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Microbial carbonates: the geological record of calcified bacterial–algal mats and biofilms

ROBERT RIDING
Department of Earth Sciences, Cardiff University, Park Place, PO Box 914, Cardiff CF10 3YE, UK
(E-mail: riding@cardiff.ac.uk)

ABSTRACT

Deposits produced by microbial growth and metabolism have been important components of carbonate sediments since the Archaean. Geologically best known in seas and lakes, microbial carbonates are also important at the present day in fluviatile, spring, cave and soil environments. The principal organisms involved are bacteria, particularly cyanobacteria, small algae and fungi, that participate in the growth of microbial biofilms and mats. Grain-trapping is locally important, but the key process is precipitation, producing reefal accumulations of calcified microbes and enhancing mat accretion and preservation. Various metabolic processes, such as photosynthetic uptake of CO_2 and/or HCO_3^- by cyanobacteria, and ammonification, denitrification and sulphate reduction by other bacteria, can increase alkalinity and stimulate carbonate precipitation. Extracellular polymeric substances, widely produced by microbes for attachment and protection, are important in providing nucleation sites and facilitating sediment trapping.

Microbial carbonate microfabrics are heterogeneous. They commonly incorporate trapped particles and *in situ* algae and invertebrates, and crystals form around bacterial cells, but the main component is dense, clotted or peloidal micrite resulting from calcification of bacterial cells, sheaths and biofilm, and from phytoplankton-stimulated whiting nucleation. Interpretation of these texturally convergent and often inscrutable fabrics is a challenge. Conspicuous accumulations are large domes and columns with laminated (stromatolite), clotted (thrombolite) and other macrofabrics, which may be either agglutinated or mainly composed of calcified or spar-encrusted microbes. Stromatolite lamination appears to be primary, but clotted thrombolite fabrics can be primary or secondary. Microbial precipitation also contributes to hot-spring travertine, cold-spring mound, calcrete, cave crust and coated grain deposits, as well as influencing carbonate cementation, recrystallization and replacement. Microbial carbonate is biologically stimulated but also requires favourable saturation state in ambient water, and thus relies uniquely on a combination of biotic and abiotic factors. This overriding environmental control is seen at the present day by the localization of microbial carbonates in calcareous streams and springs and in shallow tropical seas, and in the past by temporal variation in abundance of marine microbial carbonates. Patterns of cyanobacterial calcification and microbial dome formation through time appear to reflect fluctuations in seawater chemistry.

Stromatolites appeared at ~3450 Ma and were generally diverse and abundant from 2800 to 1000 Ma. Inception of a Proterozoic decline, variously identified at 2000, 1000 and 675 Ma, has been attributed to eukaryote competition and/or reduced lithification. Thrombolites and dendrolites mainly formed by calcified cyanobacteria became important early in the Palaeozoic, and reappeared in the Late Devonian. Microbial carbonates retained importance through much of the Mesozoic, became scarcer in marine environments in the Cenozoic, but locally re-emerged as large agglutinated domes, possibly reflecting increased algal involvement, and thick micritic reef crusts in the late Neogene. Famous modern examples at Shark Bay and Lee Stocking Island are composite coarse agglutinated domes and columns with complex bacterial–algal mats occurring in environments that are both stressed and current-swept: products of mat evolution, ecological refugia, sites of enhanced early lithification or all three?

Keywords Bacteria, biofilm, calcification, mat, microbe.

INTRODUCTION

Microbes are widespread and often abundant in Earth-surface environments (Brock *et al.*, 1994), and appear to have been so from early in Earth history (Schopf, 1983). They can live on virtually all wet sedimentary surfaces, at all depths in lakes and seas, and in sediment to depths of kilometres. Microbes interact widely with other organisms, both competitively and cooperatively, play major roles in chemical cycles that influence atmosphere–hydrosphere composition (Fenchel & Finlay, 1995; Banfield & Nealson, 1997; Ehrlich, 1998), and are extensively involved in the production, accumulation and diagenesis of sediment (Nealson, 1997; Riding & Awramik, 2000). The effects of microbial mediation on precipitation and localization of carbonate sediments are noticeable in a wide variety of depositional settings. These include marine reefs, tidal flats, lacustrine whitings, fluviatile tufas, hot-spring travertines and cave crusts, as well as subaerial calcretes and other coatings, grains and matrices within sediment. Microbial carbonates form a huge area for research. My aims here are to outline key aspects of these sediments and, in particular, to focus on some of the challenges that these studies encounter. I will necessarily be selective.

Microbes, most simply defined as all microscopic organisms, are generally considered to encompass bacteria (including cyanobacteria), fungi, small algae and protozoans (Fig. 1; Brock *et al.*, 1994). With such inclusivity, the boundaries of microbial carbonate studies are not well defined, or at least are not narrow (see Pia, 1926; Camoin, 1999). Many studies of microbial carbonates focus mainly on bacteria in general, and cyanobacteria in particular, and emphasize their ability to precipitate as well as to localize sediment. In contrast, in the case of small algae and protozoans, only their non-skeletal, e.g. trapping and binding, roles are usually included in microbial carbonate research. Small calcified organisms, such as coccolithophore algae and foraminiferal protozoans, are technically microbes, but deposits in which both can be abundant, such as the Cretaceous Chalk of north-west Europe, are not normally regarded as microbial carbonates. The reason is probably that coccoliths and tests are distinctive discrete skeletal components. In contrast, many, although not all, microbial carbonates consist of rather less clearly defined nonskeletal precipitates, together with trapped grains. The focus of microbial carbonate studies is mainly calcified biofilms and microbial mats, and their geological record.

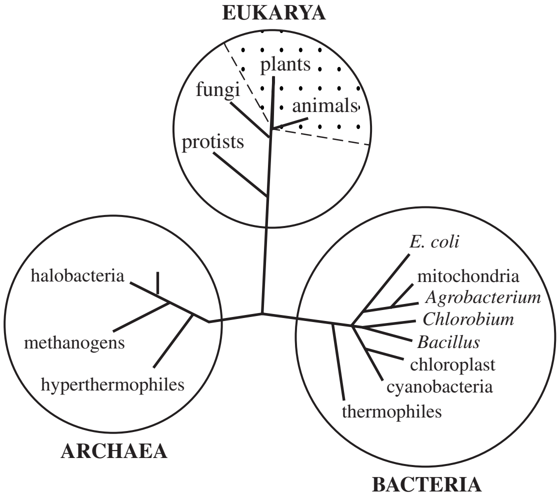

Fig. 1. Cloverleaf of life: microbial diversity (bacteria, algae, protozoans and fungi) in a molecular phylogeny perspective based on 16S rRNA gene-sequences (after Nealson, 1997, fig. 1). Microbes occupy all except the shaded area. Archaea and Bacteria are two major groupings of bacteria. Archaea include all known methane-producing bacteria (methanogens), and most bacteria living in very salt-rich (> 10% NaCl, halophiles) and very hot (> 80°C, hyperthermophiles) conditions (see Brock *et al.*, 1994). Bacteria include cyanobacteria and many other types. In contrast to bacteria, the eukaryote cell of the Eukarya contains membrane-bound cell organelles. Protists encompass most algae and protozoans.

MICROBES

Bacteria

Bacteria are the key organisms in the formation of microbial carbonates. In practice, the terms bacteria and prokaryotes are synonymous: prokaryotes lack discrete nuclei and other membrane-bound cell organelles; all other organisms are eukaryotes (Eukarya). Bacteria exhibit immense diversity (Brock *et al.*, 1994). Their phylogenetic study and classification has been revolutionized by genetic similarity comparisons, particularly based on analysis of ribosomal ribonucleic acid (rRNA) gene sequences. Although gene transfer complicates these interpretations (see Wiegel & Adams, 1998), a major result has been recognition of two distinct bacterial groups (Fig. 1), archaebacteria and eubacteria (Woese, 1987), now, respectively, termed Archaea and Bacteria (see Brock *et al.*, 1994). These names can cause some terminological confusion; here I refer in general to both groups as bacteria.

Cyanobacteria (previously variously termed blue–green algae, blue–green bacteria, cyanophytes) are very important sedimentologically. These relatively large and somewhat alga-like eubacteria are essentially aerobic phototrophs – using sunlight as energy. In shallow-water oxygenated environments they can thrive in the water column and at the sediment–water interface. Many other bacteria are anaerobic heterotrophs and can occupy dark anaerobic conditions such as sediment pore surfaces (Nealson, 1997). They mineralize (decompose) organic material to inorganic components by redox processes using electron acceptors in order of their energy-yield. This results in progressive depletion in ambient O_2, NO_3^-, SO_4^{2-} and CO_2 (see Fenchel & Finlay, 1995, p. 173). The catabolic (breakdown, usually energy-yielding) processes involved, denitrification, sulphate reduction and methanogenesis, occur successively with increasing depth in sediments. Sulphate reduction is especially important in marine environments, owing to the high sulphate concentration of seawater. As the supply of organic material is reduced, bacterial activity in sediments declines and is often slight at depths below 10–20 cm (Jørgensen, 1977; Fenchel & Finlay, 1995, p. 195).

Algae

Small algae in modern microbial carbonates (see Wallner, 1935; Walter, 1972, pp. 88–89; Golubic, 1976) are usually associated with microbial mats, where they trap and stabilize sediment. They include brown, green and red algae that are mainly relatively large filamentous forms (Scoffin, 1970; Riding *et al.*, 1991a). In contrast, diatoms are small unicellular forms, but they attach by mucilaginous stalks, secrete mucilage and locally are sufficiently abundant to be important sediment stabilizers in marine (Neumann *et al.*, 1970; Awramik & Riding, 1988) and nonmarine (Winsborough & Golubic, 1987; Winsborough, 1999) carbonate environments. In association with microbial carbonates, small calcified algae are prominent in fresh water (Wallner, 1934; Golubic, 1976), but can also be important in the sea (e.g. Dravis, 1983). Fungi become important in subaerial impermanently wetted settings, especially in soils, and are symbiotically associated with algae, and cyanobacteria, in lichens (Klappa, 1979; Jones & Wilson, 1986).

Extracellular polymeric substances

Extracellular polymeric substances (EPS), widely produced by microbes (Decho, 1990), are of central importance in the formation of microbial carbonates. EPS accumulates outside cells to form a protective and adhesive matrix that attaches microbes to substrates (Costerton *et al.*, 1978), provides physical and chemical protection, and can also aid nutrient absorption (Christensen & Characklis, 1990). Bacteria, cyanobacteria and diatoms can all secrete copious amounts of EPS. Sedimentologically important EPS exist in a variety of forms. On sediment surfaces, these range from well-defined protective envelopes surrounding cells, as in cyanobacterial sheaths, to masses that anchor and provide a favourable medium for microbial populations and communities on a scale from biofilms (100s of nanometres) to microbial mats (1000s of nanometres). In addition, microbes can form blooms (dense concentrations of phytoplanktic cells) and floccules, as in marine and lake snow (millimetric EPS-based organic aggregates suspended in the water column). These are typically complex communities which can also be sites of precipitation, as in whiting formation. Exopolymers directly promote the accretion and preservation of the biofilms and microbial mats that they help to constitute by favouring both sediment trapping and mineral precipitation.

Biofilms

Biofilms are generally submillimetric veneers of bacterial populations and communities in an EPS matrix, attached to substrates in aquatic environments. The EPS that they secrete provide stability, facilitate metabolic interaction and act as a diffusion barrier and adsorbent (Lawrence *et al.*, 1994), advantages that have drawn comparisons with eukaryote tissue (Costerton *et al.*, 1995, p. 713). Biofilms can exhibit structural heterogeneity (Wolfaardt *et al.*, 1994, fig. 4; Costerton *et al.*, 1995, fig. 8; Decho, 2000). Biofilm architecture (Lawrence *et al.*, 1991) may include a 'regular array of channels and aggregates', on a scale of 20–40 μm. The aggregates of cells form irregular three-dimensional networks separated by canal systems maintained by water currents and acting as conduits for nutrients, oxygen and waste materials. These are common in pure-culture biofilms under low-flow conditions, but mixed-species biofilms show less regular architecture. The difference could reflect nutrient-limitation in pure-culture biofilms, and niche-exploitation in mixed-species biofilms (Costerton *et al.*, 1995, pp. 719–720). Biofilms are usually only tens or hundreds of micrometres in thickness and their components can only readily be observed by electron microscopy. Biofilm sedimentology is complex (Jones, 1995); they may trap very small grains, but can be calcified by bacterial processes (Pedley, 1992; Perry, 1999).

Microbial mats

Mats are complex structures that form the accreting surface of most stromatolites and other large-scale benthic microbial carbonates. A modern living mat commonly has a thickness of millimetres, and relatively large microbes, including filamentous cyanobacteria, diatoms and filamentous algae, can create intertwined turf-like communities in which the main individual components can commonly be seen with a hand-lens. Mats readily trap micritic sediment, and where they are thick they may also trap sand or even coarser grains (Fig. 2). In addition to stability and protection, microbes require energy and nutrients. In mats these activities can be closely interrelated, involving complex syntrophic communities in which photosynthesis in the upper mat is balanced by decomposition below (Brock *et al.*, 1994, p. 636). There are steep gradients in both light and oxygen. These fluctuate diurnally (see Fenchel & Finlay, 1995, pp. 28, 181–186) and result in well-defined microbial stratification. Typically, aerobic phototrophs (cyanobacteria) are near the surface, anoxygenic phototrophs below, followed by chemo-organotrophs that require neither oxygen nor light (Revsbech *et al.*, 1983; Jørgensen *et al.*, 1983; Pierson *et al.*, 1987). The activities of these microbes determine mat calcification and preservation (Canfield & Raiswell, 1991; and see 'Other bacterial calcification' below). Algae add a further complexity to the bacterial surface community.

