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## Cross-references

[Biofilms](#)  
[Extracellular Polymeric Substances \(EPS\)](#)  
[Microbial Biomineralization](#)  
[Microbial Mats](#)  
[Microbialites, Stromatolites, and Thrombolites](#)  
[Organomineralization](#)  
[Sediment Diagenesis – Biologically Controlled Tidal Flats](#)  
[Tufa, Freshwater](#)

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## MICROBIALITES, STROMATOLITES, AND THROMBOLITES

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### Microbialite Definition

Microbialites are “organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation” (Burne and Moore, 1987, pp. 241–242).

### Introduction

Microbial carbonates are produced by the interaction of microbial growth and metabolism, cell surface properties, and extracellular polymeric substances (EPS) with mineral precipitation and grain trapping. The early lithification that is essential for the accretion and preservation of benthic microbial carbonates is both biologically mediated and environmentally dependent. Consequently, microbialite history reflects not only microbial mat evolution, but also long-term changes in seawater and atmospheric chemistry that have influenced microbial metabolism and seawater carbonate saturation state.

Microbialites are in place benthic sediments produced by microbial processes. The term “microbialite” has been most widely used to describe carbonate stromatolites, thrombolites, and similar structures that occur as domes and columns in the shallow waters of lakes and seas, but it can also apply to many additional authigenic accumulations in which microbes are locally conspicuous, such as

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some tufa, travertine, speleothem and spring, seep, and vent deposits. A series of terms and definitions were proposed between 1967 and 1987 in attempts to distinguish benthic sediments formed by microbial sediment trapping and/or precipitation. The first term, *cryptalgal*, was proposed by Aitken (1967, p. 1163) for rocks or rock structures “believed to originate through the sediment-binding and/or carbonate precipitating activities of non-skeletal algae.” The second was redefinition of *stromatolite* by Awramik and Margulis’ (1974) as “organosedimentary structures produced by sediment trapping, binding and/or precipitation as a result of growth and metabolic activity of organisms, primarily blue-green algae.” Both Aitken (1967, p. 1163) and Awramik and Margulis (1974) used blue-green algae to indicate cyanobacteria, and therefore Kennard and James (1986, p. 496) replaced *cryptalgal* by *cryptomicrobial*. The third term was *microbialite* (Burne and Moore, 1987), which effectively repeated Awramik and Margulis’ (1974) definition of *stromatolite*, thereby broadening its scope. The primary focus of all these definitions was stromatolites and thrombolites.

Research during the 1900s revealed many details concerning the nature and history of stromatolites, but it also led to nomenclatural uncertainty as it became necessary to accommodate newly recognized deposits, such as thrombolites. Aitken (1967, p. 1164) sought to clarify use of “algal” in carbonate rock descriptions by distinguishing “rocks composed of the remains of skeletal calcareous algae . . . from those formed by noncalcareous blue-green . . . and green . . . algae.” He termed the latter *cryptalgal*, defined as rocks or rock structures “believed to originate through the sediment-binding and/or carbonate-precipitating activities of nonskeletal algae” (Aitken, 1967, p. 1163). Aitken (1967, Fig. 1) regarded both thrombolites and stromatolites as *cryptalgal* deposits, distinguishing by their respective clotted and laminated macrofabrics. However, Awramik and Margulis’ (1974) proposed a broader definition of *stromatolite* as “megascopic organosedimentary structures produced by sediment trapping, binding and/or precipitation as a result of growth and metabolic activity of organisms, primarily blue-green algae.” This therefore subsumed thrombolite as a category within *stromatolite*.

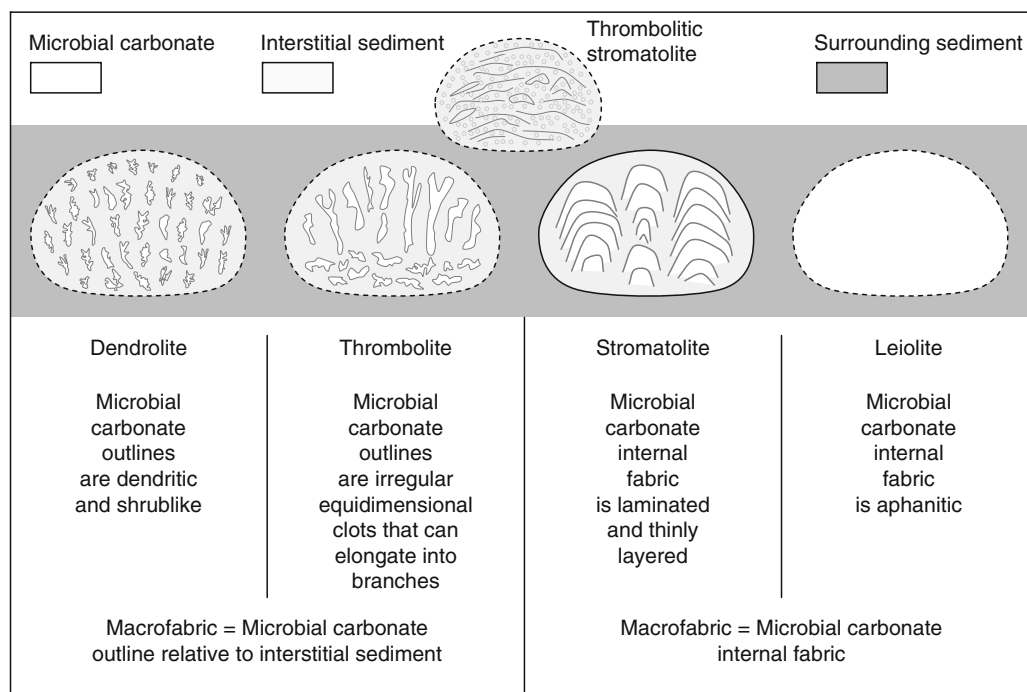
As a result of these and other developments, by the 1980s stromatolites could variously be regarded as (1) microbial and laminated (e.g., Kalkowsky, 1908; Hofmann, 1969; Krumbein, 1983), (2) microbial but not necessarily laminated (Awramik and Margulis, 1974), and (3) laminated but not necessarily organic (Semikhatov et al., 1979) (see Riding, 1999, p. 324). Since the wording of Burne and Moore’s (1987, pp. 241–242) definition of *microbialite* closely followed that of Awramik and Margulis’ (1974) definition of *stromatolite*, it therefore required return to a narrower definition of *stromatolite*, as layered or laminated structures. This relatively narrow definition was intended by Kalkowsky (1908) and is implied by his term *stromatolith*; *stromat*, Greek for “to spread out,” suggests a layer. Burne and Moore’s

(1987) new term, *microbialite*, encompassed more diverse benthic microbial deposits. The outcome of these developments was that stromatolite and thrombolite could be considered as equal categories within *microbialite*, mirroring Aitken’s (1967, Fig. 1) classification of stromatolites and thrombolites within *cryptalgal* carbonates. Subsequently, these and other varieties of *microbialite* have commonly been distinguished by their dominant internal macrofabric: stromatolite (laminated), thrombolite (clotted), dendrolite (dendritic), and leiolite (aphanitic) (Riding, 2000, pp. 189–195) (Figure 1).

Given the importance of stromatolites in the development of these concepts, this orderly arrangement of terms under the *microbialite* umbrella relied heavily on stromatolites being microbial structures. However, as soon as Kalkowsky’s (1908) article was published, researchers began to point out similarities between stromatolites and abiogenic precipitates (Reis, 1908; Bucher, 1918), and this chorus has continued ever since. Logan et al. (1964, p. 69) suggested recognition of “inorganic stromatolites”; Hofmann (1973, Fig. 5) showed the difficulty of distinguishing stromatolites from other laminites; and Semikhatov et al. (1979, p. 994) proposed a descriptive rather than purely genetic definition of *stromatolite*. Reports of essentially abiogenic stromatolites have persisted, especially in the Proterozoic (Grotzinger and Read, 1983; Grotzinger, 1989a; Pope et al., 2000). Attempts to separate abiogenic and biogenic stromatolites are obstructed by *hybrid stromatolites* (see below, Stromatolites) consisting of millimetric alternations of abiogenic crust and lithified microbial mat (Riding, 2008). Consequently, although microbial mat models seem to apply well to all or most thrombolites, dendrolites and leiolites, they do not account for all stromatolite-like deposits, particularly in the Precambrian. The implications of this complication for stromatolite interpretation as well terminology have still to be worked out.

### Microbialites in space and time

Microbes occupy a very broad range of environments, including waters of widely differing chemistry and composition, and their involvement in sedimentation is equally varied. Most microbialites are carbonate (e.g., aragonite, calcite, dolomite) in composition, but siliceous, phosphatic, iron, manganese, and sulfate examples also occur. The microbes in microbialites are dominantly bacteria, including cyanobacteria, together with small algae. From the perspective of biocalcification, *microbialite* carbonates are bioinduced. Bacteria in general exert relatively weak control over the organic site and mineralogy of calcification, and present-day microbial carbonates appear to be most widespread in environments where precipitation is inorganically favored. This environmental dependence means that where rapid cooling and degassing strongly favor mineral precipitation irrespective of organic intervention, as in hot water springs and vents, the overall sedimentary contribution of microbes may be



**Microbialites, Stromatolites, and Thrombolites, Figure 1** Microbial carbonates defined by macrofabric: leiolite (aphanitic), stromatolite (laminated), thrombolite (clotted), dendrolite (dendritic). Examples show domes and associated sediment. Not to scale. All categories are integradational. In addition to domes/mounds, overall shape can include columns, layers, and irregular masses. A complication is that leiolite and stromatolite macrofabrics are defined by features within (i.e., internal to) the microbial carbonate, such as lamination. In contrast, thrombolite and dendrolite macrofabrics are defined by the external shape of individual masses of microbial carbonate, such as clots or small shrub-like masses. Thrombolitic stromatolite (Aitken, 1967), typified by some Shark Bay columns, is internally weakly clotted and crudely laminated. It is essentially agglutinated, in contrast to Neoproterozoic and early Palaeozoic thrombolites with calcified microbial microfabrics. In the latter, the clots may be prostrate and irregular, and also vertically extended into amalgamated elongate branches (e.g., *Favosamacteria*).

relatively minor. In such cases, they influence the fabric more than the process of deposition. In contrast, where waters are less saturated for minerals, microbial activity can play a major role in sediment precipitation. These differing roles are reflected in the form and fabrics of the resulting deposits.

