

Stromatolite reef crusts, Early Cretaceous, Spain: bacterial origin of *in situ*-precipitated peloid microspar?

ROBERT RIDING* and SARA TOMÁS†

*School of Earth, Ocean and Planetary Sciences, Cardiff University, Cardiff CF10 3YE, UK (E-mail: riding@cardiff.ac.uk)

†Departament de Geoquímica, Petrologia i Prospecció Geològica, Universitat de Barcelona, 08028 Barcelona, Spain

ABSTRACT

Peloidal crusts are significant components of Early Cretaceous (Aptian) reef carbonates in eastern Spain. The crusts form steep-sided laminated deposits on coral and other skeletal surfaces. Their microfabric consists almost entirely of silt-sized peloids in fenestral microspar matrix. This microfabric contrasts with more poorly sorted and generally finer grained detrital wackestone–packstone fabrics of the adjacent reef matrix. Scarcity of incorporated grains indicates that the crusts did not trap many particles. It is proposed that the crusts are stromatolites and that peloids and inter-peloid space were created concurrently by bacterial degradation of organic matter. As they developed, inter-peloid voids were protected from infiltration of extraneous sediment by the organic-rich exterior surface of the stromatolite. Even spacing of the peloids within microspar may reflect self-organization of bacterial colonies in the decaying organic matrix. Compressed and partly amalgamated peloids marginal to burrows in the stromatolites suggest that the peloid fabrics were initially only partially lithified. The grainstone-like peloid fabric is therefore interpreted as having formed *in situ* by very early diagenetic processes driven by heterotrophic bacteria.

Keywords Cretaceous, microbial, microfabric, peloid, reef, Spain, stromatolite.

INTRODUCTION

Reef surfaces are potential sites for the accumulation of a wide range of carbonate deposits, including skeletal encrusters, stromatolites, particulate sediment and cements (James & Ginsburg, 1979). Discriminating between the last three of these components is not always straightforward. Stromatolite microfabrics, in particular, are complex and can both incorporate allochthonous particles and produce *in situ* aggregates that closely resemble allochthonous grains (Monty, 1976). This paper describes and offers an interpretation for stromatolite microfabrics that at first sight resemble peloid grainstone but which are interpreted here as having precipitated *in situ*. Such crusts appear to be widespread in modern (e.g. Land & Goreau, 1970; Macintyre, 1977, 1984;

Montaggioni & Camoin, 1993) and ancient (e.g. Scoffin, 1971; Reid, 1987; Sun & Wright, 1989) reefs. They have sparked debate concerning whether they should be regarded as microbial or cement fabrics (Macintyre, 1985). An additional key question posed by these microfabrics is how to account for the microsparite matrix that surrounds the peloids. How do grainstone-like fabrics form in autochthonous precipitates, and how is adjacent fine-grained detrital sediment excluded?

Stromatolite microfabrics are notoriously difficult to interpret (Monty, 1976; Riding, 2000). One of the most widespread is ‘grumeleuse’ (clotted) fabric (Cayeux, 1935, p. 271) consisting of irregular micritic peloidal aggregates surrounded and traversed by microspar. These aggregates and the intervening microspar areas have dimensions

generally in the range 10–100 µm and together create the spongy, clotted appearance that gives the fabric its name. At first sight there appears to be little regular organization to clotted fabric, but distinctive features are present, notably the varied but relatively small, typically silt, size of the peloids, and their generally well-spaced distribution within the microspar groundmass. Although Cayeux (1935) considered clotted fabric to result either from partial re-crystallization or mechanical deposition of peloid grains, Kaisin (1925) had earlier suggested that clotted fabric is bacterial in origin. Pia (1927, p. 36) could recognize ‘no distinct organic structure’ in clotted stromatolite microfabric, and interpreted it as a cyanobacterial deposit formed by extracellular precipitation, a view echoed by subsequent workers (Hofmann, 1969, p. 40; Gebelein, 1974; Bertrand-Sarfati, 1976; Monty, 1976).

By definition, peloids are granular micritic aggregates of uncertain origin (McKee & Gutschick, 1969). They can include allochthonous grains such as faecal pellets and micritized bioclasts (Bathurst, 1976, p. 84). Peloidal fabrics that appear to be in-place precipitates are common in reefs (Flügel & Steiger, 1981; Macintyre, 1984, 1985; Lighty, 1985, p. 378; Reid, 1987; Sun & Wright, 1989). In some cases they have been regarded as microbial, and in others as cements, although these designations are not necessarily mutually exclusive. Land & Moore (1980, p. 364, fig. 12) examined fabrics in Jamaican fore-reef slope sediments, and recognized the intrinsic problem of accounting for peloids that ‘appear to “float” in a cement matrix’. They suggested that loose peloid grains were sedimented contemporaneously with spar cement growth. This view was supported by Lighty (1985).

CaCO₃ precipitation resulting from degradation of organic matter by heterotrophic bacteria is an important lithification process in microbial mats (Krumbein *et al.*, 1977; references in Riding, 2000, p. 184). Chafetz (1986) suggested that peloids can be calcified bacterial aggregates. This is supported by association of CaCO₃ precipitation with heterotrophic bacteria in present-day mats (Paerl *et al.*, 2001), and by peloidal aggregates resembling bacterial microcolonies constituting the microfabric of calcified biofilm (Riding, 2002a). It is possible, therefore, that a general origin for clotted and peloidal microfabrics in microbial carbonates is calcification just below the sediment–water interface in microbial mats, resulting from pH rise induced by degradation of organic products by anaerobic organotrophs –

such as sulphate-reducing bacteria (Krumbein *et al.*, 1977; Pigott & Land, 1986; Visscher *et al.*, 1998; Riding, 2003). Even so, the specific origin of the grainstone-like fenestral fabric that characterizes these deposits remains an unresolved question.

GEOLOGICAL SETTING

These reef deposits are of Lower Aptian (late Early Cretaceous) age from the Maestrat Basin, which is located 50–150 km north of the city of Valencia in eastern Spain. During the Mesozoic, up to 7 km of marine carbonates, marginal siliciclastics, and estuarine carbonates accumulated in intracratonic sub-basins, including the Maestrat Basin, collectively termed the Iberian Basin, now exposed in the Cordillera Ibérica of east-central Spain (Alvaro *et al.*, 1978) (Fig. 1). The Permian–Cretaceous succession can be divided into stages of rift and post-rift development (Salas & Guimerà, 1997; Salas *et al.*, 2001). The sub-basins were subsequently inverted during the Palaeogene (Salas & Casas, 1993; Vergés *et al.*, 2002).

In the Aptian, prograding shallow water carbonate platforms up to 1100 m thick accumulated in the Maestrat Basin. Part of this sequence crops out at Benicàssim, in the south-eastern part of the Maestrat Basin, 75 km NNE of Valencia (Fig. 2). Carbonates of the Lower Aptian (K1.8 sequence of Salas *et al.*, 2001) Villarroya de los Pinares Formation overlie the basinal marls of the Forcall Formation (Fig. 3). This ~200 m thick succession consists of Forcall marls with ammonites and bivalves, followed by basal Villarroya nodular wackestones with echinoids and oysters that pass up into low angle cross-bedded bioclastic grainstones of the platform margin. The Benicàssim coral-stromatolite reef overlies these grainstones ~35 m above the base of the Villarroya Formation and is ~60 m thick. It is overlain by a further ~40 m of platform margin low angle cross-bedded ooid grainstones with orbitolinid foraminifers, followed by more than 60 m of platform interior packstones with gastropods, orbitolinids, and rudistid bivalves.