Mats in harsher environments such as hot springs and salinas are simpler and less disturbed by bioturbation than those on subtidal marine shelves. However, the details of mat complexity are often rapidly lost as the organisms die, although the organic framework persists (Défarge *et al.*, 1996). In most microbial carbonates, calcified cyanobacteria are the best-preserved microbes.

Fig. 2. Complex mat, trapping ooid–peloid sand (light coloured grains), from the surface of a subtidal dome in the tidal channel between Lee Stocking Island and Norman's Pond Cay, Exuma, The Bahamas. The mat is dominated by microbes (cyanobacteria, green algae and diatoms), but also supports a prominent canopy of hydrozoans and macroalgae (see Riding *et al.*, 1991a). Width of view ~5 cm.

PROCESSES

Many bacteria obtain nutrients and energy by degrading minerals and other compounds, and these activities are facilitated when bacteria adhere to sediment and rock surfaces. The mineral dissolution that results is a key aspect of weathering, and releases products that can be precipitated (Ehrlich, 1998). These intimate relationships between microbes and sediments make microbes of global importance in the biogeochemical cycling of elements. They are also responsible for the two main processes that create microbial carbonates: grain trapping and mineral precipitation.

Grain trapping

The size, motility, orientation and mutual relationships of microbes determine their ability to trap and stabilize sediment (see Gebelein, 1969; Monty, 1976; Golubic *et al.*, 1999) and EPS production is also important (Golubic, 1976). *Stabilization* is well seen on tidal and lacustrine flats where microbial growth occurs during pauses in sedimentation (Noffke, 1998). Firm mats form fibrous or leathery coverings and are further strengthened by desiccative early lithification. Flooding of the flats ruckles and folds mats, forming petee structures (Gavish *et al.*, 1985, p. 192). As a result, storm layers of coarse sediment alternate with mats, some of which are folded (Shinn *et al.*, 1969; Kendall & Skipwith, 1969).

Whereas microbial overgrowth stabilizes previously deposited sediment, *trapping* localizes sediment passing across mats (Black, 1933). This can involve fine to coarse, and siliciclastic as well as carbonate grains. The grade of particles trapped (Fig. 2) depends on ambient sediment supply and on mat structure (Ginsburg *et al.*, 1954). The process of trapping can involve simple physical blockage (*baffling*) of grain movement, and also adhesion on, and in, EPS. Both processes are facilitated where mats have irregular surface topography, such as that formed by relatively large microbes with abundant erect filaments, and also mats with abundant soft EPS, which may trap coarse sediment if it is available, as in some Shark Bay and Lee Stocking Island domes. In contrast, smooth mats or films with little surface topography trap only very fine grains or none at all. Trapping, the localization of hitherto mobile grains on mat surfaces, goes hand-in-hand with the dual process of *binding*: organic overgrowth of trapped grains by cells, filaments and biofilms, which incorporates them into the mat, as in the classic diagram of Gebelein (1969, fig. 14). Grains thus become the substrate for further surficial microbial growth. The mat surface rises, and accretion has occurred.

Precipitation

Although trapping was given prominence by work in modern intertidal environments (Black, 1933; Ginsburg *et al.*, 1954), and is occasionally still emphasized as the key process in the formation of stromatolites (e.g. Ehrlich, 1998), early lithification is also crucial for the formation of microbial carbonates (Walcott, 1914; Logan, 1961; Ginsburg, 1991). Conservation of accreted trapped sediment requires early lithification to strengthen the deposit, to allow microbial sediment to keep pace with or outpace surrounding sediment accumulation, and to maintain domical and columnar mats. Nonetheless, the importance of precipitation for microbial carbonates goes well beyond cementation of trapped material. Dendrolites, skeletal stromatolites and tufa stromatolites, for example, are fundamentally precipitated deposits dominated by calcified microbes, probably cyanobacteria. In addition, and significantly, other bacteria that degrade organic matter below the mat surface create conditions that result in precipitation.

Cyanobacterial calcification

Cyanobacterial calcification appears to result from creation of alkalinity gradients in mucilaginous sheaths, associated with photosynthetic uptake of CO_2 and/or HCO_3^- uptake that raises alkalinity (see Pentecost & Riding, 1986; Merz, 1992; Merz-Preiß, 1999). Preliminary assumptions made by Pentecost & Riding (1986) still appear to be valid: calcification is intimately related to the cyanobacterial mucopolysaccharide sheath, is specific (and see Défarge *et al.*, 1994a) but not obligate, and is dependent on suitable environmental conditions. Sheath impregnation appears to occur in environments where calcification is less rapid, such as lakes and pools, whereas sheath encrustation occurs in fast-flowing rapidly precipitating streams, although this requires further study (see Merz-Preiß & Riding, 1999). Although cyanobacterial calcification appears mainly to occur during life, the converse can also apply, as in desiccated *Entophysalis* in Shark Bay (Golubic & Hofmann, 1976). At the

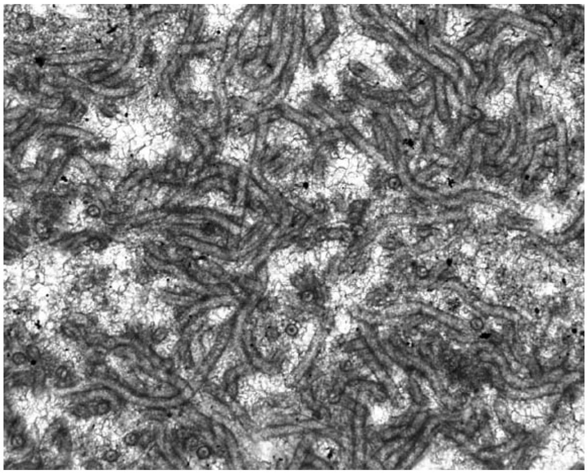

Fig. 3. *Girvanella*, a common calcified cyanobacterium in Palaeozoic–Mesozoic shallow-marine environments, preserved by sheath impregnation (low mid-Ordovician, Lunnan, northern Tarim Basin, China). Width of view = 1·5 mm.

present day, intense and widespread cyanobacterial calcification appears to be essentially a freshwater phenomenon and is scarcely known in modern subtidal environments, although it has been widespread at times in the past (Fig. 3). None the less, it occurs in present-day brackish marine environments (Rasmussen *et al.*, 1993).

EPS calcification

Microbially produced EPS can favour $CaCO_3$ precipitation by providing diffusion-limited sites that create alkalinity gradients in response to metabolic processes, and by attracting and binding calcium ions to negatively charged sites (Pentecost, 1985). However, EPS can also inhibit precipitation, depending on environmental conditions (see Arp *et al.*, 1999a). At high alkalinities, as in alkaline lakes, calcification appears not to be directly associated with living cyanobacteria because photosynthesis in these conditions will not create a sufficient alkalinity gradient in the sheath; instead, calcification preferentially occurs on surfaces poor in EPS (Arp *et al.*, 1999b).

Other bacterial calcification

A wide range of bacterial processes, in addition to photosynthesis in cyanobacteria, can lead to HCO_3^- concentration and raised alkalinity favouring $CaCO_3$ precipitation (see von Knorre & Krumbein, 2000). These include ammonification, denitrification, sulphate reduction and anaerobic sulphide oxidation (see Krumbein, 1979a; Visscher *et al.*, 1992; Castanier *et al.*, 1999). These processes are localized within decaying mats as heterotrophic bacteria degrade organic matter, including cyanobacteria (Bartley, 1996), and they lead to fine-grained precipitation, typically micritic or slightly coarser (Chafetz & Buczynski, 1992; Reitner, 1993; Défarge *et al.*, 1994b; Reitner *et al.*, 1995). These processes are of fundamental importance in the lithification of microbial mats (Krumbein *et al.*, 1977; Krumbein, 1978, 1979a, 1983, p. 495; Chafetz & Buczynski, 1992; Chafetz, 1994). The general result, in microbial carbonates containing calcified cyanobacteria, would be to create a micritic matrix around the calcified sheath material. In microbial carbonates primarily formed by agglutination of coarse sediment on and in mats, the fine-grained matrix created by synsedimentary bacterial precipitation will superficially resemble trapped fines, or micritic cement. Although the importance of these processes in the synsedimentary lithification of microbial carbonates is evident, linking particular products to specific bacterial processes remains an elusive goal. Défarge *et al.* (1996) observed diverse precipitates within stromatolitic mats. These probably nucleate at various sites: around cells, on organic and grain surfaces, and within EPS. The specific site of precipitation appears to influence the mineralogy of the precipitate. Buczynski & Chafetz (1991) found calcite, rather than aragonite, precipitation in more viscous laboratory media, and also in viscous mucilage in natural mats (Chafetz & Buczynski, 1992).

Organomineralization

Bacterially induced precipitation within mats is clearly important and complex. However, precipitation of fine-grained $CaCO_3$ in association with nonliving organic macromolecules (organomineralization; Trichet & Défarge, 1995), independent of biological activity, may also be a sedimentologically significant process (see Reitner *et al.*, 1995; Neuweiler *et al.*, 1999) that overlaps in environment, timing and product with bacterial micrite. Discrimination between these various closely associated fine-grained precipitates in ancient microbial carbonates and mud mounds is a major challenge for future research.

Whiting precipitation

Bacteria have long been linked to the precipitation of water-column carbonates such as whitings, relatively small (generally < 20 µm) $CaCO_3$ crystals (Fig. 4) in lakes and shallow seas (e.g. Bavendamm, 1932). Recently, both lacustrine and marine whitings have been specifically linked to picoplanktonic cyanobacteria (Thompson & Ferris, 1990; Robbins & Blackwelder, 1992). It remains likely, however, that algal and cyanobacterial blooms in general, together with environmental conditions that may vary seasonally, combine to stimulate precipitation through localized removal of CO_2 and HCO_3^-. If whitings are indeed water-column precipitates then their volume would be of considerable significance, potentially accounting several times over for all late Holocene bank-top lime mud on Great Bahama Bank, for example (Robbins & Evans, 1997). However, doubts continue about the nature of marine whitings (Morse & He, 1993; Thompson, 2000).

RECOGNITION

A central problem for the study of microbial carbonates concerns recognition of both the organisms and the processes involved. Many ancient microbial carbonates do not, or at least do not readily appear to, preserve clear evidence of the organisms responsible for their formation. This immediately raises the question, 'then how do we know that they are microbial'. This is not a new problem. Many early workers thought that the deposits that would come to be named stromatolites were made by simple animals. Hence, Hall (1883) named Cambrian examples, from near Saratoga Springs in New York State, *Cryptozoon* and Gürich (1906) called Early Carboniferous examples in Belgium spongiostromids, which he regarded as a new group of protozoan-like organisms that created distinctive microfabrics composed of rounded aggregates traversed by minute canals. When Kalkowsky (1908) proposed the term stromatolite he was convinced that they (and ooids) were organic, but he could not prove it, and he was not sure which organisms were responsible, although he suspected that they were simply organized plants.

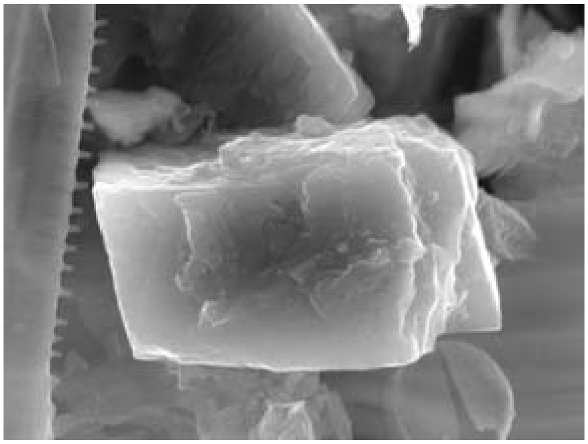

Fig. 4. Calcite whiting crystal, 8 µm long, from sediment trap at −15 m, north basin Lake Lugano, Italy, July 1992 (sample provided by A. Hofmann; see Hofmann, 1996).

The essential answers were of course provided by modern analogues. The first organisms to be confidently linked to stromatolites in this way were cyanobacteria, when Walcott (1914) compared modern freshwater cyanobacterial tufa crusts and oncoids with Proterozoic stromatolites of the Belt rocks in Montana. Bradley (1929) did the same for Eocene stromatolites in the Green River Formation of Wyoming. Cyanobacteria were further implicated as key organisms in stromatolite formation by the work of Black (1933) and Ginsburg (1955) on tidal flats in Andros Island and Florida, respectively (see Hoffman, 1973, p. 180). Thus, Logan's (1961) attribution of the Shark Bay domes to cyanobacterial trapping, while at the same time terming them *Cryptozoon*, had the resonance of 75 years research.

Yet, in spite of this, the external appearance, internal fabrics and geochemical signatures of ancient examples of microbial carbonates are usually insufficient to provide unequivocal evidence of their origins, and it is often difficult to relate organism, process and product at both micro- and macrofabric levels. The question of demonstrating biogenicity resurfaces whenever the interpretation of a deposit is sufficiently important that really firm evidence of origin is demanded. A prime example is recent discussions about earliest Archaean stromatolites in the ~3450 Ma Towers Formation (Warrawoona Group) of Western Australia (Lowe, 1980). These occur as cones, domes and layers in chertified limestones and dolostones and appear to have formed in shallow, often evaporative, basins in volcanic greenstone belts (Walter, 1994). Biogenicity problems that afflict most microbial carbonates assume critical importance in these very old deposits. Arguments have been marshalled both against (Lowe, 1994, 1995) and for (Buick *et al.*, 1995) the biological origin of these and other stromatolite-like structures older than 3200 Ma. They remain widely regarded as probably microbial in origin (e.g. Schopf, 1994; Hofmann *et al.*, 2000; Hofmann, 1999) but, as often as not, definitive evidence is scarce. Such difficulties in establishing biogenicity have had a strong influence on how terms (e.g. see 'Stromatolite', below) should be defined. Internal fabrics are a prime source of evidence concerning possible origins.

