

# Microbialites: Organosedimentary Deposits of Benthic Microbial Communities

ROBERT V. BURNE

*Baas Becking Geobiological Laboratory, PO Box 378, Canberra A.C.T. 2601, Australia*

LINDA S. MOORE

*Department of Microbiology, University of Western Australia, Nedlands W.A. 6009, Australia*

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Microbialites are organosedimentary deposits formed from interaction between benthic microbial communities (BMCs) and detrital or chemical sediments. Processes involved in the formation of calcareous microbialites include trapping and binding of detrital sediment (forming microbial boundstones), inorganic calcification (forming microbial tufa), and biologically influenced calcification (forming microbial framestones). The latter process is probably the result either of chemical changes associated with photosynthesis, or the nucleation of crystals on the polysaccharide-bearing sheaths of the microorganisms. Elevated  $\delta^{13}\text{C}$  values in these crystals may reflect isotopic fractionation associated with the biological setting of the mineralization. Microbialites contrast with other biological sediments in that they are generally not composed of skeletal remains. Once formed, the primary framework of the microbialite becomes the locus of secondary cementation. To distinguish them from bioherms and biostromes of skeletal origin, microbialite buildups are termed "microbial lithoherms" or "microbial lithostromes". The morphogenesis of these structures is a function of environmental influence, biologic and ecologic controls, and processes and rates of lithification. The internal structures of microbialites are best identified by descriptive terms that do not imply a particular origin. Terms used to describe internal structures of microbialites include stromatolitic, thrombolitic, oncotic (concentrically laminated), spherulitic, and cryptic. Consideration of the term "stromatolite" shows that it is currently used in at least three distinct ways: to refer to products of microbial sedimentation in general, to describe laminated structures of probable microbial origin, or to describe discrete laminated lithified bodies. We recommend that the term be restricted to refer to microbialites with an internal structure of fine, more or less planar laminations.

Assessment of published distinctions between thrombolites (microbialites characterised by a clotted internal structure) and stromatolites in the light of some present-day Australian occurrences shows that thrombolites are not always constructed by coccus-dominated BMCs, nor are stromatolites always constructed from filament-dominated BMCs. Although we have

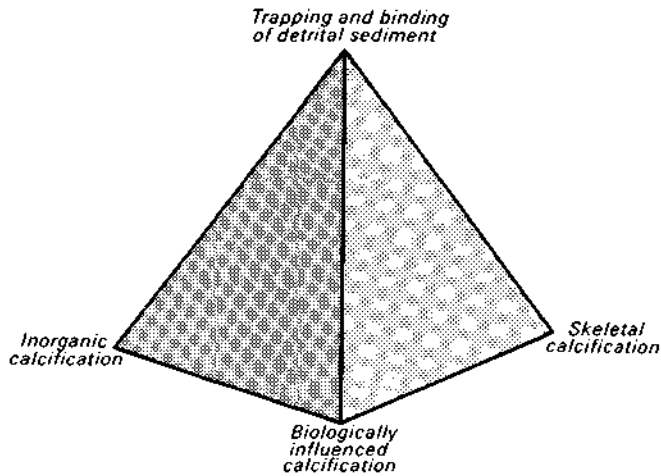
observed examples of modern thrombolitic structures forming where biogenically influenced calcification dominates, and stromatolitic structures forming where trapping and binding of either detrital sediment or seasonally precipitated carbonate dominates, both structures could be produced by other processes. It is hoped that the ability to differentiate between the processes involved in the genesis of microbialites will lead to a better understanding of such factors as the morphogenesis of microbialites, their evolution through geologic time, and their potential as tools for biostratigraphic correlation.

## INTRODUCTION

Living benthic microbial communities (BMCs) are complex ecological associations of photosynthetic prokaryotes, eukaryotic microalgae, and chemoautotrophic and chemoheterotrophic microbes (Bauld, 1986). They have evolved from prokaryotic ancestors that formed the first macroscopic record of life on Earth (Walter, 1983). Although the microbes themselves may be preserved as fossils, particularly in cherts, the geologic record of BMCs generally results from their interaction with sediments to form organosedimentary structures. Indeed, structures of this type were the only macroscopic structures produced by organisms for 3 billion years after the appearance of life on the planet. They declined in relative importance with the rise of higher life forms during the Phanerozoic, but they have been locally significant throughout geologic time. BMCs may interact with sediments in three main ways: as thin films or veils, in which the BMC is dispersed through loosely consolidated detrital sediment; as mats in which there is an intimate association of a cohesive BMC and associated trapped and bound detrital sediment; and as indurated masses (commonly of limestone) produced by mineralization closely associated with the BMC. For all these deposits we propose the term *Microbialite*.

## Definition

*Microbialites are organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and*



**FIGURE 1**—Primary processes of mineralization involved in microbialite deposition expressed as a four-way continuum. Processes of secondary cementation would be superimposed on these.

*binding detrital sediment and/or forming the locus of mineral precipitation.*

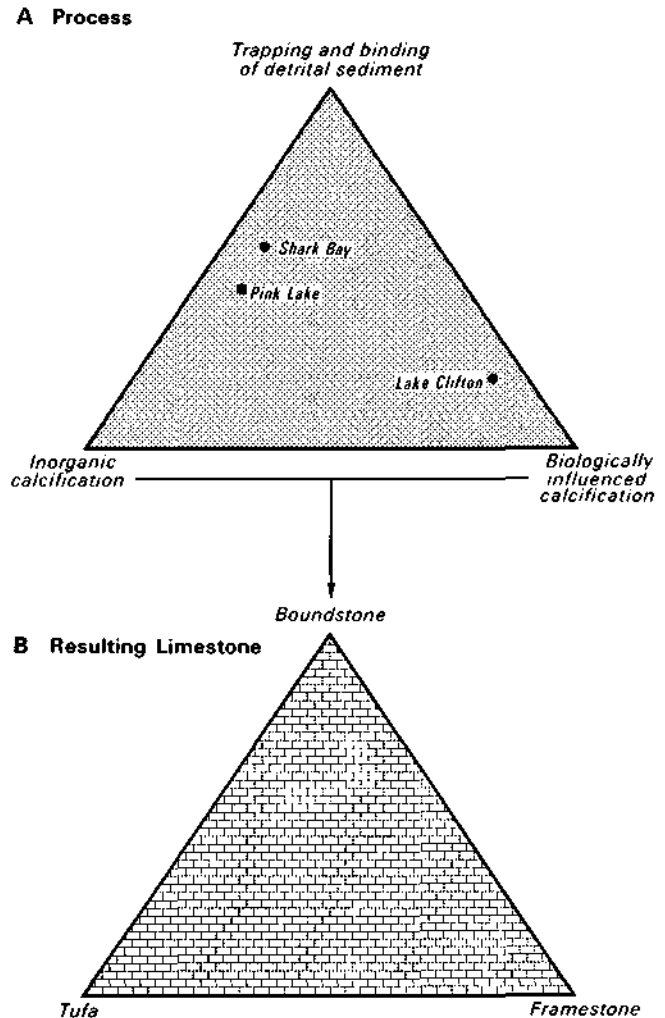
Calcareous microbialites have been traditionally classified as algal limestones (Johnson, 1961) because they are produced from BMCs, which commonly contain cyanobacteria, organisms that until recently were termed blue-green algae (Stainer, 1977, 1982). This classification has masked an important distinction: True algal limestones are largely constructed from the skeletal remains of calcareous algae, whereas calcareous microbialites generally are not.

Aitken (1967) recognized the need to distinguish rocks composed of the remains of skeletal calcareous algae from those formed by noncalcareous algae (including cyanobacteria). He proposed the term *cryptalgal sedimentary rocks* for rocks believed to have originated through the sediment-binding and/or carbonate-precipitating activities of nonskeletal algae, the designation "cryptalgal" being used because the influence of algae on the rock is more commonly inferred than observed. Although this term has been widely adopted, we suggest it be abandoned in favor of the term microbialite, because cyanobacteria are no longer regarded as algae, and other microbial components are present alongside cyanobacteria in most microbial communities.

