & Ginsburg, 2009). These microbialites are predominantly stromatolites with laminae composed of fine- to medium-sized grains and cement, though coarser textures have been diagnosed as thrombolites (Planavsky & Ginsburg, 2009; Riding, 2011). Other significant but overlooked modern peritidal microbialites include reef and cryptic crusts (Camoin & others, 1999), which are also well described from Paleozoic and Mesozoic reefs (e.g., Flügel & Steiger, 1981; Leinfelder & others, 1996). While the textures of modern peritidal deposits are fairly uniform, macrostructure varies with respect to current and wave conditions. In particular, modern peritidal stromatolites have very high relief from the seabed (though not necessarily a high synoptic relief within individual laminae), and columns often show a pronounced elongation of the major axis. In most cases, the elongation is parallel to tidal flow and perpendicular to wave crests. Overall stromatolite size also decreases away from the tidal zone toward the margins of deposits.

Biological studies of peritidal microbialites typically focus on extensive cyanobacterial communities, both for the ability of cyanobacteria to bind detrital grains and influence local carbonate saturation states (GEBELEIN, 1969; REID & others, 2000). However, many other organisms also contribute to microbialite growth, including diatoms and other algae trapping grains (AWRAMIK & RIDING, 1988) and cement precipitation mediated by heterotrophic bacteria (VISSCHER & others, 1998; REID & others, 2000). Modern stromatolites also host localized ecosystems of corals and sponges in addition to algae and microbial mats. Similar microbialite-metazoan reefs are well known throughout the Phanerozoic and Neoproterozoic (RIDING, 1991; ROWLAND & SHAPIRO, 2002; GROTZINGER, ADAMS, & SCHRÖDER, 2005). However, the relatively coarse grains and common presence of eukaryotes within modern peritidal microbialites limits their capabilities as faithful analogues for many ancient examples, especially in Precambrian environments.

Lacustrine

Microbialites are present in a number of lacustrine settings across various climates, typically as calcitic thrombolites and stromatolites with distinct micritic or micrite-microspar laminae (BURNE & MOORE, 1993; WINSBOROUGH & others, 1994; LAVAL & others, 2000; GISCHLER, GIBSON, & OSCHMANN, 2008). Lacustrine microbialites occur across a greater range of depths than within marine peritidal zones, though most deposits form near lake surfaces (e.g., KEMPE & others, 1991). Sharp depth gradients of geochemistry, temperature, and light produce distinct microbialite biofacies. For example, microbial mats within deeper lake waters often have higher vertical relief for photosynthetic organisms to access more sunlight, forming textures such as pillars or cones (LAVAL & others, 2000; ANDERSEN & others, 2011). Lake depth profiles and chemistry also change more dramatically during short-term climate fluctuations than in marine peritidal environments, especially in closed basin lakes where evaporation and precipitation dominate water budgets (see Geological Significance of Microbialites, p. 15). Relatively rapid depth and climate changes can produce distinct fabrics in lacustrine microbialites, particularly in stromatolites (FRANTZ & others, 2014; FEDORCHUK & others, 2016).

Springs

Both carbonate and silica microbialites are well known from modern hot and cold springs (WEED, 1889; JONES & RENAUT, 1997; TURNER & JONES, 2005). Modern spring microbialites are of low areal extent compared with peritidal and lacustrine examples, though wetter climates generally lead to increased discharge rates and more extensive deposits (BARGAR 1978; GUO & RIDING, 1998). Most described spring microbialites are stromatolitic, with macrostructure varying as flow gradients shift from the vent to outflow apron (WALTER, BAULD, & BROCK, 1972; JONES, RENAUT, & ROSEN, 1998). Differentiating true biologically mediated microbialites from abiogenic deposits (e.g., tufa, travertine, and sinter) is a continuing challenge, as many spring deposits are thinly laminated without the presence of microbial mats (KONHAUSER & others, 2003; RIDING, 2008). However, recent work on silica-cemented microbial textures has demonstrated exquisite preservation of microbial cells (SCHULTZE-LAM & others, 1995; KONHAUSER & others, 2001; MATA & others, 2012), though it remains to be shown if this preservation would persist through early diagenesis.

Hydrocarbon Seeps

While both stromatolitic and thrombolitic textures have been described at hydrocarbon seeps, many deposits are neither laminated nor clotted and would best be termed as leiolites (Greinert, Bohrmann, & Elvert, 2002; Shapiro, 2004a; Lloyd & others, 2010). The microstructure of seep microbialites is noteworthy for abundant non-fecal micropeloids, dissolution surfaces, yellow, bladed calcite cements, and aragonitic botryoids (Campbell, Farmer, & Des Marais, 2002), though carbonate fabrics themselves are not conclusive of a hydrocarbon source. Instead, microbial carbonates with substantially depleted $\delta^{13}C$ signatures are a common indicator of hydrocarbon seeps (Aharon, 2000) and reflect either thermogenic or biogenic methane as sources of carbon (Birgel & others, 2006). The co-occurrence of chemosynthetic metazoans alongside localized carbonate deposits within a siliciclastic lithofacies provides additional biological and sedimentary evidence for hydrocarbon seeps.