Sensitivity to environmental influence is also reflected in the secular distribution of microbialites. Without ruling out the influence of other factors – such as competition with other organisms – marine microbial carbonate abundance through time significantly reflects fluctuation in carbonate saturation state (Fischer, 1965; Grotzinger, 1990; Riding and Liang, 2005). Microbial carbonates can therefore be relatively sensitive proxies for seawater carbonate chemistry, and for atmospheric composition, since cyanobacterial sheath calcification is promoted by increased bicarbonate uptake (Merz, 1992) when  $\text{CO}_2$  levels decline (Riding, 2006).

### Scope

The term microbialite, with its emphasis on benthic microbial deposits, encompasses a wide range of sediments; what does it not cover? “Benthic” would seem to exclude both allochthonous and interstitial microbial sediments.

If so, then biogenic “whiting” deposits produced by photosynthetically induced nucleation of small  $\text{CaCO}_3$  crystals in the water column are not microbialites, and neither are diagenetic bacterially induced precipitates such as cements and concretions. However, these somewhat artificial distinctions could be blurred, as in some soil crust and beachrock deposits. On the other hand, “microbial” must exclude abiogenic stromatolites, identified in both Precambrian and Phanerozoic sediments (Grotzinger and Read, 1983; Pope et al., 2000). This is a complication, especially since microbialite (Burne and Moore, 1987) is based on a preexisting definition of stromatolite proposed by Awramik and Margulis (1974), and arose from a need for a general term to encompass stromatolite, thrombolite, and related deposits. Such difficulties of definition should be resolved by increased understanding of both present-day and ancient examples of these important and geologically widespread deposits.

### Stromatolites

#### Definition

Stromatolites are laminated benthic microbial deposits (Riding, 1991).



## Introduction

Kalkowsky (1908) proposed the term stromatolite (*Stromatolith*) for columns and domes in early Triassic playa lake oolites, but similar structures were already long known from examples such as those in the late Cambrian of New York State that Steele (1825, pp. 17–18, pl. 2) described as “calcareous concretions” and Hall (1883) named *Cryptozoon* (Figure 2). The search for present-day analogs of these ancient stromatolites led from freshwater tufa (Walcott, 1914; Roddy, 1915) and marsh deposits (Black, 1933) to marginal marine domes (Ginsburg et al., 1954) and columns (Logan, 1961). These discoveries strongly supported Kalkowsky’s (1908) inference that stromatolites are essentially microbial deposits. But optimism that they could provide appropriate analogs for all ancient marine stromatolites was tempered by studies of Precambrian examples that include significant abiogenic precipitated components (e.g., Serebryakov, 1976, p. 633; Grotzinger and Knoll, 1999, p. 314). Some definitions of stromatolite have therefore encompassed both microbial and abiogenic layered/laminated authigenic crusts that characteristically form domical and columnar morphologies.

Definitions of stromatolite range from that of Kalkowsky (1908) to that of Semikhatov et al. (1979, p. 993): “a stromatolite is . . . an attached, laminated, lithified, sedimentary growth structure, accretionary away from a point or limited surface of initiation. Although characteristically of microbial origin and calcareous composition, it may be of any origin, composition, shape, size, or age.” Understanding of Kalkowsky’s view has been hindered by a definition incorrectly attributed to him by Krumbein (1983, p. 499): “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 (1908) did not write this (see Riding, 1999, p. 323), but it has been repeated as if it were a literal translation from his paper (e.g., Ginsburg, 1991, p. 25; Feldmann and McKenzie, 1998, p. 201; Grotzinger and Knoll, 1999, p. 316; McLoughlin et al.,

2008, p. 96). Compounding this mistake, the somewhat awkward wording (use of “must not” rather than “need not”) has been cited as “paradoxical,” and “confusion” to be avoided, and also as an example of the deficiencies of genetic definitions (Grotzinger and Knoll, 1999, p. 316; McLoughlin et al., 2008, p. 96). In his 1908 paper, Ernst Kalkowsky did not provide a specific definition of stromatolite, but he did repeatedly emphasize that it is a laminated organic structure. He thought that the life forms involved were “*niedrig organisierte pflanzliche Organismen*” (simple plantlike organisms, Kalkowsky, 1908, p. 125). It is therefore reasonable to conclude that Kalkowsky essentially regarded stromatolites as laminated microbial deposits (Riding, 1999).

However, at the same time that support was growing for Kalkowsky’s (1908) biogenic interpretation of stromatolites, the contrary view was also being expressed. Reis (1908) interpreted stromatolites as inorganic precipitates, Bucher (1918) compared them with hot spring sinter. Semikhatov et al. (1979, p. 994) were also concerned by the similarities between microbial stromatolites and “morphologically similar structures of nonmicrobial origin” such as those in caves and hot springs, and therefore suggested their descriptive definition. Subsequent research has shown that some stromatolite-like deposits are essentially abiogenic (e.g., Grotzinger and Read, 1983; Grotzinger and James, 2000, p. 9). Pope et al. (2000, p. 1139) contrasted microbial and abiogenic stromatolites, and considered “isopachous stromatolites to have been dominated by chemogenic precipitation in the absence of microbial mats, and the growth of peloidal stromatolites to have been controlled by sedimentation in the presence of microbial mats.”

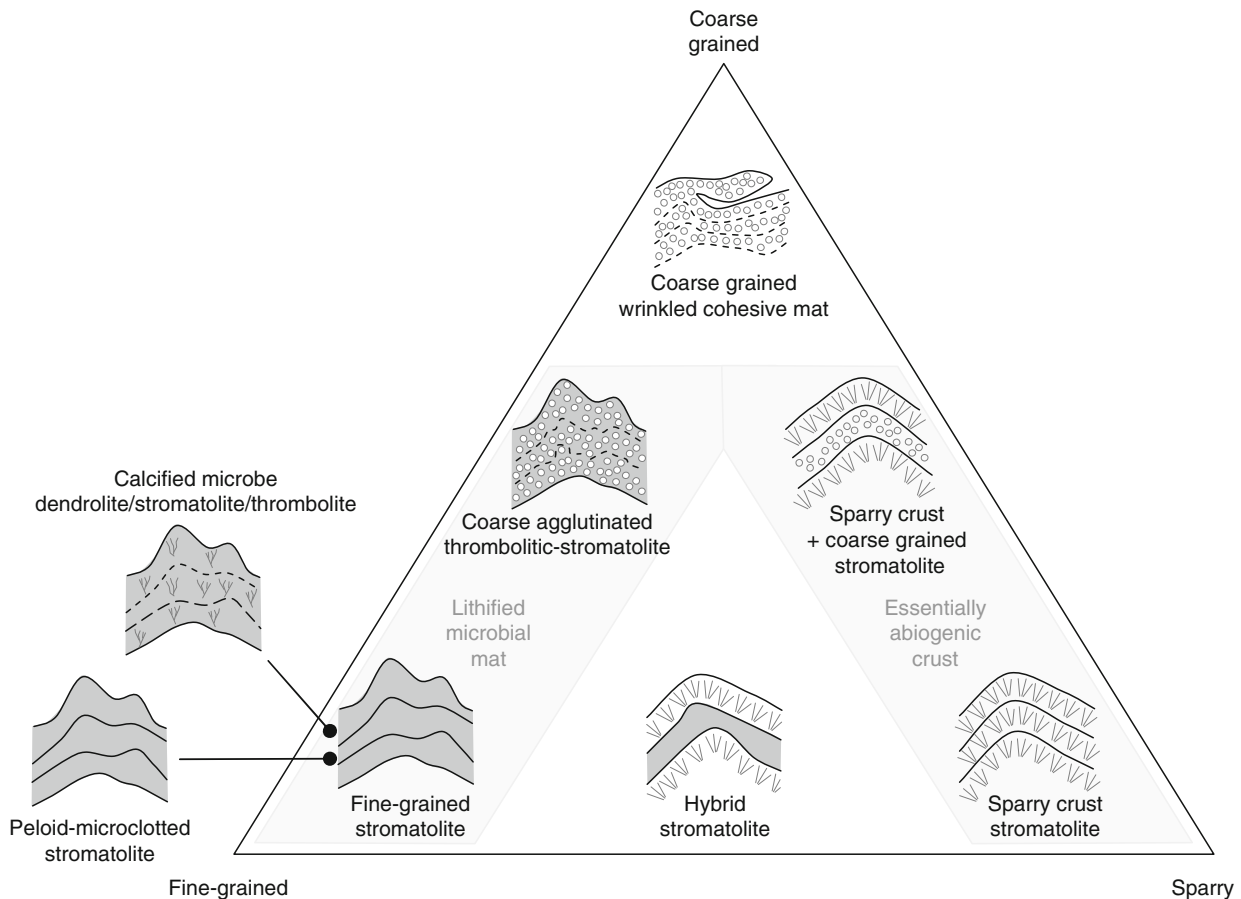
Fabric criteria can be used to distinguish abiogenic evenly layered sparry crust from fine-grained lithified microbial mats with uneven layering. In well-preserved examples, it should therefore be possible to tell abiogenic and biogenic stromatolites apart. However, as noted under microbialite, the millimetric interlayering of these two fabrics that can occur in hybrid stromatolites (Riding, 2008) makes such straightforward separation impossible. Consequently, stromatolites are regarded here, essentially, as laminated benthic microbial deposits, but they can contain abiogenic precipitates and be intimately inter-layered with them. In the marine realm, there is a strong secular perspective to this. Many Phanerozoic and Neoproterozoic stromatolites are probably essentially lithified microbial mats, whereas many older examples probably contain at least some precipitated abiogenic crust.