FABRICS AND COMPONENTS

Components and fabrics are the key to understanding the organisms and processes involved in microbial carbonates (Monty, 1973), but since many of them form at the scale of the microbes themselves, their correspondingly small size complicates their interpretation. Trapped coarse grains, calcified cyanobacteria and subordinate skeletal encrusting eukaryotes are usually the most readily recognizable components. However, many microbial carbonates are dominated by micritic fabrics whose apparent uniformity masks a range of possible origins. Although a good deal of effort has been put into describing microfabrics and the finer details of mesofabrics in ancient stromatolites, these have proved hard to categorize and even harder to interpret (see Vologdin, 1962; Bertrand-Sarfati, 1976; Komar, 1989; Knoll & Semikhatov, 1998), except where calcified microbes are present (e.g. Bertrand-Sarfati *et al.*, 1994). It is possible to distinguish a variety of principal components and tentatively to suggest origins for them (Table 1), but comprehensively relating processes to fabrics and components remains a challenging research goal.

Micrite

(i) Dense micrite. Possible microbial origins:

(I) *Calcified bacterial cells*. Dead and dying bacteria can become calcified during lysis (Krumbein, 1979a) giving rise to discrete rounded bodies, small varieties (< 1 μm) of which (Maurin & Noël, 1977) have been attributed to nanobacteria (Folk, 1993), although similar objects can form abiotically (Kirkland *et al.*, 1999) and there is continuing dispute concerning nanobacteria (Abbott, 1999).

(II) *Whitings*. These planktonic precipitates (see 'Processes', above) include micrite as well as larger crystals (Fig. 4). They have long been attributed to bacteria, and recently specifically to cyanobacterial picoplankton (e.g. *Synechococcus*, Thompson & Ferris, 1990; Thompson, 2000).

(III) *Calcified biofilm*. Bacteria preferentially adhere to grain and other surfaces for stability, and create biofilm communities that are augmented by other microbes. Consequently, some constructive micrite envelopes (Fig. 5) probably

Table 1. Common components of microbial carbonates and their possible microbial origins.

Component	Possible origins
Micrite	
dense micrite	calcified cells, microbial whitings, calcified biofilm
clotted fabric	EPS calcification and trapped micrite
calcified sheath	impregnated cyanobacterial and other sheaths
peloid	calcified bacterial aggregates
Microspar & spar	extent of microbial origin uncertain; common: in freshwater tufas on peloids in travertine shrubs on cyanobacterial filaments as crystal aggregates on bacterial cells
Allochthonous grains	trapped by microbial mats
Pores	interstices, fenestrae and growth cavities, in microbial reefs

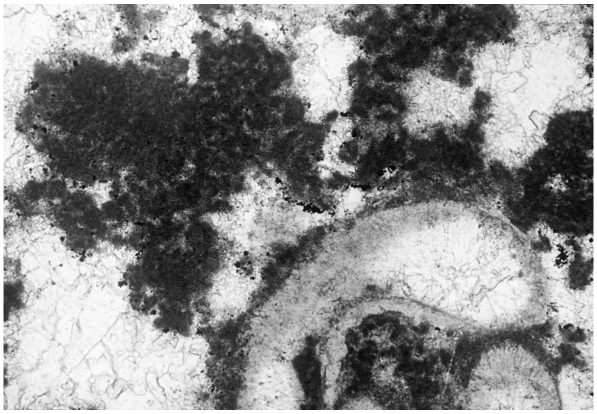

Fig. 5. Peloidal micrite veneers and clumps associated with a vermiform gastropod in skeletal stromatolite-thrombolite. Lower Carboniferous, Liddesdale, southern Scotland. Width of view, 2 mm.

represent biofilm calcification (see Kobluk & Risk, 1977; Perry, 1999; Webb *et al.*, 1999) .

(ii) Clotted fabrics. This microfabric, typically formed by an irregular sponge-like network of micrite, is widespread in stromatolites (and thrombolites, Pratt & James, 1989; but should not be confused with the *macroscopic* fabric of thrombolites). It has been referred to as spongiostrome (Gürich, 1906) and 'grumeleuse' (clotted; Cayeux, 1935, p. 271) fabric, and can grade to dense micrite (Figs 6 and 7). Vermiform fabric (Walter, 1972 – see Bertrand-Sarfati, 1976, p. 255; Pratt, 1982a) is similar. Diffusely clotted micrite appears to represent EPS calcification, although the precise origins and specific processes involved are usually not clear; it possibly also incorporates trapped micrite.

(iii) Calcified sheaths. Calcification of microbial external polysaccharide protective sheaths yields calcified fossils that are relatively readily recognizable. Many of them appear to be impregnated cyanobacterial sheaths, e.g. *Angusticellularia*, *Cayeuxia*, *Girvanella* (Fig. 3) and *Ortonella* (Fig. 7). However, the affinities of a host of other fossils, such as *Archaeolithoporella*, *Rothpletzella* and *Shamovella* (= *Tubiphytes*), which have at times been regarded as microbial, are more uncertain (Flügel, 1981; Riding, 1991a; Senowbari-Daryan & Flügel, 1993; Pratt, 1995).

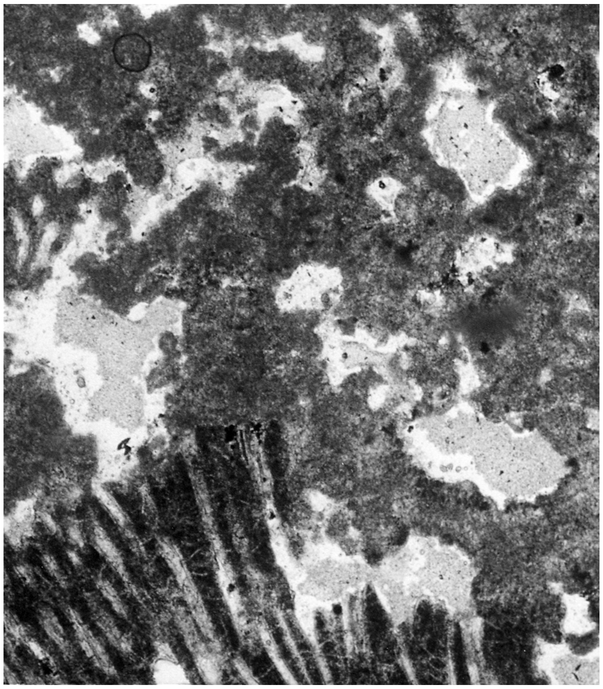

Fig. 6. Diffuse masses of clotted/spongiostrome micrite enclosing irregular uncemented pores and associated with calcified rivulariacean cyanobacteria (filaments to left and below) in a brackish-water bioherm. Pleistocene, Gulf of Corinth, Greece (see Richter *et al.*, 1979). Thin-section courtesy of Ernst Ott. Width of view, 1·2 mm.

Peloids

Granular micritic aggregates of uncertain origin (McKee & Gutschick, 1969) are a common constituent of modern tropical carbonate sediments (Illing, 1954, p. 24) and may exhibit a range of silt to sand sizes. Peloids that appear to be in-place precipitates are common in Holocene reefs (e.g. Lighty, 1985). These typically silt-size (20–60 µm) spherules of Mg-calcite have been regarded as cement fabrics (Macintyre, 1984, 1985), but also as calcified bacterial aggregates

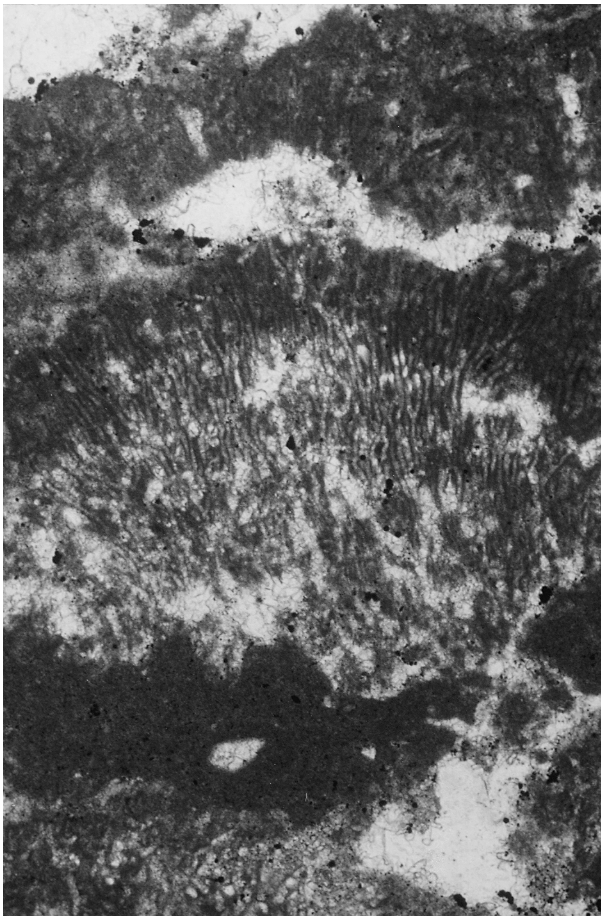

Fig. 7. Alternating laminae of dense micrite, clotted micrite, irregular fenestrae and the calcified cyanobacterium *Ortonella* (erect branching filaments in centre), in skeletal stromatolite–thrombolite. Lower Carboniferous, Liddesdale, southern Scotland. Width of view, 1·2 mm.

Table 2. Environmental distribution of microbial carbonates.

Environment	Type of deposit	Variety
Suspended		whitings in seas and lakes*
On sediment		
subaquatic	marine	domes, columns, reefs of stromatolite, thrombolite, etc.
		crusts in algal–metazoan reefs
		coated grains (oncoids, envelopes)*
	intertidal	stromatolites
	lacustrine–fluviatile	tufas and oncoids
subaerial		hot-spring travertine
		tufa mounds
		cave crusts
In sediment		
subaquatic		intergranular matrices, crusts, films, peloids
soil		calcretes, vadoids
‘diagenetic’		precipitation and transformation

*Allochthonous deposits; others are mainly authochthonous.

rimmed by euhedral calcite crystals (Chafetz, 1986). Peloids that appear to be microbial precipitates are widespread and often very common in ancient reefs (e.g. Flügel & Steiger, 1981; Reid, 1987; Sun & Wright, 1989) and stromatolites (Fig. 5).

Microspar and spar

Fibrous, equant and dendritic spar precipitates are common as external crusts and rinds on organic tissue and grain and mineral surfaces in microbial carbonates. They are well seen in freshwater tufas (Irion & Müller, 1968), karst surfaces (Jones & Kahle, 1986; Jones, 1999), coating peloids (Chafetz, 1986) and contributing to travertine shrubs (Guo & Riding, 1994). The extent to which these crusts may be microbially induced is uncertain. They also form around cyanobacterial filaments, and on bacterial cells, where they can create distinctive crystal aggregates: spherulites, rosettes, crosses and sheaf- and dumbbell-shaped fascicles (see Krumbein *et al.*, 1977; Krumbein, 1979b; Buczynski & Chafetz, 1991; Guo & Riding, 1992a; Défarge *et al.*, 1996).

Pores and allochthonous grains

Diverse voids, ranging from tiny interstices to large growth cavities (Pratt, 1995), are associated with microbial carbonates. They include irregular fenestrae, such as microspar-filled spaces in clotted fabrics (Fig. 6), and larger tidal-flat vugs (‘birdseyes’; Shinn, 1983a).

Trapped grains are important components of some microbial carbonates, such as agglutinated stromatolites. Agglutination is easy to recognize where the grains are silt- or sand-sized or larger, but trapped micrite can be difficult to distinguish from precipitated micrite in EPS. Micritized trapped grains can add to the fine-grained appearance of microbial carbonates (Hoffman, 1973, p. 183). Consequently, the relative importance of trapping and precipitation in micritic stromatolites can be unclear (Fairchild, 1991), although the clotted microfabrics resulting from biofilm calcification are more distinctive. Large grains in gravity-defying stromatolitic crusts, e.g. on overhangs (Riding *et al.*, 1991c), in otherwise micritic matrix demonstrate trapping, as does selective incorporation of grains that differ in size from those in adjacent interbeds (Riding *et al.*, 1991a, Fig. 3).

PRODUCTS

Introduction

Microbial carbonates can form extensive rock units, in reefs for example, in which they may be the principal component, or be relatively minor constituents of alga- or metazoan-dominated reefs and of allochthonous sediments. The details of these deposits that reflect organisms, processes and components are mainly microscopic, but more readily observed meso- and macroscale characters provide the main subdivisions. Microbial carbonates that form at the

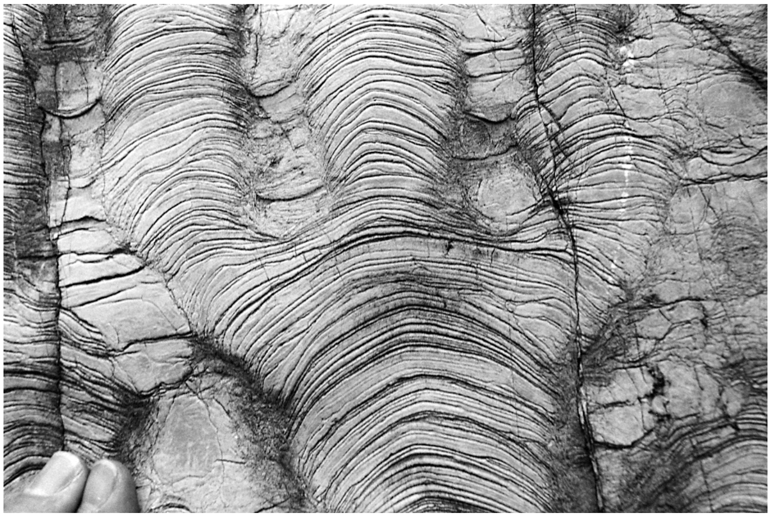

Fig. 8. Detail of branching in the stromatolite *Tielingella*. Late Mesoproterozoic (~1100 Ma) Tieling Formation, near Jixian, northern China. Width of view, 15·5 cm.

aquatic sediment surface include (i) stromatolites, (ii) thrombolites, (iii) dendrolites and (iv) leiolites. These mainly form a variety of domes, columns, thick layers and crusts (Table 2). Tufas and travertines are subaquatic or subaerial, and are generally only partly microbial. Microbial coatings on allochthonous grains form oncoids or micrite envelopes. Other subaerial or subsurface deposits which may locally have a significant microbial component include cave crusts and calcretes. Microbial deposits that form as particles in suspension, but which accumulate on lake- and sea-floors, include whitings.