ANCIENT EXAMPLES

Precambrian

The great antiquity of stromatolites cannot be overstated. Dating back nearly 3.5 billion years (Ga), stromatolites have a sporadic but impressive preserved fossil record through Archean and Proterozoic deposits (Hofmann, 2000; Schopf, 2006). Nutman and others (2016) recently report stromatolitic textures in 3.7 Ga carbonates from Isua, Greenland, but subsequent studies argue that domal and conical textures are the result of secondary alteration (Allwood & others, 2018). The oldest definitive Archean stromatolites are from the Pilbara Craton of Australia, including the 3.5 Ga Dresser Formation (Walter, Buick, & Dunlop, 1980; van Kranendonk, 2006; van Kranendonk, Webb, & Kamber, 2003), and the 3.2 Ga Strelley Pool Chert (Lowe, 1980; Allwood & others, 2006), as well as 2.7–2.5 Ga Fortescue and Hamersley Group deposits (Buick, 1992; Lepot & others, 2008; Hickman, 2012). The Kaapvaal Craton of South Africa also contains a variety of Archean stromatolites and other microbial textures, including the Buck Reef Chert, Pongola and Ventersdorp Supergroups, and the Campbellrand-Malmani Dolomite (Buck, 1980; Beukes, 1987; Beukes & Lowe, 1989; Sumner, 1997, 2000; Tice & Lowe, 2006; Homann, 2019; Wilmeth & others, 2019). Other Archean stromatolite locations include the Superior and Slave Cratons (Canada), the Dharwar and Singhbhum Cratons (India), the Yilgarn Craton (Australia), and the Zimbabwe Craton (Hofmann, 2000; Schopf, 2006).

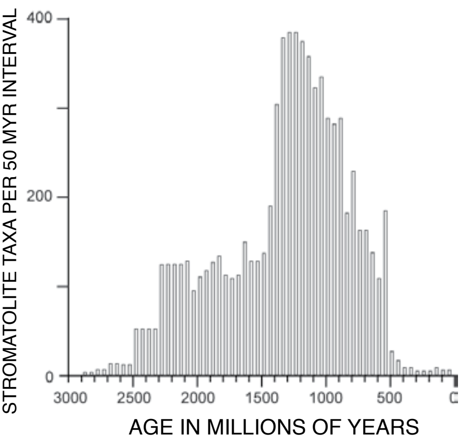

Fig. 10. Stromatolite abundance plot of Awramik and Sprinkle (1999) as presented in Riding (2006).

The Precambrian microbialite record is rich and diverse enough to suggest secular variation in stromatolitic attributes (Grotzinger & Knoll, 1999). In general, stromatolites are less common in the Archean (though this is likely a function of lack of preserved suitable facies within greenstone belts) and increase in both diversity and abundance through the Paleoproterozoic, reaching a maximum in the Mesoproterozoic (Awramik & Sprinkle, 1999) (Fig. 10). The Proterozoic increase in microbialite abundance and diversity has been linked to the development of large continents with stable continental shelves for extensive shallow-marine carbonates to form (Eriksson & others, 2006, 2007). While stromatolites and thrombolites continued to dominate shallow water carbonates during the Neoproterozoic, overall microbialite diversity decreased during this era (Grotzinger, 1990; Awramik & Sprinkle, 1999). Lacustrine and spring microbialites have also been described as early as the Archean, though smaller primary spatial extents limit the number of known locations (Buck, 1980; Buick, 1992; Djokic & others, 2017; Wilmeth & others, 2019). Many researchers have developed biostratigraphic schemes for correlating Precambrian deposits (e.g., Cloud & Semikhatov, 1969; Knoll & Semikhatov, 1998; Semikhatov & Raaben, 2000) though not without controversy, as discussed later in this chapter.