This paper examines some of the processes that may give rise to microbialites, and describes the essential characteristics of the resultant deposits. We restrict our treatment to calcareous microbialites.

#### PROCESSES THAT FORM MICROBIALITES

The four major processes involved in the formation of calcareous microbialites are trapping and binding of detrital sedimentary particles, inorganic calcification, biologically influenced calcification, and skeletal calcification. These processes are described below. Many microbialites have a composite origin, the relative importance of each of the various processes in forming individual examples may be portrayed by reference to

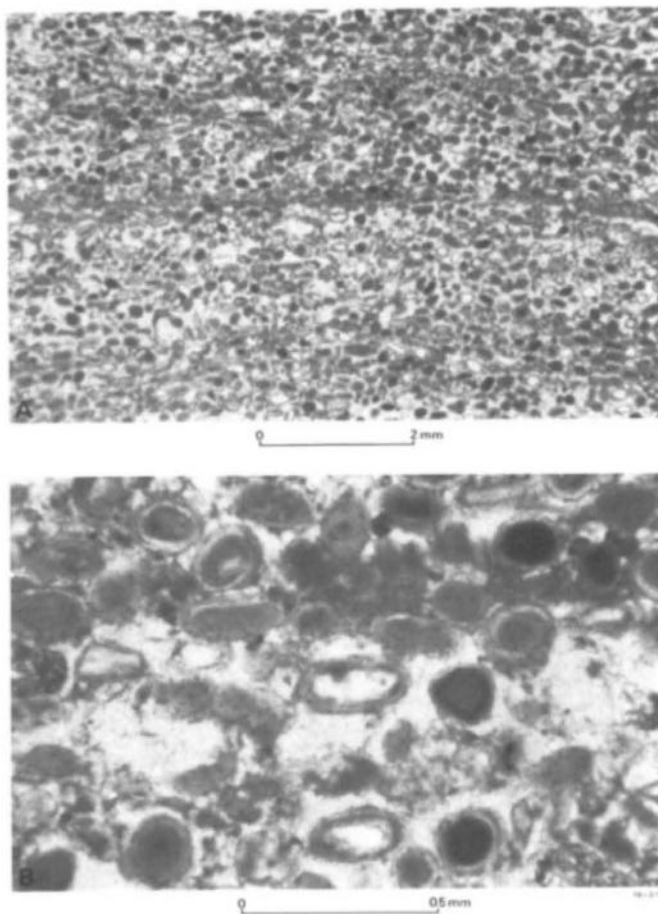


**FIGURE 2**—A) The three common processes of microbialite mineralization expressed as end members of a three-way continuum. Plotted points indicate the inferred genesis of some of the microbialites referred to in the text. B) Suggested nomenclature for limestones formed by the three primary processes shown in A.

a pyramidal diagram with each of the four processes as end members (Fig. 1, contrast with the diagram of Hoffman, 1973). As we will demonstrate, the skeletal end-member need not be considered for most microbialites, and the pyramidal diagram may therefore be reduced to a triangular plot in these cases (Fig. 2, contrast with the diagram of Riding, 1977).

As Kennard and James (1986) have pointed out, microbial limestones often defy description by schemes of limestone classification such as those of Folk (1962), Dunham (1962), and Embry and Klovan (1971). We suggest the following three names be used to differentiate between microbial limestones formed by each of the processes mentioned above (Fig. 2):

**Microbial Boundstones**—formed principally by microbial trapping and binding of detritus



**FIGURE 3—A)** Thin section of a microbialite formed by trapping and binding of detrital grains in conjunction with primary cementation; Carbla Point, Hamelin Pool, Shark Bay. **B)** Enlargement of Figure 3A. Note the abundance of detrital peloids and ooids, and the turbid opaque cements, possibly the result of biologically associated calcification within the coccoid-dominated BMC associated with these structures. Mottled white areas are impregnating resin.

**Microbial Tufa**—formed when microorganic material is incorporated during inorganic precipitation of carbonate.

**Microbial Framestones**—composed of a framework formed either as a result of biologically influenced calcification or (rarely) from microbial skeletal material (Skeletal Microbial Framestones)

Once formed, the microbialite may become the locus of passive lithification with the possible formation of a variety of carbonate cements. This cementation may commence soon after deposition, and continue through diagenesis after burial of the structure. The exact nature of the cement will depend on the post-depositional environment (Bricker, 1971; Schneidermann and Harris, 1985). The cements may either overgrow the primary crystals or they may form distinct crystal types that line and fill primary fenestrae. Continued precipitation of secondary cements and diagenetic modification of the primary

framework obscure the original structure of the microbialites. The resultant limestone may preserve little of its original microbial structure (Bradley, 1929), hence Aitken's (1967) use of the term "cryptalgal".

#### Trapping and Binding of Detrital Sediment

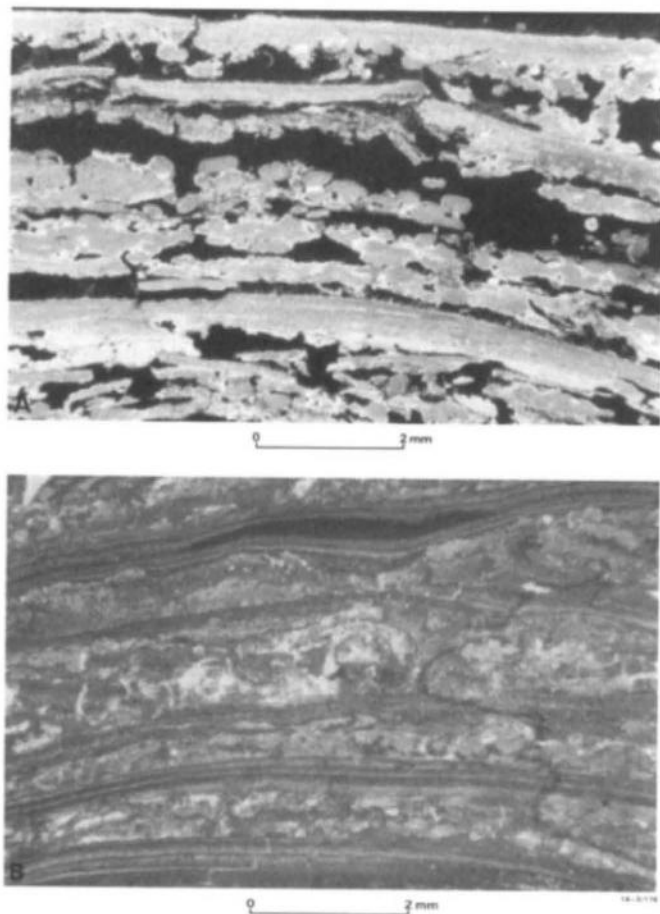
Controls on this process include the presence of a BMC capable of trapping or binding sediments, the availability of suitable detrital sediment, and the rate of supply of sediment.

The agents of trapping and binding in BMCs may include filamentous cyanobacteria, which are able to intertwine and incorporate detritus to form cohesive mat-like structures by virtue of their "sticky" surface properties, sheath hydrophobicity, and gliding motility. Similarly, coccoid cyanobacteria (which also produce mucilaginous sheaths), diatoms (some of which have either a mucilaginous coating or leave mucilaginous trails), and some eukaryotic microalgae may also contribute to the formation of microbial mats. Trapping and binding may be regulated by microbial activity, which in turn may be stimulated by sediment burial. Although difficult to prove, this would provide a mutually regulating mechanism for accumulation (Golubic, 1973). Motility of the cyanobacteria in response to diurnal variations in light intensity and longer-term upward migration at a rate sufficient to keep pace with over-all sediment accumulation are considered to be important in producing the well-laminated structure characteristic of many mat deposits (Monty, 1976). Other mats are not well laminated. The cinder mats of Abu Dhabi (Kendall and Skipwith, 1968), the crenulate mats of Spencer Gulf (Burne and Colwell, 1982), and the pustular mats of Shark Bay (Davies, 1970) are examples that have a weakly laminated or massive internal structure.