Major categories: domes, columns and crusts

Macrofabrics, usually readily distinguished in the field, are used to define major categories (Table 3) of microbial carbonate: stromatolite (laminated), thrombolite (clotted), dendrolite (dendritic) and leiolite (aphanitic). Process of origin is reflected in subcategories, such as agglutinated stromatolite and skeletal stromatolite.

Stromatolite

Definition

The term stromatolite was created by Kalkowsky (1908) as stromatolith (Greek *stromat*, to spread out, Latin *stroma*, bed covering; Greek *lithos*, stone) for lacustrine examples in the Lower Buntsandstein (lowest Triassic) in northern Germany (see Paul & Peryt, 1985). Some workers restrict the term to structures, such as domes and columns, with primary relief, but stromatolites may be originally flat deposits. Stromatolites are also not necessarily carbonate; there are siliceous (Walter *et al.*, 1972) and evaporite (Rouchy & Monty, 1981; Gerdes *et al.*, 1985; Renaut, 1993) examples (and see Hoffman, 1973, p. 346). Carbonate–siliciclastic domes occur (Martín *et al.*, 1993; Bertrand-Sarfati, 1994), and essentially flat siliciclastic examples are widespread on modern temperate tidal flats (e.g. Cameron *et al.*, 1985), where microbial mats may influence the formation and preservation of matground and other structures (Noffke, 1998; Pflüger, 1999). Many stromatolites, unlike dendrolites and thrombolites, lack calcified microbes (the main exception being skeletal stromatolites).

Table 3. Principal categories of microbial carbonate deposits.

Major categories	Variety
Stromatolite	Skeletal
	Agglutinated
	Fine-grained
	Tufa
	Terrestrial
Thrombolite	Calcified microbial
	Coarse agglutinated
	Arborescent
	Tufa
	Postdepositional – bioturbation, enhancement, secondary creation
Dendrolite	
Leiolite	

Despite being an old and widely used term, there is currently no generally accepted definition of stromatolite. Kalkowsky (1908) evidently regarded stromatolites as laminated, as the name indicates (Fig. 8), and microbial, but his long and intricate paper failed to specify a single clear definition. By the 1970s, research had revealed that: (i) not all microbial deposits are laminated, and (ii) it can be difficult to demonstrate biogenicity in ancient examples. Attempts to deal with these two complications resulted in new definitions that were as different as the problems that they attempted to resolve. In order to encompass nonlaminated deposits, one definition enlarged the term stromatolite into a broad 'genetic' term that encompassed all microbial deposits irrespective of macrofabric (Awramik & Margulis, 1974). In contrast, another definition avoided the problem of demonstrating biogenicity by being 'descriptive', and allowing stromatolite to apply to abiogenic as well as biogenic laminated deposits (Semikhatov *et al.*, 1979).

Although endorsed in the seminal 1970s publication on stromatolites by Walter (1976), the genetic definition did not discriminate between microbial deposits with markedly differing macrofabrics. As the term thrombolite (Aitken, 1967) for macroscopically clotted microbial carbonates gained acceptance, it became clear that a broad term, similar to that suggested by Awramik & Margulis (1974), was needed when referring to laminated stromatolites and clotted thrombolites as a whole, but that stromatolite would not do: it would be too confusing to try to use stromatolite simultaneously as both a specific term for laminated structures and as an umbrella term for microbial deposits in general. As a result, Burne & Moore (1987) took the Awramik & Margulis (1974) definition and applied it to a new, all encompassing, term: microbialite. This not only permitted the terms stromatolite (laminated) and thrombolite (clotted) to coexist, but subsequently fostered further nomenclatorial innovation to accommodate other macrofabrics: dendrolite for dendritic (Riding, 1991b) and leiolite for aphanitic (Braga *et al.*, 1995) forms.

However, the term stromatolite remained untouched by these clarifications. Whereas thrombolite, dendrolite and leiolite, as well as microbialite, each had single uncontested definitions, by the late 1970s the term stromatolite had three definitions, which variously viewed it as being essentially:

1 laminated and microbial (Kalkowsky, 1908);
2 just microbial (Awramik & Margulis, 1974);
3 just laminated (Semikhatov *et al.*, 1979).

Setting aside Awramik & Margulis's (1974) definition in favour of microbialite still leaves the choice between Kalkowsky's (1908) genetic definition and Semikhatov *et al.*'s (1979) descriptive definition unresolved. Semikhatov *et al.*'s (1979) definition of stromatolite has three deficiencies. (i) Its descriptive rationale conflicts with the genetic one whose usage is now well established for other microbial deposits. The terms dendrolite, leiolite and microbialite are all genetic because they are defined as microbial. (ii) It negates the essential microbial nature of stromatolites; no present-day deposits are termed stromatolites if they are not microbial. (iii) It would include laminated domes as diverse as mineral deposits, diagenetic concretions, travertine crusts and speleothem, as well as microbial deposits, within the term stromatolite. Use of dual definitions of stromatolite, descriptive for ancient and genetic for present-day examples (Ginsburg, 1991, p. 27), would not reduce these deficiencies, and could increase confusion.

Kalkowsky (1908) was convinced that stromatolites are organic, even though he could not prove it and was unsure which organisms were responsible (although he suspected simply organized plants). Consequently, his definition requires having to demonstrate biogenicity. This is not a problem in stromatolites that preserve the organisms responsible for their formation, such as skeletal stromatolites, but it can be difficult in other types. However, interpretation of microbial carbonate fabrics, including microfabrics, is improving and can provide the ability to achieve the level of confidence required to apply Kalkowsky's (1908) definition. There will, of course, be examples in which preservation will be inadequate, and in these cases uncertainty can be indicated by 'possible, probable' prefixes. This is no different from the difficulties involved in recognizing other fossils; the fact that we cannot always confidently recognize fossils in all geological situations does not prevent us usefully defining them. But it remains necessary to realize the difficulties and to apply biogenic criteria rigorously.

It could be, therefore, that not only the oldest but also the best definition of stromatolite is that of Kalkowsky (1908) which can simply be restated: '*a stromatolite is a laminated benthic microbial deposit*' (Riding, 1991b, 2000). This adds stromatolite to the suite of microbial deposits distinguished according to their differing macrofabrics, stromatolite, thrombolite, dendrolite and leiolite, with microbialite as the overarching term.

Varieties

Carbonate stromatolites vary considerably in origin and components, and also in quality of lamination. Episodic, even accretion promotes layering, including lamination (Table 4; Braga *et al.*, 1995), and may be related to seasonal growth, periodic sedimentation or both. Lamination (Gerdes *et al.*, 1991) is a key characteristic of stromatolites, and distinct and continuous lamination is typical of most Precambrian stromatolites (Walter, 1972, p. 11). It is disrupted by desiccation in intertidal to supratidal environments, and by bioturbation. Layering is thicker, and may be crude, where components are large and/or erect, as in skeletal stromatolites and dendrolites. In agglutinated stromatolites, crude lamination may be a direct result of coarse sediment supply (Walter, 1972, p. 6, fig. 4), but also suggests irregular and uneven accretion (Braga *et al.*, 1995).

Skeletal stromatolite. Stromatolites 'in which the organisms responsible for its formation are commonly preserved as calcified fossils' (Riding, 1977; also porostromate stromatolite, Monty, 1981). It is arguable whether the term skeletal is appropriate for microbial fossils (Golubic & Campbell, 1981), but it conveys the relative distinctiveness and rigidity of these calcified microbes, mainly cyanobacteria. The resulting frames also contain biofilms, trapped particles and early cements. Skeletal oncoids are widespread in Palaeozoic and Mesozoic marine environments, and in modern calcareous streams. Skeletal stromatolites appear less common, possibly because the erect filaments that usually form them disrupt lamination and thereby create dendrolitic fabrics.

Table 4. Major dome and column categories of microbial carbonates comparing macrofabrics and accretion patterns.

Term	Macrofabric	Accretion
Stromatolite	laminate	episodic
Thrombolite	clotted	irregular
Dendrolite	dendritic	irregular
Leiolite	aphanitic	irregular

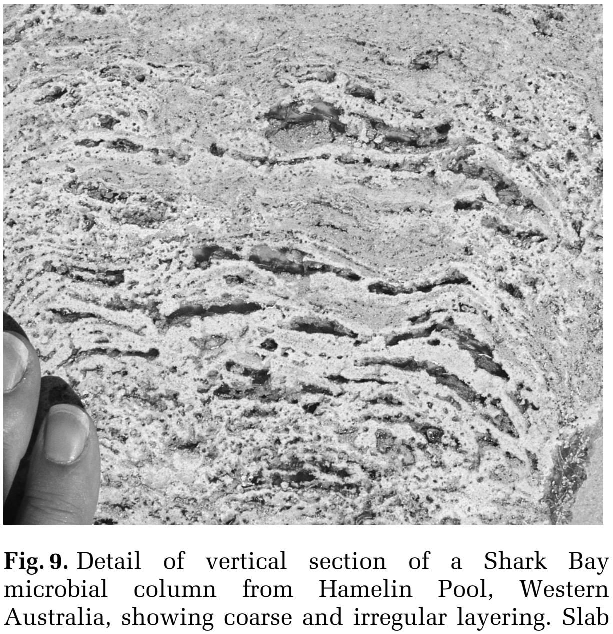

Fig. 9. Detail of vertical section of a Shark Bay microbial column from Hamelin Pool, Western Australia, showing coarse and irregular layering. Slab supplied by R. V. Burne.

Agglutinated stromatolite. 'Produced by the trapping/binding of particulate sediment' (Riding, 1991b). They may incorporate grains of any size from micrite to gravel, but are most readily recognized where the grains are silt-sized or coarser (Fig. 2). Increased coarseness appears to correlate with cruder layering, and coarse-grained microbial domes and columns are often at least partly thrombolitic, as in the famous Shark Bay (Fig. 9) and Lee Stocking Island examples. Ancient examples of coarse-grained domes are still remarkably rare (see Riding *et al.*, 1991b; Martín *et al.*, 1993; Braga *et al.*, 1995).

Fine-grained stromatolite. Interpretation of fine-grained stromatolites is a challenge. Are they agglutinated or precipitated (Fairchild, 1991), and which microbes were involved (Riding & Sharma, 1998)? These questions are compounded, especially in the Proterozoic, by the formation of a variety of distinctive morphotypes, such as digitate forms and large inverted cones, that lack direct modern analogues. Laminar intertidal stromatolites are also commonly at least partly fine grained. They occur in a variety of modern tropical environments, from the humid shores of Andros Island, where they pass laterally towards freshwater marsh with calcified cyanobacteria (Monty, 1967; Monty & Hardie, 1976), to evaporative sabkhas (Shinn, 1983b), and may be largely agglutinated. However, Neogene examples of fine-grained stromatolitic crusts and layers in coral and algal reefs could be largely precipitated (Riding *et al.*, 1991c; Montaggioni & Camoin, 1993; Reitner, 1993; Braga *et al.*, 1996), and offer both a reminder of the continuing significance of microbial carbonates in tropical reefs and a key to the past.

Tufa stromatolite. Freshwater fluviatile tufas locally exhibit oncoids (Fritsch, 1959) and thick laminated crusts formed by calcified cyanobacteria (Pentecost, 1978; Pedley, 1990) in which calcification appears largely to be by encrustation of the sheath (Merz-Preiβ & Riding, 1999). These tufa stromatolites are therefore mainly produced by precipitation of minerals on, rather than in, organic tissue (Riding, 1991b). This distinguishes them from skeletal stromatolites. However, both the specific site of precipitation and the quality of lamination differ according to environment and organisms (see 'Tufa mounds', below), and impregnation appears more common in lacustrine cyanobacteria. Tufa can include calcified algae such as *Cladophora*, *Gongrosira*, *Oocardium* and *Vaucheria* (see Wallner, 1934; Golubic, 1976) that coarsen the fabric. Locally, large tufa bioherms constructed by green algae (probably *Cladophora*) form in association with stromatolitic crusts, as in the Miocene Ries Crater Lake of southern Germany (Wolff & Füchtbauer, 1976; Arp, 1995). In lakes, tufa crusts with significant microbial (particularly cyanobacterial, diatom and green algal) components can form complex metre-scale domical mounds, for example those in Green Lake, New York (Eggleston & Dean, 1976). Cyanobacterial and associated tufa can record environmental and climatic information in stable carbon and oxygen isotope values (Andrews *et al.*, 1997).

Terrestrial stromatolite. Laminar calcretes formed by microbial activity have been termed lichen (Klappa, 1979), terrestrial (Wright, 1989) and subaerial stromatolites (Riding, 1991b). Although efforts have been made to discriminate between laminar calcrete and stromatolite (Read, 1976), and no doubt processes such as evaporation contribute significantly to $CaCO_3$ precipitation in calcretes, the local importance of microbes in calcrete formation (e.g. Krumbein, 1968) justifies the view that some calcretes may be regarded as microbial deposits (Wright, 1989; and see 'Microbial calcretes', below).