The Benicàssim reef is well-exposed at El Moltó hill, just west of the N-340 highway immediately north of Benicàssim. This outcrop displays microsolenid coral close cluster reefs to laminar frame reefs (for terminology see Riding, 2002b) with coralline and peyssonneliacean red algae, encrusting foraminifers, and stromatolitic crusts.

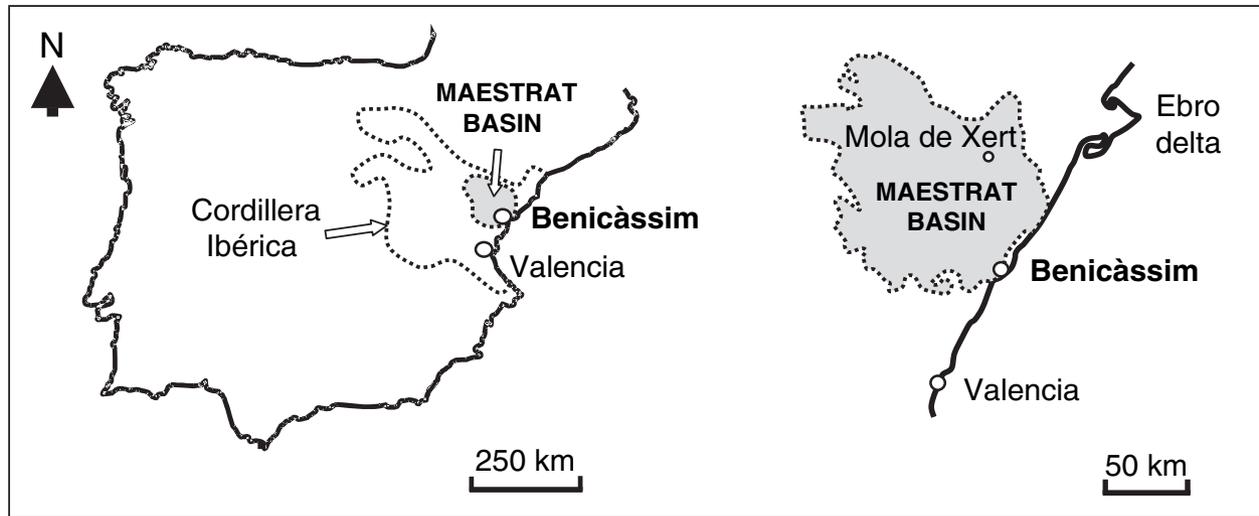


Fig. 1. Locations: Maestrat Basin and Benicàssim, eastern Spain.

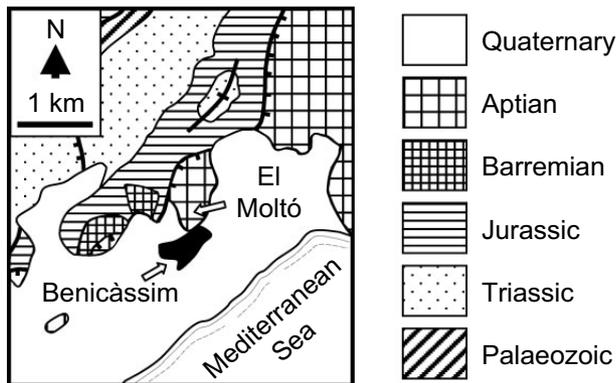


Fig. 2. Location of Early Aptian (Cretaceous) reef deposits at El Moltó, Benicàssim, eastern Spain.

The presence of corals and coralline algae indicates normal marine salinity. The microsolenids commonly occur as platy convex-up forms, several decimetres in width, resting on and surrounded by bioclastic wackestone–packstone reef matrix. The upper surfaces of the corals are typically veneered by a thin layer of skeletal encrusters (red algae, foraminifers, *Lithocodium*, etc.) succeeded by a thicker crust of stromatolite (Fig. 4). Based on outcrop area, stromatolitic crusts constitute ~20% of the total reef volume.

In the Benicàssim area, the lower part of the Villarroya succession is interpreted as a shoal complex deposit with patch reefs. Similar facies of this age are developed at Mola de Xert, ~60 km to the north (Bitzer & Salas, 2001). The sequence studied at Benicàssim appears mainly to consist of fore-reef facies due to the following: presence of platy microsolenid corals typical of low light

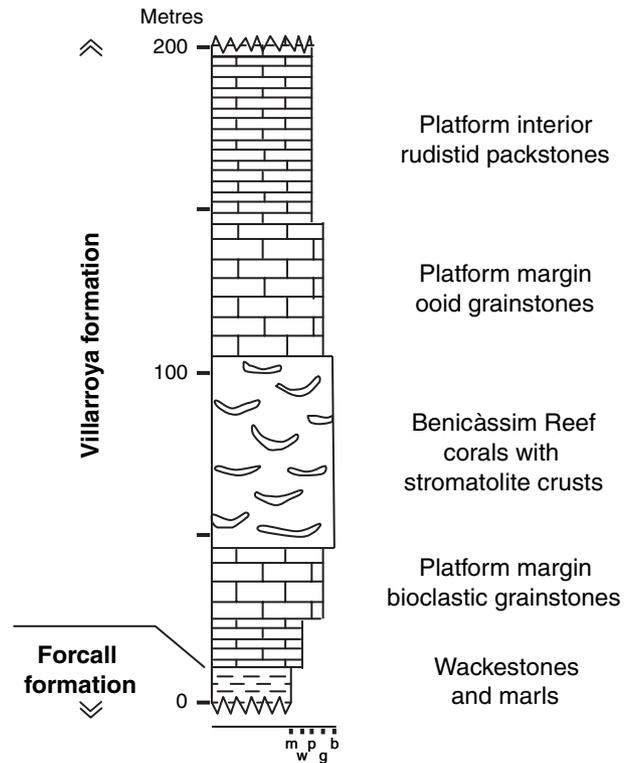


Fig. 3. Stratigraphy of the Early Aptian (Cretaceous) Benicàssim reef sequence at El Moltó.

reefal environments in the Late Jurassic and Early Cretaceous (see Rey, 1979; Insalaco, 1996; Leinfelder *et al.*, 1996; Höfling & Scott, 2002), presence of thin coralline and peyssonneliacean algal crusts, absence of shelf lagoon and of very shallow water biota, presence of a predominantly fine-grained wackestone–packstone reef matrix,