The importance of trapping and binding of detrital sediment by BMCs was first realised by Black (1933), who described the mechanical trapping of uncemented carbonate sediments in the mucilaginous sheaths of benthic cyanobacterial communities on Andros Island, Bahamas. Trapping and binding of detrital sediment are now recognised as major processes in the formation of unlithified intertidal microbial mats (Bauld, 1984; Black, 1933; Davies, 1970; Monty, 1976; Gebelein, 1969). They are also of importance in the formation of subtidal stromatolites in Hamelin Pool, Shark Bay (Logan et al., 1964; Playford and Cockbain, 1976; Playford, 1980; Burne and James, 1986), Bermuda (Gebelein, 1969), and the Exumas, Bahamas (Dill et al., 1986), where they combine with a process of early cementation to form lithified structures (Fig. 3).

#### Inorganic Calcification

Calcium carbonate is precipitated inorganically to form primary limestones in many environments, including springs, streams, waterfalls, and within caves. These deposits may be formed by evaporation of saturated solutions, but more frequently result from the loss of  $\text{CO}_2$  by degassing from supersaturated waters. Carbonate-rich ground water has a higher  $\text{pCO}_2$  than surface water in which the  $\text{pCO}_2$  is in equilibrium with that of the atmosphere. But as ground water becomes exposed to the atmosphere it loses  $\text{CO}_2$ . Re-equilibration promotes the precipitation of carbonate (Hanor, 1978; Golubic, 1973; Ferguson et al., 1982). Similar precipitation may occur



**FIGURE 4—A)** Thin section of a microbialite formed from alternating layers of trapped and bound peloids and dense plates of aragonitic micrite, interpreted as a primary precipitate. Crossed nicols. Pink Lake, Esperance Western Australia. **B)** Thin section of a microbialite considered to be an ancient analogue of that shown in Figure 4A. Note compacted structure. Amelia Dolomite, Macarthur Basin, Northern Territories, Australia.

from surface waters of high alkalinity in environments where loss of  $\text{CO}_2$  and consequent increase in pH is promoted by turbulence (e.g., waterfalls in rivers, or areas of breaking waves in marine environments), increase in temperature, or freezing.

Microbial communities favor damp environments and are associated with many areas of inorganic calcification (Scholl and Taft, 1964; Chafetz and Folk, 1982; Golubic, 1973, 1976; Pentecost, 1978, 1985; Pentecost and Riding, 1986). In these cases, the microbial population will become encrusted in the precipitating minerals, a process enhanced by the tendency of recently precipitated carbonate to become trapped on the mucilaginous surface of the microbes in the same way that detrital sediments are trapped and bound (Fig. 4). The high rate of carbonate deposition tends to bury the microbial community, which responds by either growing or gliding out of the crustal layers, only to be exposed to further burial at the surface. Seasonal variation in precipitation due to changes in water

chemistry and/or microbial growth may give rise to regular laminations within the deposits.

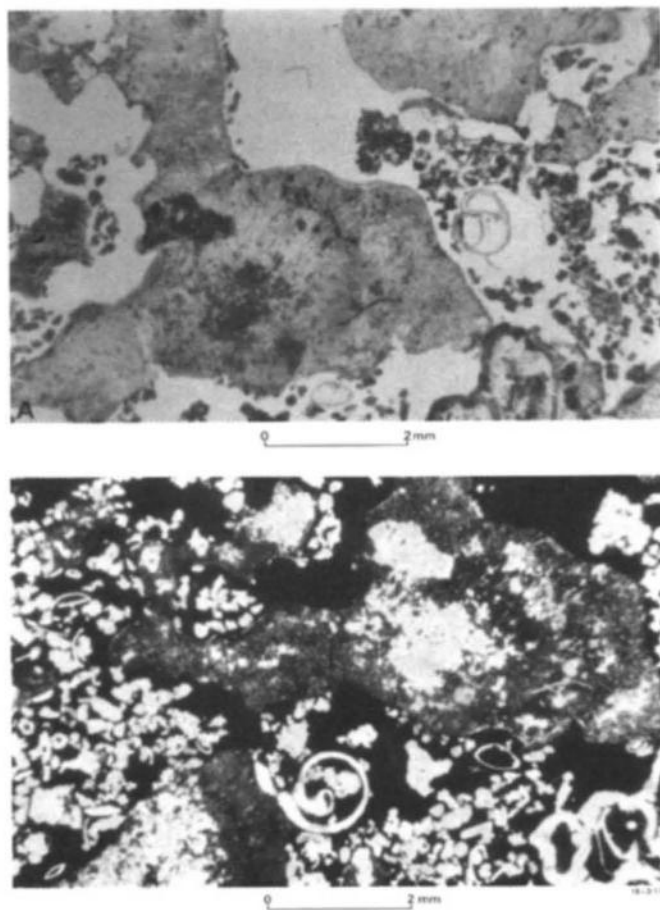
The deposits are known by a variety of terms, including tufa, travertine (a denser form), sinter, and tophus. The internal structures of tufas and travertines range from regular laminations to structures of great diversity (Chafetz and Folk, 1982; Folk et al., 1985; Walter, 1976b). The microbial community may provide a foundation for inorganic cementation and hence control for the internal structures of the tufa deposit. The microbial community may also help to establish the overall architecture of the tufa deposit, enabling the construction of the delicate structures of tufa observed at many locations worldwide, including Mammoth Hot Springs (Weed, 1889; Walter 1976b); Plitvice, Yugoslavia (Pentecost, pers. comm.); and the sea cliffs southwest of Augusta, Western Australia. According to Pentecost and Riding (1986) *Phormidium incrustatum*, *Schizothrix calcicola*, and to a lesser extent *Rivularia* are commonly found in the surface layers of tufa. Remains of the BMC may be preserved deeper in the tufa deposit, but more commonly this zone is one in which there is decay of both the original microbial community and other encrusted organic material. The destruction of this material contributes to the porosity that is characteristic of these deposits (Golubic, 1973; Pentecost, 1978).

#### Biologically Influenced Calcification

It has long been recognized that cyanobacteria participate in processes of calcification (e.g., Roddy, 1915). Black (1933) described the formation of carbonate cements associated with *Scytonema* filaments in the higher areas of the Andros marshes. Monty (1965, 1967, 1976) further described the precipitation of calcium carbonate within *Scytonema* sheaths and discussed the relative importance of this process and that of sediment trapping and binding. Golubic (1983) documented calcification in *Entophysalis* mats at Shark Bay. Golubic and Campbell (1981) described biogenically formed concretions associated with marine *Rivularia*. Thus, the precipitation of a mineral phase in a habit and environment determined by a BMC, with crystals nucleating on and within the biomass, is recognized as an important process that can eventually form primary limestones of high initial strength and porosity.

Pentecost and Riding (1986) have reviewed the subject of cyanobacterial calcification. They conclude that several cyanobacteria exhibit specificity for calcification, but none is an obligate calcifier. It has been suggested that, in the geological past, important rock-forming organisms such as *Girvanella*, *Epiphyton*, and *Renalcis* were microbes that possessed calcareous skeletons. However, Pratt (1984) concluded that *Epiphyton* and *Renalcis* were not deliberately precipitated skeletons of genetically distinct organisms but were the result of post-mortem calcification within colonies of coccoid cyanobacteria. Riding (1977) suggested that the cyanobacterium *Plectonema* sp. represents a recent example of *Girvanella*. This organism has a calcified sheath, but this is due to impregnation with micrite-sized crystals of Mg-calcite. It seems likely that the organized structures found in *Girvanella*, *Renalcis*, *Epiphyton*, and the like, were in fact formed from biologically influenced, non-skeletal calcification.