**Microbialites, Stromatolites, and Thrombolites, Figure 2** Late Cambrian (late Franconian–early Trempealeauan) stromatolite (*Cryptozoon*), Hoyt Limestone, Petrified Gardens, Saratoga Springs, New York, USA. Coin diameter ~3 cm.

## Stromatolite types

Stromatolite micro- and macrofabrics commonly intergrade with those of dendrolites and thrombolites (Figure 3). Their formation can involve up to three main processes: microbial precipitation, inorganic precipitation, and grain trapping (Figure 4). The main types represent



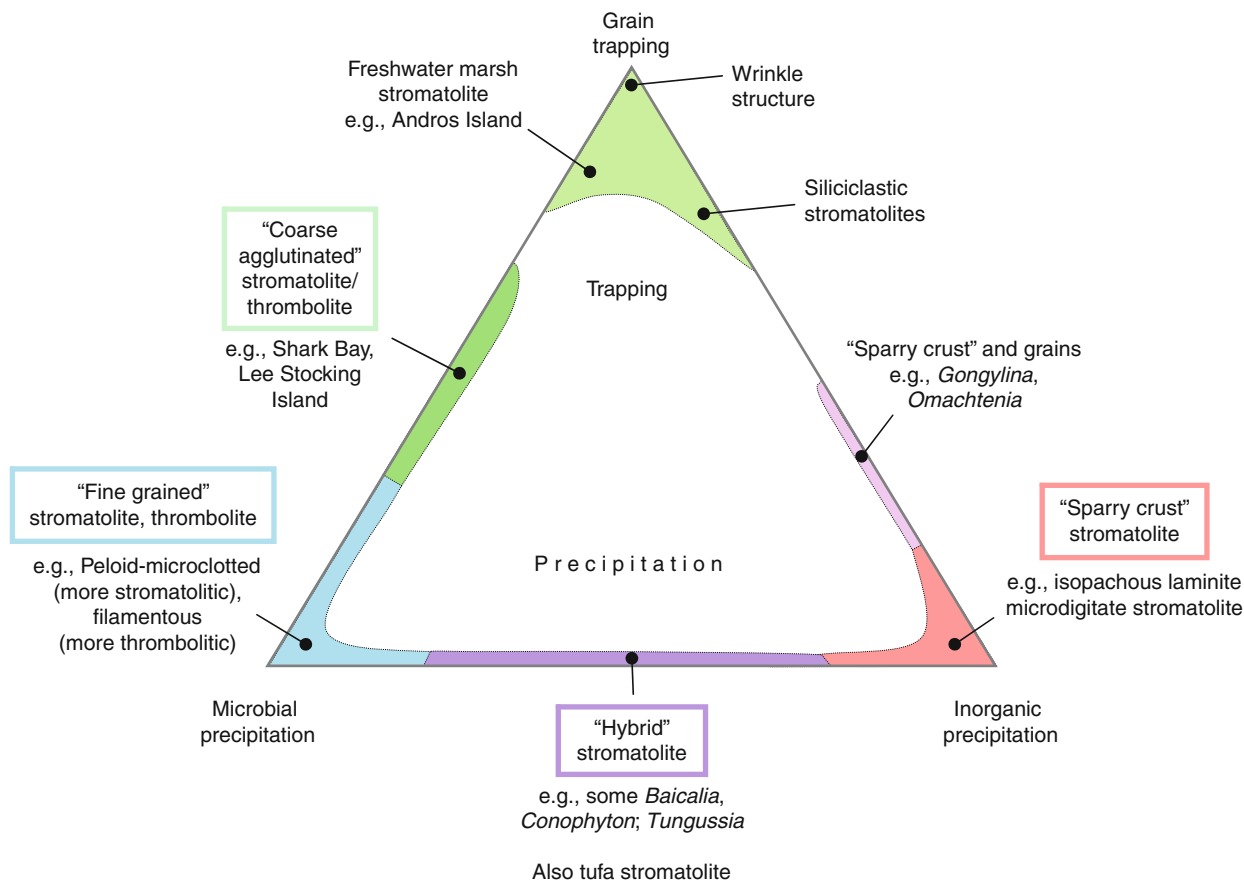
**Microbialites, Stromatolites, and Thrombolites, Figure 3** Stromatolites and thrombolites based on micro/macrob fabric. All except wrinkled cohesive mats are syngedimentarily lithified by microbial and/or abiogenic processes. Fine-grained varieties include two distinctive types: (i) stromatolites with peloidal-microclotted microfabrics and (ii) dendrolites and thrombolites with abundant filamentous and other calcified microbial microfossils.

lithified microbial mat, sparry crust, and combinations of these (“hybrid stromatolite”).

*Lithified microbial mat stromatolites* exhibit a variety of intergradational fabrics. Two main types are fine-grained and coarse agglutinated. They form diverse stratiform, domical and columnar structures and, overall, tend to show relatively uneven to discontinuous layers with relatively poor inheritance and can include abundant fenestrae. Fine-grained stromatolites appear mainly to be products of syngedimentary microbial precipitation and are dominated by fine-grained (micrite, microspar) and filamentous fabrics. Fine-grained microfabrics are typically clotted and peloidal and are probably largely produced by heterotrophic bacterial calcification (e.g., dissimilatory sulfate reduction) of EPS and other cell products. Filamentous microfabrics are dominated by tubiform microfossils such as *Girvanella* that reflect photosynthetic cyanobacterial sheath calcification, but they too have fine-grained matrices. On their own, peloid-microclotted fabrics tend to be stromatolitic, and have been termed spongiostrome (Gürich, 1906; Pia, 1927, p. 36).

Filamentous fabrics tend to be more crudely layered and grade to thrombolitic. They have been termed porostromate (Pia, 1927, pp. 36–40), skeletal (Riding, 1977), and calcimicrobial (James and Gravestock, 1990). Coarse agglutinated stromatolites/thrombolites are produced by trapping sandy sediment by uncalcified EPS and erect filaments that can include microalgae. Present-day examples include some Shark Bay and Lee Stocking Island columns. They often have crudely layered macrofabrics (Logan, 1961) and have been termed thrombolitic stromatolites (Aitken, 1967).

*Sparry crust* (Riding, 2008) can form stromatolite-like abiogenic precipitates (Grotzinger and Rothman, 1996) characterized by even, often isopachous, laterally persistent layers with good inheritance (Pope et al., 2000). They have been most widely recognized in the Palaeoproterozoic and Mesoproterozoic (Grotzinger and Knoll, 1999, Fig. 6a, b), with microdigitate forms occupying peritidal environments (Grotzinger and Read, 1983) and isopachous laminite (Jackson, 1989) relatively deeper water facies.



**Microbialites, Stromatolites, and Thrombolites, Figure 4** Stromatolitic and thrombolitic carbonates related to grain trapping, and syndimentary microbial and inorganic precipitation. Developed from Riding (2008, Fig. 12). Principal categories are coarse agglutinated, fine-grained, hybrid and sparry crust. Those dominated by microbial precipitation and/or grain trapping are microbial mats. Sparry crusts are essentially abiogenic precipitates. Hybrid stromatolites are combinations of lithified microbial mat and sparry crust. Fine-grained varieties include filamentous (also termed porostromate, skeletal, and calcimicrobial) which is more thrombolitic and peloidal-microclotted (also termed spongiostromate) which is more stromatolitic. Microbial mats dominated by trapping, but with relatively minor early lithification include freshwater marsh stromatolites (Black, 1933) and wrinkle marks (Runzelmarken, Häntzschel and Reineck, 1968) mainly in siliciclastic sands and silts. For secular distributions see Fig. 11.

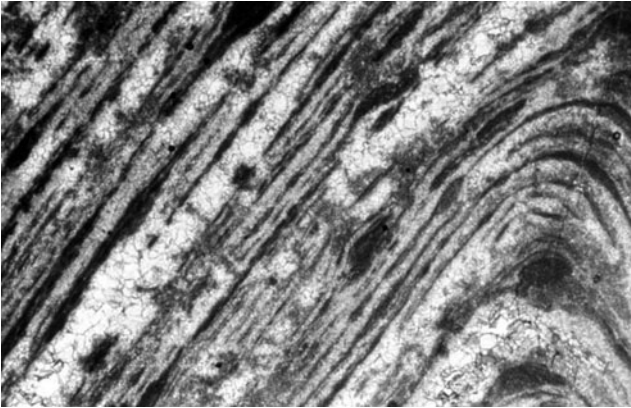
*Hybrid crust stromatolites* (Riding, 2008) typically consist of light-dark, often millimetric, alternations of sparry and fine-grained crust. These build stromatolites with well-developed even, although not usually isopachous, layering that is laterally quite persistent with generally good inheritance, as in some *Conophyton* (e.g., Walter, 1972, p. 86) (Figure 5). This layering is therefore intermediate in regularity between that of stromatolite-like sparry crust and fine-grained crust stromatolites. Hybrid crust appears to be a major component of Palaeoproterozoic (e.g., Sami and James, 1996) and Mesoproterozoic stromatolites (e.g., Petrov and Semikhatov, 2001), which can include very large domical and conical examples. Laminated freshwater cyanobacterial mats in shallow lakes of Andros Island show similarities to hybrid stromatolite, with fine-grained incipiently lithified cyanobacterial mats alternating with laminar fenestrae and elongate open voids (Monty, 1976, Fig. 4). If this structure were early lithified,

it could resemble some *Conophyton* and *Baicalia* fabrics, as Bertrand-Sarfati (1976) suggested.