Thrombolite

Definition

Thrombolite (Greek: *thrombos*, clot; *lithos*, stone), defined on the basis of Cambro-Ordovician examples of the southern Canadian Rocky Mountains (Aitken, 1967; also see Aitken, 1966), has a macroscopically clotted fabric (not to be confused with clotted *microfabric*). Thrombolite clots, more-or-less discrete rounded to irregular patches that differ in colour and/or texture from intervening areas, create a blotchy, generally unlayered, mesoscale fabric. Clots range from diffuse to distinct, and from primary to secondary. Thus, clottedness, as a character, is broader and less readily defined than lamination. As a result, although the term thrombolite has become almost as well known as stromatolite, there is some confusion surrounding it, deriving from the variety of fabrics and origins it encompasses.

Varieties

Some thrombolites, like stromatolites, are primary products of microbial calcification or agglutination. They appear to be essentially subtidal and form columns, domes, layers and thick crusts (e.g. Pratt & James, 1982; Riding *et al.*, 1991b; Armella, 1994; Kennard, 1994), but are characteristically domical metre-scale doughnut-like masses that have been termed calyptrae (Luchinina, 1973; Rowland & Gangloff, 1988; kalyptrae). Thrombolites may prove to be locally important in the Proterozoic (Aitken & Narbonne, 1989), but currently are best known to become conspicuous near the Proterozoic–Cambrian boundary (e.g. Schmitt & Monninger, 1977), and were important throughout much of the Cambrian and Early Ordovician (e.g. Armella, 1994; Kennard, 1994). The view that thrombolites could be bioturbated stromatolites, and that Late Neoproterozoic – Early Palaeozoic thrombolite formation represented a response by stromatolites to metazoan disturbance (Walter & Heys, 1985), is at odds with the evident skeletal nature of many Early Palaeozoic thrombolites (see Kennard & James, 1986; Pratt & James, 1982; Walter, 1994), although some Neogene agglutinated thrombolites do appear bioturbated. Reports of post-Ordovician thrombolites are sporadic (see Kennard & James, 1986), although they were locally important in the Jurassic (Leinfelder *et al.*, 1993; Leinfelder & Schmid, 1999). Feldmann & McKenzie (1998) suggested that ancient thrombolites may represent eukaryotic structures. This could well apply to Late Miocene agglutinated thrombolites (Riding *et al.*, 1991b), but is unsupported for Early Palaeozoic examples dominated by *Epiphyton–Renalcis–Angusticellularia* group calcified microbes.

Calcified microbial thrombolites. Thrombolite fabric can be produced by microbial calcification. Examples in the Lower Palaeozoic (Kennard & James, 1986) typically display well-defined clots (Fig. 10) and were probably formed by cyanobacteria, as were dendrolites.

In oblique or transverse sections, dendrolite fabric appears thrombolitic. Nonetheless, many Early Palaeozoic thrombolites are not so evidently formed by calcified microbes (see Kennard, 1994), and it remains to be seen just how these examples, and also the 'type' thrombolites of Aitken (1967), some examples of which show diffuse poorly defined clotted fabrics, have formed. Present-day examples associated with sponge-tissue degradation (Reitner, 1993; Reitner *et al.*, 1995) should shed some light on the complex processes whereby bacterial calcification produces thrombolitic and other fabrics.

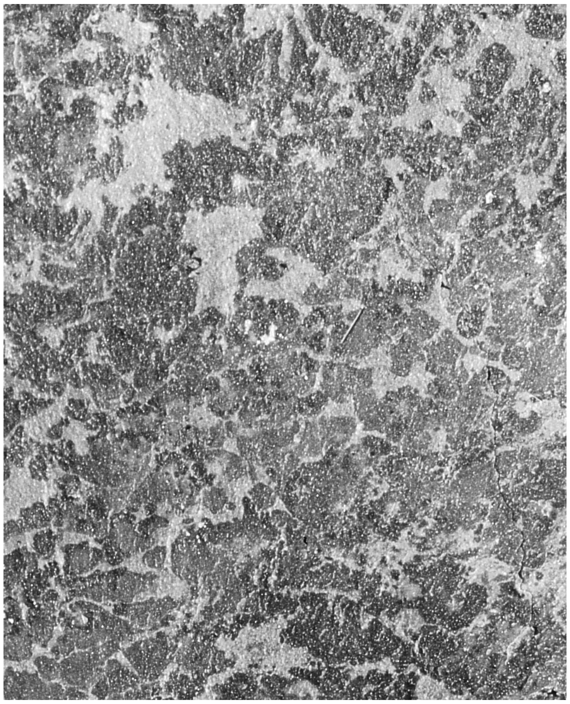

Fig. 10. Thrombolite formed by probable calcified cyanobacteria including *Tarthinia*. Lower Cambrian Lie de Vin Series, near Tiout, Morocco (see Latham & Riding, 1990). Width of view, 5 cm.

Coarse agglutinated thrombolites are best documented in the Late Miocene of SE Spain (Fig. 11; Martín *et al.*, 1993; Braga *et al.*, 1995; Feldmann & McKenzie, 1997) and show similarities to present-day Shark Bay and Lee Stocking Island domes (Riding *et al.*, 1991b). They incorporate sand- and even gravel-sized oolitic and bioclastic sediment, and commonly exhibit complex internal variation that includes stromatolitic, crudely layered blotchy, or relatively structureless fabrics. Blotchy agglutinated fabrics could be due to the coarseness of the sediment (Walter, 1972, p. 6), uneven accretion (Braga *et al.*, 1995) or other factors, including bioturbation. It has long been recognized that Shark Bay columns are often not well laminated (Fig. 9; Logan, 1961), although they are widely termed stromatolites. However, coarse agglutinated Neogene domes evidently differ from Early Palaeozoic thrombolites that are dominantly calcified microbial in structure, and do not usually display such relatively well-defined clots (but see Feldmann & McKenzie, 1998). Further work may recognize the blotchy appearance of Neogene examples as a distinct fabric type, but at present they can be regarded as a variety of thrombolite.

Arborescent 'thrombolites'. Palaeozoic thrombolites are commonly associated with decimetric dendritic fabrics (larger than dendrolite fabric which is typically centimetric) that have also been termed thrombolite (e.g. Schmitt & Mon-

Fig. 11. Coarse-grained, mainly oolitic, agglutinated composite leiolite–stromatolite–thrombolite domes. Messinian (Upper Miocene), Joyazo, Almería, Spain (see Riding *et al.*, 1991b). The dome in the left foreground is ~1 m wide.

Fig. 12. Dendrolite with dark centimetric bush-like fabrics formed by the probable calcified cyanobacteria *Gordonophyton* and *Tarthinia*. Mid-Cambrian Zhangxia Formation near Jinan, Shandong, China. Width of view = 14 cm.

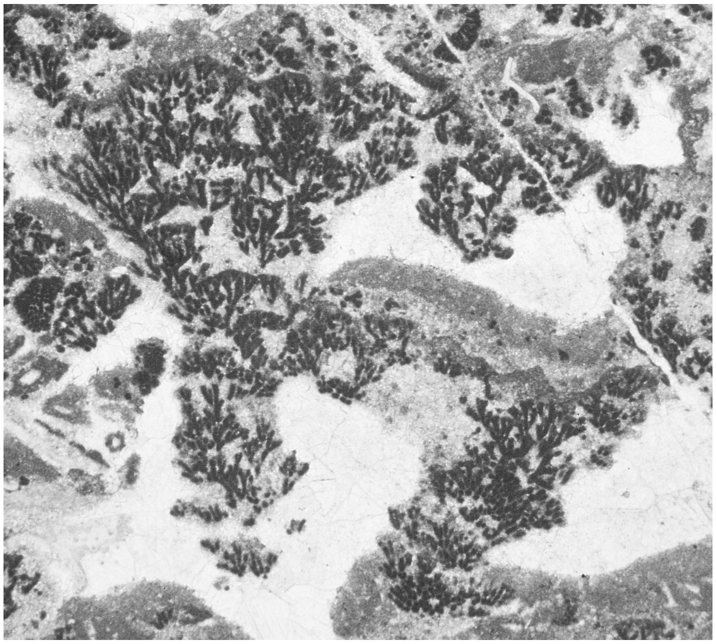

Fig. 13. Photomicrograph of dendrolite skeletal framework mainly formed by the probable calcified cyanobacteria *Gordonophyton*. Mid-Cambrian Zhangxia Formation near Jinan, Shandong, China. Plane polarized light. Width of view = 8·5 mm.

ninger, 1977; Pratt & James, 1982; Armella, 1994; type 1 of Kennard, 1994). Similar fabrics occur in the Jurassic (Leinfelder *et al.*, 1993). These show a transitional relationship with thrombolites, and also possibly with dendrolites.

Tufa thrombolites (new term). Just as intense $CaCO_3$ encrustation on organic surfaces generates distinctive tufa stromatolite fabrics, clotted fabrics can form in freshwater lakes and streams (Moore & Burne, 1994). At Kelly Lake, British Columbia, Ferris *et al.* (1997) suggested that thrombolitic fabrics reflect a greater degree of calcification than in stromatolites.

Post-depositional thrombolites. Clotted macrofabrics can be syndepositionally produced, diagenetically enhanced or diagenetically created. This adds a dimension to thrombolite studies that does not appear to apply to stromatolites. Some of the blotchy fabrics in Neogene agglutinated thrombolites resemble bioturbation patterns, and clots in skeletal thrombolites are commonly diagenetically enhanced by partial recrystallization and/or replacement, including selective dolomitization of matrix between clots (Fig. 10). Clotted fabrics in carbonates appear in some cases to develop secondarily, as in some Late Proterozoic 'thrombolites' (e.g. Mesoproterozoic Wumishan Fm, near Beijing, China).

Dendrolite

Definition

Dendrolite (Greek *dendron*, tree; *lithos*, stone; Riding, 1991b, p. 34) has a macroscopic centimetric bush-like fabric (Fig. 12), typically produced by calcified microbes. Dendrolites, like stromatolites and thrombolites, form large domes

Fig. 14. Tufa pinnacles formed by precipitation localized by calcium-rich spring-water entering an alkaline lake subaqueously. Fall in lake-level has exposed the pinnacles, which are each approximately 0·5–1 m diameter. Mono Lake, California.

and columns, and also extensive reefal masses that may be organized into large ovoid doughnut-like calyptrae. Unlike stromatolites and thrombolites, they are only known to form by microbial calcification, and not by agglutination of particles.

Varieties and distribution

Like thrombolites, dendrolites in hand-specimen consist of areas differing in colour and/or texture from intervening areas. But whereas in thrombolites these areas are rounded to irregular, in dendrolites they are bushy or tree-like, with vertically erect or radial orientation. Dendrolites lack lamination, but are commonly layered, reflecting irregularity in accretion. This results in coarse but well-defined layering in domes and columns. Regular accretion produces massive deposits as in some Early Cambrian reefs. The constituent dendroids range from small shrub-like forms to elongate radial fingers that grade towards arborescent forms that have been regarded as thrombolites (see 'Arborescent thrombolites', above). In oblique or transverse section, dendrolites resemble thrombolites.

Although 'dendriform' stromatolites (Aitken, 1989) and *Angusticellularia*-like calcified fossils (Turner *et al.*, 1993) are known from the Neoproterozoic, the earliest documented dendrolites remain Early Cambrian. They are best known from rocks of Cambrian to Early Ordovician and Late Devonian age, where they are built by calcified microbes belonging to one or more of the *Epiphyton*, *Renalcis* and *Angusticellularia* groups (Fig. 13; Riding, 1991b). In these time intervals, dendrolites were commonly major reef builders, either on their own or in association with sponges, such as archaeocyaths and *Archaeoscyphia* in the Cambrian – Early Ordovician and stromatoporoids in the Devonian (e.g. Mountjoy & Riding, 1981).

Leiolite

Definition

Leiolite (Greek *leios*, uniform or smooth, *lithos*, stone) has a relatively structureless, aphanitic, macrofabric lacking clear lamination, clots or dendritic fabrics. The term is founded on examples in the Late Miocene of SE Spain (Braga *et al.*, 1995, p. 347) where leiolites form large domes in association with stromatolites and thrombolites (Fig. 11). Leiolite fabric may reflect irregular accretion (Table 4) and/or compositional homogeneity, as in well-sorted oolite sand (Braga *et al.*, 1995) and in micritic reefal crusts, for example in Jurassic sponge reefs (Leinfelder *et al.*, 1993; Dupraz & Strasser, 1999; Leinfelder & Schmid, 1999).

The temptation to give microbial crusts and domes a well-known label, such as stromatolite or thrombolite, may have obscured the fact that many of these deposits lack the macrofabrics implied by such names. 'Stromatolitic' crusts are sometimes only weakly laminated (e.g. Riding *et al.*, 1991c, fig. 9b), and well-known modern domes and columns, such as at Shark Bay and Lee Stocking Island, include portions that appear leiolitic.

Other categories

Large homogeneous concentrations, exemplified by stromatolite, thrombolite and similar domes and masses, are not the only significant deposits of microbial carbonates, although they are perhaps the most noticeable. Many other microbial carbonates (Table 2) are commonly, although not always, intimately associated with carbonates of other origins. They can be locally important in spring, soil and cave deposits, as coated grains in a variety of depositional environments, in benthic sediments accumulated from water-column precipitation and in intergranular deposits, including cements. All deserve far fuller treatment than I can attempt here.

Spring microbial carbonates

Hot-spring travertine. As hot groundwater charged with calcium and bicarbonate in solution reaches the surface, pressure reduction, cooling and evaporation promote evasion of CO_2. Precipitation is localized around the vents, and lateral facies change is rapid as precipitated crusts give way to pool and marsh deposits (Guo & Riding, 1999). These travertines are exemplified by Mammoth Hot Springs (Wyoming), Rapolano Terme (Tuscany), and Pamukkale (western Turkey). Close to vents they appear mainly abiogenic, although microbial carbonates locally form close to springs (Guo & Riding, 1992b) and as crusts on $CaCO_3$ crystal layers (Guo & Riding, 1992a). The suggestion that small shrub-like precipitates in travertine pools and marshes are microbial (Chafetz & Folk, 1984) has some support from petrographic (Guo & Riding, 1994) and isotope studies (Guo *et al.*, 1996), but see also Pentecost (1990), Jones & Renaut (1995) and Chafetz & Guidry (1999).