What, then, is the nature of this process? Pentecost and Riding (1986) found that most calcifying cyanobacteria have



**FIGURE 5—A)** Thin section showing biologically associated calcification of filamentous BMC forming irregular lithified areas (meso-clots) interspersed with cavities containing detrital sediment of peloids and shells. White areas are impregnating resin. Field Station Transect, Eastern side of Lake Clifton, Western Australia. **B)** Similar view to Figure 5A but under crossed nicols. Note growth of carbonate crystals within the felted mass of calcified filaments.

gelatinous sheaths 2–10  $\mu\text{m}$  thick. Exceptions are *Scytonema* and *Plectonema*, which have non-gelatinous sheaths. Most calcifying forms belong to the Oscillatoriaceae, including *Plectonema*, *Schizothrix calcicola*, and *Phormidium incrustatum*, although other groups are important, including *Scytonema hoffmannii* and *Rivularia haematites* (Monty, 1976; Pentecost and Riding, 1986). The coccoid form *Pleurocapsa* also calcifies, and Golubic (1983) has reported post-mortem calcification in *Entophysalis*. The resultant mineralization may take a variety of forms, including rhomb-like crystals within and upon the sheath, acicular crystals within the sheath, platy crystals on the sheath surface, or dendritic crystallites within and beyond the sheath. Crystal masses may surround several trichomes (Pentecost and Riding, 1986). Calcification may consist of impregnation of sheath material by crystals (which ultimately results in the formation of macaroni-like tubes) or the encrustation of sheath material to form an external crust. This process of mineralization forms molds of small intertwined and felted

groups of sheaths rather than individual filaments (Fig. 5) (Bradley, 1929).

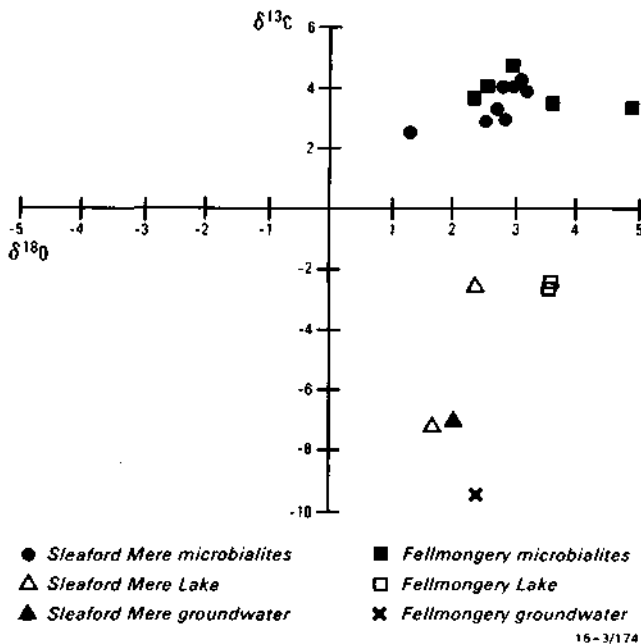
The process of calcification around elements of a microbial community is clearly biologically associated in some way. It has generally been related to photosynthesizing cyanobacteria removing  $\text{CO}_2$  from saturated waters, with consequent elevation of pH and precipitation of  $\text{CaCO}_3$  (Hassack, 1888; Bradley, 1929; Scholl and Taft, 1964; Taylor, 1975; Golubic, 1973; Halley, 1976). This process is biologically controlled, but mineralization is inorganic. Raven (1970, 1980) has demonstrated that calcification may be promoted by the ability of some plants to transport  $\text{HCO}_3^-$  ions into their structure in low-pH environments and release  $\text{OH}^-$  ions. However, Pentecost and Riding (1986) report that, although photosynthetic activity plays an important part in the calcification of eukaryotic algae, it is not an important factor in cyanobacterial calcification, because cyanobacteria have no special anatomical features to promote calcification, and because growth rates are generally low. They concede that photosynthesis may become an important factor in areas of high biomass and low water flow.

Krumbein (1979) has suggested that chemo-organotrophic bacteria may be implicated in the process of carbonate precipitation via the degradation of organic matter previously produced by photosynthesis. This process has been further discussed by Walter (1983). Other non-photosynthetic processes of biologically induced calcification have been described by Lyons et al. (1984), Dalrymple (1966), and Krumbein and Cohen (1977).

Pentecost (1985) considers that calcification may be due to the heterogeneous nucleation of carbonate cements on and within sheath material. The ionizable carboxylic acid groups contained in the polysaccharide sheaths of cyanobacteria may attract calcium ions and provide favourable sites for the nucleation of carbonate crystals. Cyanobacterial calcification of this type is therefore only partly within the influence of the organism since it requires both suitable environmental conditions favoring the precipitation of  $\text{CaCO}_3$  and the presence of organic matter such as sheath material to provide sites for crystal nucleation. A laminated deposit may form as a result of chemotaxis or thermotaxis (Pentecost, 1978). A comparable process for the calcification of ooids has been proposed by Ferguson et al. (1978), and Davies et al. (1978).

The ions required for carbonate precipitation may be derived either from overlying saturated lake or sea water (Eggleston and Dean, 1976) or from saturated spring water flowing up through underlying sediments (Scholl and Taft, 1964; Moore et al., 1984; Moore, in press). The mineralogy of the precipitated carbonate is generally consistent with that expected from inorganic precipitation from the surrounding water (Pentecost and Riding, 1986), and examples of calcite, aragonite, and monohydrocalcite cements have been documented (Burne and Moore, 1986).

It may be difficult to distinguish these biologically influenced cements from trapped crystals or from an inorganically deposited cement. The use of stable-carbon isotopes offers one possibility for the distinction between inorganic and biologically influenced cements. Carbonate precipitated as a result of physical or chemical processes will have an isotopic signature similar to that of the dissolved carbonate in the water from which it was



**FIGURE 6**—Stable-isotope values of microbial carbonates, lake water, and groundwater feeding marginal springs for Sleaford Mere and Lake Fellmongery, South Australia. Note that, while the  $\delta^{18}\text{O}$  values of the carbonates and the water are similar, the  $\delta^{13}\text{C}$  values of the carbonates are markedly heavier than are those of the co-existing water. The  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values for the water were obtained from separate samples.  $\delta^{18}\text{O}$  values are expressed relative to PDB.

precipitated. If, however, biological processes are influencing or promoting precipitation, this should be evident from the isotopic data, owing to fractionation of the carbon isotopes. For example, the preferential use of the lighter isotope  $^{12}\text{C}$  during photosynthesis results in an enrichment of  $^{13}\text{C}$  in the surrounding microenvironment of the organisms (Borowitzka, 1982; Calder and Parker, 1979). In waters close to  $\text{CaCO}_3$  saturation, the uptake of  $\text{CO}_2$ , for instance, would be sufficient to bring about an imbalance in the carbonate equilibria, and carbonate could precipitate from solution (Turner and Fritz, 1983). The preferential use of  $^{12}\text{C}$  will leave the resulting inorganic carbon precipitated as carbonate enriched in  $^{13}\text{C}$ , i.e., it will have a positive  $\delta^{13}\text{C}$  value, while the organic component will be depleted in  $^{13}\text{C}$ , i.e., it will have a negative  $\delta^{13}\text{C}$  value.