#### Intertidal mats and wrinkle structures

At the present day, intertidal and supratidal sediments are commonly colonized by cyanobacteria dominated mats in siliciclastic (e.g., Cameron et al., 1985; Stal et al., 1985), evaporitic (e.g., Gerdes et al., 2000), and carbonate (Black, 1933; Logan et al., 1974) environments (Figure 6). Where these mats are cohesive, but insufficiently early lithified, they do not show significant accretion but nonetheless stabilize layers of sediment. These microbialites that were unlithified during their formation can be preserved in place, and also imprinted and disrupted, e.g., by desiccation and water movement. They and their incorporated sediment may be cracked, curled, and folded, and this syndimentary deformation can be preserved after burial. Such patterned surfaces in





**Microbialites, Stromatolites, and Thrombolites,**  
**Figure 5** *Conophyton garganicum*. The fabric is interpreted as Hybrid stromatolite composed of alternating submillimetric layers of fine-grained lithified microbial mat and light-colored essentially abiogenic sparry layers. Middle Riphean, Russia, stratigraphic unit and locality not known. Specimen donated to Geological Survey of Canada by M.A. Semikhatov; photograph courtesy of Hans Hofmann. Width of view 8 mm.



**Microbialites, Stromatolites, and Thrombolites,**  
**Figure 6** Wrinkled microbial mat with carbonate sediment; supratidal flat, Crane Key, Florida Bay, USA. Red pen cap ~5 cm long.

Mesoproterozoic limestones were named *Kinneyia* by Walcott (1914, p. 107, pl. 11, Fig. 3) and subsequently linked to “Runzelmarken” (wrinkle marks, Häntzschel and Reineck, 1968) and other mat-related structures (Hagadorn and Bottjer, 1997). They have also been termed microbially induced sedimentary structures (MISS) (Noffke et al., 1996). The exact origins of these bedding plane structures are probably complex and varied (Porada et al., 2008) but they have been widely linked to deformation of microbial mats and have been used to infer the presence of mats in the Proterozoic (Horodyski, 1982) and Archaean (Noffke et al., 2006).

### Siliciclastic stromatolites

In contrast to wrinkle structures, siliciclastic stromatolites can possess large domical morphologies and considerable synoptic relief. They are much scarcer than carbonate stromatolites, and are only known from mixed siliciclastic-carbonate environments that provide both siliciclastic grains and the early lithification required to maintain their support (Martín et al., 1993). Most examples are Palaeozoic, e.g., Ordovician (Davis, 1968), Devonian (Draganits and Noffke, 2004), Carboniferous (Bertrand-Sarfati, 1994), and Permian (Harwood, 1990), but diverse examples also occur in the late Miocene of South-east Spain (Martín et al., 1993; Braga and Martín, 2000). Based on the proportion of siliciclastic grains they contained, Martín et al. (1993) recognized three compositional types: “carbonate,” <10%; “siliciclastic-carbonate,” 10–50%; and “sandstone,” >50%. They are typically metric, locally decametric, domes with both stromatolitic and thrombolitic macrofabrics, associated with marginal marine beach (Braga and Martín, 2000), fan-delta and conglomeratic debris-flow deposits (Martín et al., 1993), and also with oolitic stromatolites–thrombolites (Braga et al., 1995). Sediment within the more siliciclastic domes includes abundant quartz, mica, and lithic fragment sand, and occasional quartz and metamorphic rock granules and pebbles.

### Thrombolites

#### Definition

Thrombolites (Greek: *thrombos*, clot; *lithos*, stone) are “cryptalgal structures related to stromatolites, but lacking lamination and characterized by a macroscopic clotted fabric” (Aitken, 1967, p. 1164).

#### Introduction

Aitken’s (1967) seemingly straightforward definition of thrombolite contained the seeds of more confusion than might have been anticipated. Since stromatolites are generally regarded as internally laminated; it could be expected that thrombolites are internally clotted. However, stromatolitic laminae are internal features of microbial carbonate, whereas “clot” could be used to describe both the external shape and internal structure of microbial carbonate (Figure 1). Aitken’s (1967) descriptions of Cambro-Ordovician examples, and his emphasis that thrombolite clotted fabric is macroscopic, have directed most researchers to regard “clots” as centimetric patches of microbial carbonate within interstitial sediment. In this view, a thrombolite dome consists of numerous such clots within lighter colored interstitial detrital matrix. Consequently, the dome has an overall macroclotted fabric, but the individual clots themselves are not necessarily internally composed of smaller clots, although they can be. This contrasts with stromatolitic domes in which each individual stromatolite is internally laminated and its shape is described separately, e.g., as domical, columnar, digitate, etc.

Aitken's (1967) concept of clots as patches of microbial carbonate within matrix is appropriate where they are irregularly rounded, but in digitate thrombolites the patches elongate into decimetric branches (e.g., Armella, 1994, Fig. 9) and use of "clot" to describe these is awkward. If some of Aitken's (1967) thrombolite domes contain dendritic fabrics, as seems likely, then why did he stress their clotted macrofabric? A likely explanation is that, in domes composed of radial branches, any section other than a vertical one through the dome center (e.g., Armella, 1994, Fig. 9) tends to show clot-like rounded outlines of oblique sections of branches. If this is correct, then to be consistent the branches should also be regarded as clots. This approach was followed by Armella (1994) and Kennard (1994) (although they used *thromboid* as an equivalent term to clot) to describe rounded lobate patches and elongate columns alike. There seems little doubt that this is what Aitken (1967) intended, and Shapiro (2000, p. 166) recognized that he used clot to describe the thrombolite columns themselves. Nonetheless, in describing similar branched Cambro-Ordovician thrombolites (*Favosamaceria*), Shapiro (2000) and Shapiro and Awramik (2006) broadened "clot" to refer to both millimetric clots within the branches and centimetric clots embedded in interstitial sediment. And there is a further complication. Aitken (1967) suggested that poorly laminated columns at Shark Bay are "thrombolitic stromatolites." As a result, in addition to describing Cambro-Ordovician domes with well-defined fine-grained clots, thrombolite has been applied to agglutinated present-day microbial columns in which the clots are much less distinct patchy fabrics.

These complications of usage still require clarification. At present, it is safe to say that "clot" (and the equivalent terms mesoclot and thromboid) has not been used consistently in thrombolite studies. It has been applied to millimetric patches within microbial carbonate, to centimetric lobate patches and also extended columns of microbial carbonate surrounded by detrital carbonate sediment, to transverse sections of these columns (here termed pseudoclots), and to diffuse patches of trapped sand, as well as to secondarily enhanced clots. Given these complications, it is understandable that earlier workers often referred to thrombolites as "unlaminated stromatolites" (e.g., Aitken, 1967, p. 1166; Pratt, 1982a; Schopf and Klein, 1992, p. 1202). Nonetheless, thrombolites can generally be regarded as benthic microbial carbonates with macroclotted fabric.

### Thrombolite types

Two main types of thrombolite are calcified microbe and coarse agglutinated (Riding, 2000, pp. 192–193). Both intergrade with microbial mat stromatolites and primarily reflect the presence of major components that form irregular aggregates rather than thin layers. Nonetheless, the two types have quite distinct origins:

- (i) *Calcified microbe thrombolites* include the classic Cambro-Ordovician examples described by Aitken (1967) and also by Pratt and James (1982) and Kennard and James (1986). Aitken (1967) noted that burrows and trilobite fragments are common in these thrombolites, and examples of similar age often show mottled interiors and stromatolitic outer coatings (Figure 7). They consist of clots composed of framework whose most recognizable components are calcified microfossils, such as *Girvanella* filaments and *Renalcis* botryoids. The clots may be irregular centimetric amoeboid forms (Figure 8) or extend vertically into elongate (Armella, 1994, Fig. 9) meandriform and laterally amalgamated (Pratt and



**Microbialites, Stromatolites, and Thrombolites, Figure 7** Late Cambrian (Trempealeuan) thrombolite column with mottled interior (within dotted line) and dark stromatolitic coating (between white arrows). Smoky Member, Nopah Fm, Dry Mountain, California, north-western Death Valley National Park, USA. Pen ~15 cm long.



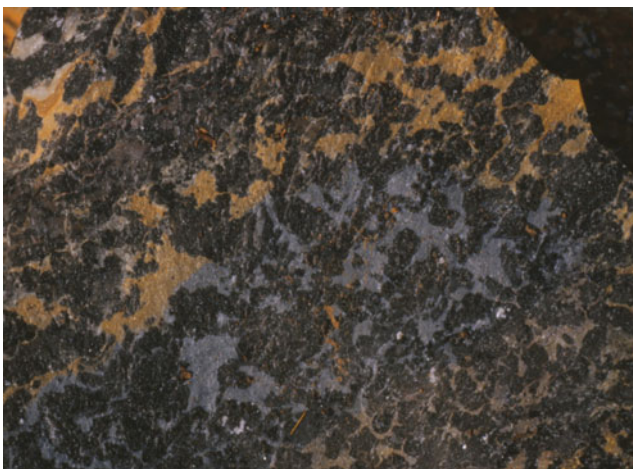
**Microbialites, Stromatolites, and Thrombolites, Figure 8** Late Cambrian (Trempealeuan) thrombolite, Smoky Member, Nopah Fm, Dry Mountain, California, north-western Death Valley National Park, USA.



