



Growth dynamics and ecology of Upper Jurassic mounds, with comparisons to Mid-Palaeozoic mounds

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Abstract



The Mid-Palaeozoic, including the Late Jurassic, was a time of both widespread coral reef growth and pronounced mound formation. A comparison of mound features and their general setting highlights, despite all differences, general similarities in overall growth dynamics. Mound formation was frequently driven by discontinuous patterns, particularly by background sedimentation. In many examples, episodes of mound stabilisation by early lithification, growth of microbolite crusts and winnowing of fines was followed by growth episodes of benthic fauna under reduced to negligible background sedimentation. This pattern of variable sedimentation and organic buildups may have occurred in different orders and magnitudes, inducing a fractal pattern in some mound complexes. A composite approach in estimating growth rates of mounds demonstrates that high-frequency oscillations necessary for growth of most mounds might have ranged from a few thousand years to 4th and 5th order Milankovich cycles that were superimposed by autocyclic factors. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Biologically induced carbonate mound structures rich in micrite are a common element throughout major parts of earth history and occur in a great variety of subtypes and variable environmental settings. Some long intervals of geological time were dominated by mounds, with true framework reefs lacking (Early and Late Palaeozoic), while in other geological intervals (e.g., Mid-Palaeozoic and Late Jurassic), mounds frequently co-occurred with shallow-water framework reefs (cf. James and Bourque,

1992). During the latter episodes, mounds encompassed a great variety of types, some even displaying characteristics transitional into shallow-water framework reefs. The general palaeogeographic settings of time intervals rich in both mounds and reefs are comparable to a large degree. Global sea-level was mostly rising or relatively high, which resulted in wide tropical–subtropical shelf areas and associated epeiric seas. Tropical carbonate shelf morphologies were largely dominated by ramps, some modified by local or regional tectonics into steepened ramps or even rimmed shelves. Climate was generally equilibrated, possibly resulting in reduced water circulation, with episodes of oxygen depletion (expressions of which are the common black shales and bituminous

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limestone intervals formed during these times; Leinfelder et al., 1994).

During the Late Jurassic, mounds were especially common along the northern Tethys margin and its adjacent shelf seas. These complexes have been the subject of many papers, most focusing on sponge–microbolite mud-mounds that developed within deeper ramp settings. A wide Upper Jurassic sponge mound belt can be traced across Europe from southern Portugal and southeastern Spain, through southwestern France, northern Switzerland, and southern Germany, into central Poland and Romania. In Germany, these well-documented mounds represent the ‘classic’ examples of sponge–microbial reefs (Wagenplast, 1972; Gwinner, 1976; Flügel and Steiger, 1981). Such deeper-water siliceous sponge-bearing microbial mud-mounds are also reported from the subsurface off eastern North America (Nova Scotia; Eliuk, 1978; Jansa et al., 1982) and other non-European regions such as Caucasia (Kuznetsov, 1993) and Argentina (Legarreta, 1991). They also appear in the Lower Jurassic of Portugal (Duarte et al., 2000), Morocco (du Dresnay et al., 1978), and in the Middle Jurassic of Spain (Giner and Barnolas, 1979). Besides these deeper-water ‘classical’ mound occurrences, there are several examples of mound development in shallow-water environments (e.g., Upper Jurassic of Portugal and Spain). These complexes are generally composed of scleractinian corals, stromatoporoids, detrital mud and minor amounts of binding microbial crusts (Nose, 1995).

During Mid-Palaeozoic times (Ordovician–Late Devonian), mounds developed mainly in the Baltoscandian region (e.g., Upper Ordovician of Lake Siljan), in eastern North America (e.g., Ordovician of Western Newfoundland; Pohler and James, 1989; Stenzel and James, 1995), and in the Canadian Arctic and Michigan Basin regions (Silurian; Narbonne and Dixon, 1989; Pratt, 1995). Silurian mounds also occur on the Gaspé Peninsula, Québec (e.g., Bourque and Gignac, 1984). Devonian mounds are reported from the Canadian Rocky Mountains (Alberta; Pratt, 1995), Northern Africa (Algeria and Morocco; Wendt, 1993; Wendt et al., 1997), the Rhenohercynian belt in western and central Europe (Belgium, Rhenish Slate Mountains, Harz Mountains; Burchette, 1981; Struve, 1986; Bourque and Boulvain, 1993; Weller, 1995; Boulvain and Coen-Aubert, 1997; Pohler et al., 1999),

Australia (Wood, 1999) and from Poland (Holy Cross Mountains; e.g., Racki, 1992).

Mid-Palaeozoic mounds generally developed as stromatactis- and cement-rich horizons with variable metazoan content (e.g., bryozoans, corals, stromatoporoids, crinoids). Although mostly initiated in deeper water, many of these mounds display shallowing-upward successions. The latest stages developed in fairly shallow water (see below; cf. Wood, 1999).

In this study, we present an overview of the great variety of mound types existing in the Jurassic, and give a first brief outline of representative Mid-Palaeozoic mound types. We also discuss the controlling mechanisms leading to the development of different mound types in shallow and deeper-water settings, and compare the Jurassic and Mid-Palaeozoic examples in order to get a better understanding of the general processes and prerequisites involved in mound formation.

1.1. Terminology and definitions

1.1.1. Mounds

According to James and Bourque (1992), mounds can be subdivided into three categories, which we, to a large extent, adopt in this paper: (1) microbial mounds, dominated by peloidal or dense micrite produced by calcifying benthic microbial associations (thrombolites, stromatolites, leiolites); (2) skeletal mounds, in which skeletal metazoans (e.g., corals, sponges) are largely prevailing; and (3) mud-mounds, predominantly composed of detrital mud (Fig. 1).

There is still ongoing debate as to what actually constitutes an ancient reef or mound, resulting in many different definitions and review articles about the terms reef, mound, buildup, etc. (Heckel, 1974; Wilson, 1975; James, 1983, 1984; James and Bourque, 1992; Bosence and Bridges, 1995, and others). We define the term “reef” in a broad, pragmatic way, as encompassing all carbonate structures with organic control during growth and a laterally restricted extension, which may have developed a weak or pronounced positive relief (cf. Tucker and Wright, 1990; Flügel and Flügel-Kahler, 1992). In contrast to some definitions which differentiate between reefs and mounds in terms of hydrodynamically stable organic framework formation (James and Bourque, 1992), we characterise mounds as a subtype of reefs, representing lenticular or knobby bodies, which mainly consisted of

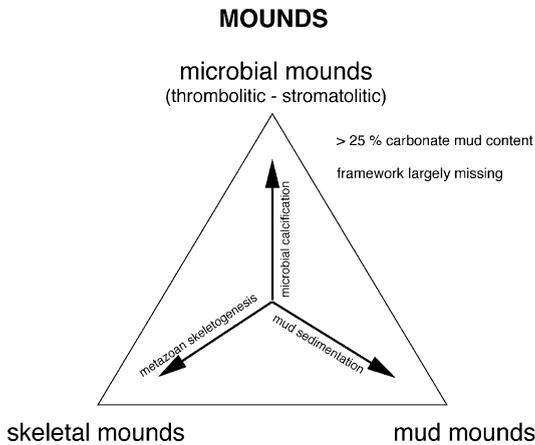


Fig. 1. Process related compositional classification of mound types used in this paper.

dense micritic carbonate with varying amounts of bioclasts, organic bindstones and benthic metazoans. The micritic carbonate might have been originally deposited as soft mottled mud, or it might have been microbially precipitated carbonate ('leiolites'; Braga

et al., 1995) that was indurated soon after its formation. In this paper, mounds are defined as structures containing more than 25% of detrital or microbially generated structureless micrite. These structures developed in both deep and shallow waters, generally low-energy environments such as deep basins, lower slopes, slope/shelf breaks, intra-shelf areas and lagoons. Our definition of mounds follows several review articles (James, 1983, 1984), and its usage has continued in recent textbooks (Tucker and Wright, 1990).

1.1.2. *Stromatactis*

There is a long-lasting discussion about the definition and genesis of stromatactis, which remain enigmatic structures. Most authors agree upon the following essential criteria for defining stromatactis: sparitic structures embedded in micrite-dominated carbonate; flat to undulose smooth lower surface; digitate upper surface; internal sediment present; sparitic areas form a three-dimensional network (e.g., Bourque and Boulvain, 1993). There is, however, no real consensus about the inclusion of early diagenetic

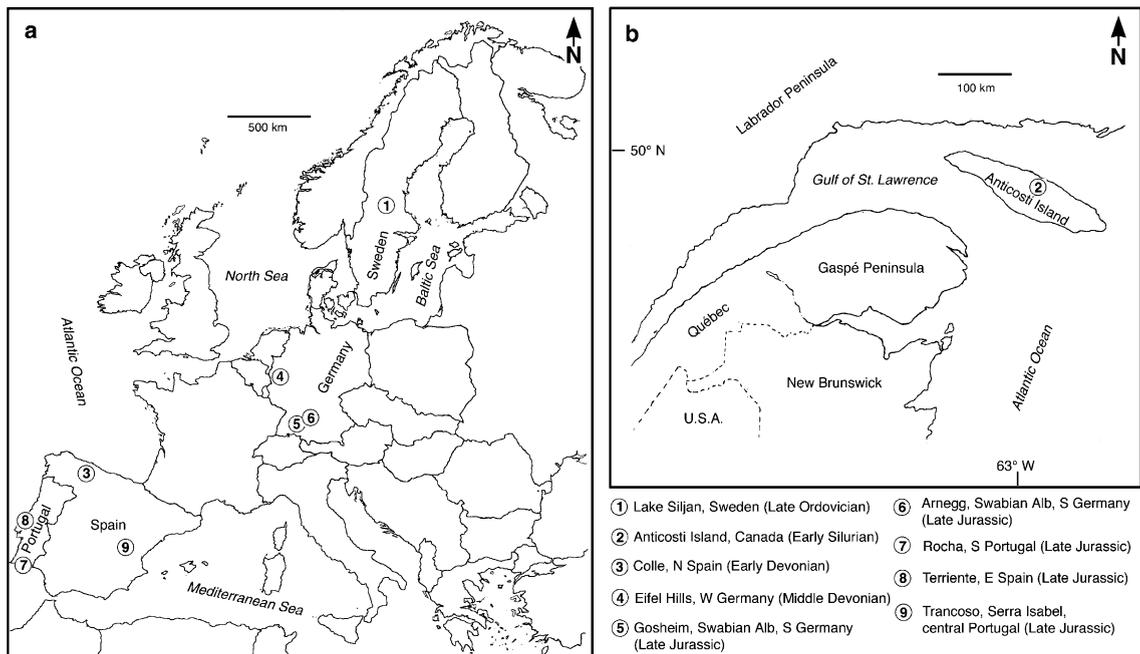


Fig. 2. Location map of investigated mound sites in Europe (a) and in SE Canada (b).

cements in the definition. According to Bathurst (1982), ‘radial–fibrous cements’ are a prerequisite for qualifying a structure as stromatactis, whereas Bourque and Boulvain (1993) somewhat more generally require ‘isopachous cement crusts’. Flügel (1982), by contrast, does not include cements in his definition of stromatactis at all. In our view, it is at least questionable to include diagenetic features such as cements in the definition of a sedimentary or biogenic structure, especially considering that radial–fibrous cements are not diagnostic for stromatactis and do occur in other cavities. However, as isopachous cements are regarded as a prerequisite for genuine stromatactis by most authors, we accept this view here, and consequently, adopt the definition of Bourque and Boulvain (1993). Furthermore, we follow the practicable terminology of Matyszkiewicz (1997), who also uses the definition of Bourque and Boulvain (1993), thus, clearly restricting the term ‘stromatactis’ to spar networks. When referring to the cavity system itself,

the term ‘stromatactis cavities’ is used. Isolated cavities that do not form a network but share all other characteristics of true stromatactis are termed ‘stromatactis-like cavities’. The latter term is also used for cavities without isopachous cements.