Taylor (1975) reported  $\delta^{13}\text{C}$  values of +4.5 for the monohydrocalcite cements and of -20 for their associated organic matter in the microbial carbonates of Lake Fellmongery, South Australia. By comparison, the  $\delta^{13}\text{C}$  value of the lake water that we analysed in 1986 was -2.7. Taylor interpreted the elevated  $^{13}\text{C}$  values of the cements to be the result of carbonate formation in an evaporative basin, stating that "the isotopic data suggest that the 'beach rock' has not been secreted by the algae, but rather that it has been precipitated from saline waters."

Taylor's results, however, comply with the  $\delta^{13}\text{C}$  values that might be expected as a result of isotopic fractionation brought about by biological processes. Similar elevated  $\delta^{13}\text{C}$  values for

microbial carbonates, as compared with lake waters, have been encountered in several other Australian lake deposits (Fig. 6), which again supports the contention that stable-carbon isotopes may be used as a method of determining the origin of precipitates and cements. This technique requires further research, however, as it is possible that rapid inorganic precipitation may promote isotopic fractionation, and that carbonate nucleation on sheath material may not involve significant fractionation.

#### Skeletal Calcification

The term "skeletal calcification" is used here in the sense of a strictly directed biological process in which metabolism produces an organized mineralized structure with a predetermined form. Although calcification in some cyanobacteria has been described as resembling skeletal formation (Golubic and Campbell, 1981) it is not a strictly directed biological process. The only common constituents of BMCs that secrete metabolised skeletons are diatoms, which are siliceous. Diatoms are important constituents of BMCs associated with many presently forming Australian microbialites, but their remains are never the dominant constituent of the resulting lithified framework.

In our studies of Australian lakes we have yet to encounter benthic microbial communities that contain sufficient quantities of skeletal material to construct a primary limestone framework, although uncemented sediments rich in the remains of diatoms are well known.

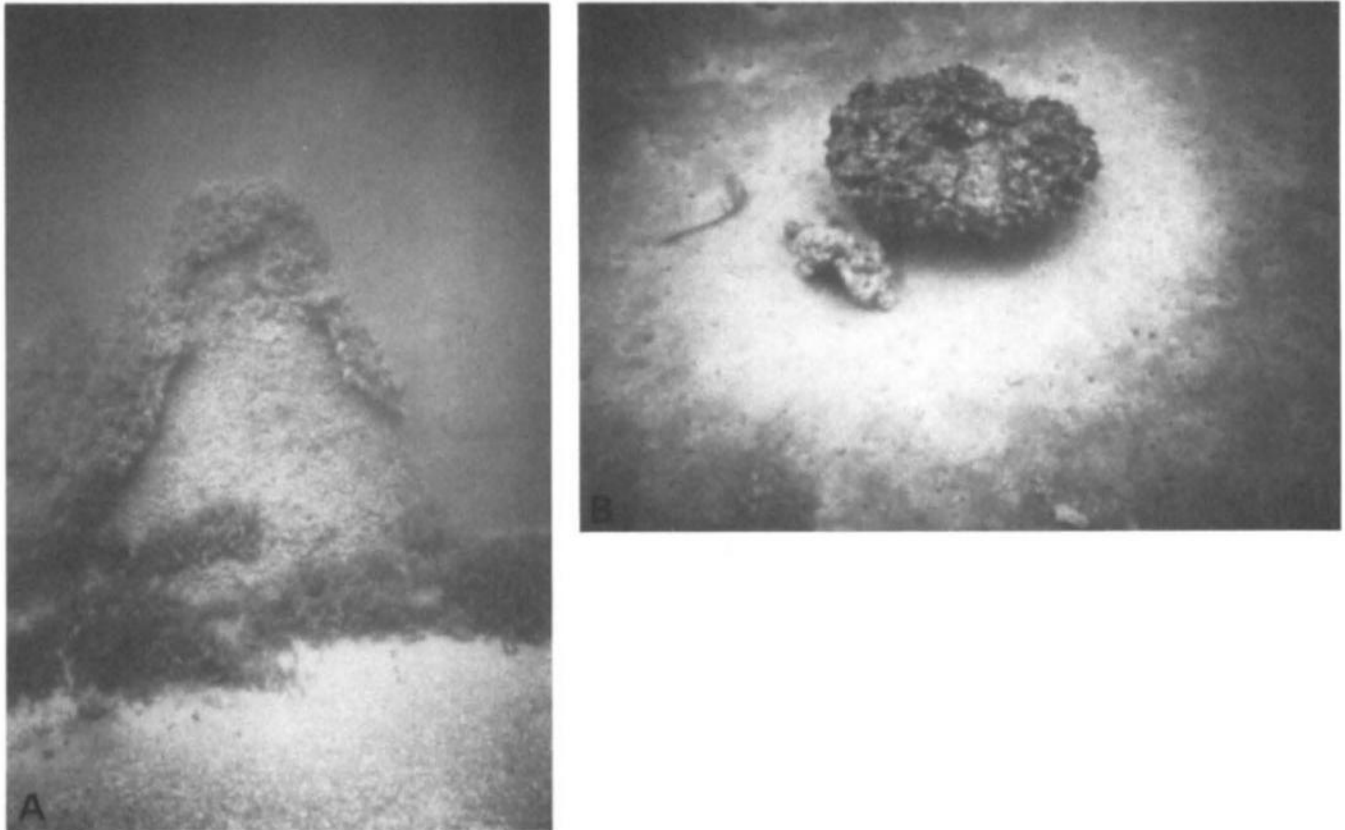
Walter (1972) cited several examples of modern stromatolites constructed by eukaryotic algae, including red algae, which form calcareous crusts. Calcareous red algae construct both fixed (Ginsburg and Schroeder, 1973) and unattached concentric calcareous rhodoliths. However, although some red algae are microscopic, they are not generally regarded as microbes and, hence, their deposits cannot strictly be referred to as microbialites.

Riding (1977) proposed the term "skeletal stromatolites" for "... stromatolites constructed by calcification of organisms which are not obligate calcifiers and which, when uncalcified, are still capable of constructing stromatolites". Monty (1981) rejected this term on the grounds that the calcified structures were not proper metabolised skeletons. It is clear from Pentecost and Riding (1986) that Riding did not intend to imply that skeletal stromatolites were other than calcified stromatolites. Furthermore, he did not intend to imply that they did not possess genetically determined skeletons. This being the case, we agree with Monty (1981) that the term "skeletal stromatolites" should be abandoned.

#### DEPOSITIONAL FORM

Trapping and binding of detrital sediments produces unlithified but cohesive mound-shaped structures and flat microbial mats. The latter deposits are probably the most extensively studied products of microbial sedimentation (see review in Golubic, 1973). They have been referred to as *stratiform stromatolites* (Walter, 1976a), *potential stromatolites* (Krumbein, 1979), *cryptogalaminated carbonates* (Aitken, 1967), and *algal laminated sediments* (Davies, 1970).

Processes of calcification develop indurated frameworks. These may take a number of forms, including isolated, unat-



**FIGURE 7—A)** Subaqueous conical microbial lithoherm 85 cm high in water 1.5-m deep. Note exfoliation of calcified outer shell and charophytes colonizing the lower flanks. The structure is not cemented to the substrate; Mt. John transect, eastern side of Lake Clifton, Western Australia. **B)** Unattached, subaqueous “pustular doughnut” lithoherm. Note small burrows in surrounding sediment and light aureole, adjacent to the structure, caused by shedding of diatomaceous material. Lithoherm is 18 cm in diameter and lies at 1.5-m water depth. Same specimen as in Figures 5 and 10E. Field Station Transect, eastern shore of Lake Clifton, Western Australia.

tached bodies such as those of Lake Clifton (Fig. 7) (Moore et al., 1984) or attached buildups. The latter are well-developed in Shark Bay (Fig. 8) (Playford and Cockbain, 1976), the Exumas (Dill et al., 1986), and in several present-day lakes (Eggleston and Dean, 1976; Casanova, 1986) where they often dominate the peripheral environment (Fig. 9). They occur in a number of forms such as isolated heads, coalescent mounds, or irregular sheets. The presence of these rigid porous masses on the lake floor or sea bed has great ecological significance. They provide shelter for crustaceans, fish, and insect larvae; a firm substrate for epilithic colonization; and a source of food for grazing metazoans.