James, 1982, Figs. 9, 12) branches named *Favosamaceria* by Shapiro and Awramik (2006), (Figure 1). The clots are surrounded by detrital sediment infill. Progression from irregular clots to elongate branches has confused descriptive terminology. Shapiro (2000) suggested that in branched forms the clots typical of thrombolites are to be found within the branches, although Aitken (1967) seems to have regarded the columns as clots. James and Gravestock (1990) used “calcimicrobe” (calcified microbial microfossil) to refer to filamentous and botryoidal fossils that are common in Cambrian reefs. These typically form dendrolite (Figure 9) and thrombolite (Figure 10) fabrics and include calcified cyanobacteria such as *Angusticellularia*, *Botomaella*, and *Girvanella*, and also *Epiphyton* and *Renalcis*, whose affinities are less certain. Calcified microbe thrombolites are widespread in shallow marine



**Microbialites, Stromatolites, and Thrombolites,**  
Figure 9 Dendrolite, Middle Cambrian, Zhangxia Formation,  
near Jinan, Shandong, China



**Microbialites, Stromatolites, and Thrombolites,**  
Figure 10 Thrombolite, early Cambrian, near Tiout, Anti-Atlas  
Mountains, Morocco. Width of view 8 cm.

environments during the Neoproterozoic and early Palaeozoic.

- (ii) *Coarse agglutinated thrombolites* are largely composed of fenestral microbially trapped sandy sediment within finer-grained microbially lithified matrix. They are closely associated with coarse agglutinated stromatolites (Figures 3 and 4) that Aitken (1967, p. 1171) described as “thrombolitic-stromatolites.” They are only known in the late Neogene and their development appears to be linked to the rise of algal-cyanobacterial mats able to trap coarse sediment.

Coarse-grained thrombolites in the late Miocene of South-east Spain are closely associated with stromatolite fabrics in composite domes and columns up to 1.5 m high and 4 m across (Martín et al., 1993; Braga et al., 1995; Feldmann and McKenzie, 1997). They include oolitic examples in which clotted fabric is produced by irregular fenestrae up to 15 mm in size (Riding et al., 1991a, p. 123). Braga et al. (1995, Fig. 8, pp. 358–359) attributed the formation of these thrombolite fabrics to “a complex of irregular agglutination, microbial calcification, skeletal encrustation, and erosional processes.”

Logan (1961) regarded Shark Bay columns as stromatolites but recognized that the lamination is often poor, describing some as “crudely laminated with laminae of 1–10 mm. in thickness” (p. 526, pl. 1, Fig. 4). Playford and Cockbain (1976, p. 403) observed that “Hamelin Pool stromatolites range from unlaminated (thrombolites) to finely laminated; most show only crudely developed lamination.” Walter (1972, p. 64) attributed “the crude lamination of many Shark Bay stromatolites” to the thick irregular mats and coarse sediment. Logan et al. (1974, p. 154) related carbonate fabric to mat type, with thick irregular pustular mat dominated by *Entophysalis* in particular producing “unlaminated to poorly laminated” fenestral fabric, and Gebelein (1974) suggested that clotted fabric could reflect degradation of organic material. Similar Bahamian subtidal columns (Dravis, 1983) are coarse-grained and crudely laminated (Dill et al., 1986) and it has been suggested that abundant algae, including diatoms in these mats contribute to the coarse texture and poor lamination typical of both Shark Bay (Awramik and Riding, 1988) and Bahamian (Riding et al., 1991b) columns.

*Mesozoic-Cenozoic thrombolites:* Thrombolites are also common in the mid-late Jurassic (e.g., Leinfelder et al., 1993; Parcell, 2002; Kopaska-Merkel, 2003; Mancini et al., 2004), often in association with sponges and stromatolites in deeper water (e.g., Jansa et al., 1988; Leinfelder et al., 1994, p. 37; Dromart et al., 1994) and with corals in shallow-water (e.g., Bertling and Insalaco, 1998; Dupraz and Strasser, 1999; Olivier et al., 2003; Olivier et al., 2006; Helm and Schülke, 1998, 2006). They exhibit a variety of forms, including

arborescent and pendant that commonly occur as thick crusts on frame-building invertebrates, and are also closely associated with a variety of problematic encrusting organisms such as *Bacinella*, *Lithocodium*, and *Shamovella/Tubiphytes*, as well as annelids and foraminifers (Leinfelder et al., 1993, Fig. 6; Olivier et al., 2003, Fig. 4). Similar – but more often stromatolitic – crusts occur in late Neogene, including present-day, scleractinian reefs (Riding et al., 1991c; Montaggioni and Camoin, 1993; Leinfelder et al., 1993, pp. 222–224), and provide important clues to the formation of microbial carbonate microfabrics (Reitner, 1993; Reitner et al., 2000). In addition, the macrofabrics of these Mesozoic-Cenozoic examples broadly resemble those of early Palaeozoic calcified microbe thrombolites, but with significantly different skeletal components. Their microfabrics are fine-grained, with peloids and microclotted micrite (Olivier et al., 2006, Fig. 9), similar to those of many lithified microbial mat stromatolites.

*Tufa thrombolite and stromatolite* (Riding, 2000, pp. 191, 194) forms in calcifying lakes and streams as a result of cyanobacterial calcification that includes sheath impregnation and encrustation, together with calcification of associated microbes. It was compared with freshwater tufa that first led to recognition of links between stromatolites and cyanobacteria (Walcott, 1914; Roddy, 1915). These complex fabrics show considerable variety due to local differences in organisms and the extent of biocalcification and external encrustation. There are similarities between tufa stromatolites and hybrid crust stromatolites (Riding, 2008, p. 88) (Figure 4).

Kennard and James (1986, p. 498) noted that, although “poorly laminated and partially clotted microbial structures” occur on some present-day hypersaline marine shorelines (Laguna Mormona, Shark Bay) and in some lakes of various salinities (Great Salt Lake, Lake Clifton, Green Lake), in these examples “individual microbial clots are generally poorly defined” and “form an irregular, botryoidal-like, mesoscopic fabric that is unlike any of the fabrics observed by us in Lower Paleozoic thrombolites.” However, Moore and Burne (1994, pp. 23) considered that thrombolites in brackish to normal marine Lake Clifton, Western Australia, do closely resemble some early Palaeozoic examples in mesoclot shape and “the interframework of infilled fenestrae” and they pointed out that in Lake Clifton filamentous cyanobacteria (*Scytonema*) are important in thrombolite formation. Moore and Burne (1994, p. 21) noted that fine laminae, initially present in the Lake Clifton structures, are syndimentarily destroyed during mesoclot formation as carbonate precipitation continues, and also that the interframework fenestrae are intrinsic features “primarily related to the topography of the surface of the developing microbialite rather than to excavation of the structure by metazoan activity.” Great Salt Lake “algal mounds,” that consist of precipitated aragonitic framework and internal sediment (Halley, 1976, p. 439, Fig. 3), have a sub-centimetric thrombolitic fabric. Ferris et al. (1997)

suggested that thrombolitic fabrics in Kelly Lake, British Columbia, reflect a greater degree of calcification than in stromatolites.

*Post-depositional thrombolites* Aitken (1967, p. 1171) noted that thrombolite macroclots are prone to accentuation by recrystallization. This emphasizes a fundamental difference from stromatolites, whose laminae are essentially primary and not likely to be significantly enhanced by diagenesis. In contrast, clots could be significantly enhanced, e.g., by selective dolomitization, and in some cases secondarily produced, e.g., by bioturbation.

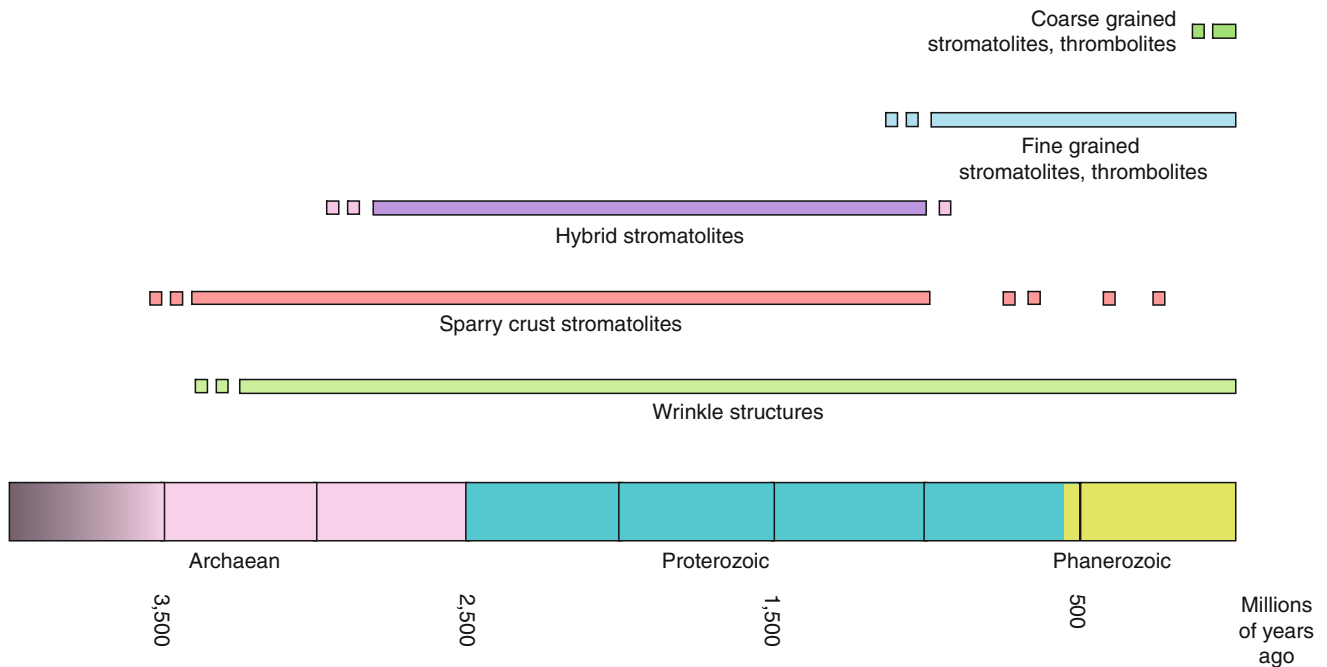
### **Stromatolites and thrombolites through time**

Microbialite types are generally long ranging. Nonetheless, they show some distinctive differences in time distribution (Figure 11). Marine sparry crusts and hybrid stromatolites are typically Precambrian, and fine-grained stromatolites and thrombolites mainly range Neoproterozoic to the present day. Wrinkle structures show the longest range, whereas lithified coarse-grained carbonate thrombolites and stromatolites are only known from the past 10 Ma or less.