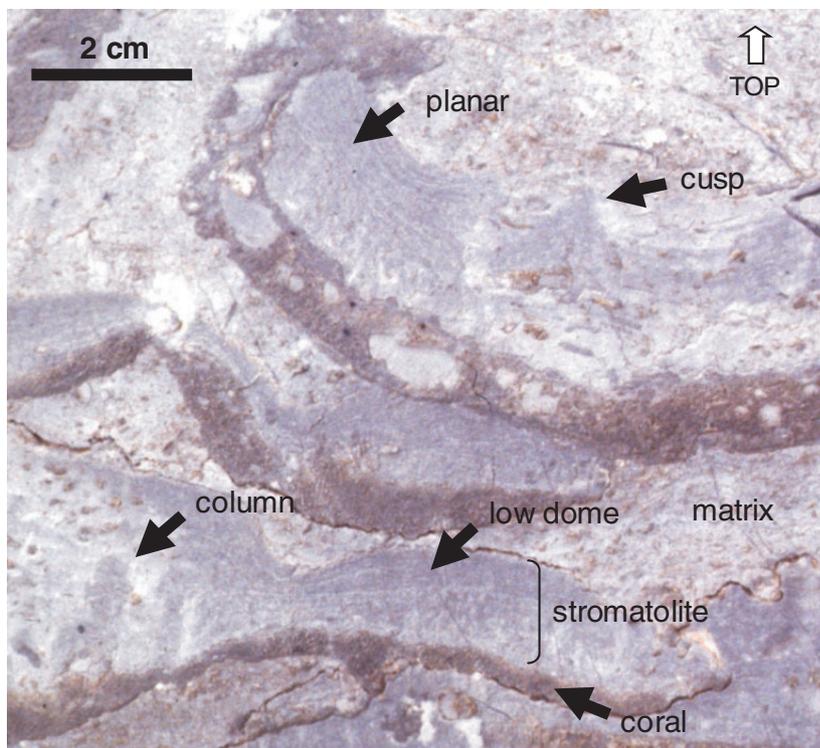


Fig. 4. Detail of Benicàssim reef outcrop at El Moltó showing laminar microsolenid corals (dark brown) (locally with recurved margins), centimetric stromatolite veneers (grey) and intervening particulate matrix (light colour). Stromatolites preferentially encrust upper surfaces of corals, and exhibit columnar, cusped, domical and planar forms. Lamination is best developed in low domical and, especially in this example, planar stromatolites. Some contacts are stylolitized.

and the stratigraphic relationship with the underlying relatively deep water Forcall basal marls.

STROMATOLITE

Morphology and macrofabric

The term stromatolite is used here to refer to laminated microbial deposits (Riding, 1999). The Benicàssim stromatolitic crusts range from steep-sided irregular columns to smoothly domical masses (Fig. 4). The platy corals are generally 5–50 cm in width, and the overlying stromatolite crusts are up to ~5 cm thick. Club-shaped individual columns, up to ~5 mm in width and ~15 mm high, grow up from thin stromatolitic veneers on the upper surfaces of the corals. More commonly, these columns are closely juxtaposed on the tops of the corals, forming complex surfaces with intervening spaces occupied by fine-grained sediment. In vertical section, invaginations in the steep-sided stromatolite margins contain ‘islands’ of particulate sediment surrounded by stromatolite (Fig. 5). These islands are probably contiguous with the adjacent reef matrix. Planar and smooth low domical stromatolites, locally with cusped morphologies, veneer most of the upper surfaces of corals, probably in response to reduced sediment accumulation

(Fig. 4). Contacts between the stromatolites and adjacent to overlying particulate reef-matrix sediment are sharp, although lack of colour contrast can obscure them in thin section (Fig. 5). Stromatolitic lamination is most distinct on weathered surfaces. It is more irregular and poorly developed on steep sided columns, and better developed on planar and low domical forms where differential weathering shows relatively even, millimetric, spacing and good continuity (Fig. 4). In thin section, lamination is locally irregularly crustose with steep sides and overhangs, and is made conspicuous by fabric variations with darker layers of densely packed peloids alternating with lighter layers of more open packing (Fig. 6).

Microfabrics

The stromatolite microfabric is almost entirely fenestral peloid ‘grainstone’ in contrast to adjacent poorly sorted, fenestrae-free detrital wackestone–packstone reef matrix (Figs 7 and 8A and B). Allochthonous fine sand size particles, including recognizable bioclasts, are locally incorporated into the stromatolite (Fig. 8C), but are generally scarce and volumetrically insignificant. The peloids that dominate the stromatolite microfabric range widely in size but generally are <70 µm, and often <50 µm across. The density of



Fig. 5. Microsolenid coral with thin skeletal crust overlain by thicker stromatolite veneer showing steep-sided protuberances with marginal invaginations. Upper surface of stromatolite outlined. Thin section.

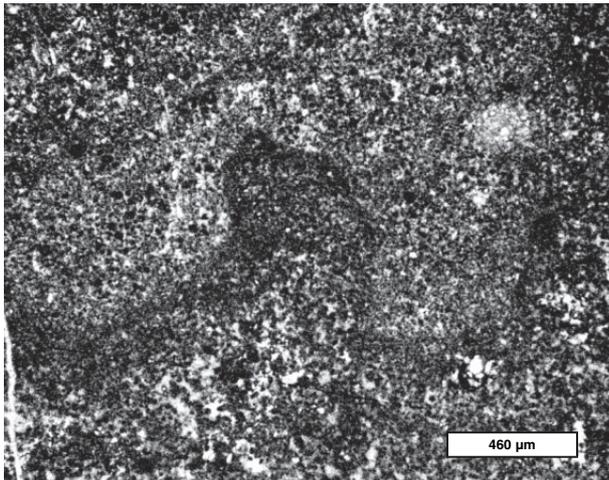


Fig. 6. Irregular crustose layering within stromatolite, emphasized by variations in peloid packing density that generate lighter and darker layers. Note steep sides to laminae. Thin section.

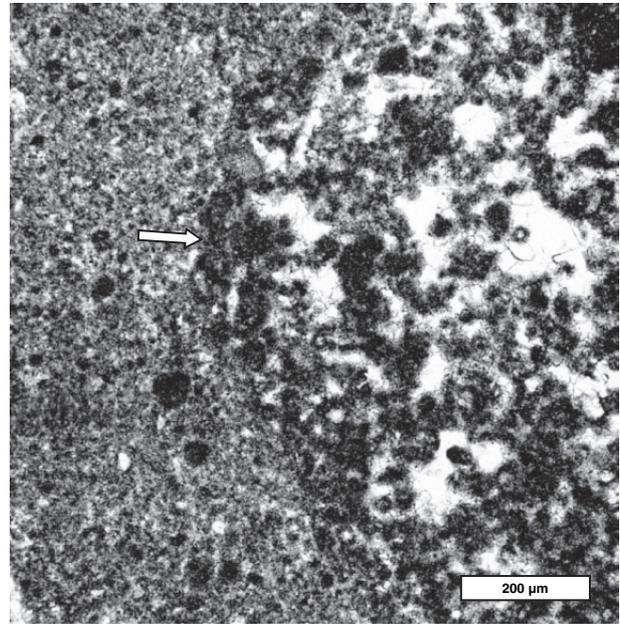


Fig. 7. Steep-sided to overhanging contact between stromatolite (right) and detrital reef matrix (left). Note well-defined contact (arrow) with matrix, and contrast between fenestral clotted peloid microspar stromatolite microfabric and wackestone–packstone of the matrix. If the peloid microspar fabric had formed inorganically it would have precipitated at the sediment–water interface surface, and particulate micrite would be expected to have draped over it, filling voids between peloids. This is not seen, and the open fenestrae are interpreted as evidence that organic material provided the medium in which peloids nucleated and prevented entry of particulate lime mud from the adjacent wackestone–packstone matrix (see Fig. 9). Thin section.

peloid spacing varies, and contributes to lamination. Nonetheless, within small areas peloids typically show relatively evenly spaced distribution in a microspar to sparite matrix. Peloid margins differ in distinctness. Some have relatively well-defined margins with simple outlines (Fig. 8D). Others form irregular clusters that lack well-defined boundaries and occur as aggregates within aggregates, creating a complex clotted fabric within fenestral microspar (Fig. 8E). Locally clusters of very irregular sinuous fenestrae up to 250 μm across are present (Figs 7 and 8A and C).