Tufa mounds, pinnacles and towers. Spectacular carbonate towers form where calcium-rich spring water emerges subaqueously in alkaline lakes, triggering precipitation of $CaCO_3$ minerals. Well-known examples include Pyramid Lake, Nevada (Benson, 1994), Searles Basin, California (Scholl, 1960), Lake Van, Turkey (Kempe *et al.*, 1991), and Mono Lake, California (Fig. 14). Microbial activity has been suggested as a major factor in the precipitation of alkaline lake spring tufas (e.g. Scholl & Taft, 1964; Kempe *et al.*, 1991), but it seems likely that physicochemical processes based on mixing of spring and lake waters should be the principal factor localizing precipitation, although microbes are likely to have a significant role in determining microfabric. However, early diagenetic changes, such as ikaiite to calcite transformation, can seasonally destroy primary fabrics in cold lakes (Shearman *et al.*, 1989).

Microbial calcretes

In terrestrial stromatolites, cyanobacteria, fungi and lichens can be important influences on precipitation, mineralogy and fabrics, including the formation of micritic and microscopic dendritic, needle and spherulitic fabrics (Jones & Kahle, 1985, 1986; Jones & Wilson, 1986; Wright, 1986; Jones & Pemberton, 1987; Wright *et al.*, 1988; Verrecchia & Verrecchia, 1994; Verrecchia *et al.*, 1995). Larger vadoid nodules also form and can be confused with subaqueous oncoids (see Peryt, 1983a).

Microbial cave surface deposits

Cave crusts can support microbial populations that variously influence precipitation, mineralogy, solution, alteration and fabrics of carbonate deposits (Jones, 1995, 1999). An example is moonmilk (Mondmilch), a soft paste-like or powdery deposit in which microbes occur (Thrailkill, 1976; Gradzinski *et al.*, 1997) and from which calcifying bacteria have been isolated (Mason-Williams, 1959).

Microbially coated grains

Oncoids (Onkoid, from Greek *onkos*, nodule, Heim, 1916, p. 566) are unattached spherical stromatolites (oncolites, originally Pia, 1927, p. 37) that were widespread in ancient marine environments until at least the Jurassic or Cretaceous (Peryt, 1983b). Modern marine examples are scarce, but heavily calcified cyanobacterial oncoids are common in unpolluted calcareous lakes and streams. Some micrite envelopes on grains (Bathurst, 1966; creating cortoids, Flügel, 1982) may be microbial coatings.

Microbial intergranular and 'diagenetic' deposits

The influence and importance of microbes in a wide range of early diagenetic precipitation and transformation involving carbonate minerals, including cementation, concretion formation, dolomite formation, recrystallization and replacement, has long been realized. Many details remain to be elucidated (see, e.g. Berner, 1971a,b; Irwin *et al.*, 1977; Jones, 1985; Compton, 1988; Middleburg *et al.*, 1990; Vasconcelos *et al.*, 1995; De Craen *et al.*, 1999; Wright, 1999; Machel & Foght, 2000)

Microbial whiting deposits

These micrite to silt-grade precipitates are best known, as benthic deposits, from lacustrine varve-like layers, where organic-, silica- (diatom frustules) and carbonate-laminae alternate, reflecting seasonal variations in surface water productivity and precipitation (e.g. Kelts & Hsu, 1978). The carbonate laminae incorporate calcified algae (*Phacotus*) but the dominant fraction is made up of calcite rhombs (Fig. 4) and other aggregates, mainly less than ~20 µm in size, that have often been suggested to have a microbial origin (see 'Processes, Whiting precipitation').

TIME TRENDS

It is to be expected that over 3500 Myr microbial carbonates will have changed, as microbes and other organisms evolved and Earth-surface environments altered (Fig. 15). The classic view is that microbial carbonates, largely in the form of stromatolites, were widespread and abundant during much of the Precambrian, but that Phanerozoic competition from metazoans and other eukaryotes progressively relegated them to environmentally protected refuges, such as intertidal flats in general, and hypersaline Shark Bay in particular. How true is this, what changes can we perceive in the character, abundance and distribution of microbial carbonates in space and time, and to what extent can controlling factors be disentangled?

Archaean–Proterozoic

Origination

Carbon-isotope values in the Isua Group of southern Greenland are evidence for the existence of microbes at 3800 Ma (Schidlowski, 1988), but currently the oldest tangible fossils are bacteria-like filaments comparable in size to cyanobacteria, in cherts in the ~3450-Ma Towers Formation of the Warrawoona Group of Western Australia (Awramik *et al.*, 1983). Stromatolites are present in the same unit (Lowe, 1980); thus, neatly, the oldest microbes and oldest microbial carbonates co-occur. However, doubts have been raised about the biogenicity not only of these Warrawoona stromatolites but of all stromatolite-like structures older than 3200 Ma (Lowe, 1994). The balance of opinion continues to favour

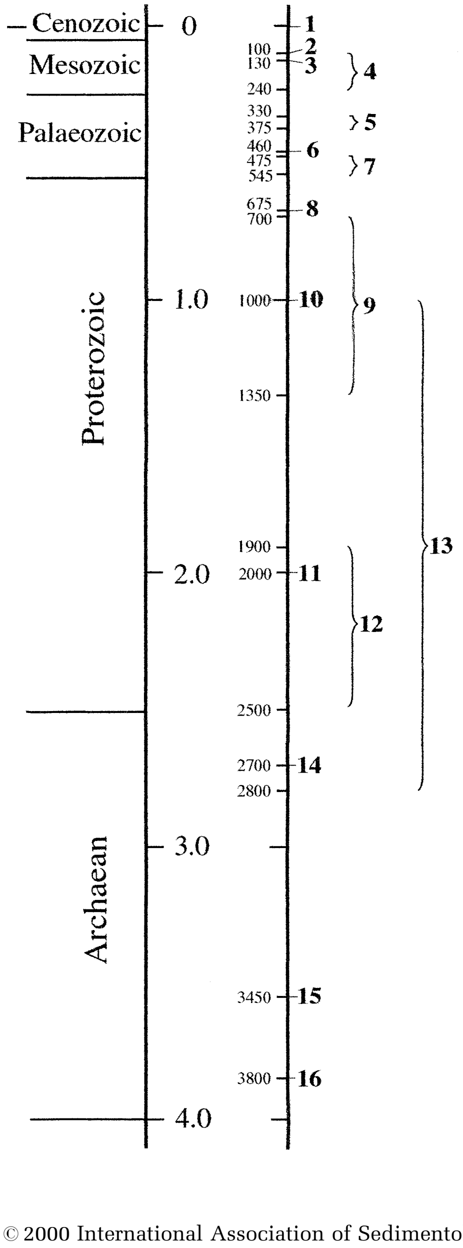

Fig. 15. Key developments in the history of microbial carbonates. Cyanobacterial calcification episodes (CCEs): Riding (1994b). Time-scale: Harland *et al.* (1990), except for base of Cambrian (Bowring *et al.*, 1993). **1**: 0–6 Ma, Late Neogene micritic reef crusts and coarse domes-columns. **2**: 100 Ma, Late Mesozoic decline of marine microbial carbonates. **3**: 130 Ma, first diatoms (Tappan, 1980). **4**: 100–240 Ma, Mid-Triassic to Early Cretaceous CCE. **5**: 330–375 Ma, Late Devonian to Early Carboniferous CCE. **6**: 460 Ma, stromatolite decline (Fischer, 1965). **7**: 475–545 Ma, Cambrian – Early Ordovician CCE, abundant thrombolite–dendrolite. **8**: 675 Ma, stromatolite decline (Awramik, 1971). **9**: 700–1350 Ma, Late Proterozoic CCE. **10**: 1000 Ma, stromatolite decline (Walter & Heys, 1985). **11**: 2000 Ma, stromatolite decline (Grotzinger, 1990). **12**: 1900–2500 Ma, Early Proterozoic CCE. **13**: 1000–2800 Ma, Late Archaean – Proterozoic stromatolite acme. **14**: 2700 Ma, definite cyanobacteria, probable algae (Brocks *et al.*, 1999). **15**: 3450 Ma, first stromatolites (Lowe, 1980), probable cyanobacteria (Awramik *et al.*, 1983). **16**: 3800 Ma, isotope evidence of microbes (Schidlowski, 1988).

their being microbial (Buick *et al.*, 1995; Hofmann *et al.*, 1999; Hofmann, 2000), but this debate is a reminder of the need for objective biogenicity criteria for ancient stromatolites (see Buick *et al.*, 1981; Walter, 1994, pp. 272–274).

Reports of Archaean stromatolites increased from 11 in 1980 (Walter, 1983) to 32 in the latest compilation (Hofmann, 2000). Nonetheless, their significance continues to outweigh their number, because they record all that is currently known about microbial carbonates during a critical 1000 Myr of early Earth history. The oldest examples are domes, cones and layers in chertified limestones and dolostones. Their typical sedimentary settings, ephemeral often evaporative basins on small cratons subjected to prolonged volcanism, might be a reason for their scarcity (Walter, 1994). Similarly, marked increases in stromatolite abundance, size and diversity at about 2800 Ma (Walter, 1994; Hofmann, 2000) could reflect increased craton size and more stable conditions.

Fig. 16. Microdigitate stromatolites less than 1 cm in height in partly silicified dolomite. Mid-Mesoproterozoic (~1300 Ma) lowermost Wumishan Formation, near Jixian, northern China. Width of view = 13 cm.

Acme

Twenty or more stromatolite morphotypes have been recorded from the late Archaean (Hofmann, 2000). The scale and diversity of this development, for example in the Cambellrand part of the Transvaal Supergroup of South Africa (Beukes, 1987), sets the scene for the Early Proterozoic. The immense period from 2800 Ma to the end of the Mesoproterozoic (1000 Ma) was the Golden Age of stromatolites. Diverse morphotypes, ranging from stratiform and microdigitate stromatolites (Fig. 16) on tidal flats, through shallow subtidal domes and branching columns (Fig. 8), to deep-water cones, participated extensively in the creation of carbonate platforms and the first extensive reefs (Hoffman, 1974; Grotzinger, 1989; Fig. 17). Sea-floor carbonate precipitates complicate interpretation of Archaean and Early Proterozoic stromatolites (Grotzinger, 1994; Grotzinger & Knoll, 1999; Sumner, 2000). An example is the microdigitate forms with distinctive radial fibrous microfabric that first became abundant at about 2700 Ma (Hofmann, 2000). They have been given Linnaean-style names, such as *Asperia* and *Pseudogymnosolen* (Liang *et al.*, 1985), but have also been termed tidal-flat tufas (Grotzinger & Read, 1983), and there has been debate about their biogenicity (in favour: Grey & Thorne, 1985; against: Hofmann & Jackson, 1987).

Fig. 17. Detail of a bioherm composed of *Baicalia*-type stromatolites. Bhander Limestone, possibly ~1000 Ma, near Satna, Madhya Pradesh, India.

Proterozoic stromatolite decline

It could be argued that it is less remarkable that stromatolites eventually declined, than that they prospered for so long. Nonetheless, probably the most evident and remarked upon aspect of microbial carbonate history is the decline of stromatolites from their 2800–1000 Ma acme. Treatment of this topic resembles that of the Decline and Fall of the Roman Empire: was it inevitable, was it quick, when did it start, were the causes simple or complex? Discussion of possible reasons clearly necessitates establishment of the essential facts; but this is easier said than done. Fischer (1965, pp. 1208–1209) and Cloud & Semikhatov (1969) noted stromatolite decline, but they recognized it from the mid-Ordovician onwards. This raises the question whether Proterozoic decline simply continued into the Early Palaeozoic (there was certainly dramatic decline from the Late Cambrian to Late Ordovician), or whether there was significant Early Palaeozoic recovery, not only of microbial carbonates in general, owing to the spectacular rise of dendrolites and thrombolites, but of stromatolites too. There is some evidence to support this latter view.

Proterozoic stromatolite decline was first clearly recognized from examination of stromatolite taxonomic data. Precambrian stromatolites provided rare potential for the subdivision and correlation of sedimentary sequences otherwise lacking in macrofossils. Their abundance and, in particular, their variety of shape fostered taxonomic studies with a practical aim: Proterozoic biostratigraphy. This approach, pioneered on sequences in the northern Urals and Siberia (see Cloud & Semikhatov, 1969; Semikhatov, 1980), was applied widely (see Bertrand-Sarfati & Walter, 1981) but raised many questions. Are stromatolite taxa consistently defined? Does stromatolite shape reflect organisms (Fenton & Fenton, 1937, p. 1941), environment (Logan *et al.*, 1964), abiogenic accretion patterns (Grotzinger & Rothman, 1996; Grotzinger & Knoll, 1999) or combinations of these (Serebryakov, 1976)? Which is more significant: microfabric, macrofabric or external shape? Does the stratigraphy work and, if so, is it because the microbes evolved or because the environments changed with time, or both? It has been suggested that external morphology mainly reflects environmental controls whilst microfabric reflects organic influences (see Semikhatov & Raaben, 1999), but the details of these questions have still largely to be resolved.