### **Archaean and Proterozoic**

Stromatolites are relatively scarce in Archaean rocks until nearly the end of the eon. Their history begins with ~3.45 Ga coniform examples in the Pilbara region of Western Australia. These show fine continuous laminae (Lowe, 1980, 1983) and sparry microfabrics (Hofmann et al., 1999, Fig. 3). Their origins, and those of other Pilbara stromatolites, have been debated (e.g., Lowe, 1994, 1995; Buick et al., 1995), with recent studies supporting a biogenic origin (Hofmann et al., 1999, p. 1260–1261; Allwood et al., 2006, p. 717). Wrinkle and associated structures also suggest the presence of microbial mats in ~2,900 Ma siliclastic sediments of South Africa (Noffke et al., 2008), but these too are generally scarce. However, stromatolites are abundant in the ~2.55 Ga Campbellrand-Malmani carbonate platform of South Africa, locally forming elongate domes 10 m across and 40 m or more in length (Beukes, 1987, p. 9). In addition, these late Archaean carbonates contain distinctive “fenestrate microbialites” (Sumner and Grotzinger, 2004) consisting of millimetric to centimetric areas of light colored cement outlined by thin net-like layers (Figure 12). These have been interpreted as wispy convoluted microbial mats that were encrusted by calcite as they formed (Sumner, 1997a, b).

Large, often decametric, stromatolites are also conspicuous components of Proterozoic carbonate platforms (e.g., Grotzinger, 1986, p. 833; Petrov and Semikhatov, 2001, Fig. 6, p. 269). Where they are well preserved, they often show interlamination of sparry and micritic layers (e.g., Sami and James, 1996, p. 217). These dark-light layers that appear to represent alternations of lithified mat and abiogenic crust, are typical of “hybrid stromatolites” and are well seen in some *Conophyton* and *Baicalia* (Riding,



**Microbialites, Stromatolites, and Thrombolites, Figure 11** Approximate time distributions of major categories of marine microbialites. Coarse agglutinated mats are mainly Neogene. Fine-grained mats and thrombolites are mainly Neoproterozoic and Phanerozoic. Marine “sparry” and “hybrid” crusts are mainly Archaean and Proterozoic. Wrinkle structures range Archaean to present-day. For some possible controls, see [Figure 14](#).

2008). Such incorporation of thin abiogenic sparry crusts appears to have contributed significantly to the size and relief of stromatolites throughout the Palaeo- and Mesoproterozoic. During the same period, extensive sheets of very small “microdigitate” stromatolites, typically <5 mm wide and <20 mm high (Hoffman, 1975, p. 262) were common in shallow peritidal environments ([Figure 13](#)). These “tufas” have been interpreted as essentially abiogenic (Grotzinger and Read, 1983).

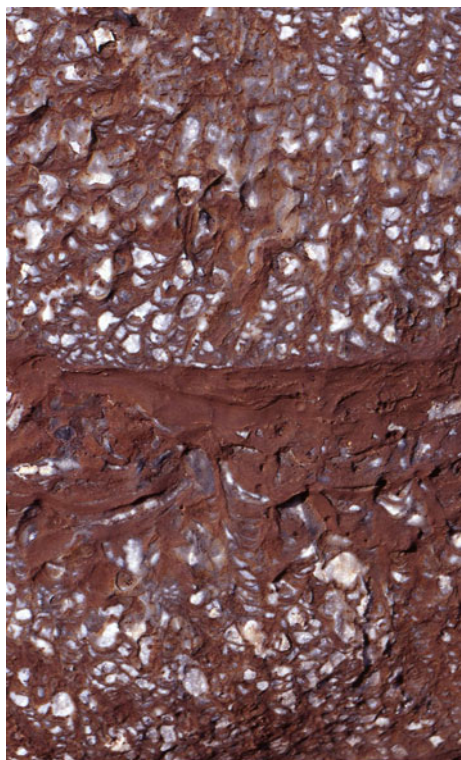
An important control on Archaean-Proterozoic stromatolite formation was gradual decline in seawater carbonate saturation state (Grotzinger, 1989b; Grotzinger and Kasting, 1993). This progressively reduced stromatolite abundance (Grotzinger, 1990) and mediated a long-term trend from sparry crust to micritic carbonate sediments (Grotzinger and Kasting, 1993; Kah and Knoll, 1996). Transition to carbonate mud-dominated platforms ~1,400–1,300 Ma ago (Sherman et al., 2000) preceded the appearance of sheath-calcified cyanobacteria ~1,200 Ma ago (Kah and Riding, 2007). This significant transition, which led to Neoproterozoic development of calcimicrobial thrombolites (Aitken and Narbonne, 1989; Turner et al., 1993, 2000a, b), could reflect induction of CO<sub>2</sub>-concentrating mechanisms (CCM) in cyanobacteria in response to fall in CO<sub>2</sub> levels below a threshold near ten times present-day levels (Riding, 2006) ([Figure 14](#)). CCMs are responses to reduced availability of inorganic carbon for photosynthesis, and in cyanobacteria include active bicarbonate uptake that

locally increases sheath pH, promoting calcification (Merz, 1992). Calcified filaments, such as *Girvanella*, altered microbial carbonate fabrics, disrupting stromatolite layering and promoting thrombolitic macro-clotted fabric. In subtidal environments, Neoproterozoic stromatolites are commonly interlayered with thrombolites with filamentous, clotted, and spongy “cellular” fabrics (Aitken and Narbonne, 1989) comparable with those of Cambro-Ordovician thrombolitic bioherms (Turner et al., 1993; 1997, p. 441, 449; 2000a, [Figs. 6e, 8h](#) and i).

### Stromatolite decline

Stromatolites show long-term decline in abundance that may have commenced as early as the Palaeoproterozoic (Grotzinger, 1990) and is still observed in the Phanerozoic. Fischer (1965) suggested that decline since the Ordovician could reflect both reduction in carbonate saturation and competition by eukaryotes. Competition was subsequently emphasized when it appeared that marked late Proterozoic fall in stromatolite morphotypic diversity coincided with metazoan evolution (Awramik, 1971), but inception of decline prior to the appearance of metazoans implicates reduction in saturation state as the major influence (Grotzinger, 1990). It was also suggested that Cambrian thrombolites reflected disruption of stromatolites by burrowing organisms (Walter and Heys, 1985, pp. 150–151). However, Cambrian-Ordovician thrombolite fabrics are dominated by calcimicrobes that resist disruption (Kennard and James, 1986, p. 494) and





**Microbialites, Stromatolites, and Thrombolites,**  
**Figure 12** Fenestrate microbialite. Meshwork of large fenestrae (white) outlined by thin curved dark layers. Late Archaean Campbellrand-Malmani platform, South Africa. Width of field  $\sim 16$  cm.



**Microbialites, Stromatolites, and Thrombolites,**  
**Figure 13** Microdigitate stromatolite, silicified after carbonate. Wumishan Formation, Mesoproterozoic,  $\sim 25$  km north of Beijing, China. Width of view  $\sim 25$  cm.

it has since been recognized that thrombolites appeared in the Neoproterozoic (Aitken and Narbonne, 1989), and possibly  $\sim 1.9$  Ga in the Palaeoproterozoic (Kah and Grotzinger, 1992).

This leaves the question of the significance of trends in stromatolite diversity. Stromatolite shape reflects original

synoptic relief, determined by accretion rate relative to adjacent sediment (Figure 15). Low relative accretion rate results in low relief that makes stromatolites more prone to lateral incursion by sediment, thereby fostering complex shapes such as digitate forms (Figure 16). In contrast, high relative accretion rate results in high relief and simple shapes, such as domes and cones. Consequently, although mid-Proterozoic increase in morphotypic diversity, e.g., in branched stromatolites, has been regarded as a proxy for abundance, it more likely reflects low synoptic relief due to reduced relative accretion rate. Paradoxically, therefore, increased diversity could be sign that stromatolite growth was in decline due to reduced microbial growth and/or reduction in syndimentary lithification.