Burrows

The stromatolites are traversed by ~ 200 μm wide sinuous, spar-filled burrows. These have dark densely clotted margins of uneven thickness that show gradational contacts to the adjacent stromatolite fabric (Fig. 8F).

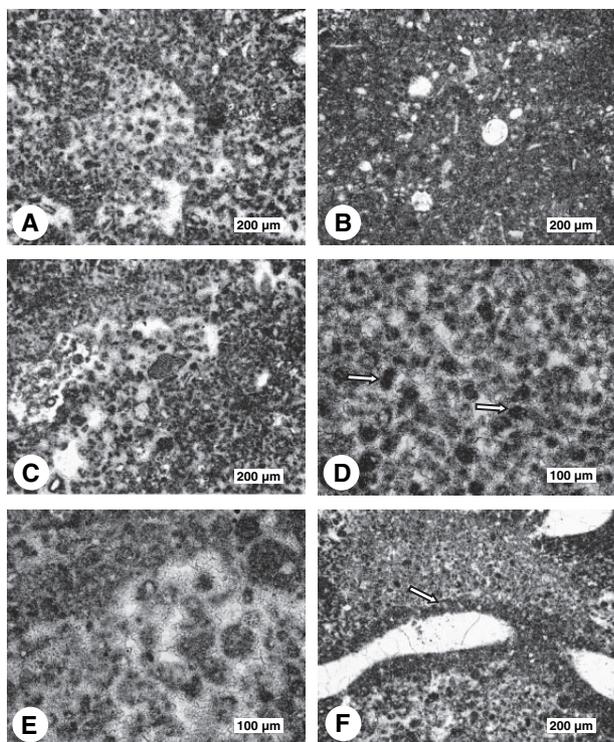


Fig. 8. Photomicrographs of stromatolite and associated reef matrix microfabrics. (A) Stromatolite fabric dominated by silt-sized peloids distributed in a clotted to microspar matrix. Fenestrae are locally present (e.g. lower centre). A few recognizable incorporated allochthonous particles are present. (B) Wackestone–packstone bioclastic reef matrix that occurs adjacent to the stromatolites. Note the poor sorting and absence of extra-skeletal pore spaces. (C) Peloidal stromatolite fabric with incorporated bioclast (centre). Note irregular distribution of denser fabric with more closely spaced peloids to right, and more open fabric with fewer peloids scattered in a clotted and fenestral fabric to the lower left. (D) Stromatolite microfabric. Note relatively good ‘sorting’ and even spacing of peloids within ubiquitous microspar matrix. Some peloids (examples arrowed) have relatively well-defined margins. (E) Stromatolite microfabric composed of diffuse peloidal aggregates with poorly defined boundaries creating clotted fabric surrounded by sinuous fenestrae. Peloids differ in size and shape and contrast with ‘well-sorted’ peloids, some of which have distinct margins, as seen in panel D. (F) Burrows within stromatolite interpreted to have formed in semi-consolidated material. Note the dark dense peloid micrite rims to the burrows, with uneven margins (arrow) that grade into adjacent peloid microspar stromatolite fabric.

DISCUSSION

‘Autochthonous grainstone’ peloid microfabric

In Benicàssim stromatolites, grainstone-like peloid fabric is well-developed and pervasive. It

contrasts markedly with the wackestone–packstone fabric of the adjacent reef matrix (Fig. 7). How did the apparently open-space fenestrae of this fabric develop, and why were such voids not infilled by particulate micrite from the adjacent wackestone–packstone matrix? The proposals put forward here are that: (1) this juxtaposition of wackestone–packstone matrix and fenestral peloid ‘grainstone’ is a key to understanding the origin of these peloidal stromatolite fabrics, (2) the peloids and clotted micrite represent products of organic decay immediately below the sediment–water interface, and (3) the peloidal fabric formed *in situ* during very early synsedimentary diagenesis. The organic matter probably included a combination of extracellular polymeric substances (EPS), soluble biomolecules, and inert biomass (see Laspidou & Rittmann, 2002), representing the products of microbial biomass growth, death, and hydrolysis (see Scuras *et al.*, 1998).

The relatively even spacing of the peloidal aggregates and the open-space fabrics that separate the aggregates may reflect the spatial arrangement of the original bacterial microcolonies in the degrading organic matrix. Aggregates of bacterial cells can form organized patterns (Budrene & Berg, 1991), in response to growth and directed cell movement (Wimpenny, 1992). Factors that may be involved in determining these patterns include nutrient gradients, chemotaxis, motility, intercellular signalling, and the protection imparted by cell aggregation (Eisenbach, 1996; Ben-Jacob, 1997). Growth patterns are most easily observed as two-dimensional outlines on agar plates (Budrene & Berg, 1991). Fluorescence *in situ* hybridization and confocal laser scanning microscopy (e.g. Sekiguchi *et al.*, 1999; Okabe *et al.*, 2004) have been used to elucidate the distribution of cells in biofilms and other aggregates in three-dimensions, but it remains difficult to image the three-dimensional spatial arrangement of cells (Barranguet *et al.*, 2004). Despite the inevitable loss of cell detail, stromatolite clotted fabrics, exemplified by grainstone-like peloid ‘cements’, could represent the overall spatial self-organized distributions of bacterial microcolonies – as is also likely in calcified biofilms (Riding, 2002a).

Despite forming adjacent to particulate matrix (Fig. 7), relatively few allochthonous grains were incorporated into the stromatolites (Fig. 8C). The possibility that micrite was trapped cannot be ruled out, but overall the stromatolite fabric consistently contains less micrite than the adjacent matrix (Figs 7 and 8A and B). This might indicate that the stromatolite had a non-sticky