Various terms have been used previously to describe these structures, including algal reefs (Bradley, 1929), algal boundstones (Warren, 1982), algal tufa (Warren, 1982), algal mounds (Halley, 1976), algal biostromes (Carozzi, 1962), stromatolites (Moore et al., 1984), stromatolitic bioherms (Eggleston and Dean, 1976), and beach rock (Taylor, 1975). The variety of these terms is confusing, especially as they all pertain to the same sedimentary products: it seems that none of them is truly appropriate. The use of the term “reef” implies large-scale

structures that present a hazard to navigation and are capable of developing independent sedimentary facies (Johnson, 1961; Cumings, 1932) or, in more modern usage, a sedimentary system within itself (James, 1983). The term is inappropriate for decimeter-scale structures such as those figured by Bradley (1929). The deposits may however coalesce to form reefs (Logan, 1961; Playford and Cockbain, 1976; Moore et al., 1984) or, more correctly, microbial buildups (c.f. Heckel, 1974). The terms “bioherm” and “biostrome” (Cumings, 1932) have no connotations of scale and are therefore more appropriate. Indeed, Cumings (1932), who introduced the terms, cited the algal banks of Karatta Lake (now known as Lake Fellmongery) described by Mawson (1929) as examples of bioherms. In his field description, however, Mawson interpreted the banks to be of coralline-algal origin, i.e., that they were composed of skeletal remains. The loss of the samples prevented his (and, later, Cumings’s) realization that they were in fact constructed by the non-skeletal precipitation of monohydrocalcite as spherular aggregates in a microenvironment associated with microorganisms (Taylor, 1975). While the terms “bioherm” and “biostrome” are appropriate for



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**FIGURE 8—A)** Sub-tidal lithoherms formed from coalescing columns. Note colloform BMC covering entire structure, and associated macro-algae, fish, and surrounding sediment with abundant bivalve shells (*Fragum*). Structures are 1.7-m high and occur in water 2-m deep; Carbla Point, Hamelin Pool, Shark Bay. **B)** Sub-tidal club-shaped lithoherms. Note colloform BMC colonizing the crests of the structures, and vertical flanks colonized by macro-algae (including *Acetabularia*). These columns are occasionally partially buried by migration of ooid sand-waves. Structures are 20–40 cm high, water depth is 1.5 m; 1.5 km southwest of Flagpole Landing, Hamelin Pool, Shark Bay.

skeletal deposits, because they are defined as being formed by the remains of sedentary organisms, these terms are not appropriate for the deposits of biologically influenced non-skeletal cementation, and we propose that the terms “microbial lithoherms and lithostromes” be used for these deposits.

The term *lithoherm* was coined by Neumann et al. (1977) for deep-water rocky carbonate mounds formed by the sub-sea lithification of successive layers of trapped sediment and deposited skeletal debris. The term was proposed to signify a morphological expression of sub-sea lithification, and to emphasize the primary role of this chemical process in a biological build-up. Implicit in this was the need to distinguish lithoherms from build-ups resulting from the skeletal deposition of carbonate. Although our use of the term lithoherm represents a slight modification of the original definition, we, like Neumann et al. (1977), and Aitken (1967) before them, recognize the need to distinguish sediments of skeletal origin from those of non-skeletal origin. We do this by restricting the terms bioherm and biostrome to deposits constructed largely of skeletal material (c.f. Krumbein, 1979), and by using the terms microbial lithoherm and lithostrome for deposits in which the calcified framework is the product of biologically influenced, non-skeletal

precipitation resulting from the effect of the BMC on the physicochemical microenvironment.

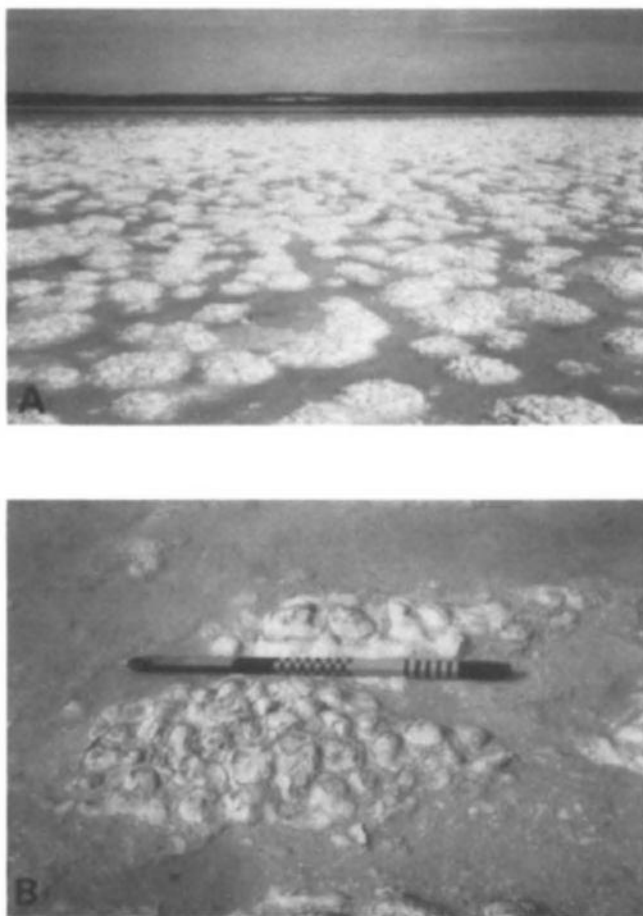
Although there is a relationship between lithoherm form and environmental influences parallel to that which influences the form of hermatypic-coral bioherms (James, 1983), the morphogenesis of microbialites is dependent on additional factors. As well as environmental influences, it reflects a complex interaction between the composition of the BMC, the ecology of the BMC and the associated biota, and the processes of lithification. There is a need for extensive research into the subject of microbialite morphogenesis.

#### INTERNAL STRUCTURE, TOGETHER WITH A DISCUSSION OF THE TERMS “STROMATOLITE” AND “THROMBOLITE”

Microbialites may contain a variety of macroscopic internal structures (Fig. 10). These are best identified initially by descriptive terms, rather than terms that automatically imply formation from a particular environment, BMC, or process.

Confusion surrounding the use of “stromatolite” has become





**FIGURE 9—A)** Nests of small domical microbialites forming a lithostrome around the seasonally inundated periphery of Pink Lake, Esperance, Western Australia. **B)** Close-up of a nest of domical microbialites shown in Figure 9A. Note the perfect, egg-shell-thin layering revealed on the damaged crests. Surfaces are naturally smooth. Mannion-scale is 60 cm long.

an obstacle to progress in the understanding of microbial sedimentation. This term was originally coined by Kalkowsky (1908) to describe masses of limestone possessing a fine, more-or-less planar lamination (in contrast to the concentric lamination of oolitic grains), in which “lower vegetal organisms” initiated the precipitation of calcium carbonate. This definition has undergone gradual revision (e.g., Cloud, 1942, Gary et al., 1973; Hofman, 1973; Krumbein, 1983; Logan, 1961; Logan et al., 1964; Davies, 1970; Aitken, 1967; Awramik and Margulis, 1974; Semikhatov et al., 1979) with the incorporation of concepts such as formation by lime-secreting algae (Cloud, 1942), attachment (Semikhatov et al., 1979), sediment trapping and binding (Logan, 1961; Walter, 1976a), and interactions between microbial activity and the physical and chemical environment (Krumbein, 1979). However, as Pentecost and Riding (1986) have pointed out, there has been persistent difficulty in satisfactorily defining the term. This has been due to the

absence, in most ancient examples, of direct evidence for the organisms responsible for the formation of the stromatolites. Buick et al. (1981) suggested that, although the original use of the term stromatolite continues amongst field geologists, stromatolite specialists have mostly abandoned the original definition in favor of one of two conflicting views: that *stromatolites must have a particular form of laminated morphology, but may have any type of sedimentary origin* (e.g., Semikhatov et al., 1979), or that *stromatolites may have any morphology, but must have an organosedimentary (particularly microbial) origin* (e.g., Awramik and Margulis, 1974).