2. Jurassic mound types: some case studies

Abundance and composition of macrobenthic elements (corals, siliceous sponges) and the grade of calcifying microbial precipitation allow differentiation of four mound types in the Upper Jurassic of Iberia and southern Germany (Fig. 2). The main biogenic constituents of these mounds are scleractinian corals, siliceous sponges and microbolites and their broad compositional patterns can be illustrated on ternary plots such as that shown in Fig. 3. There is a large compositional gap along the ‘corals and coralline sponges–microbolites’ axis in Fig. 3, because scler-

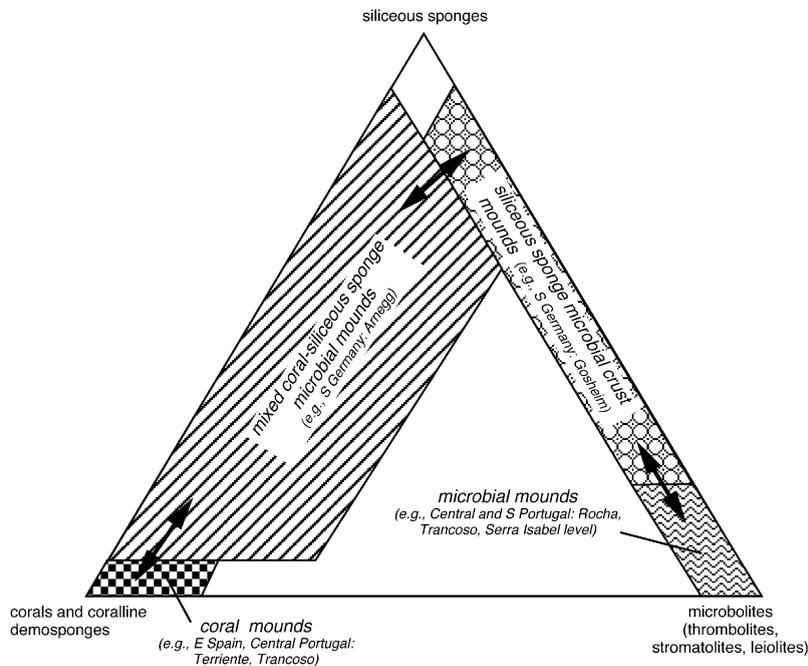


Fig. 3. Upper Jurassic mound types. The most important constituents of Upper Jurassic mounds are microbolites, siliceous sponges and corals/coralline sponges, and a minimum content of 25% (by volume) carbonate mud. The two white fields are not found in nature. The larger void area is positioned between corals/coralline sponges and microbolites, and is due to the high frame-building potential of scleractinian corals, which were associated with early lithifying microbial crusts. They formed genuine reef frameworks but not mounds. Siliceous sponges alone (smaller void area) could not form mounds, although exceptionally, sponge-framework reefs did occur. The arrows schematically mark observed vertical facies transitions.

actinian corals in association with microbial crusts typically formed stable framework reefs capable of constructing bioherms with a pronounced, steep flanked relief (Leinfelder et al., 1993), and hence did not form mounds. Such coral–microbolite reefs were mainly situated in shallow high-energy platform settings with only subordinate deposition of carbonate mud. A second gap occurs near the ‘siliceous sponge’ corner and reflects the restricted capability of siliceous sponges, especially hexactinellids, to form elevated structures on the sea floor. Although some sponges might have been relatively effective in trapping mud, hexactinellid sponges were only capable of forming reef structures when associated with microbial crusts (Leinfelder et al., 1993). Without these crusts, hexactinellid sponges could only have formed biostromes. However, lithistid demosponges rarely formed true framework reefs during the Middle Jurassic of France (Palmer and Fürsich, 1981).

2.1. Coral mounds

Mud-rich mound structures containing significant scleractinian corals are found within the Celtiberian range of Spain and the Lusitanian Basin of central Portugal (Nose, 1995). In the Lusitanian Basin (e.g., Trancoso; Figs. 4 and 5), coral mounds developed

as small lense-like bodies with thicknesses of 3–4 m and lateral extent of 6–10 m. The coral fauna is dominated by thick branching forms (*Microsolena*, *Dendraraea*) and very irregularly shaped colonies of *Convexastrea minima*. Microsolenid forms clearly dominate the association. *Microsolena* and *Dendraraea* formed ramose colonies reaching 0.7 m in height. Additional corals are the dendroid *Thecosmilia dichotoma*, the large solitary *Montlivaltia* cf. *obconica* and the fragile dendroid *Goniocora socialis* (cf. Nose, 1995). As well as terebratulid brachiopods, encrusting coralline demosponges (*Neuropora lusitanica*) and echinoid remains occur. The groundmass is composed of grey bioclastic mud.

The Spanish examples (e.g., Terriente; Fig. 6) represent small knobby coral mounds interfingering with well-bedded oncoid–intraclast–wackestone/floatstone. Individual reef bodies are 2–3 m in height and 2–4 m in lateral extent. The fauna is predominantly composed of massive corals (*Fungiastrea*, *Comoseris*, *Thamnasteria*) and chaetetids (*Ptychochaetetes*). Distinct thin layers within the patch reefs are characterised by occurrences of fragile dendroid corals (*Goniocora*, ?*Stylosmilia*). Within the interstitial muddy sediment, *Girvanella*-bearing oncoids provided local substrates for the initial settlement of reef



Fig. 4. Upper Jurassic coral mound from the central Lusitanian Basin; Trancoso, Portugal. Note branching coral colony (?*Dendraraea*) (arrow).



Fig. 5. Micritic coral mound facies with branching *Dendraranea* (left and right margin); note thin microbial coatings on biogenic components. Trancoso, central Lusitanian Basin; scale bar, 1 mm (thin section L 15).

building metazoans. Patch reefs graded upward into debris-rich massive coral biostromes that extended to several hundred metres (Fezer, 1988; Nose, 1995).

These mound examples are interpreted to have grown under slightly elevated influxes of detrital carbonate mud within calm lagoonal platform set-

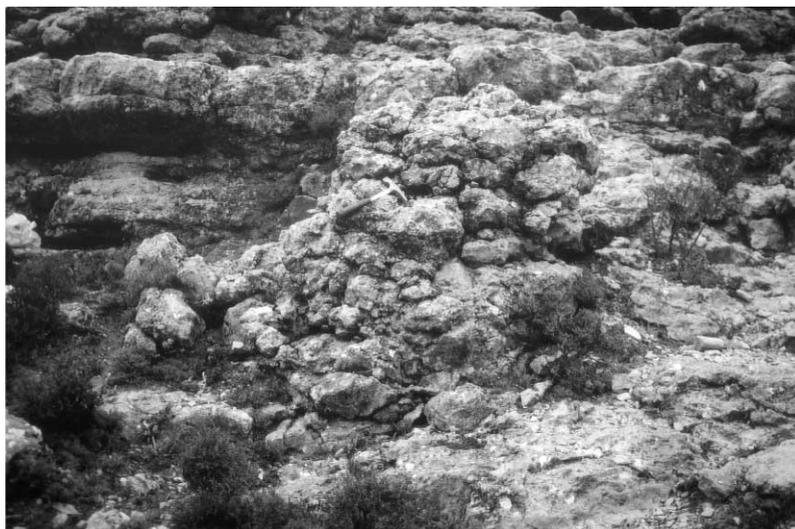


Fig. 6. Upper Jurassic coral mound from the Celtiberian Range, Terriente, eastern Spain.

tings (Leinfelder et al., 1994; Nose, 1995). The predominantly branching morphologies of strongly morphovaryable corals in the Portuguese example contrast with the more massive morphotypes in the patch reefs from the Celtiberian range in eastern Spain. Lack of encrusters and nonenveloping, stacked growth bands of coral branches in the Portuguese examples show, that corals were partially buried in sediment during life and are thus a strong indicator of limited, but continuous, background sedimentation (Nose and Leinfelder, 1997; Nose, 1999). The dominance of more massive corals in the Spanish mounds suggests that carbonate mud was mostly in suspension rather than being continuously deposited on the coral surfaces. Consequently, sedimentation rates must have been lower than in the Portuguese occurrences, allowing for the growth of low relief corals and, temporarily, of oncoids. In both examples, the coral fauna is strongly dominated by clonal multiseptate thamnasterioid taxa with highly porous skeletons. These features are thought to be indicative of scleractinian corals that were

capable of efficiently removing fine sediment particles from their surfaces (Hubbard and Pocock, 1972; Leinfelder, 1986). Hence, the adapted fauna, the low rate of microbial encrustation, and the high mud content all point to a sediment-stressed environment (cf. Leinfelder et al., 1993). The shelf geometry was characterised by low-angle, homoclinal (Celtiberian range, eastern Spain) or distally steepened ramp profiles (Lusitanian Basin, Portugal). The mud-rich reefs developed in low-energy shallow back-barrier or back-reef environments (Nose, 1995).

2.2. Siliceous sponge–microbial mud-mounds

Siliceous sponge–microbial mud-mounds are abundant in the Upper Jurassic of the Swabian and Franconian Alb of southern Germany (e.g., Wagenplast, 1972; Gwinner, 1976; Flügel and Steiger, 1981; Geyer and Gwinner, 1984; Meyer and Schmidt-Kaler, 1990; Selg and Wagenplast, 1990; Leinfelder et al., 1994; Leinfelder and Keupp, 1995). Sponge reef development

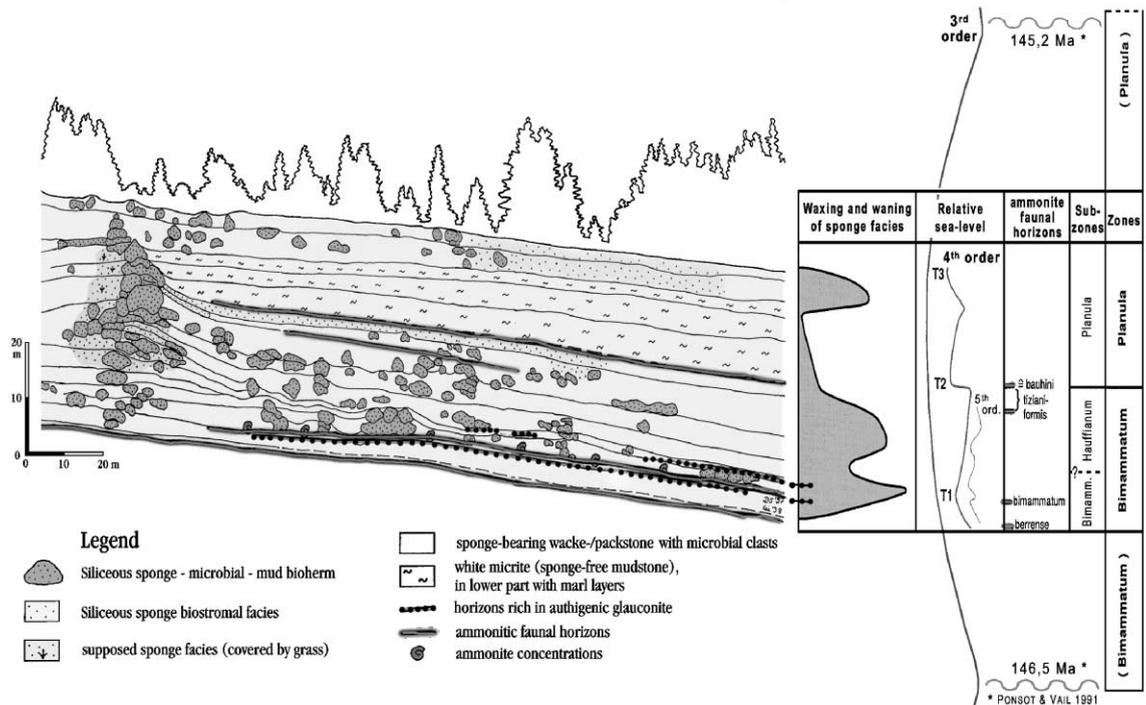


Fig. 7. The main part of the Klingenthal sponge mound complex, SW Germany, reaching from the Upper Oxfordian Bimammatum Zone to the Lower Kimmeridgian Planula Zone. Bimamm. = Bimammatum, ord. = order, T = transgression. Modified from Leinfelder (in press).

reached its maximum during the Late Kimmeridgian, when large parts of the outer ramps on the northern Tethyan shelf, including southern Germany, were covered by sponge mounds.