Nonetheless, stromatolite taxonomy proliferated numerous quasi-Linnaean form-genera and -species which, if the uncertainties are overlooked, represent an impressive data set. Plots of stromatolite taxa revealed a dramatic latest Proterozoic decline, commencing at ~675 Ma, that coincided with the current perceptions of metazoan evolutionary diversification (Awramik, 1971). Subsequent re-examination of these data suggested that decline commenced earlier, near 1000 Ma, although it remained sharpest later in the Neoproterozoic (Walter & Heys, 1985). However, qualitative abundance data suggest a much earlier commencement of decline near 2000 Ma (Grotzinger, 1990, fig. 6; Grotzinger & Knoll, 1999, p. 345, fig. 11). Thus, the bare bones of these various assessments suggest that stromatolite decline commenced either at 2000, 1000 or 675 Ma. Despite these disparities, and the continuing uncertainties about the significance of the taxonomic data, there is widespread agreement that stromatolite abundance and morphological diversity was much reduced after ~1000 Ma (Meso-Neoproterozoic boundary), and that microdigitate and coniform varieties in particular became far less common (Walter *et al.*, 1992, p. 259).

Phanerozoic

Despite possible Neoproterozoic (Aitken & Narbonne, 1989) and Palaeoproterozoic (Grotzinger & Hoffman, 1983) antecedents, thrombolites appeared dramatically near the base of the Cambrian, prompting initial suggestions that they might represent burrowed stromatolites, but more closely reflecting the development of abundant calcified microbes, particularly the *Epiphyton*, *Angusticellularia* (= *Angulocellularia*) and *Renalcis* groups (Riding, 1991b). During the Cambrian and Early Ordovician, thrombolites and dendrolites participated extensively in reef formation, either in association with metazoans such as archaeocyaths or alone (Copper, 1974). Stromatolites also remained important, and may have been relatively more abundant during the Late Cambrian (Zhuravlev, 1996), but they contrast with typical Proterozoic stromatolites: the distinctive coniform and microdigitate forms had disappeared, branched stromatolites were scarce and columnar forms often show thrombolitic interiors (Kennard, 1994, fig. 3). The Early Palaeozoic thus marked both a recovery for microbial carbonates and an alteration in their character.

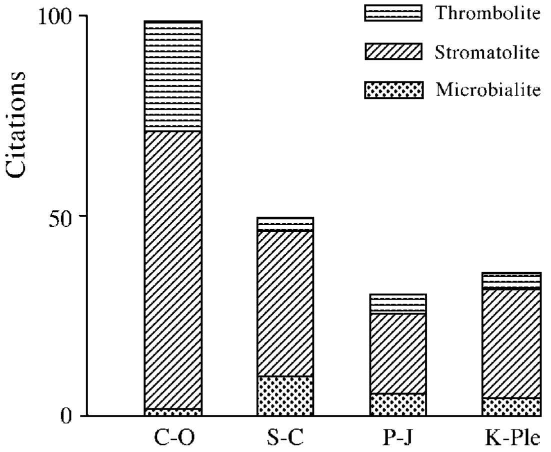

Fig. 18. Numbers of GEOREF citations (August 1999) of 'microbialite', 'stromatolite' and 'thrombolite' for four Phanerozoic intervals: Cambro-Ordovician 106 Myr, Silurian–Carboniferous 149 Myr, Permian–Jurassic 144 Myr, Cretaceous–Pleistocene 146 Myr (Harland *et al.*, 1990). These rough data suggest rapid initial decline followed by relatively minor changes in abundance of microbial carbonates during the remainder of the Phanerozoic.

The mid-Ordovician appearance of bryozoans, tabulate corals, stromatoporoid sponges and other skeletal metazoans was a major change for reef-building (Fagerstrom, 1987, p. 343). However, stromatolites remained both important and conspicuous in reefs, as in those of the Chazy of Quebec and Vermont (Pitcher, 1964), and detailed studies of younger reefs throughout much of the remainder of the Palaeozoic and Mesozoic usually reveal the continuing importance of microbial carbonates up until the present day, as perceptively noted by Pratt (1982a,b; see also Fagerstrom, 1987; Geldsetzer *et al.*, 1988; Monty *et al.*, 1995; Webb, 1996). This can be briefly demonstrated from just a few examples, including older literature: Silurian of England (Scoffin, 1971) and Alaska (Soja, 1994); Devonian of Western Australia (Wray, 1967); Carboniferous of Japan (Ota, 1969); Permian Capitan reef complex (Babcock, 1977); Triassic of the Dolomites (Fois & Gaetani, 1984); Jurassic of southern Germany (Gwinner, 1976); Cretaceous of Arizona (Scott, 1981). However, microbial carbonates appear to have been scarcer in the Palaeogene (see Webb, 1996, pp. 955–956). Miocene revival is largely focused on the Mediterranean area, which could represent unusual conditions. Nonetheless, sites in SE Spain present instructive examples of coarse-grained stromatolites, thrombolites, leiolites (Fig. 11) and also micritic reefal crusts (Riding *et al.*, 1991b,c; Martín *et al.*, 1993; Braga *et al.*, 1995, 1996).

It is tempting therefore to suggest that the stromatolite decline from the mid-Ordovician onwards, noted by Fischer (1965), actually marks the time when microbial carbonates became subsumed within (or themselves subsumed!) algal–metazoan reefs. Plots of references to microbial carbonates, albeit based on crude data, support the view that, following abrupt decline in the Early Palaeozoic, microbial carbonates exhibit no marked changes in abundance through the remainder of the Phanerozoic (Fig. 18). Nonetheless, a notable feature within this broad pattern is temporal variation in calcified microbe abundance (see 'Cyanobacterial calcification events'). Modern marine carbonate environments continue to host a diversity of microbial deposits (Browne *et al.*, 2000). These include stromatolite–thrombolite reefal crusts and matrices (Montaggioni & Camoin, 1993; Reitner, 1993; Webb *et al.*, 1998). Coarse-grained domes, such as at Shark Bay and Lee Stocking Island, may reflect changes in mat communities (see 'Microbial evolution', and 'Modern analogues' below).

Cyanobacterial calcification events

Supersaturation with respect to carbonate minerals varies environmentally in natural waters and directly affects microbial carbonate sedimentation, as can be seen by comparing tufa stromatolite formation in freshwater, at one extreme, with the absence of shallow-marine domical stromatolites from cold marine waters at the other. It has been suggested that variation in abundance of marine calcified cyanobacteria through geological time could reflect temporal variation in the saturation state of seawater (Riding, 1991a) and that cyanobacterial calcification events (CCEs; Riding, 1992) also broadly coincide with periods of unusual abundance of ooids and marine cements. These environmentally controlled calcification events (Riding, 1993) are especially marked in the Cambrian to Early Ordovician, Late Devonian and Permian–Triassic. If CCEs represent periods of elevated carbonate saturation, they may correspond with one or more of the following: high global temperature (which enhances precipitation rate); low sea-level and low skeletal abundance (which increase availability of calcium and bicarbonate); and development of alkalinity pumps from stratified basins

Fig. 19. Large molar tooth-shaped microbial column, partly buried by ooid sand dunes at a depth of 10 m in a channel between Lee Stocking Island and Norman's Pond Cay, Bahamas. Strong tidal currents supply sediment, deter competitors and may facilitate early lithification. Column top and sides are colonized by a diverse mat community (see Fig. 2).

(see Riding, 1993). Phanerozoic CCEs have been suggested to reflect saturation states > 0·8 (Merz-Preiß & Riding, 1999; and see Kempe & Kazmierczak, 1994). Instead of simple unidirectional decline, the temporal distribution of microbial carbonates appears patterned in response to fluctuations in seawater chemistry.

DISCUSSION

The Precambrian enigma

Episodic abundances shown by marine calcified cyanobacteria during the Phanerozoic (Fig. 15) are only weakly matched in the Proterozoic (Riding, 1994b), in which calcified cyanobacteria are unexpectedly scarce. Although a variety of microbes could have been involved in building Precambrian stromatolites, it has been widely assumed that cyanobacteria were the principal ones. With locally intense synsedimentary carbonate precipitation (Grotzinger, 1989), Proterozoic carbonates would be expected to incorporate abundant calcified cyanobacterial microfossils. Their actual scarcity has been termed the 'Precambrian enigma' (Riding, 1994b). A possible explanation is that cyanobacteria were less important than has been generally assumed in stromatolite formation in the early mid-Proterozoic (Riding, 1994b, p. 432; Riding & Sharma, 1998). Reduction in calcification potential (Grotzinger, 1990), and environmental impact such as increasing oxygen levels on noncyanobacterial bacteria, together may have contributed to Proterozoic stromatolite decline (Riding, 1997). However, additional factors, such as nucleation problems (Knoll *et al.*, 1993) or phosphate levels (Merz-Preiß, 2000), could well have been important.

Competition

Grazing, or competition for habitats, by eukaryotes has long been an attractive explanation for the perceived Precambrian abundance and relative Phanerozoic scarcity of stromatolites. One of the possible causes advanced by Fischer (1965, pp. 1208–1209) to account for stromatolite decline from the mid-Ordovician onwards was competition with algae, but although Monty (1973) supported algal competition as a factor, attention dramatically switched to invertebrates following Garrett's (1970) suggestion that gastropod grazing was responsible for the apparent restriction of well-developed microbial mats to intertidal environments on the Bahama Banks. This view of metazoan competition was greatly strengthened when Awramik (1971) related the sharp late Proterozoic reduction in stromatolite diversity to metazoan appearance and rapid diversification at, and just prior to, the Neoproterozoic–Cambrian boundary. The realization that microbial carbonates continue in importance during the Phanerozoic (Pratt, 1982b) has damaged this hypothesis less than might have been expected, possibly because Phanerozoic reefal microbial carbonates usually appear quite different from Precambrian stromatolites, and also because the occurrence of the Shark Bay columns in an environment that is at least seasonally hypersaline is an ever-present reminder of the concept of stromatolite survival in stressed refugia.

Competition is difficult to test. It has even been suggested (Vologdin, 1962; Monty, 1973, p. 603) that microbial competition with metazoans delayed metazoan radiation, and therefore that microbial decline in the Neoproterozoic may have favoured metazoan emergence. In the same vein, in Early Cambrian reefs where dendrolites are often volumetrically dominant, it has been suggested that archaeocyath sponges were outcompeted by calcified microbes (see Riding, 1997).

Refugia

A concept directly derived from that of metazoan competition, is that when and where metazoans are scarce, stromatolites will become more abundant. It is consistent with the relative abundance of marine stromatolites on desiccated tidal flats, and with the presence of *Cryptozoon*-like columns in Shark Bay where hypersalinity seasonally reduces potential grazers (Logan, 1961, p. 520). It is not necessarily weakened by the existence of even larger columns in normal-salinity waters at Lee Stocking Island (Dill *et al.*, 1986) because these can be regarded as current-stressed (Fig. 19). The concept has also been invoked to account for the unusual abundance of large microbial carbonate domes in the Western Mediterranean about the time of the Late Miocene Messinian Salinity Crisis (Martín & Braga, 1994). It can similarly be applied to intervals during the Phanerozoic when metazoans were temporarily reduced by mass extinction. This view of stromatolites as 'disaster forms' during the first 4–5 Myr of the Early Triassic, immediately following the end-Permian event, was suggested by Schubert & Bottjer (1992; but see Soja, 1994). However, it could also be that some of the conditions connected to extinction events, such as raised temperatures and/or the saturation state of seawater with respect to $CaCO_3$ minerals, actually favour microbial carbonate formation irrespective of competitive interactions (Riding, 1997).

Importance of lithification

A discrete hypothesis that can stand in opposition to that of eukaryote competition to account for the distribution of microbial carbonates in time and space is the microbial calcification model, emphasizing both the importance of calcification in the formation of microbial carbonates and the environmental factors that significantly control it. Recognition of the importance of lithification for microbial carbonates is not new. Walcott (1914), Logan (1961, p. 520), Fischer (1965), Monty (1973, p. 614; 1977, pp. 23–24), Serebryakov & Semikhatov (1974) and Gebelein (1976, p. 505), and more recently Ginsburg (1991, p. 32) and Reid & Browne (1991), have all in various ways stressed that microbial carbonate formation depends on early lithification as well as on processes such as grain trapping. Without calcification, microbial carbonates can neither form nor be maintained and preserved.

The microbial calcification model proposes that microbial calcification is essentially micritic, metabolically induced, but environmentally dependent, calcification of extracellular polymeric substances (EPS), as biofilm or sheath mucilage. This process produces both clotted (spongiostrome) fabrics and calcified (porostromate) fossils, accounts for most microbial carbonates and is postulated to be the principal factor, after microbial growth, controlling their distribution and abundance in time and space. This has a number of implications:

1 Agglutinated micritic stromatolites are geologically scarce, and are perhaps most widely seen in Cenozoic intertidal environments.

2 The majority of microbial micrite is neither particulate grains nor external cement, but represents initial internal, micritic calcification of organic tissue (biofilm and sheath) that is promoted by metabolic activity and environmentally facilitated.

3 Micritic impregnation results in the formation of both spongiostrome and porostromate fabrics.

4 The scarcity of recognizable calcified cyanobacterial sheath in clotted microbial micrites suggests that spongiostrome fabrics, including those in Precambrian stromatolites, are formed by calcification of EPS biofilms created mainly by noncyanobacterial bacteria.

5 Steep-sided micritic stromatolites in the Precambrian indicate early lithification, interpreted as biocalcification. If calcified cyanobacteria are scarce, it suggests that other bacteria were responsible for these deposits.

6 The history of microbial carbonates mainly reflects calcification potential, both biological and environmental.

7 Calcification outweighs metazoan competition in determining the abundance and distribution of microbial carbonates.

8 Trapping and binding (agglutination) of particulate sediment is a relatively minor process in the history of microbial carbonate formation.

If these inferences are substantially correct, then the temporal, and spatial, distribution of microbial carbonates should correspond to enhanced environmentally facilitated precipitation, such as ooids and early cements.