Thus, there are at least three current uses for the term “stromatolite”:

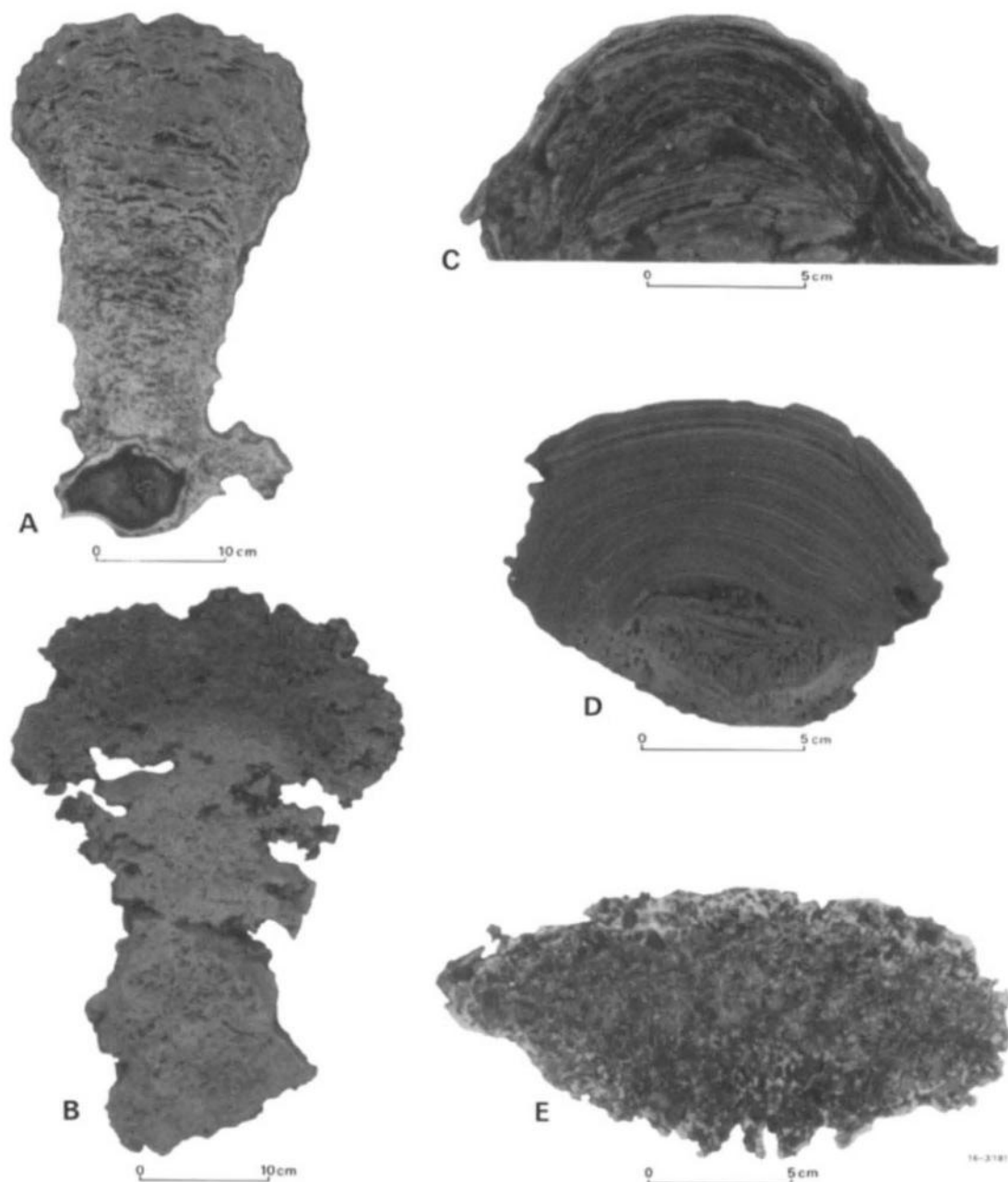
1. To refer to the products of microbial sedimentation (*sensu* Awramik and Margulis);
2. To describe laminated structures of probable microbial origin (*sensu* Kalkowsky); and
3. To describe discrete laminated lithified bodies (*sensu* Semikhatov et al.).

The definition of Walter (1976a), derived from that of Awramik and Margulis (1974) (“organosedimentary structures produced by sediment trapping, binding and/or precipitation as a result of the growth and metabolic activity of micro-organisms, principally cyanophytes”) has gained wide acceptance (Walter, 1976a; Buick et al., 1981). Ironically, it intentionally excludes reference to the one essential element of Kalkowsky’s definition, the laminations. Although this definition is now firmly entrenched in biological and geological usage, we advocate a return to Kalkowsky’s original meaning for “stromatolite”, and use it to refer to one possible internal structure of a microbialite.

Kennard and James (1986) suggest that three classes of microbial buildups can be differentiated on the basis of their internal structure: clotted *thrombolites* (a term introduced by Aitken in 1967), laminated *stromatolites*, and undifferentiated *microbial boundstones* composed of a vague, mottled, or massive cryptic fabric.

Kennard and James (1986) term the mesoscopic components of thrombolites *mesoclots* (equivalent to the clots of Aitken, 1967), which, in the Cambrian examples they describe, are said to be predominantly composed of microstructures (which they do not illustrate) resulting from *in-situ* calcification of coccoid-dominated communities. We consider that, although coccoid communities may have dominated the formation of Cambrian examples, *thrombolitic mesoclots are not necessarily the product of coccoid communities*. Very similar structures, forming from calcified filamentous communities and containing a variety of distinctive textures imparted by calcified filaments, are found in microbialites in present-day lakes, e.g., at Lake Clifton, Western Australia (Moore et al., 1984) and at Sleaford Mere, South Australia (Warren, 1982), (Figs. 5, 10e).

Kennard and James (1986) describe stromatolites as composed of layers or laminae (stromatoids, *sensu* Kalkowsky, 1908), which they interpret to have been constructed predominantly by continuous filamentous mats rather than by discontinuous coccoid colonies. Again, we caution against overgeneralization, and cite the following examples of stromatolites in which the constructing microorganisms were not



**FIGURE 10—A)** Impregnated slice through a sub-tidal, club-shaped lithoherm from 1.5 km southeast of Flagpole Landing, Hamelin Pool, Shark Bay. Note basal attachment to a flint pebble, and laminated fenestral, stromatolitic structure. Specimen is similar to those in Figures 3 and 5B. The structure consists of trapped and bound detrital sediment cemented by primary calcification, in part of biologically associated origin. **B)** Impregnated slice through a club-shaped lithoherm from the intertidal zone, mid-way between Flint Cliff and Flagpole Landing, Hamelin Pool, Shark Bay. The composite structure shows a basal section composed of a laminated structure, formed sub-tidally and now extensively disrupted by boring. Note the internal sediment within the borings. The 10-cm-thick upper zone is a mottled deposit formed in the intertidal zone by calcification associated with a pustular, *Entophysalis*-bearing BMC of the type described by Golubic (1983). The lower zone was originally stromatolitic, but boring has resulted in a less regular structure. The upper part is thrombolitic. **C)** Domical laminated stromatolite from Pink Lake, Esperance, Western Australia (c.f. Figs. 4A and 9). Note alternations of precipitated sheets of aragonite and zones of detrital peloids associated with the remains of a BMC. Impregnated slice. **D)** Stromatolite from Marion Lake, South Australia (von der Borch et al., 1977) showing regular laminations comparable with those in Figure 10C. Slice. **E)** Impregnated slice through the “pustular doughnut” lithoherm shown in Figure 7B. Note the thrombolitic structure formed by mesoclots of calcified cyanobacterial filament felts, infilled by unconsolidated detrital sediment rich in gastropod and ostracod shells. Field Station Transect, eastern side of Lake Clifton, Western Australia.