A typical and well-exposed example occurs on the western Swabian Alb near Balingen, in Gosheim (Klingenthalde quarry; Fig. 7). Biostratigraphically, the Gosheim reef complex extends from the *Bimammatum* Subzone (Upper Oxfordian) to the lower *Planula* Zone (Lower Kimmeridgian according to Schweigert and Callomon, 1997). In lithostratigraphic terms, it extends from the upper 'Weißjura alpha' to the lower 'Weißjura beta'. These well-bedded limestones with intercalated marly layers represent a cephalopod-rich deep-ramp facies. Most of the carbonate mud was probably exported from shallow platform areas where productivity was high (Pittet et al., 2000). The Gosheim reef complex exhibits a remarkable pyramidal architecture with a thickness of almost 50 m and a maximum lateral spread of 200 m. Consisting of numerous smaller mounds, the reef complex displays a 'fractal' geometry, making it possible to track cycles of several orders. In this complex, hexactinellid sponges clearly dominate the reef metazoans over lithistid

sponges. Shallow-water forms such as colonial corals, stromatoporoids or chaetetids were lacking. Tiny solitary corals with diameters of 4–6 mm occurring in the mound complex are interpreted as deep-water forms. Microbolites consisted of thrombolites and a relatively high proportion of leiolites, the latter often grading into allochthonous mud (Fig. 8).

The development of the reef complex commenced at the base of the *Bimammatum* Subzone, when sedimentation shifted from siliciclastic to carbonate domination (see Schweigert and Callomon, 1997 for a discussion of applying biozones to high-resolution biostratigraphy). The abundance of glauconite which generally forms in deep, cold water (Odin and Fullagar, 1988; Baumgärtner and Krautter, 1999), together with many boreal and subboreal ammonite forms (e.g., *Amoeboceras praebauhini*, *A. bauhini*, *Ringsteadia flexuoides*; det. G. Schweigert, Stuttgart) that were restricted to these levels, suggests water depths of at least 60 to 100 m. That the Gosheim reef complex grew in cold water is further corroborated by the presence of hexactinellids, which today are restricted to water temperatures below 15 °C (see discussion in Krautter, 1997). However, horizons containing boreal

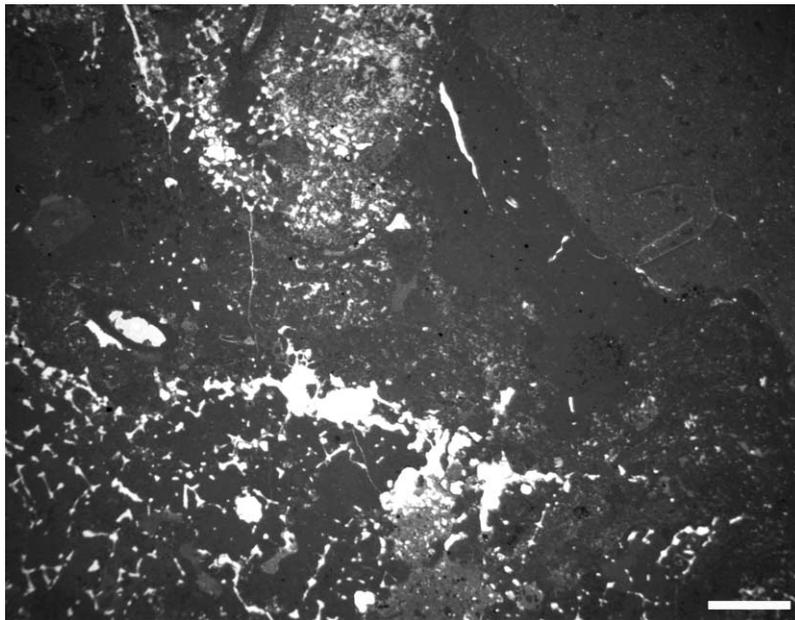


Fig. 8. Siliceous sponges overgrown by dense to peloidal microbial crusts (arrow); Gosheim, Swabian Alb, Germany, Upper Oxfordian; scale bar, 2 mm (thin section O5).

and subboreal ammonites also contain Mediterranean forms such as *Sowerbyceras*, which suggests the presence of a thermocline. The smaller bottom-dwelling (cold-water) ammonites probably lived within the sponge reefs whereas the larger tropical forms swam in shallow and warmer water.

The mound complex is most laterally extensive directly above the Bimammatum faunal horizon, which is positioned within the Bimammatum Subzone (Fig. 7). This level is marked by a dense, sheet-like cluster of numerous metre-sized mounds, a high content of glauconite, and giant sponges up to 2 m in diameter, probably the largest known Jurassic sponges. Ammonites and belemnites are also greatly enriched within this horizon. These faunal and lithological characteristics support stable depositional conditions and very low sedimentation rates, possibly during a sustained transgression. After this phase of maximum lateral extension of the mound complex, reef growth apparently waned rapidly, resulting in smaller and much more localised occurrences, especially above the *bauhini* horizon. The mounds expanded laterally for the last time in the Planula Zone. Reef growth was terminated by a phase of lime mud deposition that totally covered the reef complex following this period of time.

Fine biostratigraphic resolution and a distinctive sedimentary architecture allow pulses of mound growth to be correlated with global sea-level curves, and permit a finer sequence stratigraphic resolution than would have been possible from biostratigraphy alone (Fig. 7). The Gosheim reef complex formed during a dominant but unsteady 3rd order transgression, which was characterised by a change from strongly reduced to slightly elevated sedimentation rates, and which was modulated by 4th and 5th order sea-level fluctuations (Leinfelder working group, unpublished results). Cycles of even higher order are detectable within the single, metre-size mounds (Reich, 1995). Facies patterns within individual mounds are variable, but a common sequential trend may be recognised.

1. Siliceous sponges sporadically started to grow, commonly “rooted” in a marly layer.
2. Mound formation began, dominated by microbolite growth.
3. Mound growth was commonly followed by mud-rich deposition.

The succession might have been repeated several times in larger mounds.

In an allocyclic interpretation, the marls represent lowstand deposition, the siliceous sponge–microbolite growth corresponds to transgressive conditions, and the mud-rich capping facies represents highstand conditions. However, the repeated small-scaled succession of sponge settlement followed by microbolite growth was probably autocyclic. Mound architecture and the internal mound successions were probably controlled by overlapping allo- and autocyclic processes (Leinfelder working group, unpublished results). Hence, we feel that the spectacular Gosheim reef complex serves as a classic example for dynamic allocyclic and biological controls on mound formation. In addition, it serves to illustrate the importance of adjustment of delicate equilibria, particularly of microbolite formation and the accumulation of allochthonous mud, in the growth of sponge–microbial mounds.

2.3. Coral–siliceous sponge–microbial mounds

This mound type was particularly well developed within large scale successions that graded from siliceous sponge microbial mounds into coral reefs (e.g., Arnegg, Swabian Alb, southern Germany, Upper Kimmeridgian), and was consequently, probably transitional between shallow-water coral facies and deeper-water siliceous sponge facies. The Arnegg mounds were intercalated in a well bedded, bioclastic slope facies which, in certain layers, was first stabilised by platy microsolenid and fungiid corals (e.g., *Thamnasteria*, *Microsolena*). The mounds measure 7–10 m in height and 15–20 m across. Their composition is highly variable and they contain many different coral taxa. Low-integrated phaceloid and dendroid corals (*Montlivaltia*, *Thecosmilia*, *Enallhelia*) are more common than high-integrated thamnasterioid forms (*Dimorpharaea*, *Microsolena*, *Thamnasteria*). Sponges are dominated by lithistid demosponges, but coralline demosponges (*Neuropora*) and calcareous sponges also occur. Several microbiotic elements such as ‘*Tubiphytes*’,¹ recently reinterpreted as a miliolid

¹ Although *Shamovella* is the correct name for the genus *Tubiphytes* (Riding, 1993), the name ‘*Tubiphytes*’ in quotation marks is still used here for the Jurassic forms; for taxonomic details, refer to Schmid (1995).

foraminifer (Schmid, 1995, 1996), and the agglutinating worm tube *Terebella* grew on the skeletal substrates. Sediment within the mounds includes considerable amounts of mud, but mud-supported fabrics are speckled by grain-supported lenses and tongues containing intraclasts, ooids and bioclasts. Microbial crusts commonly developed either as nonlaminated peloidal to dense thrombolites or as stromatolites. Stromatolitic laminae preferentially formed within grainy sediments, whereas thrombolites were most abundant in mud-rich areas. The internal fabric of the mounds suffered early diagenetic fracturing, presumably caused by gravitational slumping (Nose, unpublished results). Gravitational processes, feasible as tilted geopetal fills, suggest depositional gradients of approximately 30° (Latenser, 2000). The combination of detrital mud, loose particles (intraclasts, ooids), early lithified microbial mats, and gravitational processes (including fracturing) led to a characteristic fenestral fabric with stromatactis-like cavities (Fig. 9). The cavities were commonly cemented by early fibrous calcite, followed by late isometric blocky calcite. After formation of the first fibrous cement, eloidal micritic sediment formed geopetal fabrics. Stromatactis-like cavities within peloidal to dense micritic sediment are primary structures that were probably produced by microbes, and therefore, cannot be related to syndepositional slumping.

Mound development started discontinuously, whenever the shedding of bioclastic debris terminated, most likely through autocyclic lateral migration of fan lobes (Nose, unpublished results). Reef growth on deactivated fan lobes was also described from the

Jurassic of the Lusitanian Basin, Portugal (Leinfelder, 1994). Initial patchy growth of lithistid sponges and branching corals accounted for the accumulation of muddy sediment. Grain-supported tongues could have been produced from occasional shedding of nonskeletal and skeletal particles from still active fans on upper slope regions. The mounds developed considerable positive relief due to the presence of stabilising microbial crusts (cf. Leinfelder et al., 1993). On the down-slope flank, the mounds exhibit very distinctive interdigitation with adjacent bioclastic beds. These contacts can be explained by multiphase, syndepositional slumping and sliding (Brunton, personal communication). Hence, we conclude that these mounds grew on a steepened slope and had a pronounced positive relief with relatively steep and unstable flanks. Faunal composition (lithistid sponges and corals) and the estimated steepness of the underlying slope suggest a water depth in the range of 30–40 m.

2.4. Microbial mounds

Microbial mounds are relatively common in the Jurassic (cf. Leinfelder and Schmid, 2000). A spectacular example is the large Rocha mound in the Lower Kimmeridgian of eastern Algarve, Portugal. It is a thrombolitic microbialite bioherm 30-m thick, comprising several stacked biostromes (Ramalho, 1988; Leinfelder et al., 1993; Schmid, 1996), and is embedded in marly deep-ramp facies of the upper Peral beds. This microbialite mound is, to a very large extent, composed of thrombolites with a pillar-like

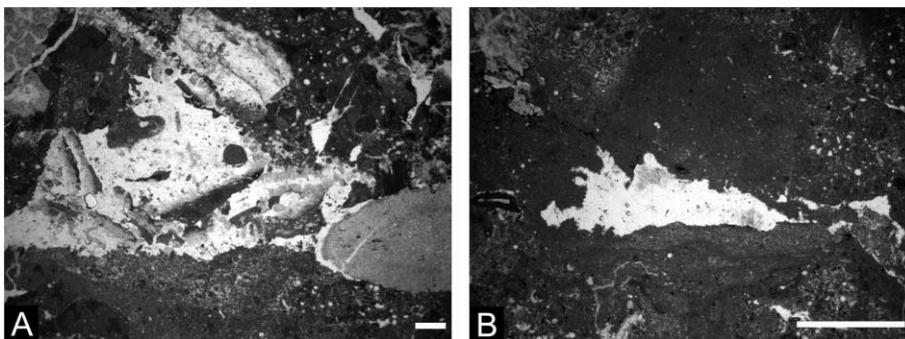


Fig. 9. (A) Irregular stromatactis-like cavity within mixed coral–siliceous sponge facies; Arnegg, Swabian Alb, Germany, Upper Kimmeridgian; scale bar, 1 mm (thin section RK 30). (B) Stromatactis-like cavity with peloidal, partly stromatolitic internal sediment, locality see (A); scale bar, 3 mm (thin section OR 8).