Microbial evolution

The significance of temporal changes in mat communities (Awramik *et al.*, 1976) for microbial carbonate history may have been underestimated,

Fig. 20. Shark Bay columns at Carbla Point, Hamelin Pool, Western Australia, stranded in the intertidal zone due to Holocene relative sea-level fall. The main columns developed subtidally but have acquired an intertidal caps (see Fig. 21). Columns are ~25 cm high. Photograph courtesy of S. M. Awramik.

probably because clear evidence of the impact of microbial evolution on carbonate deposition remains limited. The oldest microbial filaments at ~3450 Ma (Awramik *et al.*, 1983) are cyanobacterium-like. Oscillatoriacean-like filaments are present in the 2750-Ma Fortescue Group, also of Western Australia (Schopf & Walter, 1982). Biomarkers of similar age (2600–2700 Ma) confirm the presence of not only cyanobacteria but also eukaryotes, presumably algae, by this time (Brocks *et al.*, 1999). The earliest reported body-fossils of algae are 2100 Ma (Han & Runnegar, 1992). Although it seems reasonable to expect that algae should have been involved in Proterozoic stromatolites (Walter, 1972, pp. 90–91), there is still little information concerning occurrences of either algae or bacteria other than cyanobacteria in Proterozoic microbial carbonate communities (e.g. Walter *et al.*, 1992, p. 255; but see Riding & Sharma, 1998). At the same time, it is noteworthy that evidence for cyanobacteria is sparse in subtidal Proterozoic stromatolites (Grotzinger & Knoll, 1999, p. 349; but see Bartley, 1996). It has been assumed that stromatolite morphotypes reflect particular microbial communities (Fenton & Fenton, 1937, p. 1941) and suggested that microbial evolution is reflected by Proterozoic stromatolite fabrics and possibly morphotypes (Semikhatov *et al.*, 1979), although again there seems little firm evidence to support this (but see Awramik & Semikhatov, 1979; Knoll & Semikhatov, 1998). Nonetheless, the diversity of Proterozoic stromatolite shape and microstructure is striking and contrasts with the Early Palaeozoic.

Early Palaeozoic development of dendrolites and thrombolites may at least partly represent cyanobacterial evolution (Riding, 1994b). It has been suspected that microbial carbonates have progressively incorporated bacteria, cyanobacteria and algae (Riding, 1991b; Walter, 1994; Fig. 8), yet there is little specific evidence (but see Feldmann & McKenzie, 1997) of significant algal involvement in microbial dome formation until late in geological history. Diatoms became abundant during the Cretaceous. These relative new-

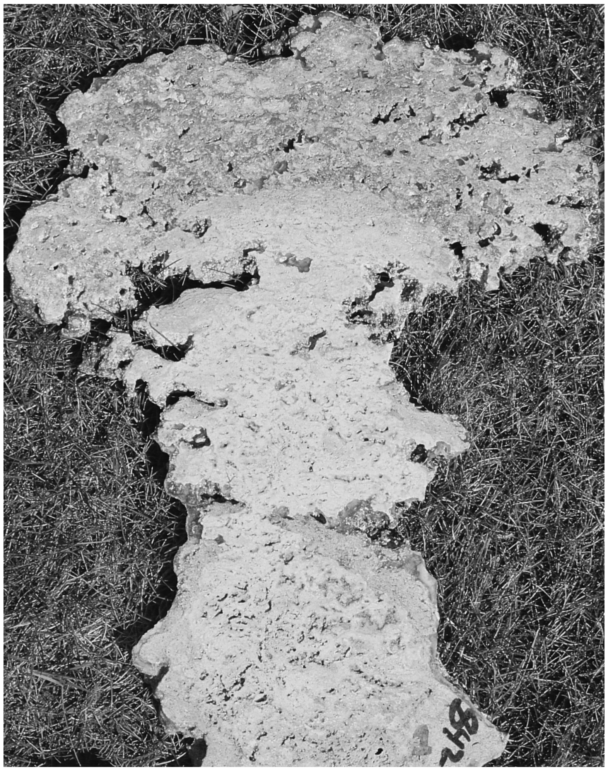

Fig. 21. Vertical section of a Shark Bay microbial column from Hamelin Pool, showing the lower narrow subtidal part and darker expanded intertidal cap. Cap is 25 cm wide. Slab courtesy of R. V. Burne.

comers may have transformed the trapping ability of some mat communities (Awramik & Riding, 1988). Coarse-grained agglutinated domes and columns are not restricted to the Cenozoic (Bertrand-Sarfati, 1994); but the best-known examples are all Neogene. These include carbonate and also carbonate–siliciclastic stromatolites, thrombolites and leiolites in the Late Miocene of SE Spain (Riding *et al.*, 1991b; Martín *et al.*, 1993) as well as Shark Bay and Lee Stocking Island examples. This relatively recent development of coarse-grained domes contrasts with the concept of long-term decline of microbial carbonates.

Modern analogues

Major developments, such as Walcott's (1914) recognition of the importance of cyanobacteria and lithification, Black's (1933) emphasis on sediment trapping, and Logan's (1961, p. 520) inference of the possible importance of metazoan predation, were all derived from examination of modern analogues. However, the diversity and long history of microbial carbonates permits modern analogues to distract as well as inform. After all, stromatolite research has been viewed as a succession of dogmas (Hoffman, 1973; Monty, 1977) largely arising from uncritical application of modern analogues.

Shark Bay and Lee Stocking Island

Modern marine microbial carbonates are well known in tidal flat settings, and are becoming increasingly evident in coral–algal reefs, but without doubt the most famous examples are restricted to seasonally hypersaline embayments of the Indian Ocean in Western Australia (Figs 20 and 21). It was tempting to regard these impressive modern microbial carbonate columns, at Hamelin Pool in Shark Bay, as analogues for Proterozoic examples (Logan, 1961), but it was soon recognized that this view is too simple (Hoffman, 1973, p. 188; Playford & Cockbain, 1976, pp. 408–409). Shark Bay columns contain much trapped coarse sediment, are often only crudely layered, and in places are thrombolitic or leiolitic. In contrast, many Proterozoic microbial carbonates are fine-grained and well-laminated stromatolites. A possible explanation for the coarse-grained nature of Shark Bay (and also Lee Stocking Island) subtidal columns is the floral composition of their mat communities. In addition to cyanobacteria, algae, and in particular diatoms and chlorophytes, are conspicuous mat-components in both Shark Bay and Lee Stocking Island (Fig. 2) columnar stromatolites (Awramik & Riding, 1988; Riding *et al.*, 1991a). These algae are generally larger than cyanobacteria and may be responsible for trapping the coarse sediment that is typical of these columns and that distinguishes them from most pre-Cenozoic stromatolites, although it must be remembered that this does not exclude the continuing importance of cyanobacteria in dome formation (Golubic & Browne, 1996).

Therefore, rather than being precise analogues for the Precambrian, these well-known modern examples of peritidal microbial columns instead possibly represent a relatively modern development in which algae have combined with prokaryotes to produce complex, faster growing and more effective sediment-accreting communities (Awramik & Riding, 1988). If this is correct, the question arises whether and where modern analogues for Precambrian stromatolites actually exist.

Temporal controls

The essential prerequisite for a good explanation of the historical development of microbial carbonates is confident recognition of their distributions. The emerging picture cannot yet be described as detailed or complete, but, based on the information to hand, can we reach a reasonable preliminary assessment?

The competition hypothesis, for long an influential concept, has encountered serious obstacles. Research on the older Proterozoic has pushed back the timing of stromatolite decline [although algae (Brocks *et al.*, 1999) and metazoans (Seilacher *et al.*, 1998) are also being reported earlier], but the Phanerozoic persistence, and success, of microbial carbonates in coexistence with invertebrates challenges the view that grazing and competition for space are major limiting factors. It has also never been made clear whether the anticipated effects of eukaryotes on microbial carbonates are attributed directly to grazing or to competition for substrate. On the other hand, was the dramatic Early Palaeozoic appearance of thrombolites and dendrolites in part a calcification response to provide protection? Yet potential early grazers in the Cambrian were small (Farmer, 1992) and, in any case, Archaean and Proterozoic stromatolites show all the signs of early lithification. Nonetheless, when we look again at the present day, it is striking that the most impressive examples of microbial carbonates are large domes and columns in, at least partly, stressed environments, whether by salinity or tidal currents, at Shark Bay and Lee Stocking Island. The less impressive, but volumetrically far more abundant, laminar stromatolites on tidal flats are also in environments that are severely stressed by desiccation and temperature fluctuation. Thus, although the initial strengths of the competition hypothesis have been weakened, it cannot yet be dispensed with.

The calcification model emphasizes the overriding importance of the environment in facilitating early lithification. It suggests that the supersaturation state of seawater waxed and waned, directly influencing microbial carbonate accretion and therefore abundance. The weaknesses of the competition hypothesis are strengths for the calcification model. Inception of decline in abundance of stromatolites relatively early in the Proterozoic could reflect changing water conditions that are also reflected in abiogenic precipitates (Grotzinger, 1990; Grotzinger & Knoll, 1999). The Phanerozoic development of microbial carbonates is patterned by fluctuations expressed in cyanobacterial calcification episodes (CCEs; Riding, 1992) that may also occur in the Proterozoic (Riding, 1994b), and which can speculatively be related to factors such as temperature (Riding, 1992) that influenced the saturation state with respect to $CaCO_3$ minerals (Merz-Preiß & Riding, 1999). Thus, early Proterozoic decline, Cambrian resurgence and Phanerozoic episodicity, which beleaguer the competition hypothesis, are accounted for by the calcification model. Not least, it offers a mechanism to account for significant Phanerozoic fluctuations in abundance of microbial carbonates. But how does the calcification model fare when confronted with the presence of Shark Bay and Lee Stocking Island columns in apparent stressed refugia? The concept of eukaryote competition as a determining factor (e.g. Gebelein, 1976; Walter & Heys, 1985) fits well with the present-day occurrence of marine microbial carbonates in hostile environments, including hypersaline lagoons, desiccated tidal flats and areas of highly mobile sediment (Awramik, 1971, p. 825). But these environments may also enhance carbonate precipitation. Shark Bay and Lee Stocking Island are, respectively, swept by waves and currents that can promote early cementation. On intertidal flats, evaporation has a similar effect. These could therefore not simply be refuges from metazoan interference, but environments of rapid early lithification, as are freshwater lakes and pools with heavily calcified tufa stromatolites (Riding, 1997).

On the other hand, as algal evolution provided new components for mat ecosystems, their trapping and calcification abilities may have altered. Have diatoms, originating during the Mesozoic, made a major change to sediment stabilization and accretion? Are the coarse-grained domes and columns of Shark Bay and Lee Stocking Island simply the expression of the improved abilities of such regenerated communities to accumulate sediment (Awramik & Riding, 1988)?

Experience generally shows us that one-sided views ultimately fail to account for complex situations. Surely, environmental effects, biological interactions and microbial evolution must all have importance. The range of possibilities and the time and space involved, not to mention the diversity of microbial carbonates, all counsel against hard and fast conclusions. Indeed, could everyone be right?: stromatolite abundance decline commenced around 2000 Ma (Grotzinger, 1990), diversity decline commenced around 1000 Ma (Walter & Heys, 1985) and was greatest after 675 Ma (Awramik, 1971, 1991), in response to a combination of factors; cyanobacterial evolution together with fluctuations in calcification (Riding, 1992, 1994b) and the effect of emergence of invertebrates and algae (Fischer, 1965; Garrett, 1970) strongly patterned the development of Phanerozoic microbial carbonates, in which incorporation of newly evolved microbes added yet another factor (Awramik & Riding, 1988). Thus, despite possible inhibition in marine environments owing to the relatively low saturation state of seawater, the present day reveals diverse microbial carbonates, coexisting in abundance with algae and invertebrates in reefs, colonizing stressed tidal flats, locally creating spectacular columns in bays and channels, and forming in freshwater and hot-spring environments where $CaCO_3$ precipitation is facilitated. Whereas competition can inhibit or modify mat growth, lithification can independently determine preservation and accretion. So we might contrast microbial carbonate development in high-competition/low-calcification environments with that in low-competition/high-calcification situations, and so on. How we test these ideas and attempt to disentangle overlapping controls such as competition, lithification and microbial evolution, while avoiding the cycle of dogmatism that has so long prevailed in microbial carbonates, is the continuing challenge, but we can be confident that the results will be more surprising than our preconceptions.

CONCLUDING REMARKS

Microbial carbonates have the longest geological history and most extensive facies distribution of all biogenic carbonates. For much of the Precambrian they are the most conspicuous evidence of life on Earth. Yet they rely on synsedimentary calcification that is not fully organically controlled. Biological factors, such as microbial evolution and competition with metazoans, must have had a significant influence, but ecological interactions in particular may have been over-emphasized in attempts to account for fluctuations in the abundance of microbial carbonates in marine environments during the past 1000 Myr. The role of environmental factors suggests that geological variations in microbial calcification could be a proxy for fluctuations in the supersaturation state of seawater with respect to carbonate minerals that have affected the accretion, abundance and preservation of these deposits in space and time.

There is continuing need to document the geological distribution of microbial carbonates. Present-day examples, such as domes and columns at Shark Bay and Lee Stocking Island, are not simply occupying stressed refugia, and these 'analogues' show clear differences from the much older microbial carbonates with which they have often been compared. It is curious that, in many respects, the Archaean and Proterozoic history of microbial carbonates should be better known, or at least appear more clear, than that of subsequent periods. A partial explanation must be the difficulty of recognizing and interpreting microbial carbonates amongst Phanerozoic skeletal fabrics. As large subaqueous domes and columns, microbial carbonates possess an evident and impressive geological record, but mixed with algal and invertebrate skeletons their significance can be obscured. Recognition of microbial carbonates will be aided by improved understanding of their microfabrics. These commonly fine-grained textures remain the key to the evolutionary history, and to the environmental and ecological interactions, of the microbes that contributed to their formation. The significance of variations in these fabrics, and recognition of the organisms and processes that have produced them, are key goals. They can be achieved by detailed comparative and interdisciplinary studies of present-day and ancient examples.

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