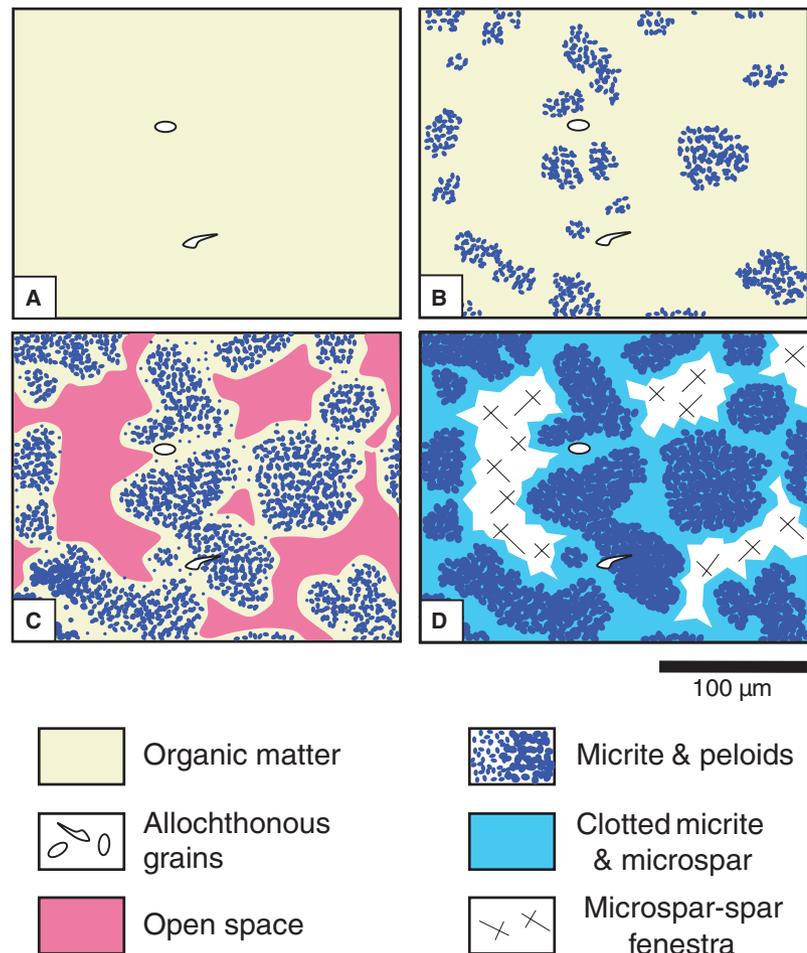
surface, ranging from firm and gelatinous to hard (see *Timing of lithification*) that did not readily trap detrital material. In addition, the stromatolite surfaces are often steep-sided (Figs 5 and 7), which could also discourage incorporation of grains.

Proposed origin of peloid microfabric

The mechanism proposed here to account for this distinctive peloid 'grainstone' fabric is that it formed *in situ* during very early diagenesis, due to calcification driven by degradation of organic compounds by heterotrophic bacteria, and that the inter-peloid spaces developed secondarily as organic matter was removed (Fig. 9). The following details are inferred. Immediately below the stromatolite surface, heterotrophic bacteria degrade organic material, primarily microbial cell tissue and EPS products, derived from the uppermost stromatolite layer. Decay and hydrolysis drive calcification of bacterial aggregates that

form the nuclei of peloids. Degradation of organic matter results in shrinkage that opens small spaces as well as larger fenestrae between enlarging calcified peloids. The spatial distribution of aggregating bacterial colonies determines the even spacing of the peloidal masses. The latter creates a self-supporting microframe. The open spaces of this 'grainstone' fabric are preserved by microspar cements that precipitate in these water-filled spaces between the peloidal aggregates. The outer organic layer of the stromatolite prevents extraneous material from filling the inter-peloid spaces forming just below the surface. Because these spaces develop secondarily around calcifying bacterial microcolonies within the stromatolite, they constitute an autochthonous, very early diagenetic, fabric that is not present at the sediment–water interface. In this model, therefore, peloid microspar originated as an *in situ* precipitate within an organic matrix, even though the texture mimics poorly sorted peloid grainstone.

Fig. 9. Model suggesting stages of development of peloid microspar fabric by heterotrophic bacterial degradation of initial organic matter near the stromatolite surface: (A) organic matter (bacterial cellular material and extracellular polymeric substances) with very minor incorporation of allochthonous particles; (B) nucleation of micrite-sized CaCO_3 crystals in vicinity of bacterial clusters initiates clotted peloidal aggregates; (C) degradation of organic matter results in shrinkage, opening fenestrae between enlarging micritic clots and peloids; (D) residual organic material around peloids is lithified by nucleation of clotted micrite–microspar; microspar–spar cements precipitate in the water-filled fenestrae that have opened between these peloidal aggregates. Subsequent minor re-crystallization aggrades fabrics, micrite grains become relatively uniform and peloid boundaries are blurred. Component outlines based on an area within Fig. 8E.



Timing of lithification

The generally sharp contact with adjacent matrix and locally steep to overhanging surface of the stromatolites (Figs 5 and 7) are consistent with early lithification and/or a gelatinous mat. Further indication that the inter-peloid cement is syngedimentary is that locally the peloids appear to float in the cement (Fig. 8A and E). This intrinsic feature of such peloid 'grainstone' crust fabrics was recognized by Land & Moore (1980) from Jamaican reefs, where they are evidently early marine in origin (Land & Goreau, 1970, p. 457). It is possible that final filling of fenestrae occurred during burial diagenesis. It is therefore inferred that internal features of this peloid 'grainstone' fabric, together with their external contacts with adjacent matrix, primarily reflect early marine lithification. There is evidence that the accreting stromatolite had a firm but not rigid consistency. This is deduced from the margins of burrows where clotted peloid material has been amalgamated into a micritic rind with a sharp margin at the burrow surface, and a diffuse and uneven distal margin (Fig. 8F). Truncation of grains that would indicate a brittle lithified fabric is not observed. Instead, the dense dark material forming the burrow 'lining' consists of partly amalgamated peloids. Possible explanations for the dense burrowed walls are that the burrow margins were more densely colonized by heterotrophic bacteria because oxidants such as O₂ and SO₄²⁻ were more rapidly supplied by flow through the burrows, or that they are due to amalgamation by the physical pressure of burrowing activity. These mechanisms are not mutually exclusive, and are both consistent with burrowing while the stromatolites were forming and in a gelatinous and semi-lithified condition. At the same time, the stromatolite fabric was strong enough to support the burrow wall.

Similar variations in bacterial density, in response to nutrient and oxidant supply and length of surface exposure, might account for differences in fabric density, and therefore darkness/lightness, that contribute to lamina formation (Fig. 6). Following the initial phase when lithification was proceeding and the microfabric was developing in the presence of decaying organic material, the stromatolite became fully lithified before there was sufficient overburden in the accreting reef sediment to compact the fenestral peloid fabric. This would be consistent with the view that, due to semi-lithification, the stromatolite surface was sufficiently firm to

reduce significant incorporation of allochthonous grains into the stromatolite.

Microbes

There is no direct information concerning specific microbes that may have been responsible for these stromatolites. Stromatolite-building non-calcifying autotrophs are inferred to have created biomass and associated organic products that were then subjected to heterotrophic decay inducing calcification, presumably in anoxic conditions. Studies of active stromatolite-forming processes are required to elucidate this further.