Fig. 10. Microbial mound facies with allochthonous sediment stored between thrombolite pillars, Rocha, Algarve, Portugal, Peral beds, Lower Kimmeridgian; scale bar, 1 cm (sample ROC 2).

growth form. Individual pillars measure several centimetres across (Fig. 10). Detrital mud was trapped among the pillars and consequently, formed occasional lenses or tongues. Together with structureless leiolitic crusts, this dense micrite comprises approximately 20–25% of the structure, making the Rocha bioherm a mound by the definition used here. The only reef metazoans in this mound are scarce siliceous sponges that are mainly restricted to three distinct levels in the upper part of the mound. Microencrusters comprise the low-diversity *Terebella*–‘*Tubiphytes*’ association and hint at a relatively deep marine setting (i.e., below storm-wave base; Schmid, 1996). The ‘*Tubiphytes*’ tests are relatively small in diameter, which further constrains the depositional setting to deep ramp (Schmid, 1996). Taking into account the conspicuous scarcity of reef metazoans, dysaerobic to poikiloaerobic conditions (poikiloaerobic according to Oschmann, 1991) probably prevailed during mound

growth and led to short periods of sponge growth during oxygenated phases (Leinfelder et al., 1993). This interpretation is further corroborated by high glauconite contents within the mound and surrounding facies, and clusters of the probable chemosymbiotic bivalve *Aulacomyella* within the mound structures (Leinfelder et al., 1993; Werner et al., 1994).

Metre- to decimetre-sized microbial mounds are also found in the Lower Kimmeridgian of the Lusitanian Basin in west-central Portugal. Together with other reef types, they are particularly common in the Serra Isabel level which is enclosed by deep-ramp Abadia marls, silts and sandstones. This level is characterised by siliceous sponge-bearing thrombolitic muddy biostromes, muddy thrombolitic mounds, crinoid meadows and moderate- to high-diversity coral–thrombolite patch reefs in a strongly condensed succession (Werner et al., 1994; Nose, 1995). Except for some poorly preserved siliceous sponges, reef metazoans are absent, and the mounds contain the same low-diversity microencruster association as found in the Rocha mound described above. A dysaerobic to poikiloaerobic shallow outer ramp setting can therefore also be deduced for the Serra Isabel mounds (Leinfelder et al., 1994). A special feature of these mounds is their abundant stromatactis-like cavities, which may reach several centimetres in diameter (Fig. 11; Schmid, 1996). In the microbially dominated parts of these mounds, the cavities are mainly produced by early-lithifying thrombolitic crusts, which sheltered the areas from intermittent lime mud sedimentation. In contrast to the thrombolites, the micritic sediment was subject to early diagenetic compaction, thus enlarging the cavities. In mud-rich parts of the mounds, the cavities can be attributed to gravitational processes which are visible not only in the fabric but also in numerous broken *Terebella* worm tubes (Fig. 11A), a feature which is otherwise very uncommon.

3. Growth rates of Jurassic microbolites and mounds

As demonstrated above, microbolites are an essential constituent of Jurassic mounds. The determination of microbolite growth rates, however, proves to be difficult since no genuine modern or Recent analogues to Jurassic reefal microbolites exist. The cryptic cave

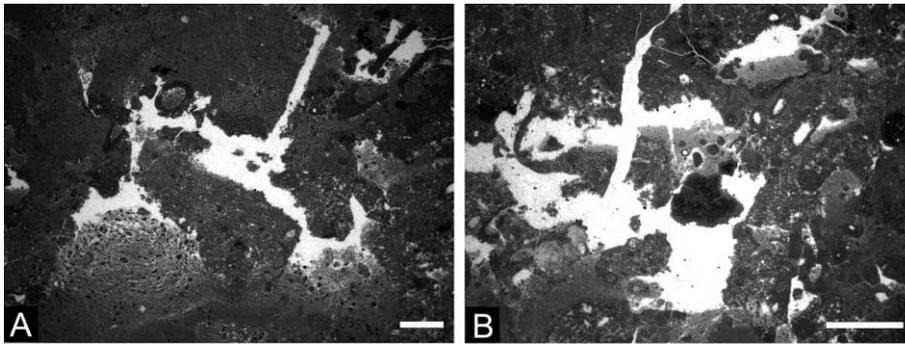


Fig. 11. (A) Stromatolite-like cavity linked to early diagenetic fractures most probably due to gravitational slumping, which is also indicated by broken *Terebella* worm tubes (arrow); Serra Isabel level near Amalal ridge, central Lusitanian Basin, Portugal, Lower Kimmeridgian; scale bar, 1 mm (thin section G2). (B) Several stromatolite-like cavities linked to early diagenetic fractures, locality see (A); scale bar, 2 mm (thin section AMA 5).

microbolites of Lizard Island (Reitner, 1993) exhibit very low net growth rates of 10 to 15 mm/1000 years or 10–15 B (Bubnoff units). However, a corrosion effect caused by intercalated iron–manganese biofilms amounts to 40% net volume loss (Reitner, 1993) and produces several discontinuous surfaces. Considering this, the value for microbial crust growth in the absence of interruptions can be corrected to about 20 B.

Taking this value as a base, a relatively large time span of 1.5 Ma would be required for the growth of the 30-m-thick thrombolitic mound at Rocha (see above). Since this mound is almost exclusively constructed by microbolites, it seems best suited for growth rate examination. The deep-ramp Peral beds, in which the mound is intercalated, are dated as extending from the Middle Oxfordian to the Lower Kimmeridgian (Marques, 1983). Assuming an approximate time span of 7 Ma, a sedimentation rate of 29 B results. This is in general agreement with the sedimentation rate of 35 B that can be calculated for the bedded marly limestone facies of the Swabian Alb (400 m in ca. 11 Ma; cf. Geyer and Gwinner, 1984; Ponsot and Vail, 1991). These rates are mean values for several million years net accumulation and include all hiatuses. For the Swabian sponge mound-bearing facies (about 600-m thick), a value of 55 B results. Selg and Wagenplast (1990) estimated sedimentation rates of 60 B for the Kimmeridgian of the Swabian Alb, taking decompaction into account. These values are consistent with the relatively low carbonate production that has to be expected in water depths exceeding 10–15 m (Schlager, 1981).

The Rocha thrombolite mound probably established itself during a period of limited or nonsedimentation; however, evidence in the form of numerous marine-sediment-filled pockets and cavities among the thrombolite pillars (Fig. 10) suggests that growth continued into periods of increased, possibly episodic sedimentation. If microbial growth kept up with sedimentation, it is reasonable to presume that mound growth also did. Hence, we conclude that the rate of mound growth was in the vicinity of 55 B, the rate estimated for the sponge–microbolite facies of the Swabian Alb. Accordingly, the mound would have formed within a time span of 550 ka. Because no major interruptions in mound development have been recognized, this estimate probably still represents a minimum value; microbial crusts probably were able to grow faster. However, relatively fast microbolite growth has only been postulated for shallow-water coral thrombolite reefs, where it can be deduced from established coral growth rates (Nose and Leinfelder, 1997). In these shallow-water reefs, corals were closely intergrown with microbolites to form a reef framework. This suggests that the microbolites might have grown as fast as the corals, some 1–2 mm/year (Schmid, 1996). Transferring this value to the deep-ramp Rocha mound yields a minimum duration of mound growth of 30 ka. This value is certainly much too low, considering the lack of fast-growing metazoans and the dysphotic conditions that probably slowed down microbolite growth. Overall, we believe that it took the Rocha mound between 30 and 550 ka

to grow. A more realistic and conservative estimate is that mound growth took place over an interval of 100 to 500 ka. If correct, this suggests that mound growth was influenced by 4th order sea-level changes, and supports the conclusions of Kendall and Schlager (1981) that sea-level changes of 4th and 5th order played prominent roles in controlling carbonate platform development.

High-resolution biostratigraphic data can also help to determine growth rates of the sponge–microbial mound complex of Gosheim described above. The maximum development time for the entire complex is about 700 ka; however, maturity analysis of authigenic glauconite in two pronounced glauconitic levels within the mound suggests two sediment hiatuses of about 20 to 200 ka each (Baumgärtner, Stuttgart, in preparation). It is likely therefore that the complex is significantly younger than 700 ka.

As in most mounds elsewhere, the individual mounds contain few physical sedimentary structures. There are, however, some 30 pronounced bedding planes in the mound complex (Fig. 7), suggesting periods of time when physical sedimentation occurred rather than mound growth. Judging from these bedding planes, we roughly estimate that only two-thirds of the interval of time that was available for mound growth actually saw mound growth, which calculates to approximately 300 ka actual growth time ($(700,000 - 200,000) \times 2/3$). Given the mound thickness of 50 m, an annual minimum growth rate of 0.16 mm/year results. An average mound of 1-m thickness within the complex would therefore have grown in about 6000 years.

Another approach to constraining mound growth rates is by comparison with coral–microbial reefs. In many coral–microbial reefs, microbolite crusts could keep up with coral growth and in these complexes, growth rates of microbolites could be up to several millimetres per year. If microbolite crust growth rates of about 1 mm/year are accurate for the Gosheim mounds, the crust-rich metre-sized bioherms should each have grown in about 1000 to 3000 years. A maximum of 30 mounds are amalgamated in the central area of the complex, which would result in an aggradation time of no more than 100 ka, indicating a preservation potential of only 14.5% (since 100 ka of active growth represents 14.5% of the available time span of 700 ka). This seems more realistic than the

above approach since metre-sized, strongly encrusted hexactinellid sponges, which can make up a large proportion of a single mound, were certainly not older than several hundreds of years (Barthel and Tendal, 1994). Growth rates of about 1 mm/year, together with a preservation potential of only 15–20%, may be realistic for other sponge mounds.

4. Comparison with Mid-Palaeozoic mounds

By providing selected examples of Mid-Palaeozoic mounds, we have attempted to demonstrate that Jurassic and Mid-Palaeozoic mounds have structural similarities. This in turn may improve our understanding of the nature and evolution of mechanisms that controlled mound formation. Numerous publications exist, which summarise characteristics and origins of Mid-Palaeozoic mounds from many localities around the world (e.g., Belgium, Southern France, Sardinia, central Sweden, Northern Africa, Canadian Arctic, Northern America, Australia; e.g., Gnoli et al., 1981; Ross et al., 1975; Jaanusson, 1978; Wendt, 1993; Wendt et al., 1997). In Mid-Palaeozoic times (Ordovician–Devonian), mounds developed generally as stromatolitic mud-rich buildups and differ from their Jurassic counterparts in terms of composition and overall distribution of characterising metazoans (e.g., corals, stromatoporoids, siliceous sponges, crinoids, bryozoans, brachiopods). Besides various stromatolitic mounds from the Middle and Late Ordovician (e.g., Meiklejohn Peak, Nevada, USA; Siljan Lake, Central Sweden), Mid-Palaeozoic mounds also include the Upper Devonian (Frasnian) so-called ‘*récifs rouges*’ (cf. James and Bourque, 1992; Bourque and Boulvain, 1993) from Belgium, the Frasnian mounds from the Harz mountains (Rübeland mud-mound; Weller, 1995) and the Canning Basin (‘Glenister knolls’; Wood, 1999), as well as the spectacular Givetian mud-mounds from Algeria and Morocco (Wendt, 1993; Wendt et al., 1997). Some of these structures were considered to have been initiated in deeper water, but grew into fairly shallow water with higher-energy regimes (‘*récifs rouges*’; ‘Glenister knolls’, Canning Basin; Boulvain and Coen-Aubert, 1997; Wood, 1999). Others grew exclusively in deeper water (100–200 m; e.g., Algeria), or at moderate water depth (several tens of metres, e.g., Morocco; Wendt, 1993; Wendt et al., 1997) (see Fig. 12).