### Snowball Earth

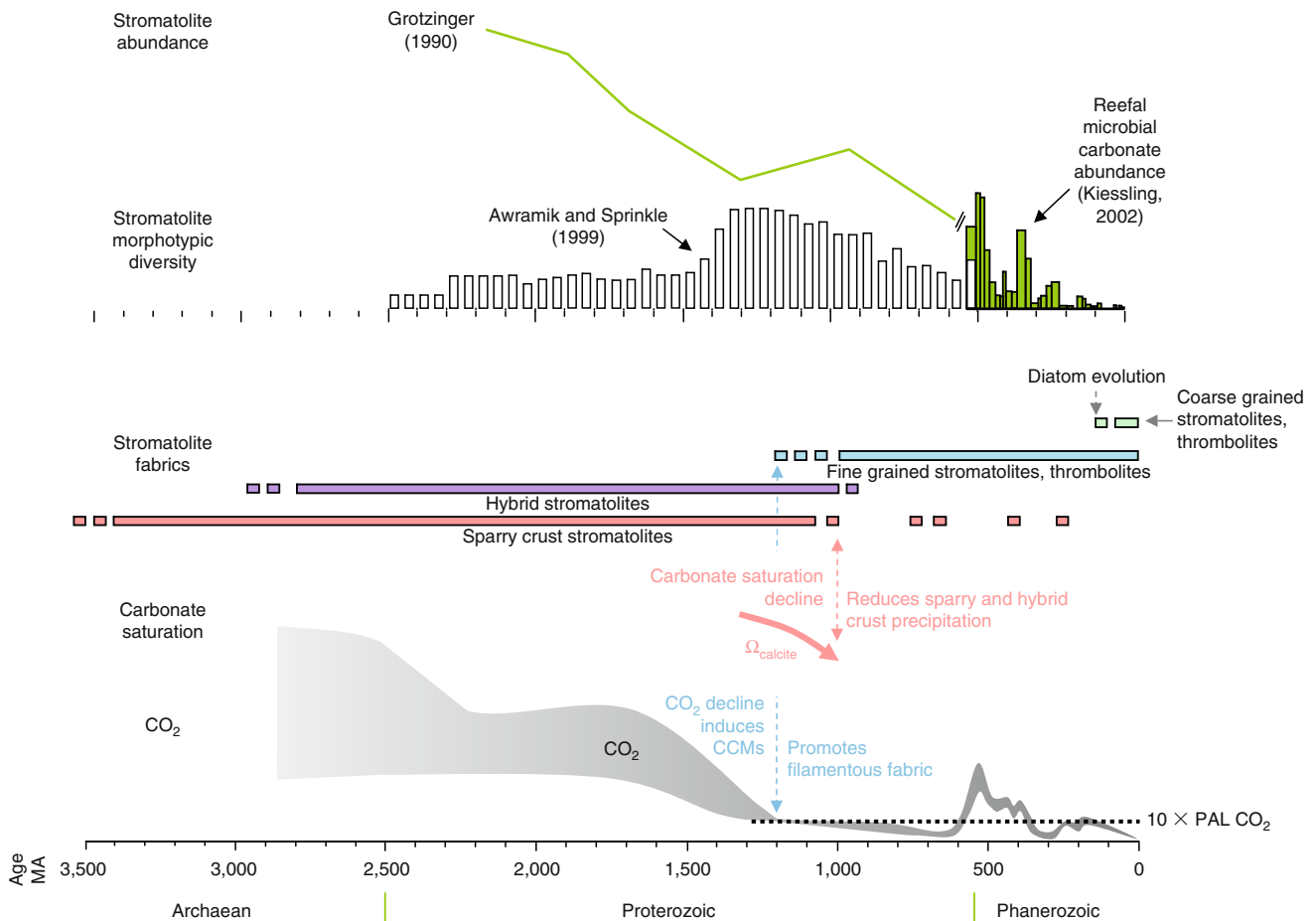
The prolonged warm Mesoproterozoic interval (Jenkins, 2003) was followed by Neoproterozoic (Sturtian,  $\sim 0.7$  Ga Ma, Walter et al., 2000; Marinoan,  $\sim 0.635$  Ga, Bodiselsch et al., 2005) glaciations. Lower temperature and  $p\text{CO}_2$  levels would have decreased seawater saturation state, hindering microbial calcification generally. Cooling would also have favored diffusive entry of  $\text{CO}_2$  into cells and therefore may have slowed CCM development, further reducing cyanobacterial calcification. Nonetheless, microbialites are locally conspicuous in Cap Carbonates that immediately follow glacial deposits (e.g., Hoffman and Schrag, 2002; Corsetti and Grotzinger, 2005). Cap Carbonates have been suggested to reflect precipitation from seawater highly saturated for carbonate minerals as a result of alkaline upwelling and enhanced terrestrial weathering (Grotzinger and Knoll, 1995; Hoffman and Schrag, 2002). In the  $\sim 600$ – $700$  Ma Noonday Dolomite of California, narrow laterally amalgamated stromatolites define tubes of intervening detrital sediment fill (Figure 17). The overall organization of some Cambro-Ordovician *Favosamaceria* thrombolites (Shapiro and Awramik, 2006) resembles these “tubestones” (Corsetti and Grotzinger, 2005, p. 360).

Following Neoproterozoic “snowball” glaciations, global warming and  $\text{O}_2$  rise could have reactivated CCM development, and rising temperature, calcium (Brennan et al., 2004), and  $p\text{CO}_2$  (Berner and Kothavala, 2001) levels would have increased seawater saturation state, stimulating microbial calcification (Riding, 2006). This favored microbialite resurgence, and dendrolites, thrombolites, and stromatolites all became widespread in the early Cambrian (Rowland and Shapiro, 2002) (Figure 18).

### Phanerozoic

#### Secular distribution

Both reefal microbial carbonates (Kiessling, 2002, Fig. 16) and calcified cyanobacteria (Arp et al., 2001) decline in abundance during the Phanerozoic, but this trend shows marked fluctuations. They are common in the late Cambrian-early Ordovician and late Devonian-early Mississippian, and scarce during the Cenozoic.



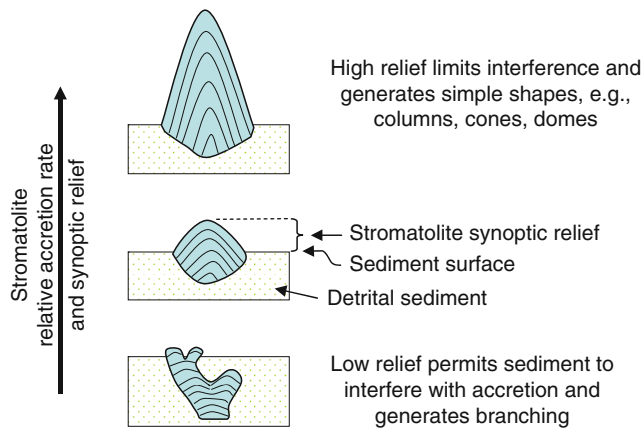
**Microbialites, Stromatolites, and Thrombolites, Figure 14** Some secular trends and possible controls on microbial carbonate developments. Proterozoic stromatolite abundance (Grotzinger, 1990) and morphotypic diversity (Awramik and Sprinkle, 1999), together with Phanerozoic reefal microbial carbonate abundance (Kiessling, 2002). These suggest overall long-term decline for at least the past 1,000 Ma. Reduction in both Sparry Crust and Hybrid stromatolites  $\sim 1,000$  Ma ago may reflect decline in seawater carbonate saturation (Grotzinger, 1990). Stromatolite-like sparry crust occurs sporadically in the Phanerozoic, particularly in evaporite basins (Pope et al., 2000). Increase in thrombolites  $\sim 1,200$ – $1,000$  Ma ago could reflect development of cyanobacterial sheath calcification, reflecting inception of  $\text{CO}_2$ -concentrating mechanisms (CCMs) as  $\text{CO}_2$  levels declined to  $\sim 10$  times present atmospheric level (PAL) (Riding, 2006). Inferred Proterozoic  $\text{CO}_2$  trend based on Sheldon (2006), Kah and Riding (2007), Hyde et al. (2000) and Ridgwell et al. (2003). Phanerozoic  $\text{CO}_2$  trend from Berner and Kothavala (2001, Fig. 13). Threshold for CCMs ( $10 \times \text{PAL } \text{CO}_2$ ) based on Badger et al. (2002). Late Neogene inception of Coarse agglutinated stromatolites and thrombolite could in part reflect incorporation of diatoms into microbial mats and also generally low values of seawater carbonate saturation.

Fischer (1965) suggested that eukaryote competition and reduction in carbonate saturation state contributed to stromatolite decline from the Ordovician onward.

**Carbonate saturation:** Comparison with seawater saturation state for  $\text{CaCO}_3$  minerals calculated from modeled seawater and  $\text{CO}_2$  values shows broad positive correspondence with peaks of microbial/cyanobacterial carbonate abundance during much of the Palaeozoic and Mesozoic (Riding and Liang, 2005), supporting Fischer (1965). Lack of correspondence during the interval  $\sim 120$ – $80$  Ma ago (when calculated saturation ratio is high but microbial carbonate abundance was low) could reflect removal of carbonate deposition by pelagic plankton that significantly reduced actual saturation state.

**Competition:** The role of metazoan competition in late Proterozoic and early Palaeozoic stromatolite history is uncertain, and it is debatable whether metazoan grazing significantly affected stromatolite development (Pratt, 1982b) so long as carbonate saturation was high enough to ensure extensive early lithification of microbial mats. Nonetheless, it seems likely that from at least the mid-Ordovician onwards, overgrowth by skeletonized algae and invertebrates inhibited the formation of domical stromatolites and thrombolites. Subsumed within complex reef structures, microbial carbonates would instead have formed patchy and irregular crusts on and around skeletal organisms. Nonetheless, they were often important reef components (Kiessling, 2002, Fig. 16).





### Microbialites, Stromatolites, and Thrombolites,

**Figure 15** Hypothetical interpretation of the significance of stromatolite shape. Shape is determined by synoptic relief that in turn reflects accretion rate of the stromatolite surface relative to adjacent sediment. In this view, enhanced stromatolite accretion generates high relief and simple shapes, such as columns, cones, and domes. In contrast, relatively low stromatolite accretion results in low relief. As a result, the stromatolite surface is prone to overlap by adjacent sediment, generating branching and irregular margins.