Comparisons

Present-day stromatolites are well known in a few impressive locations such as Shark Bay, Western Australia, and Lee Stocking Island in the Bahamas, but they are much more widespread in less obvious reefal environments, such as reef interstices and fore-reef locations (Brachert & Dullo, 1991; Camoin & Montaggioni, 1994; Webb *et al.*, 1998). Stromatolites with fabrics resembling those of Benicàssim can be found in many Phanerozoic reefs. Encrusting stromatolites with clotted and pelleted fabric are common and sedimentologically important in Silurian reefs of western England (Scoffin, 1971, pp. 199–201). Diverse peloidal fabrics in Yukon Triassic reefs include micritic crusts constituting ~25% of the rock (Reid, 1987, p. 897). The general occurrence of 'dense and knobby', 'vaguely laminated' crusts up to 3 mm thick on the upper surfaces of macroskeletons (Reid, 1987, p. 897) resembles that of the Benicàssim stromatolites, but the Yukon examples appear to be more micritic and although some of the peloids are ~20 µm in size, others range from 100 to 300 µm (Reid, 1987, p. 897, fig. 8). Crusts interpreted as *in situ* microbial precipitates on corals in Late Jurassic reefs of SE England, closely resemble Benicàssim stromatolites. They are 2–30 mm thick, include irregular dark layers, and are almost entirely composed of 10–60 µm size peloids (Sun & Wright, 1989, p. 178, fig. 8). Thin (1–6 mm) clotted micritic crusts are present on upper surfaces of microsolenid corals in Late Jurassic reefs in England (Ali, 1983) and France (Insalaco, 1996, p. 177).

Features of the Benicàssim stromatolites are similar to those described from a number of Holocene reef crusts. Land & Goreau (1970, p. 457) recognized the importance of isopachous

cements and pelleted micrite crusts for early marine lithification of Holocene reefs at Discovery Bay, Jamaica. Pelleted micrite forms 'smooth to knobby crusts' up to ~2 cm in thickness. Although Land & Goreau (1970, p. 460) failed to recognize cells or chlorophyll in fresh crust samples, they suspected organic involvement in their formation. Macintyre (1977, p. 507) described similar crusts on reef corals in Panama with 'peloidal (20–60 μ) or clotted texture', and regarded them as submarine cements. Peloids very similar to those in Benicàssim stromatolites occur in sponge borings in Early Holocene reefs in Florida (Lighty, 1985, fig. 11). The peloids, ~40 μ m in size, with 'open mosaic' fabric and microspar rims, were interpreted as an 'end-product of cementation' in which peloids may have nucleated during suspension in cavities (Lighty, 1985, pp. 133–134) (see also Land & Moore, 1980, pp. 363–364). Lighty (1985, p. 133, fig. 12f) also described surficial crusts composed of peloids overlain by detrital reef sediment.

Macintyre (1984, p. 232) recognized that organic decay processes could be involved in marine cement formation. Chemical and isotopic analyses suggested that bacterial sulphate reduction could be a control on marine cementation in Jamaican reefs (Pigott & Land, 1986). In overall size and shape, the vertically elongate projections on Benicàssim stromatolites (Fig. 5) resemble those of crusts from both Tahitian coral reefs (Montaggioni & Camoin, 1993, fig. 3) and Lizard Island reef caves (Reitner, 1993, pl. 2, fig. 1). The irregular crustose layering within the Benicàssim stromatolites (Fig. 6) also resembles that of Lizard crusts (Reitner, 1993, pl. 3, fig. 6). In size and shape, Benicàssim peloids and associated clotted fabrics resemble Lizard examples forming 'within organic slime pockets' in sponge borings (Reitner, 1993, pl. 4, fig. 3). Late Pleistocene deepwater (500–2700 m depth) stromatolite crusts from the Red Sea (Brachert, 1999) also have features in common with Benicàssim stromatolites. They are centimetric crusts and columns formed by irregularly overlapping crustose laminae, with 'peloids producing a grumulous structure' (Brachert, 1999, p. 218). Incorporated pelagic detritus constitutes 5% or less of these Red Sea stromatolites. Similar Early Holocene crusts, on ledges of vertical reef fronts at depths of 150–200 m, accumulated at rates of 3.5–10 mm per 1000 years (Brachert & Dullo, 1991). Brachert (1999, p. 227) inferred that these early lithified fabrics were 'induced by microbial activity'.

Benicàssim stromatolites, together with many of these selected modern and ancient examples, closely correspond to fabrics previously regarded as peloidal marine 'cements' (e.g. Macintyre, 1985). They exhibit a distinctive microfabric dominated by silt-sized peloids relatively evenly spaced in microspar matrix. In contrast, many other examples of stromatolites have more diverse components – a wider size-range of peloids, calcified filaments, bushy micrite, and a higher proportion of trapped grains – and consequently more complex microfabrics (Monty, 1976). These can include reefal crusts (e.g. on corals in Late Miocene reefs of SE Spain) that appear to combine extraneous detritus and diverse *in situ* precipitates (Riding *et al.*, 1991, p. 810).

These wide variations in stromatolite fabrics presumably reflect differences in the microbes and processes involved. On the basis of Benicàssim and similar examples, it can tentatively be suggested that simple peloid microspar stromatolite crusts may typically, if not exclusively, represent deeper water and/or low light environments. Possibly they reflect dominance of heterotrophic processes by microbially driven *in situ* calcification within degrading organic matrices. However, more information is required concerning the environmental distribution and, especially, the microbial composition of both these and other reefal crusts to further understand their significance.

SUMMARY AND CONCLUSIONS

Stromatolitic crusts that formed steep sided layers and masses on platy microsolenid corals and other skeletal reef builders were volumetrically and sedimentologically important components of Early Aptian platform margin carbonates in the Maestrat Basin, eastern Spain. They stabilized reef-front sediment and constitute ~20% of the reef volume. The stromatolites are internally homogeneous with a distinctive clotted peloidal fenestral fabric. There are few incorporated allochthonous grains and no well-defined calcified microfossils. The peloids are typically evenly spaced in a microspar matrix that gives the appearance of peloid grainstone. However, adjacent fine-grained particulate reef matrix lacks both microspar and fenestrae and did not fill the apparent open spaces within the stromatolite. It is proposed that the stromatolite was initially predominantly composed of bacterially produced organic material undergoing calcification and that open spaces formed within it during early diagenesis as the organic matter,

primarily cell tissue and EPS products, was removed by heterotrophic degradation. The fenestral spaces open around calcifying bacterial aggregates that form the peloids. The even distribution of the peloids within a microspar groundmass might reflect the original spatial arrangement of the bacterial microcolonies in the degrading organic matrix. The developing inter-peloid spaces were separated from the external environment by the living, organic-rich, stromatolite surface. This formed a barrier to infiltration of external detritus into the stromatolite.

Although the stromatolite microfabric resembles peloid grainstone, the interpretation is that it formed *in situ* during very early diagenesis by bacterial calcification and that the inter-peloid spaces developed secondarily as organic matter degraded. The resulting clotted peloidal masses probably created self-supporting microframes, a form of microbial reef fabric. The scarcity of allochthonous detritus suggests that the stromatolite surface was insufficiently soft or sticky to trap sediment, otherwise more particles of reef matrix would have been trapped at the accreting surface. Burrows traversing the stromatolites do not cross-cut grains. Instead they have dark distally diffuse margins that may represent amalgamation of still soft peloids by pressure of the burrowing organism and/or dense colonization by heterotrophic bacteria. If this is correct, it suggests that the stromatolite was only partially lithified when burrowing took place.