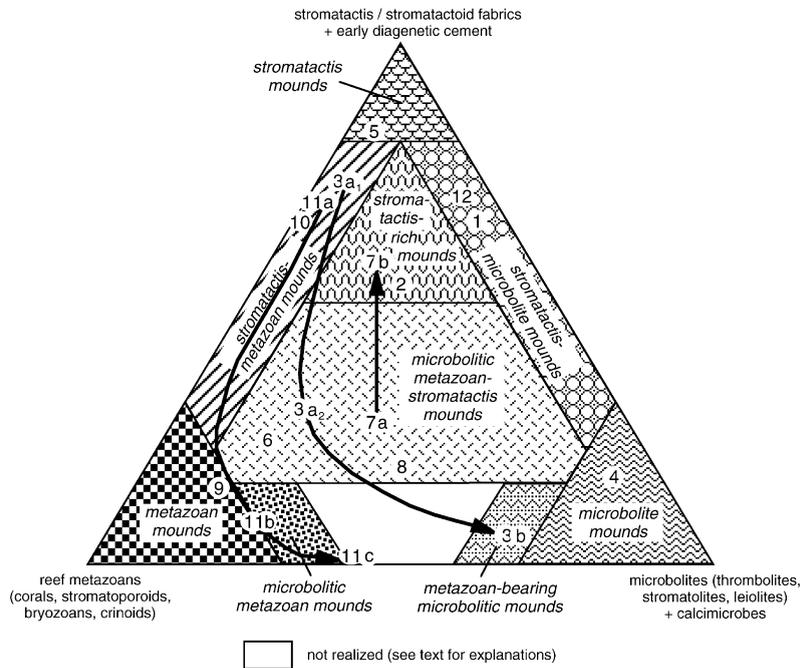


Fig. 12. Mid-Palaeozoic mound types (Upper Ordovician–Devonian), the mounds are characterised by a minimum content of 25% (by volume) carbonate mud. Since stromatactis and stromatactis-like cavities are much more abundant in Mid-Palaeozoic mounds than their Jurassic counterparts, the top of the triangle is designated ‘stromatactis fabrics’. Siliceous sponges, which were not as abundant in the Mid-Palaeozoic, are combined with ‘reef metazoans’. Selected localities from different time intervals are indicated by numbers: 1 — Siljan area, Sweden, Upper Ordovician, Boda Limestone (personal observations, cf. Beutinger, 1996); 2 — Anticosti Island, Canada, Lower Silurian, Jupiter Fm., East Point Member (personal observations, cf. Copper, 1988); 3 — Gaspé, Canada, Upper Silurian [3a — Gros Morbe Member, 3b — Anse à la Barbe Member] (Bourque and Raymond, 1988; Bourque and Boulvain, 1993); 4 — Southwestern Alaska, Silurian/Devonian boundary, Holitna Basin (Clough and Blodgett, 1988); 5 — Montagne Noire, France, Lower Devonian, Emsian (Flajs and Hüssner, 1993; Flajs et al., 1995); 6 — Colle, Cantabria, Spain, Lower Devonian, Emsian, La Vid Fm (personal observations); 7 — Kerpener Weinberg, Eifel, Germany, Middle Devonian, Eifelian, Ahbach Fm., Hallert Member [7a — base, 7b — core] (personal observations, cf. Pohler et al., 1999); 8 — Nohn, Eifel, Germany, Middle Devonian, Eifelian, Ahbach Fm, Hallert Member (personal observations, cf. Kaldun, 1998); 9 — Rauhheck, Eifel, Germany, Middle Devonian, Givetian, Loogh Fm. (personal observations); 10 — Algeria, Middle Devonian, Givetian (Wendt et al., 1997); 11 — récifs rouges, Belgium, Upper Devonian, Frasnian [11a – c = vertical facies succession A–C] (Bourque and Boulvain, 1993); 12 — Rübeland, Harz, Germany, Upper Devonian, Frasnian, Elbingerode complex (Weller, 1995).

The main constituents of Mid-Palaeozoic mounds are stromatactis (including early diagenetic cement), metazoans (including bryozoans, crinoids, sponges and corals) and microbolites (thrombolites, stromatolites and/or leiolites). Stromatactis and stromatactis-like cavities are both much more abundant in Mid-Palaeozoic mounds than in Jurassic mounds (Fig. 3). Mid-Palaeozoic mounds are also more morphologically and compositionally diverse, perhaps owing to the longer time span than afforded by the Jurassic. The compositional void along the ‘metazoans–microbolites’ axis in Fig. 3 is much

smaller than the gap between corals, coralline demosponges and microbolites that typifies the Jurassic examples. Mid-Palaeozoic metazoans (stromatoporoids, rugose and tabulate corals) may have had a weaker reef-building potential than modern-type scleractinian corals. Judging from the volumetrically minor role played by microbolites in Mid-Palaeozoic reefs, calcifying microbial communities were probably less effective reef builders in the Mid-Palaeozoic (especially in agitated shallow water) than they were in the Jurassic (cf. May, 1997; Nose et al., 1999).

Our comparative approach is based on our own (re-)investigations and descriptions of selected mound localities. Our study sites (Fig. 2) were in Upper Ordovician strata in central Sweden, Lower Silurian strata in eastern Canada, Middle Devonian strata in the Eifel Hills (Rhenish Slate Mountains), and Lower Devonian strata in the Cantabrian Mountains (northern Spain). Many of these mounds exhibited a prominent vertical facies zonation as shown in Fig. 12.

4.1. Siljan Lake (central Sweden), Upper Ordovician

In the Siljan district, carbonate mounds are known from two stratigraphic intervals of Caradocian and Ashgillian age. The mounds are intercalated in the nodular mudstone succession of the central Baltoscandian epicontinental shelf (Jaanusson, 1979, 1982; Middleton et al., 1991). For our comparative approach, this paper only deals with the Upper Ordovician mound level (Boda Limestone sensu Thorslund, 1935).

The Boda mounds of the Siljan area developed as huge elongated carbonate lenses with maximum lateral extents of 1000 m and maximum thicknesses of 100–140 m (Jaanusson, 1982). A massive core facies with abundant stromatactis cavities and cement patches, in some cases amounting to more than 50% of the rock volume (Jaanusson, 1979; Middleton et al., 1991; Beutinger, 1996), can be distinguished from bedded flank facies containing marly intercalations, and very fossiliferous intervals. Flanking beds, especially in upper parts of the mounds, are locally (e.g.,

Osmundsberget) rich in rugose and tabulate corals (*Bodophyllum osmundense*, *Acantholithus*, *Catenipora*, *Palaeofavosites*, *?Propora*; cf. Jaanusson, 1982), brachiopods (e.g., *Eoplectodonta*, *Eospirigera*, *Diceolusia*; cf. Jaanusson, 1982; Beutinger, 1996; Copper, personal communication) and cystoids (*Eucystis*, *Tetreucystis*; cf. Jaanusson, 1982).

Parts of the core facies and thick-bedded flanking beds commonly reveal a polymicritic thrombolitic fenestral fabric (Fig. 13; Beutinger, 1996). Thrombolites are composed of fenestral biomicrites containing ostracodes, fenestrate bryozoans and crinoid remains (Pratt, 1995; Beutinger, 1996). Small irregular to stromatactis-like fenestrae commonly filled with internal sediment can be distinguished from much larger (at least several centimetres) stromatactis cavities (Figs. 14–16). The latter displayed thick radial fibrous cement crusts, whereas the smaller counterparts revealed only drusy blocky calcite cements.

Isolated sponge spicules (e.g., tetractandine and hexaxone spicula; Fig. 13A) commonly occur. Although Early and Mid-Palaeozoic hexactinellid sponges rarely formed fused spicules, one relatively well preserved specimen of a rigid hexactinellid sponge was found within the Boda mound core facies by Beutinger (1996). Occasionally, cavities within the thrombolitic micrite exhibit scalloped surfaces, indicative of sponge-boring activity (Neuweiler, personal communication), and hence, of syndepositional ?microbial lithification (Fig. 17). Similar fabrics also occur within the extant lithohermes in the Straits of Florida (Neumann, personal communication).

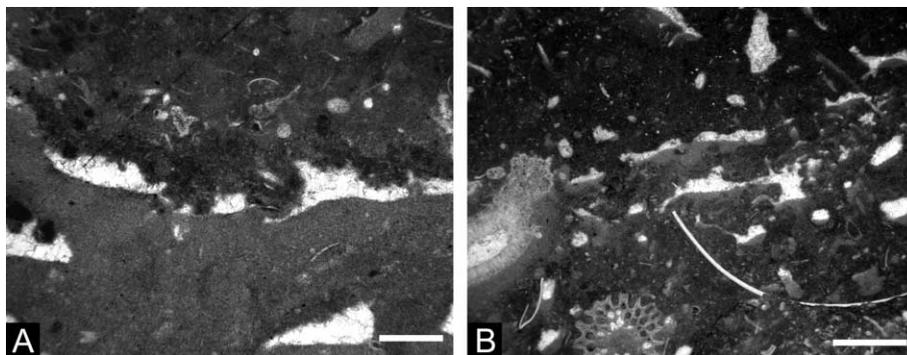


Fig. 13. (A) Stromatactis-like cavity beneath thrombolitic layer; Skålberget, Lake Siljan, central Sweden, Upper Ordovician Boda Limestone; scale bar, 1 mm (thin section S 26). (B) Peloidal thrombolitic fabric with small stromatactis-like cavities; Osmundsberget, locality see (A); scale bar, 2 mm (thin section O V 1b).

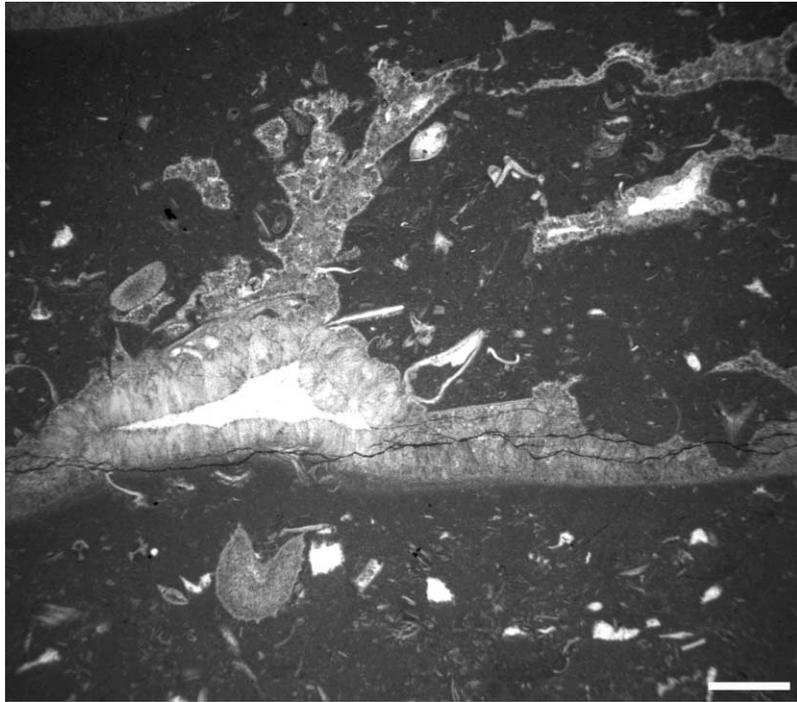


Fig. 14. Stromatactis cavities with thick isopachous radial fibrous cement crusts; Osmundsberget, Lake Siljan, central Sweden, Upper Ordovician Boda Limestone; scale bar, 2 mm (thin section O V 1(a)).