### Microbialites, Stromatolites, and Thrombolites,

**Figure 16** *Gymnosolen*, digitate stromatolite, Dali, China, ~1.0 Ga.

*Disaster biotas*: The concept of stromatolite decline resulting from algal-metazoan diversification (Fischer, 1965; Garrett, 1970; Awramik, 1971) has also given rise to that of stromatolite resurgence in the aftermaths of mass extinctions (Schubert and Bottjer, 1992, p. 885). In this view, if metazoans can competitively exclude microbial carbonates then temporary reduction in metazoan abundance and diversity in the immediate aftermaths of mass



### Microbialites, Stromatolites, and Thrombolites,

**Figure 17** Laterally amalgamated columnar stromatolites (light color) separated by slightly darker tubular fills of detrital sediment. Noonday Dolomite, late Neoproterozoic, Mesquite Mountains, California, USA.

extinctions should permit temporary increase in microbial carbonates. Schubert and Bottjer (1992, 1995) interpreted early Triassic stromatolites as “post-mass extinction disaster forms.” However, whereas microbial carbonate reefal abundance also increased noticeably in the aftermath of late Devonian extinction, it did not increase following end-Ordovician, end-Triassic, and end-Cretaceous mass extinctions (Riding, 2006). Nonetheless, it is likely that in these situations, unconstrained by algal and invertebrate reef organisms, microbial mats were able to develop distinctive morphologies, and large domes, columns, and digitate structures have been reported, e.g., at the Permian-Triassic boundary in Sichuan, China (Kershaw et al., 1999).

*Thrombolites*: Flügel (2004, p. 378) suggested that thrombolite abundance also declined after the Cambrian, although they were still locally conspicuous, e.g., in the Silurian (Kahle, 2001), Devonian (Shapiro, 2000, p. 166), Mississippian (Webb, 1987, 2005), and near the Permian-Triassic transition (Kershaw et al., 1999; Ezaki et al., 2008). Thrombolites have been widely reported in the mid-late Jurassic (see Mesozoic-Cenozoic thrombolites, above), broadly coincident with the last major peak of abundance of calcified marine cyanobacteria (Arp et al., 2001, Fig. 3d).

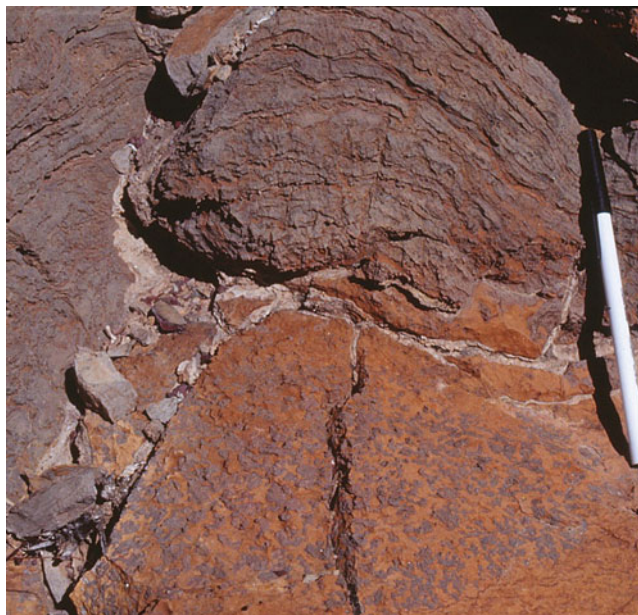
*Evaporite stromatolites*: In addition to metazoan extinction, localized increase in carbonate saturation in evaporite basins will favor microbialite development. Pope et al. (2000, p. 1139) noted that isopachously laminated stromatolites, which they considered to be dominantly abiogenic, are well developed in association with major evaporite successions and cited examples in the Proterozoic and Phanerozoic, including the Silurian Michigan Basin of North America and the late Permian Zechstein Basin of northern Europe (Pope et al., 2000,



Figs. 7, 9). These conditions therefore marked temporary returns to conditions that promoted formation of the sparry and hybrid crusts typical of the Archaean and early Proterozoic.

#### Neogene coarse-grained thrombolitic stromatolites

Well-known present-day examples of columns and domes occur in wave- and current-swept environments at Shark Bay (Logan, 1961) and the Bahamas (Dravis, 1983; Dill



**Microbialites, Stromatolites, and Thrombolites, Figure 18** Late Cambrian (Trempealeuan) thrombolite overlain by stromatolite, Smoky Member, Nopah Fm, Dry Mountain, California, north-western Death Valley National Park, USA. Pen ~15 cm long.

et al., 1986; Riding et al., 1991b; Reid et al., 2000). They accrete bioclastic and ooid sand, and have crudely layered (Logan, 1961) and thrombolitic (Aitken, 1967, p. 1171) fabrics. Several factors conspire in their formation: water movement, mat community, and seawater chemistry. High-energy grainy conditions facilitate trapping by lifting sand to the accreting mat surface, and simultaneously deter overgrowth by reefal encrusters (Dill et al., 1989, p. 10). At Shark Bay, seasonal hypersalinity also limits competitors. Together with rapid accretion this allows decimetric, and locally metric, columns to develop. Accretion is high because the mats are thick and soft, with abundant EPS (Decho et al., 2005). In addition to cyanobacteria, they contain diatoms and filamentous green algae that enhance trapping ability (Awramik and Riding, 1988; Riding et al., 1991b). The upper mat remains soft and sticky because it is largely uncalcified, and the early lithification necessary to support these large columns mainly occurs in, or below, the lower part of the mat. Microbial lithification by sulfate reduction (Visscher et al., 2000) is limited to very thin micritic crusts (Reid et al., 2000), cyanobacterial sheaths are uncalcified (Reid et al., 2000, p. 992), and calcification of algal filaments mainly occurs in cavities (Dravis, 1983; Whittle et al., 1993, p. 224). Formation of these coarse-grained thrombolitic stromatolites is therefore largely due to their thick, soft, EPS-rich mats. These in turn reflect a combination of Cenozoic circumstances: (i) seawater saturation state that is too low for cyanobacterial sheath impregnation, but permits early lithification and (ii) the presence of fast-growing microalgae, such as diatoms, which – from a geological standpoint – are relative newcomers to mat communities (Figure 14). Coarse-grained thrombolitic stromatolite domes and columns are well developed in the late Miocene of South-east Spain (Riding et al., 1991a; Braga et al., 1995; Feldmann and McKenzie, 1997) (Figure 19) but are not known in older rocks.



**Microbialites, Stromatolites, and Thrombolites, Figure 19** Coarse-grained, oolitic, composite leiolite-stromatolite-thrombolite domes, late Miocene (Messinian), Joyazo, Almería, South-east Spain. Red pen, lower left, ~15 cm long.

## Summary

During the Archaean and much of the Proterozoic, both microbial mat growth and abiogenic precipitation were involved in stromatolite development that, locally, was particularly abundant from the latest Archaean to early Neoproterozoic (Grotzinger and Knoll, 1999). The combination of these biogenic and abiogenic factors was responsible for the rapid growth that enabled stromatolites, ranging from extensive small microdigitate sheets (Grotzinger and Read, 1983) to decametric domes (e.g., Hofmann, 1998, pl. 8a), to dominate carbonate platforms for 1,500 million years. Well-preserved stromatolites with dark-light lamination (Sami and James, 1996; Petrov and Semikhatov, 2001) suggest that lithified mat growth alternated with abiogenic sparry crust precipitation on a millimetric scale to form inter-layered hybrid crust stromatolites (Riding, 2008).

Decline in sparry crusts and hybrid stromatolites ~1,000 Ma ago probably largely reflects reduction in seawater saturation (Grotzinger, 1990). This change also broadly coincided with the inception of cyanobacterial sheath-calcification in the Mesoproterozoic. This important development may reflect induction of CO<sub>2</sub>-concentrating mechanisms (CCM) to assist photosynthetic carbon uptake as CO<sub>2</sub> levels declined (Riding, 2006). It transformed microbialite fabrics, and calcified microbe thrombolites and stromatolites with filamentous fabrics were conspicuous in shallow subtidal environments until the early Ordovician. Subsequently, stromatolites and thrombolites were widely subsumed within algal-invertebrate reefs. In these closely packed habitats, they lacked space to develop classic dome and column morphologies, and instead mainly formed reefal crusts and irregular masses. Only where competitors were environmentally excluded, or absent (as in mass extinction aftermaths), did microbial domes briefly develop extensively.

Both competition and declining carbonate saturation limited the abundance of marine microbialites from the Ordovician onwards (Fischer, 1965), and they are much less widespread and abundant in the Cenozoic than in the Palaeozoic. But microbialite communities have the ability to reinvent themselves. Diatoms together with other microalgae have significantly enhanced mat trapping ability. In environments where reefal overgrowth is limited, and coarse grains abundant, these soft mats can create large coarse-grained columns, as at Shark Bay and Lee Stocking Island. Internally these have distinctive crudely layered thrombolitic stromatolite fabrics (Aitken, 1967); in external shape, they closely resemble some Palaeoproterozoic stromatolites.

Microbialites have changed significantly during their extraordinarily long history in shape, size, fabrics, and abundance. They have responded to microbial evolution, to environmental changes that have affected both carbonate sedimentation and microbial metabolism, and to the evolution of other organisms. To add to this complexity, whereas stromatolites are essentially lithified microbial mats, they may be intimately associated with abiogenic crusts.

Microbialites archive important geobiological changes in atmospheric composition, seawater chemistry, mat evolution, and biotic interaction. Their study continues to offer many challenges and opportunities.

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## Cross-references

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## MICROBIAL-METAL BINDING

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### Definition

The accumulation of metal cations to microbes, largely through adsorptive processes to the outer cellular surfaces.

### Overview

All bacteria have low isoelectric points (below pH 2 in most cases), and consequently, they interact with soluble metal cations and have them intimately associated with their surfaces (Harden and Harris, 1953). Considering their ubiquity in the near-surface environment and their characteristically large surface area-to-volume ratios, bacteria can have a significant influence on metal mobility and speciation in these settings.

Some bound metals (e.g., Ca and Mg) serve the purpose of stabilizing the negative charges of the anionic functional groups, and thus are relatively “fixed” into place, while other metals are much more exchangeable and provide a temporary positive charge to counter the negative charge induced by the deprotonation of the cell’s surface functional groups (Carstensen and Marquis, 1968). The strength of the metal–microbial bond is quantified by the surface complexation/binding constant ( $K_M$ ), where M refers to the specific metal of interest. The greater its surface complex formation constant, the less likely