Stromatolite crusts are widely distributed in reefs of many ages. However, variations in the stromatolitic microfabrics may reflect significant differences in the microbial communities and processes responsible for stromatolite formation. Benicàssim reefal stromatolites shed light on the origin of microbial carbonate microfabrics, and in particular the hitherto unexplained formation of autochthonous 'grainstone' alongside fine-grained particulate matrix. The bacterial peloid microspar fabric described here is distinctive: it is dominated by silt-sized peloids distributed in locally fenestral microspar matrix, and includes relatively few detrital grains. It is very similar, probably identical, to fabrics previously thought to represent peloidal cements. It can be speculated that stromatolite peloid 'grainstone' fabrics such as those at Benicàssim represent a distinctive type of low light stromatolite that was relatively early lithified, incorporated little detritus, and developed an *in situ*-precipitated microfabric dominated by well-spaced silt-sized peloids in microspar matrix during early diagenesis. In these

respects it differs from more complex stromatolitic fabrics that may contain less well-sorted peloids together with bushy micrite fabrics, calcified microfossils and agglutinated detritus in a micritic matrix.

This distinctive fabric may be characteristic of a widespread type of microbial carbonate present in reefs throughout the Phanerozoic whose identity has not only been confused with cements but also with stromatolites that trap and bind allochthonous grains such as peloids. Stromatolite crusts similar to those at Benicàssim may prove to be widespread and sedimentologically important in reefs both ancient and modern. Further studies of reefal stromatolitic crusts are needed to elucidate the distributions, origins and significance of the variety of microfabrics present.

ACKNOWLEDGEMENTS

S. Tomás' research at Cardiff was supported by Spanish Ministry of Science and Technology Research Project BTE-2002-04453-CO2-01. We are most grateful to C. Martín-Closas and R. Salas for generous help and encouragement. We benefited greatly from the perceptive and constructive comments and suggestions of D. Sumner and an anonymous reviewer. We thank I. Montañez for meticulous editorship.

REFERENCES

- Ali, O.E. (1983) Microsolenid corals as rock-formers in the Corallian (Upper Jurassic) rocks of England. *Geol. Mag.*, **120**, 375–380.
- Alvaro, M., Capote, R. and Vegas, R. (1978) Un modelo de evolución geotectónica para la Cadena Celtibérica. *Acta Geol. Hisp.*, **14**, 172–177.
- Barranguet, C., van Beusekom, S.A.M., Veuger, B., Neu, T.R., Manders, E.M.M., Sinke, J.J. and Admiraal, W. (2004) Studying undisturbed autotrophic biofilms: still a technical challenge. *Aquat. Microb. Ecol.*, **34**, 1–9.
- Bathurst, R.G.C. (1976) *Carbonate Sediments and their Diagenesis*, 2nd edn. Developments in Sedimentology 12. Elsevier, Amsterdam, 658 pp.
- Ben-Jacob, E. (1997) From snowflake formation to growth of bacterial colonies II: cooperative formation of complex colonial patterns. *Contemp. Phys.*, **38**, 205–241.
- Bertrand-Sarfati, J. (1976) An attempt to classify late Precambrian stromatolite microstructures. In: *Stromatolites* (Ed. M.R. Walter) Developments in Sedimentology 20, pp. 251–259. Elsevier, Amsterdam.
- Bitzer, K. and Salas, R. (2001) Simulating carbonate and mixed carbonate-clastic sedimentation using predator-prey models. In: *Geologic modeling and simulation: sedimentary systems* (Eds D.F. Merriam and J.C. Davis), pp. 169–204. Kluwer Academic/Plenum, New York.