Additional core facies types comprise bioclastic bryozoan grainstone, dasycladacean (*Palaeoporella*) boundstone and trilobite floatstone/rudstone. Besides *Palaeoporella*, some other algae and microencrusters occur, including *Hedstroemia*, *Vermiporella*, ?*Girva-*

nella and *Wetheredella tumulus* (Beutinger, 1996). Flanking beds are mainly composed of crinoid-rich grainstone/packstone, brachiopod- and crinoid-rich marl as well as the coral brachiopod-rich units mentioned above. Among crinoid stems, synarthrial stem

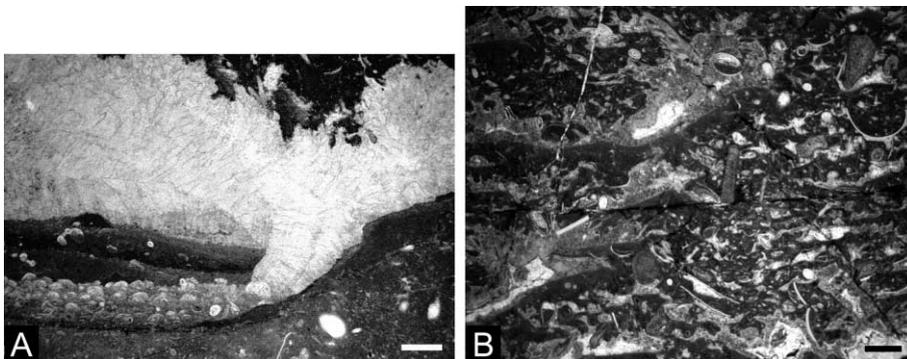


Fig. 15. (A) Multiple layers of internal sediment with ostracode packstone layer at the base, Jutjärn, Lake Siljan, central Sweden, Upper Ordovician Boda Limestone; scale bar, 1 mm (thin section J V 3a). (B) Numerous stromatactis cavities within bioclastic wackestone, locality see (A); scale bar, 1 mm (thin section J IV 2).

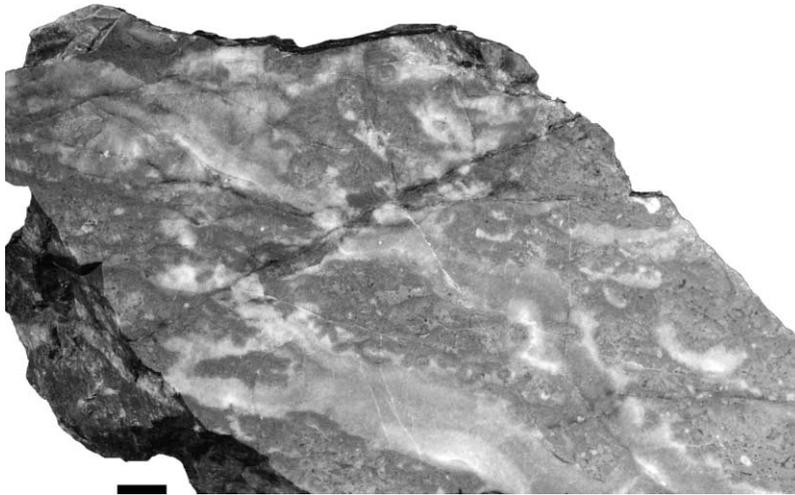


Fig. 16. Stromatactis-rich mound facies from the Upper Ordovician Boda Limestone, Lake Siljan, central Sweden; scale bar, 1 cm (sample J V 4).

morphologies belonging to the genus *Ristnacrinus* are abundant and indicate a strongly rheophilic character of the crinoid fauna (Donovan, 1988).

The morphology of the mounds is commonly “mushroom-like”, suggesting that mounds prograded over the flanking beds. The mounds are considered to

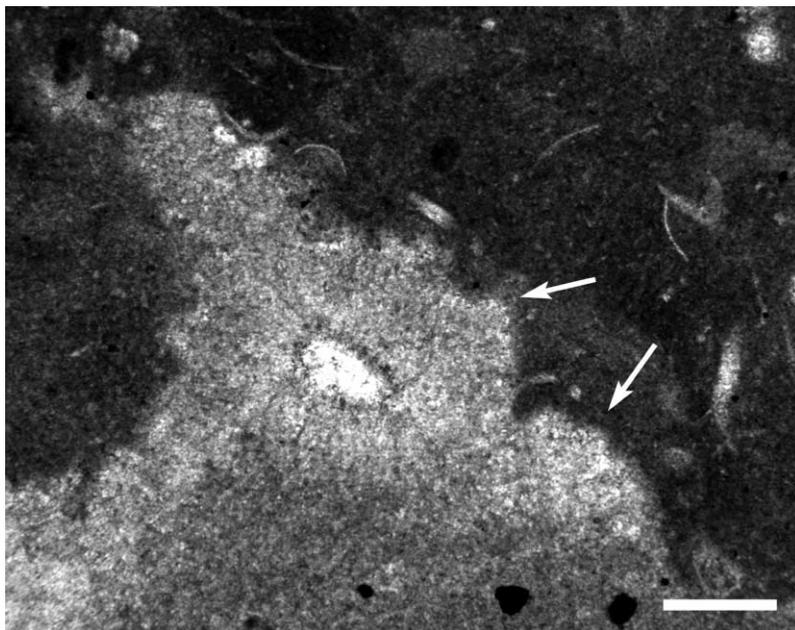


Fig. 17. Small stromatactis cavity beneath mottled, partly clotted micrite. The scalloped cavity boundary surface (arrows) is indicative of sponge-boring activity (Neuweiler, pers. commun.); Skålberget, Lake Siljan, central Sweden, Upper Ordovician Boda Limestone; scale bar, 0.5 mm (thin section S 26).

have formed prominent elevations over the sea floor (Jaanusson, 1982). Although depth of mound growth is still a matter of debate, the presence of green algae (e.g., *Palaeoporella*) points to their formation well within the photic zone. Grainstone beds and lenses within the core facies suggest deposition during weak to occasionally moderate turbulence, probably above storm wave base. However, the occurrence of the orthid deep-water brachiopod *Dicoelosia* within the upper flanking beds, even though associated with tabulate and rugose corals, suggests deposition below storm wave base (cf. Jaanusson, 1982; Jin and Copper, 1999).

Jaanusson (1979) assumed that the mounds lithified syndepositionally, but he thought that early lithification was due to inorganic precipitation of carbonate cement among carbonate grains. In our opinion, the common thrombolitic fabric in many parts of the mound core facies clearly indicates microbial, and hence, an organic nature of the mound sediment. We conclude that inorganic precipitation of extensive radial fibrous cement and microbially induced calcification both contributed to mound formation in the Boda Limestone. Siliceous sponges might also have contributed significantly to the accumulation of biomicritic sediment. However, a predominantly sponge-derived formation of mounds and stromatactis cavities (Bourque and Boulvain, 1993) is not likely a given argument of Pratt (1995). He observed that thromboids and microbial crusts were commonly the primary framework surrounding stromatactis, that many mud-mounds lacked sponge spicules, and that spicules or

sponge fragments were not common in grainstone lenses or geopetal sediments within stromatactis.

Jaanusson (1979, 1982) suggested that the Boda mounds might be comparable to modern lithoherms in the Strait of Florida (Neumann et al., 1977; Messing et al., 1990; Paull et al., 2000). There are marked similarities between the modern lithoherms and the Boda mound facies. Both display early lithified crusts in association with detrital fine grained sediment. The crusts within the lithoherms are characterised by relatively smooth hard upper surfaces and less consolidated, irregular lower surfaces. The sediment between successive crust levels is poorly cemented and was probably prone to winnowing. The detailed observations of Messing et al. (1990) led us to conclude that the modern crust–detrital sediment associations structurally resemble stromatactis-bearing polymicritic fabrics of many ancient mounds. Our observations on lithoherm material provided by A.C. Neumann support these conclusions. Messing and his colleagues argued that the shape and structure of the lithoherms was mainly controlled by strong currents and that they reflect differences in current velocities. The rheophilic character of the crinoids within the Boda Limestone also points to substantial current flow during mound growth. We conclude that the Boda mounds might be fossil counterparts of the modern lithoherms; however, given that they contain green algae, the Boda mounds probably developed in much shallower water. Consequently, the modern lithoherms can be regarded as living fossil reefs that survived in a deep water refuge.

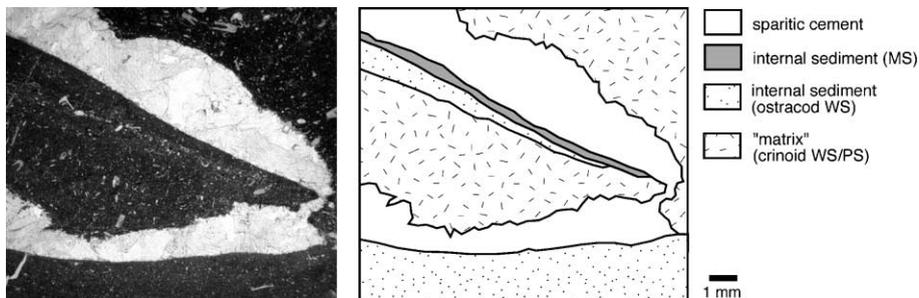


Fig. 18. Connection between two stromatactis cavities with internal sediment, mound facies, Anticosti Island, Canada (Lower Silurian, East Point Member, Jupiter Formation) (thin section ANT 14/2.1). WS = wackestone, PS = packstone. A reconstruction of this mound is shown in Fig. 21.

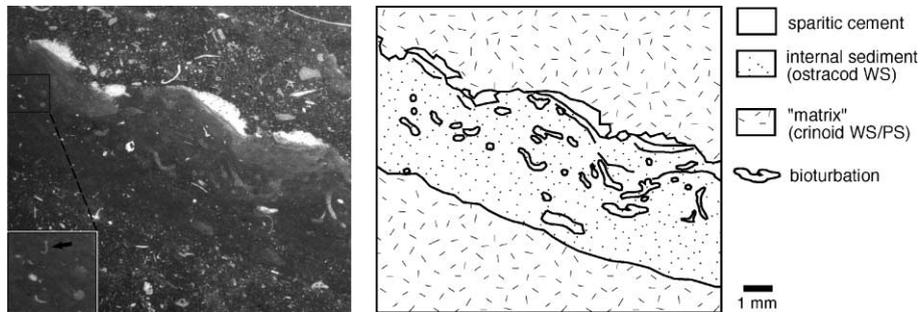


Fig. 19. Stromatactis cavity in a mound from Anticosti Island, Canada (Lower Silurian, East Point Member, Jupiter Formation); the internal sediment has been bioturbated, probably by cryptic ostracodes (arrow) (thin section ANT 14/2.2a). WS=wackestone, PS=packstone. A reconstruction of this mound is shown in Fig. 21.

4.2. Anticosti Island (Canada), Lower Silurian

The Ordovician to Silurian strata of Anticosti Island in eastern Canada contain a variety of reefal buildups, most of which exhibit mound morphologies (e.g., Copper, 1988). The mud-mounds in the Lower Silurian East Point Member of the Jupiter Formation are especially rich in stromatactis fabrics (Figs. 18–20). These widespread mounds average 3 m in thickness and 10 m in width. The reef-building association is dominated by crinoids, and contains subordinate numbers of brachiopods and bryozoans. The crinoid-rich mound matrix consists of wackestone and packstone and contains numerous stromatactis cavities that form a three-dimensional network. The cavities are, to a large extent, arranged in layers and must have been produced and kept open by currents flowing through the mound (Fig. 21). Water flow partly eroded material from the mound

and partly imported calcareous mud into the cavities from outside the mound. This scenario is consistent with the model for stromatactis genesis outlined by Pratt (1982) and also agrees with observations of extant lithoherms in the Straits of Florida (see above).

Ostracode carapaces are a minor constituent of the mound matrix, but these shells frequently dominate internal sediment within cavities, suggesting that the stromatactis cavity system formed a protected habitat for a cryptic ostracode fauna. The ostracodes are also the correct size (up to 0.8-mm long) to have produced the numerous small burrows that frequently mottle the internal sediment (Fig. 19). Epifaunal ostracode traces are common in modern sediments (personal observations; Voigt and Hartmann, 1970), but fossil examples are also known (Bandel and Quinzio-Sinn, 1999). Danielopol et al. (1996) provide descriptions of extant ostracode faunas from the shallow subsurface. Given

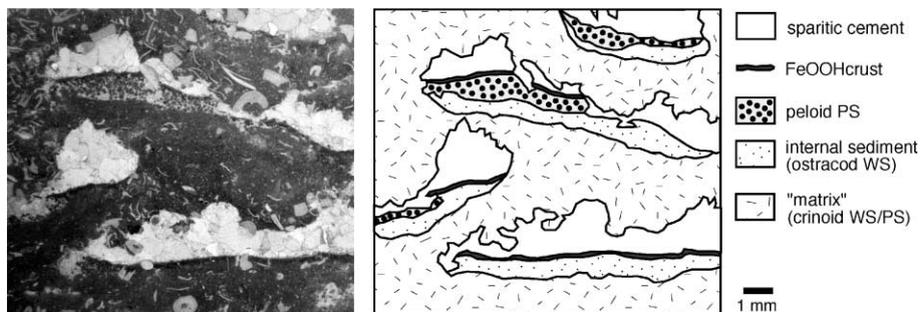


Fig. 20. Stromatactis cavities with peloidal internal sediment of probable microbial origin, mound facies, Anticosti Island, Canada (Lower Silurian, East Point Member, Jupiter Formation) (thin section ANT 14/2.4). WS=wackestone, PS=packstone. A reconstruction of this mound is shown in Fig. 21.