There are several features of Precambrian stromatolites that segregate them from younger, Phanerozoic counterparts. Precambrian stromatolites are fine grained, with most Archean and Paleoproterozoic forms dominated by crystalline microfabrics (Riding, 2008). It has been argued that Precambrian stromatolites are more likely to host abiotic crystal precipitate layers than their Phanerozoic counterparts (Grotzinger & Knoll, 1999). Precambrian deposits contain extremely large stromatolites, measured in tens of meters in height and diameter, including size ranges that are not known from the Phanerozoic (Beukes, 1987; Fralick & Riding, 2015). In contrast, ministromatolites one to several millimeters across are most common in the Neoarchean and Paleoproterozoic (Hofmann & Jackson, 1987; Medvedev & others, 2005). Upper Paleoproterozoic and Mesoproterozoic marine stromatolites display many diverse macrostructures rarely observed in Phanerozoic deposits, including simple and complexly branching forms (Cloud & Semikhatov, 1969; Awramik & Sprinkle, 1999). In terms of size, fabric, and morphology, uniformitarian principles do not allow for clear correlation from modern marine stromatolites to the vast Precambrian record.

Phanerozoic Marine and Lacustrine

Phanerozoic marine microbialites are noteworthy for their relatively simplistic morphologies compared with Proterozoic forms. Even when comprising kilometer-scale bioherms and biostrome deposits, most Phanerozoic microbialites are dominated by simple centimeter- to meter-scale, unbranched columns composed of irregular but roughly parallel laminae. Detrital grains become increasingly important fabric components over time, typically as fine- to medium-grained sediments. Another noteworthy development in Phanerozoic (and Neoproterozoic) microbialites is the addition of algae, foraminifera, poriferans, and other metazoans to the construction. The role of metazoans ranges from passive benthic filter feeders that use the rigid developing microbialite as a base to active constructors (Dupraz & Strasser, 1999; Kershaw, Zhang, & Lan, 1999; Ricardi-Branco & others, 2018).Thrombolites first appear in the Neoproterozoic (though there are reports from the Paleoproterozoic) and are common in the middle Cambrian through Lower Ordovician (Kennard & James, 1986; Kah & Grotzinger, 1992; Rowland & Shapiro, 2002). Thrombolites also increase in abundance during the Devonian, Mesozoic, and locally in the Neogene (Kennard & James, 1986; Shapiro, 2000). The fossil record of dendrolites is still poorly established, but deposits are abundant in the Cambrian with potential resurgences in the Devonian and Jurassic (Shapiro & Awramik, 2000). It is likely that previously published reports of thrombolites will be revised as dendrolites with further study, as the two forms were not distinguished in the past. Oncoids, which had been present since the Archean, also saw an increase in abundance during the Cambrian, as well as the appearance of filamentous *Girvanella* microfossils (Shapiro, 2004b).

It is important to note that Phanerozoic lacustrine and fluvial stromatolites can be quite diverse with respect to macrostructure, with many forms developing columns and pseudocolumns on upper surfaces. In microstructure, lacustrine stromatolites are typified by more regular, repeating couplets of laminae, often separated by sharp boundaries. Primary cement fabrics such as botryoids and isopachous bladed calcite are also more common in lacustrine stromatolites than their marine counterparts (Casanova, 1994), and a challenge of lacustrine stromatolite description and terminology is differentiating organically mediated accretion from presumably abiogenic tufa (Riding 2008; Petryshyn & Corsetti, 2011).

GEOLOGICAL SIGNIFICANCE OF MICROBIALITES

Hofmann (1973) detailed 15 different geological topics where microbialites can be utilized, ranging in scale from geopetal indicators to evidence for the oldest life on Earth. Subsequent studies have further expanded the significance of microbial deposits, particularly in the fields of geochemistry, geobiology, and astrobiology. Rather than cover each topic in detail, this section lists several applications for researchers to consider when studying microbialites. A unifying principle behind many of these applications is that as benthic trace fossils, microbialites can faithfully record *in situ* biological, sedimentary, and geochemical conditions during formation.

MICROBIALITES AS FACIES INDICATORS

For many geologists, a significant value of microbialites is their use as facies indicators. For example, microbialite facies definitions have recently become important after the announcement of vast carbonate reservoirs in the deep pre-salt deposits of offshore Brazil, which may be microbialite or tufa in origin (Awramik & Buchheim, 2012; Muniz & Bosence, 2015). Yet, like most carbonate deposits, there are few generalities that apply to the vast rock record, and uniformitarian principles do not always apply to ancient microbialites. In particular, the utility of stromatolites has been hampered due to what has been termed the Shark Bay Effect. Although Black (1933) described modern stromatolites from the intertidal flats of Abaco Island, Bahamas, the forms were small and the widespread applicability was not realized. The discovery of meter-scale buildups in Shark Bay, Western Australia (Logan, 1961) revolutionized the field and provided a key analog of a restricted marine, hypersaline, intertidal setting. Subsequently, nearly all fossil stromatolite buildups were interpreted—or reinterpreted—as hypersaline and intertidal, even when the deposit lacked additional criteria for recognition such as mudcracks, herring-bone crossbeds, or evaporate molds. Therefore, the discovery of morphologically similar stromatolites in subtidal, normal marine tidal channels of Eleuthera (Dravis, 1983) and the Exuma (Dill & others, 1986) Islands, Bahamas, opened the door to much broader interpretation of microbialite depositional environments.