- Brachert, T.C.** (1999) Non-skeletal carbonate production and stromatolite growth within a Pleistocene deep ocean (Last Glacial Maximum, Red Sea). *Facies*, **40**, 211–228.
- Brachert, T.C. and Dullo, W.-C.** (1991) Laminar micrite crusts and associated foreslope processes, Red Sea. *J. Sed. Res.*, **61**, 354–363.
- Budrene, E.O. and Berg, H.C.** (1991) Complex patterns formed by motile cells of *Escherichia coli*. *Nature*, **349**, 630–633.
- Camoin, G.F. and Montaggioni, L.F.** (1994) High energy coral-algal-stromatolite frameworks from Holocene reefs (Tahiti, French Polynesia). *Sedimentology*, **41**, 655–676.
- Cayeux, L.** (1935) *Les Roches Sédimentaires de France; Roches Carbonatées*. Masson, Paris, 463 pp.
- Chafetz, H.S.** (1986) Marine peloids; a product of bacterially induced precipitation of calcite. *J. Sed. Petrol.*, **56**, 812–817.
- Eisenbach, M.** (1996) Control of bacterial chemotaxis. *Mol. Microbiol.*, **20**, 903–910.
- Flügel, E. and Steiger, T.** (1981) An upper Jurassic sponge-algal buildup from the northern Frankenalb, West Germany. In: *European Fossil Reef Models* (Ed. D.F. Toomey), *SEPM Spec. Publ.*, **30**, 371–397.
- Gebelein, C.D.** (1974) Biologic control of stromatolite microstructure: implications for Precambrian time stratigraphy. *Am. J. Sci.*, **274**, 575–598.
- Höfling, R. and Scott, R.W.** (2002) Early and mid-Cretaceous build-ups. In: *Phanerozoic Reef Patterns* (Eds W. Kiessling, E. Flügel and J. Golonka), *SEPM Spec. Publ.*, **72**, 521–548.
- Hofmann, H.J.** (1969) Attributes of stromatolites. *Geol. Surv. Can. Pap.*, **69-39**, 58 pp.
- Insalaco, E.** (1996) Upper Jurassic microsolenid biostromes of northern and central Europe: facies and depositional environment. *Palaeoclimatol. Palaeoecol. Palaeogeogr.*, **121**, 169–194.
- James, N.P. and Ginsburg, R.N.** (1979) The seaward margin of Belize barrier and atoll reefs. *Int. Assoc. Sedimentol. Spec. Publ.*, **3**, 191 pp. Blackwell, Oxford.
- Kaisin, F.** (1925) Les calcaires oolithiques de l'étage viséen. *Ann. Soc. Sci. Brux.*, **44**, 365.
- Krumbein, W.E., Cohen, Y. and Shilo, M.** (1977) Solar Lake (Sinai). 4. Stromatolitic cyanobacterial mats. *Limnol. Oceanogr.*, **22**, 635–656.
- Land, L.S. and Goreau, T.F.** (1970) Submarine lithification of Jamaican Reefs. *J. Sed. Petrol.*, **40**, 457–460.
- Land, L.S. and Moore, C.H.** (1980) Lithification, micritization and syndepositional diagenesis of biolithites of the Jamaican Island slope. *J. Sed. Petrol.*, **50**, 357–370.
- Laspidou, C.S. and Rittmann, B.E.** (2002) A unified theory for extracellular polymeric substances, soluble microbial products, and active and inert biomass. *Water Res.*, **36**, 2711–2720.
- Leinfelder, R.R., Werner, W., Nose, M., Schmid, D.U., Krautter, M., Laternser, R., Takacs, M. and Hartmann, D.** (1996) Paleocology, growth parameters and dynamics of coral, sponge and microbolite reefs from the Late Jurassic. In: *Global and Regional Controls on Biogenic Sedimentation. I. Reef Evolution* (Eds J. Reitner, F. Neuweiler and F. Gunkel), Research Reports, Göttinger Arb. Geol. Paläont., Sb 2, pp. 227–248, Georg-August-Universität, Göttingen.
- Lighty, R.G.** (1985) Preservation of internal reef porosity and diagenetic sealing of submerged early Holocene barrier reef, southeast Florida shelf. In: *Carbonate Cements* (Eds N. Schneidermann and P.M. Harris), *SEPM Spec. Publ.*, **36**, 123–151.
- Macintyre, I.G.** (1977) Distribution of submarine cements in a modern Caribbean Fringing Reef, Galeta Point, Panama. *J. Sed. Petrol.*, **47**, 503–516.
- Macintyre, I.G.** (1984) Extensive submarine lithification in a cave in the Belize Barrier Reef Platform. *J. Sed. Petrol.*, **54**, 221–235.
- Macintyre, I.G.** (1985) Submarine cements – the peloidal question. In: *Carbonate Cements* (Eds N. Schneidermann and P.M. Harris), *SEPM Spec. Publ.*, **36**, 109–116.
- McKee, E.D. and Gutschick, R.C.** (1969) Analysis of lithology. In: *History of the Redwall Limestone of Northern Arizona* (Eds E.D. McKee and R.C. Gutschick), *Geol. Soc. Am. Mem.*, **114**, 97–124.
- Montaggioni, L.F. and Camoin, G.F.** (1993) Stromatolites associated with coralgal communities in Holocene high-energy reefs. *Geology*, **21**, 149–152.
- Monty, C.L.V.** (1976) The origin and development of cryptalgal fabrics. In: *Stromatolites* (Ed. M.R. Walter), *Developments in Sedimentology 20*, pp. 193–249. Elsevier, Amsterdam.
- Okabe, S., Kindaichi, T., Ito, T. and Satoh, H.** (2004) Analysis of size distribution and areal cell density of ammonia-oxidizing bacterial microcolonies in relation to substrate microprofiles in biofilms. *Biotechnol. Bioeng.*, **85**, 86–95.
- Paerl, H.W., Steppe, T.F. and Reid, R.P.** (2001) Bacterially mediated precipitation in marine stromatolites. *Environ. Microbiol.*, **3**, 123–130.
- Pia, J.** (1927) Thallophyta. In: *Handbuch der Paläobotanik*, Vol. 1 (Ed. M. Hirmer), pp. 31–136. Oldenbourg, Munich.
- Pigott, J.D. and Land, L.S.** (1986) Interstitial water chemistry of Jamaican reef sediment: sulfate reduction and submarine cementation. *Mar. Chem.*, **19**, 355–378.
- Reid, R.P.** (1987) Nonskeletal peloidal precipitates in Upper Triassic reefs, Yukon Territory (Canada). *J. Sed. Petrol.*, **57**, 893–900.
- Reitner, J.** (1993) Modern cryptic microbial/metazoan facies from Lizard Island (Great Barrier Reef, Australia) – formation and concepts. *Facies*, **29**, 3–40.
- Rey, J.** (1979) Les formations bioconstruites du Crétacé inférieur d'Estremadura (Portugal). *Géobios Mém. Spéc.*, **3**, 89–99.
- Riding, R.** (1999) The term stromatolite: towards an essential definition. *Lethaia*, **32**, 321–330.
- Riding, R.** (2000) Microbial carbonates: the geological record of calcified bacterial-algal mats and biofilms. *Sedimentology*, **47** (Suppl. 1), 179–214.
- Riding, R.** (2002a) Biofilm architecture of Phanerozoic cryptic carbonate marine veneers. *Geology*, **30**, 31–34.
- Riding, R.** (2002b) Structure and composition of organic reefs and carbonate mud mounds: concepts and categories. *Earth Sci. Rev.*, **58**, 163–231.
- Riding, R.** (2003) Bacterial carbonates: process and product in time and space. *British Sedimentological Research Group, 2003 Annual Meeting*, Leeds, England, 20–22 December 2003. Programme and Abstracts, p. 96.
- Riding, R., Martín, J.M. and Braga, J.C.** (1991) Coral stromatolite reef framework, Upper Miocene, Almería, Spain. *Sedimentology*, **38**, 799–818.
- Salas, R. and Casas, A.** (1993) Mesozoic extensional tectonics, stratigraphy and crustal evolution during the Alpine cycle of eastern Iberian basin. *Tectonophysics*, **228**, 33–55.
- Salas, R. and Guimerà, J.** (1997) Estructura y estratigrafía secuencial de la Cuenca del Maestrazgo durante la etapa de rift jurásica superior-cretácica inferior (Cordillera Ibérica oriental). *Bol. Geol. Minero Esp.*, **108**, 397–402.
- Salas, R., Guimerà, J., Mas, R., Martín-Closas, C., Meléndez, A. and Alonso, A.** (2001) Evolution of the Mesozoic Central Iberian Rift System and its Cainozoic inversion (Iberian Chain). In: *Peri-Tethyan Rift/Wrench Basins and*

- Passive Margins* (Eds P.A. Ziegler, W. Cavazza, A.H.F. Robertson and S. Crasquin-Soleau), Mémoires du Muséum national d'Histoire naturelle, Paris, **186**, pp. 145–185.
- Scoffin, T.P.** (1971) The conditions of growth of the Wenlock Reefs of Shropshire (England). *Sedimentology*, **17**, 173–219.
- Scuras, S., Daigger, G.T. and Grady, C.P.L.** (1998) Modeling the activated sludge floc microenvironment. *Water Sci. Technol.*, **37**, 243–250.
- Sekiguchi, Y., Kamagata, Y., Nakamura, K., Ohashi, A. and Harada, H.** (1999) Fluorescence *in situ* hybridization using 16S rRNA-targeted oligonucleotides reveals localization of methanogens and selected uncultured bacteria in mesophilic and thermophilic sludge granules. *Appl. Environ. Microbiol.*, **65**, 1280–1288.
- Sun, S.Q. and Wright, V.P.** (1989) Peloidal fabrics in Upper Jurassic reefal limestones, Weald Basin, southern England. *Sed. Geol.*, **65**, 165–181.
- Vergés, J., Fernández, M. and Martínez, A.** (2002) The Pyrenean orogen: pre-, syn-, and post-collisional evolution. In: *Reconstruction of the Evolution of the Alpine-Himalayan Orogeny* (Eds G. Rosenbaum and G.S. Lister), *J. Virtual Explor.*, **8**, 57–76.
- Visscher, P.T., Reid, R.P., Bebout, B.M., Hoefft, S.E., Macintyre, I.G. and Thompson, J.A., Jr.** (1998) Formation of lithified micritic laminae in modern marine stromatolites (Bahamas): the role of sulfur cycling. *Am. Mineral.*, **83**, 1482–1494.
- Webb, G.E., Baker, J.C. and Jell, J.S.** (1998) Inferred syngenetic textural evolution in Holocene cryptic reefal microbialites, Heron Reef, Great Barrier Reef, Australia. *Geology*, **26**, 355–358.
- Wimpenny, J.W.T.** (1992) Microbial systems. *Adv. Microb. Ecol.*, **12**, 469–522.

Manuscript received 6 October 2004; revision accepted 8 February 2005