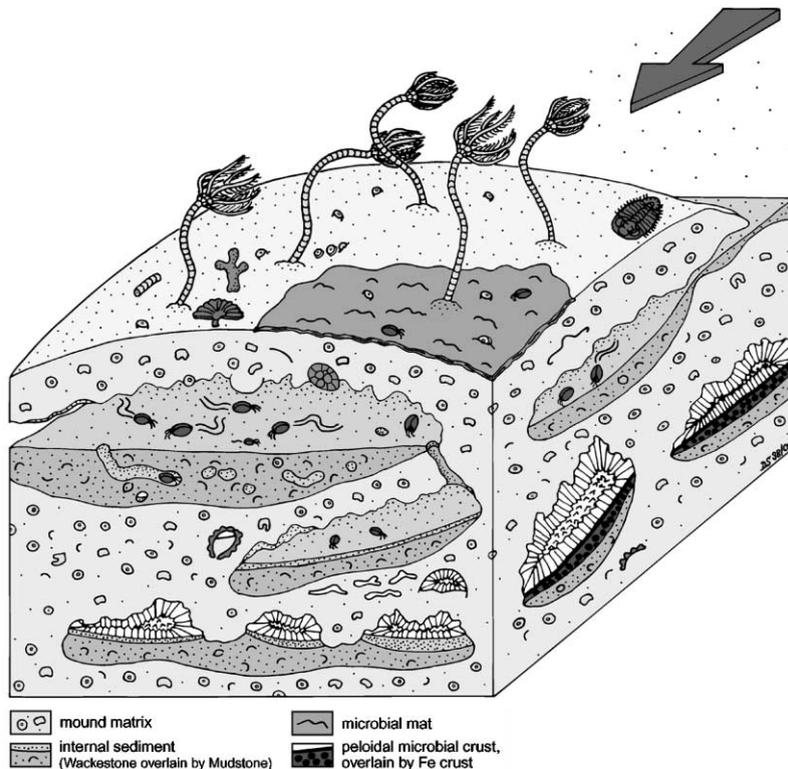


Fig. 21. Reconstruction of a stromatolite-rich mud-mound from the Lower Silurian of Anticosti Island, Canada (Jupiter Formation, East Point Member) (detail; figure not exactly to scale). The mound surface was inhabited by a reef association dominated by rheophilic crinoids. Some bryozoans, brachiopods and trilobites were also present. Sedimentation rates oscillated and calcifying microbial mats developed during sediment-starved episodes. This resulted in stabilisation and enhanced calcification of the topmost mound layer. Water currents, symbolised by an arrow, were able to winnow some unlithified sediment beneath the mound surface. Subsequently, cavities filled up with micritic internal sediment, which was mainly imported from outside the mound. A cryptic ostracode association commonly thrived in such partially filled cavities, and bioturbated the internal sediment. Within some deeper stromatolite cavities, isopachous cement crusts developed during early diagenesis. See text for further explanation.

the high abundance of ostracodes within the stromatolite cavities, it is possible that the small animals contributed, to some extent, to keeping the cavity system open by their bioeroding activity.

Microbial mats were common everywhere on the mound surface and may have also grown atop internal sediment within cavities. The presence of microbial mats within the mound structure is supported by occasional iron and peloidal crusts within cavities (Fig. 20), which are not found elsewhere within the mound and are thus considered to be microbial *in situ* precipitates. Ultimately, the microbial mats within and atop the mound complex may have provided a food source for the ostracodes. Stromatolite cavities even richer in ostracode carapaces were found in samples of Beutinger

(1996) in Upper Ordovician strata of the Siljan area in Sweden (Fig. 15A; see above), possibly indicating that cryptic ostracode faunas within stromatolite cavities are a widespread, but as yet, unreported phenomenon.

The layered arrangement of the stromatolite cavities was probably caused by periodic stabilisation of the mound surface by microbial mats, which grew when sedimentation was slow. The microbial mats themselves typically did not calcify to form stromatolitic or thrombolitic fabrics, but instead, induced rapid lithification of the underlying sediment. This, in turn, produced an inhomogeneous layered fabric whereby unlithified layers could be internally eroded by currents. The resulting layered cavities were gradually filled with micritic internal sediment rich in ostracode

carapaces, which differs markedly from the surrounding crinoid-rich mound matrix. Erosion of cavity roofs would probably have only provided limited micritic sediment, hence, much of the material that comprises the sediment fill within cavities must have been imported from other parts of the mound, or from entirely outside of the mound complex. As the voids filled, the connections among cavities gradually constricted. Consequently, currents waned and internal sediment became finer (e.g., grading from wackestone to mudstone). Finally, internal sedimentation ceased altogether, leaving most cavities partly open. Within some deeper stromatactis cavities, isopachous cements developed during early subsequent diagenesis.

4.3. Colle Mounds, Cantabrian Mountains (northern Spain), Lower Devonian

The Lower Devonian (Emsian) succession (La Vid Formation) of the Cantabrian Mountains typically shows minor reef development, except for some levels that contain abundant rugose corals (*Synaptophyllum* biostromes; Stel, 1979; Soto, 1982; Fernández et al., 1995), or tabulate corals (mainly favositids and alveolitids). Large numbers of small mud-rich mounds are also intercalated within a marly thin-bedded crinoid limestone succession, 5 m thick, containing small wedge-shaped fistuliporid bryozoans.

Some layers within the crinoid limestones are rich in cystoids or rhynchonellid brachiopods (cf. Fernández et al., 1995). The mounds range in width from 4 to 6 m and reach up to 1 m in thickness (Fig. 22). They are composed of red to green, dense polymicritic mudstone/floatstone. The macrobiota, never exceeding more than 25% by volume, are dominated by bryozoans, crinoids and brachiopods. The polymicritic sediment contains small irregular fenestrae up to 1–2 mm across (Fig. 23), some of which display micritic geopetal infillings. The first generation of polymicrite contains the macrobiota and fenestrae and is clearly bioturbated, indicating that it was deposited as unconsolidated mud. This first generation of mud must have been lithified relatively quickly as it is also penetrated by numerous borings. The rapid lithification was probably due to stabilisation of the burrows by their producers and microbial activity. The latter is suggested by microbial coatings and stromatolitic structures within the first generation of polymicrite. The second sediment generation consists of recrystallized mud with some coprolites, but no other fossil types. A detailed facies analysis of these mound structures from the La Vid Formation is in preparation (Mendez-Bédia et al., in preparation). A similar mound type was described from the basal Devonian of the southeastern United States (Gibson et al., 1988).



Fig. 22. Small lense-like bryozoan–crinoid mud-mound from the Lower Devonian of the Cantabrian mountains, Colle, Spain.

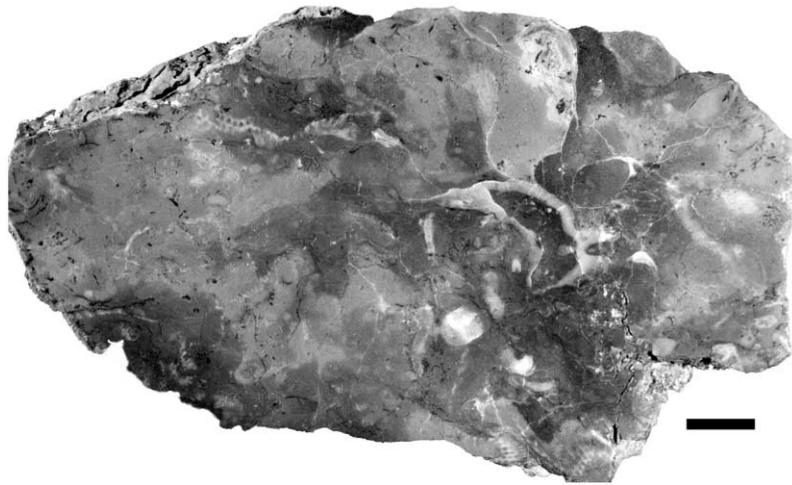


Fig. 23. Polymictic mud-rich mound facies; La Vid Formation, Lower Devonian, Cantabrian Mountains, Colle, Spain; scale bar, 1 cm (sample COL 10).

4.4. Eifel Hills (Rhenish Slate Mountains), Middle Devonian

In contrast to prolific reef development in the eastern Rhenish Slate Mountains ('Bergisches Land', 'Sauerland'), mounds in the Middle Devonian succession of the Eifel Hills are uncommon. They have only been reported from Upper Eifelian and Lower Givetian strata in the Hillesheim syncline (Struve, 1986; Birenheide et al., 1991; Pohler et al., 1999) and Givetian from the Blankenheim syncline (Schröder, personal communication).

The Upper Eifelian example is exposed in the well-known 'Weinberg' quarry (cf. Struve and Werner, 1984; Struve, 1986; Haas, 1994). It consists of a 40-m-thick mound and is composed of scattered massive to platy stromatoporoids, embedded in peloidal to dense mudstone and wackestone (Pohler et al., 1999), containing crinoids and brachiopods. Stromatolite-like cavities cemented by early fibrous and later blocky calcite are locally abundant (Figs. 24 and 25). Underlying strata are mainly composed of thin to thick, well bedded, crinoid grainstone/rudstone with very thin encrusting plates of alveolite tabulates (mainly *Platyaxum*). The limestones alternate with thin marl horizons bearing branching thamnoporoid and alveolite tabulates. At the very base of the mound (No. 7a in Fig. 12), massive to thick-bedded fenestral crinoid limestone (Fig. 26) contains rela-

tively thick platy stromatoporoids. Some layers have been stabilised by microbes, producing a wavy to lens-like fabric. The core facies (No. 7b in Fig. 12) consists of stromatolite-rich peloid bioclast packstone with sheet-like fistuliporid bryozoans. The fistuliporids probably had a binding function and may have contributed to cavity formation (Fig. 25). Abundant centimetre-sized stromatolite cavities clearly form a

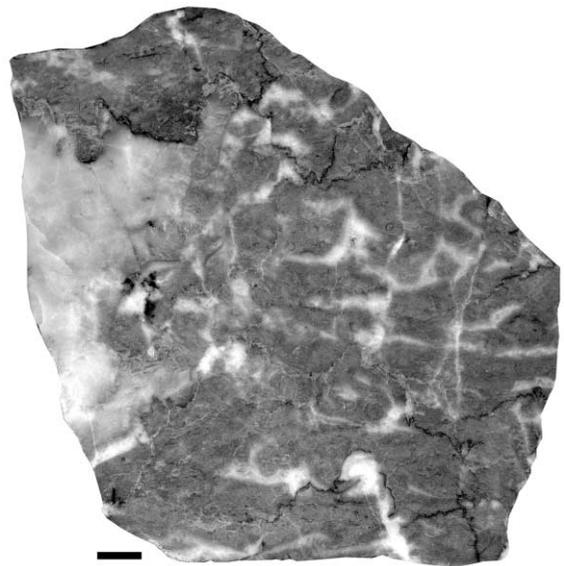


Fig. 24. Stromatolite-rich mound core facies from the 'Weinberg' mound, Upper Eifelian, Eifel Hills; scale bar, 1 cm (sample WB).