filamentous. The classical laminated sub-tidal stromatolites of Hamelin Pool, Shark Bay (Figs. 3, 8, 10a,b) are colonized and presumably created by a microbial community dominated by both coccoid and filamentous cyanobacteria, coccoid and filamentous eukaryotic algae, and diatoms. Bradley (1929) figured a laminated stromatolite apparently constructed by coccoid organisms. Well-laminated stromatolites consisting of alternations of egg-shell-like layers of inorganic aragonite precipitate and calcified microbial layers dominated by coccoid cyanobacteria and photosynthetic bacteria occur in hypersaline Pink Lake (also known as Lake Spencer), near Esperance, Western Australia (Figs. 4a, 9, 10c). These structures probably record seasonal alternations of the growth of a BMC, and aragonite precipitation. The structures are very similar to the sub-fossil stromatolites from Marion Lake, South Australia (Fig. 10d). Von der Borch et al. (1977) considered that the relative absence of preserved microbial filaments in these stromatolites was due to their destruction during cementation and diagenetic alteration, rather than being evidence for the original BMC being dominated by coccoid forms. However, microfossils preserved in chertified examples of similar stromatolites (*Stratifera undata* Komar 1966) from the Late Proterozoic of Brazil have been shown to contain coccoid, rather than filamentous, microbial remains (Fairchild and Subacius, 1986). Comparable stromatolites (Fig. 4b) are known from the Proterozoic Amelia Dolomite of the Northern Territory, Australia (Muir in von der Borch et al., 1977).

Kennard and James (1986) provide other distinguishing points between stromatolites and thrombolites: stromatolites, the diagnostic components of stromatolites, include structures comprising rhythmic layers of trapped and bound detrital particles, whereas mesoclots, the diagnostic components of thrombolites, rarely include trapped and bound material; stromatolites are rarely associated with skeletal metazoans (this is not the case for modern sub-tidal stromatolites, see Fig. 8), whereas thrombolites are often associated with a shelly biota; and stromatolites commonly contain laminoid fenestrae, whereas thrombolites commonly contain tubular fenestrae and irregular shelter cavities. Our observations of present-day microbial lithoherms generally endorse these textural differences. This suggests that, at least in the examples we have studied, the distinction between thrombolites and stromatolites is not so much a function of the composition of the associated BMC but rather a reflection of whether the framework of these structures was constructed by biologically influenced calcification or by trapping and binding either of detrital sediment or of a precipitated mineral phase.

Thus the mesoclots that form the primary rigid framework of the thrombolites described by Kennard and James (1986) result from the calcification of microbial communities. The primary framework had significant micro-relief within which unbound particles accumulated. There is evidence that the accreting thrombolites were commonly inhabited by an abundant and diverse skeletal and soft-bodied metazoan fauna. The relatively minor importance of sediment trapping and binding in these structures may reflect either rapid rates of calcification, or a BMC dominated by cyanobacteria with non-sticky sheaths. Cambrian thrombolites represent a complex, fossilized microbial-metazoan ecosystem. We consider that a modern example

of such a system is provided by the pustular doughnut structures found in Lake Clifton, Western Australia (Figs. 5, 7b, 10e) (Moore et al., 1984). Here, mineralized aggregates of the filamentous cyanobacterium *Scytonema* form an irregular framework of mesoclot-like structures between which unconsolidated sediments, including ostracod and gastropod shells, accumulate.

In contrast, BMCs associated with laminated stromatolites such as those described by Kennard and James (1986) were able to trap and bind sediment. The trapped and bound detritus was then lithified by early cements. Excellent modern-day examples of structures of this type are provided by the subtidal stromatolites of Shark Bay (Burne and James, 1986) (Fig. 3), and of the Bahamas, i.e., Eluthera (Dravis, 1983) and Exuma (Dill et al., 1986). In these cases the laminations are composed of trapped sediment similar to that found in the intervening sand bodies. It has been suggested that the early lithification of these structures is *entirely* the result of the formation of an abiological early cement (Golubic, 1983; Logan et al., 1964; Dill et al., 1986), but microscopic examination of the Shark Bay (Fig. 3) examples suggests that the lithification may be partly the result of calcification of spherical microbial bodies (Fig. 2a).

While recognizing that there are these differences of origin between *some* thrombolites and stromatolites, we caution against using terms that describe all microbialites with a particular form of internal structure in a way that implies a particular mode of formation. Similar internal structures might be produced by quite different processes. For example, while we agree with Kennard and James (1986) that many Cambrian thrombolites are not former stromatolites that have been disrupted by metazoan bioturbation, as has been suggested by Walter and Heys (1985), we believe that such activity could give rise to a thrombotic microbialite (Fig. 10b), including some of those described by Aitken (1967) and Radke (1980). Therefore we propose that the following terms be employed only to describe the internal structures of microbialites:

- Stromatolitic structure (Kalkowsky, 1908)—Fine, more or less planar lamination
- Thrombotic structure (Aitken, 1967)—A clotted texture
- Cryptic structure (Aitken, 1967; Kennard and James, 1986)—A vague, mottled, or patchy texture attributed to microbial activity
- Oncolitic structure (Pia, 1927; Peryt, 1981)—Concentric laminations
- Spherulitic structure (Taylor, 1975)—Spherular aggregates

Thus, a stromatolitic microbialite may be referred to as a *stromatolite*, a thrombotic microbialite as a *thrombolite*, an oncolitic microbialite as an *oncolite*, and the remaining two categories as *cryptic microbialites* and *spherulitic microbialites*.

## CONCLUSION

Despite more than a century of research, including particularly important work over the past 30 years, the study of microbialites is presently in a state of some disarray. Taxonomists have pragmatically attempted to apply a Linnean-type system of nomenclature to stromatolites, and have tested their use in biostratigraphic correlation. Sedimentologists have recognized the importance of environmental controls on microbio-

alite morphogenesis and, although rejecting the taxonomical approach, have suggested the use of descriptive classifications. Sedimentologists have, however, made little progress in the application of process-orientated approaches of facies analysis to microbialites. Microbiologists have tended to concentrate their studies on unlithified microbial mats that represent recent analogues of only a small proportion of ancient microbialites. The situation has been further complicated by the confusion associated with the ambiguous meaning of the term "stromatolite" commented on above.

It is hoped that an increased awareness of the nature and variety of sedimentation associated with benthic microbial communities will further our understanding of the important group of resulting sedimentary rocks, and enable a more integrated approach to their study. The ability to differentiate between the various processes involved in the formation of microbialites (Fig. 2), together with a better appreciation of the role of the BMC in constructing the structures, is a first step towards eventually understanding such problems as the relative influence of biological and environmental controls on microbialite morphogenesis; the degree to which variation in microbialites is due to evolutionary change in BMCs on the one hand and environmental controls on the other; and the possible use of microbialites for stratigraphic correlation, particularly in the Precambrian.

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We feel clearly that we are only now beginning to acquire reliable material for welding together the sum total of all that is known into a whole; but, on the other hand, it has become next to impossible for a single mind fully to command more than a small specialized portion of it.

I can see no other escape from this dilemma (lest our true aim be lost for ever) than that some of us should venture to embark on a synthesis of facts and theories, albeit with second-hand and incomplete knowledge of some of them—and at the risk of making fools of ourselves.

—Erwin Schrödinger