While the diversity of microbial forms produces many unique sedimentary facies, there are several trends in the facies applicability of microbialites that are corroborated across multiple studies. A few general observations are listed below, with the volume edited by Riding and Awramik (2000) providing an excellent resource for more detailed comparisons of different facies models. In most deposits, microbialites form on flooding surfaces, with stromatolites occurring in shallower water than thrombolites do. Stratiform deposits are typically indicative of intertidal conditions, as is the case with crinkly microbial mats. In plan view, if a significant major axis develops, it is likely that the axis parallels the dominant current. Branching appears to be related to an increase in sedimentation relative to growth rates. Other models will no doubt be added as additional studies are published.

BIOSTRATIGRAPHY OF MICROBIALITES

The biostratigraphic utility of microbialites remains a debated topic. Since microbialites are produced by microbial ecosystems rather than by individual organisms, biostratigraphic studies are often highly scrutinized (Grotzinger & Knoll, 1999; Bosak, Knoll, & Petroff, 2013). However, even though microbial structures are not subject to the same evolutionary patterns that govern eukaryotic index fossils, Proterozoic deposits often contain temporally constrained patterns of unique stromatolite morphologies. Early observations led Soviet scientists to employ a biostratigraphic zonation for the Siberian Platform (see reviews in Cloud & Semikhatov, 1969). Similar patterns have subsequently been described across various Proterozoic basins, most notably in Australia (Grey & Thorne, 1985; Hill, Cotter, & Grey, 2000). Most stratigraphic studies are restricted to intra-basinal deposits, though some have attempted to expand correlations between cratons (Medvedev & others, 2005; Grey, Hill, & Calver, 2011). A few case studies have also employed microbialites for correlation in early Phanerozoic deposits (Shapiro & Awramik, 2000, 2006). The governing forces behind widespread changes in Proterozoic stromatolite morphologies still remain enigmatic, potentially representing large-scale shifts in climate, biology, or geochemical cycles (Semikhatov & Raaben, 2000).

MICROBIALITES AS SIGNALS OF ENVIRONMENTAL CHANGE

Microbialite abundance and diversity broadly decrease across the Phanerozoic, and relatively sudden increases in microbialite deposits appear to be linked to shifts in climate, metazoan ecology, or both. For example, the end-Devonian and end-Permian mass extinctions are associated with increased microbialite abundance, as reviewed in Mata and Bottjer (2012). Many studies note the expansion of microbialites across ramp, platform, and shelf environments after the end-Permian mass extinction, the most devastating in Earth history (Schubert & Bottjer, 1992; Baud, Cirilli, & Marcoux, 1997; Baud, Richoz, & Pruss, 2007; Pruss & others, 2006; Kershaw & others, 2007; Mata & Bottjer, 2011). While the end-Devonian event was less severe regarding metazoan diversity, microbialites flourished during the aftermath (Playford, 1980; Wood, 2000; Webb, 2002; Whalen & others, 2002). Various hypotheses exist as to why microbialite abundances are less pronounced during other mass extinctions, including ecospace competition from bioturbating and reef-building organisms, as well as carbonate availability (Mata & Bottjer, 2012).

In addition to providing sedimentary evidence for ecological shifts, microbialites have the potential to record geochemical signatures of climate and environmental change. Stromatolites can contain especially detailed records of local geochemistry over time, with each layer representing a distinct period of microbial growth and mineral precipitation. Strong climate signals are observed from stromatolites within closed lake systems, where concentrations and isotopes of stable elements are controlled by variations in evaporation and precipitation (Talbot, 1990). Studies of lacustrine stromatolites have focused on several Cenozoic climate changes relevant to modern interest, including the Early Eocene Climatic Optimum and Plio-Pleistocene trends (Abell & others, 1982; Frantz & others, 2014; Petryshyn & others, 2016), with occasional studies investigating Mesozoic environments (de Wet & Hubert, 1989; Woo & others, 2004). Geochemical analyses of microbialites from any age or environment need to first analyze diagenetic and/or metamorphic alteration of minerals before collecting data, especially in easily altered carbonate minerals.

CONCLUSION

More than three billion years of interactions between microbial mats and their surrounding environments has produced a staggering diversity of microbialites. Many macroscale morphologies and mesoscale textures are specific to certain times and facies, and a detailed analysis of every form of microbial deposit would require a separate treatise for adequate description. Instead, this chapter represents a quick overview of terminology for basic field and petrographic analysis, as well as several geological applications to consider after discovery and description. The reader is invited to further investigate specific topics presented by consulting the reviews and primary literature cited throughout this chapter.

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