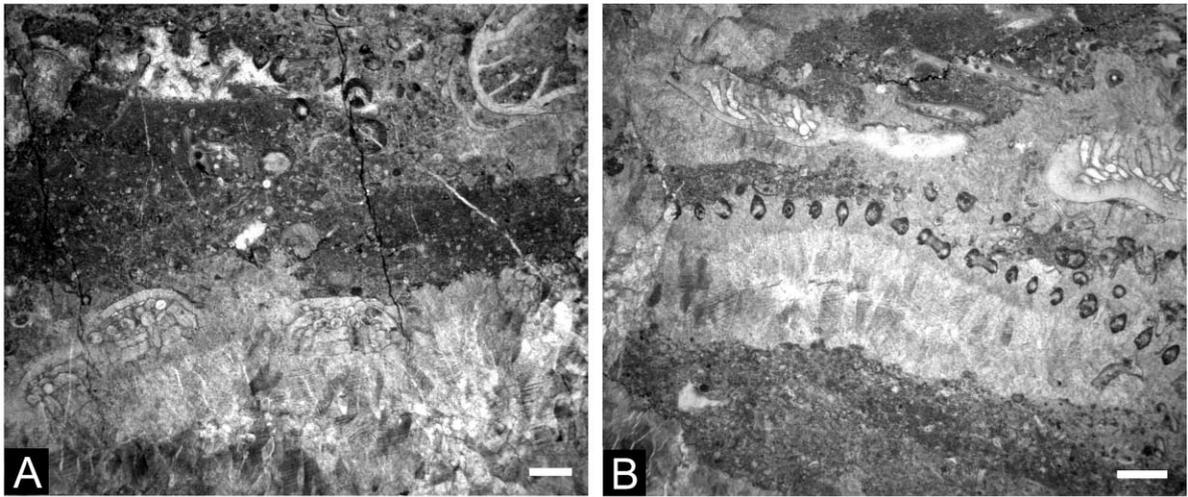


Fig. 25. (A) Thick radial fibrous cement crust within stromatactis cavity with fistuliporid bryozoans at the roof; 'Weinberg' mound, core facies, Upper Eifelian, Eifel Hills; scale bar, 1 mm (thin section KWB 3). (B) Numerous bryozoans (fistuliporid forms and others) at the roofs of stromatactis cavities, locality see (A); scale bar, 1 mm (thin section KWB 3).

three-dimensional network. Toward the top, the mound grades into a stromatoporoid reef which is strongly dolomitized, possibly reflecting depositional shallowing (see Pohler et al., 1999).

The Lower Givetian example is located close to the 'Weinberg' and is well-exposed in the 'Rauhheck'

quarry. The mound encompasses a massive stromatoporoid-coral core at least 20-m thick, grading vertically into 7 m of medium- to thin-bedded limestones, rich in stromatoporoids, alveolitids, thamnoporoids, and heliolitids. Flank facies interfinger with marly shale-bearing solitary rugose corals (Struve and

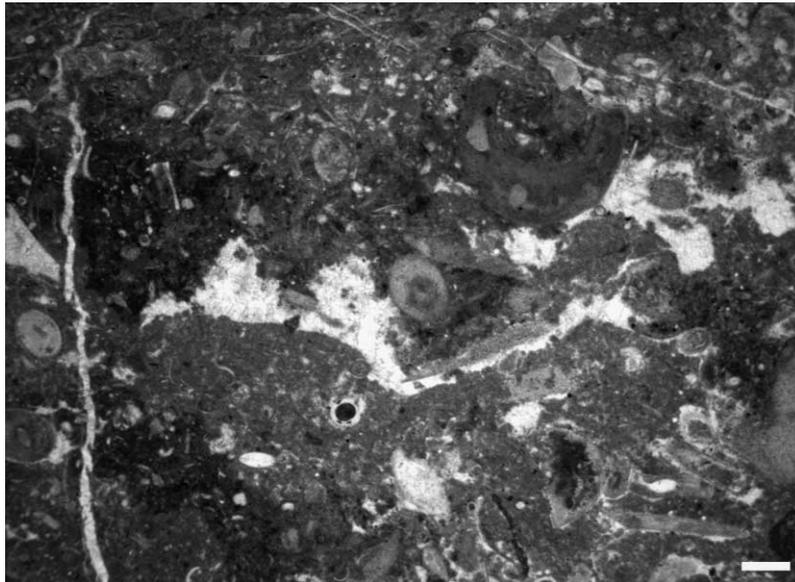


Fig. 26. Stromatactis-like cavities within crinoidal wackestone/packstone; 'Weinberg' mound, basal facies, Upper Eifelian, Eifel Hills; scale bar, 1 mm (thin section KWB 1).

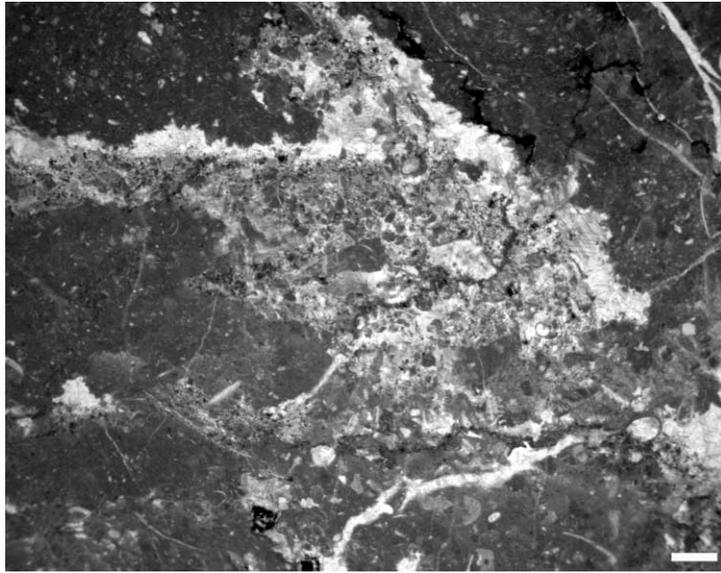


Fig. 27. Stromatactis-like cavity with bioclastic peloidal internal sediment. Note the thrombolitic fabric at the middle left margin; Rauhheck quarry, Lower Givetian, Eifel Hills; scale bar, 1 mm (thin section RH 2).

Werner, 1984; Birenheide et al., 1991). The distribution of the stromatoporoids varies considerably, from dense clusters to patches with scattered specimens. The mound sediment ranges from bioclastic and intra-clastic rudstone, to floatstone. The latter grades into fenestral polymicritic wackestone with a peloid-rich, thrombolitic to leiolitic fabric, and is likely to have been microbial in origin (Figs. 27 and 28).

Mound development in both localities appears to have been genetically linked, although they were not time equivalent structures. According to Birenheide et al. (1991), reef development in both cases took place on a local submarine rise, tectonically controlled by synsedimentary active north–south-trending faults (cf. Fuchs, 1965). Such syndepositional structural control on reef development and facies distribution

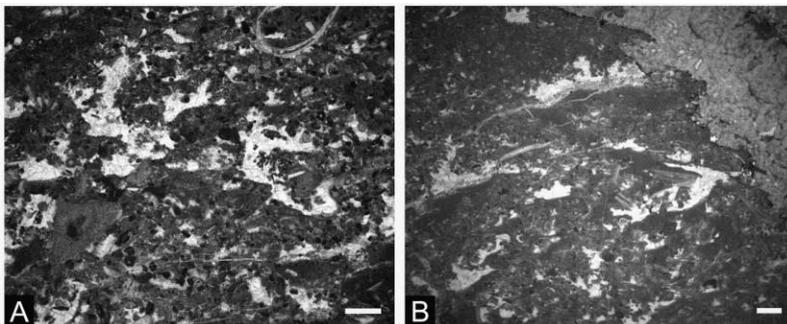


Fig. 28. (A) Network of small stromatactis-like cavities within peloidal bioclastic wackestone, Rauhheck quarry, Lower Givetian, Eifel Hills; scale bar, 1 mm (thin section RH 3). (B) Stromatactis-like cavities within polymicritic peloidal wackestone. Note stromatoporoid in the upper right corner, locality see (A); scale bar, 1 mm (thin section RH 3).

was also reported from the eastern part of the Rhenish Slate Mountains, where north–south-trending faults, orientated perpendicular to the Rhenohercynian shelf margin, account for an abrupt facies transition from deeper-water organic-rich, dark grey limestones ('Odershäuser Kalk'), to shallow-water reefal limestones (Krebs, 1969). Tectonic control would explain the somewhat exotic massive mounds in a relatively shallow and uniform intra-shelf environment with predominantly biostromal reef development (cf. Krebs, 1974; Winter, 1977).

5. The stromatactis problem

Stromatactis and stromatactis-like structures are a major constituent in Mid-Palaeozoic mounds, but also are abundant in some Jurassic mounds. As previously discussed, there is significant debate about the terminology and definitions of these enigmatic structures. In at least some of the mound examples cited in this paper, particularly those of Jurassic age, stromatactis-like cavities are thought to have been formed, in part, due to gravitational processes (Arnegg, Swabian Alb; Serra Isabel, Portugal). It is likely that the unstable shelf position (Arnegg: relatively steep slope; Serra Isabel: distal slope break) induced syndepositional gravitational formation of irregular to stromatactis-like cavities. Small-scaled discontinuities (between metazoans and sediment or microbolites and allochthonous sediment) were especially prone to disruption by gravitational slumping. In Arnegg, stromatactis-like cavities commonly developed directly above stromatolites within bioclastic allochthonous sediment. The formation of sheet-like stromatactis cavities in response to gravitational slumping or deformation structures is also suggested by Stenzel and James (1995) for shallow-water stromatactis mud-mounds from the Silurian of Newfoundland.

In the Mid-Palaeozoic, but also to some extent in the Jurassic, a major prerequisite for the formation of stromatactis and stromatactis-like cavities seems to have been the selective laminar lithification of the sediment, probably due to microbially mediated calcification (Pratt, 1982; see also Fig. 21). Subsequent winnowing beneath the crusts, as well as gravitational sliding or slumping, created and modified the cavity system.

6. Controls on mound formation — a comparative approach

Modern counterparts for the Mid-Palaeozoic and Late Jurassic mounds are extremely rare, possibly because sea level was relatively higher in those times than in the Cenozoic. Lower sea levels would be less likely to permit development of homoclinal shelf ramps, which was the favoured site for mound development in the Mid-Palaeozoic and Silurian time intervals. The lack of modern analogues in conjunction with the great diversity of Phanerozoic mound types strongly hampers attempts to resolve general factors and processes controlling mound formation and morphology. Nevertheless, the few modern examples that have been recognised offer some help in interpreting the ancient mound complexes:

- Lithoherms in the Florida Strait can serve as a model for the growth of stromatactis mounds, since they represent the only reasonable modern analogue for the formation of stromatactis-type cavities associated with episodes of early lithification and winnowing (cf. Neumann et al., 1977; Messing et al., 1990; Paull et al., 2000).

- Spectacular, large, deep-water hexactinellid sponge mounds were recently discovered in the subarctic sea off western Canada (Conway et al., 1991; Krautter, 2000), and they are the only known example where rigid hexactinellids grow on top of fine mud and also accumulate fine mud by baffling. However, this sediment is siliciclastic in composition, and any role of microbial processes in mound development has yet to be resolved. It is presently unclear if these mounds represent valid models for the growth mechanisms of Phanerozoic mud-mounds.

In this paper, we have attempted to demonstrate that detailed and comparative analysis of mound composition and architecture at various scales is necessary in order to correctly resolve mound development. It is probably a gross oversimplification to conclude that all mounds formed in quiet, mostly deep-water settings, or that a large number of mounds owe their origin to the intimate association of siliceous sponges and microbial activity (e.g., Bourque and Boulvain, 1993). Nevertheless, despite all of the time- and environment-related differences in macrofaunal and sedimentary composition, as well as variations in size and morphology, mounds share the

following common features, albeit in variable degrees or proportions:

- A matrix of originally unconsolidated (soft) mud, as evidenced by bioturbation, partial winnowing or infilled pockets and cavities. Cavities are frequently characterised by horizontal tops.

- Crust-type microbolites (thrombolitic, stromatolitic, leiolitic) that are variable in abundance and morphology. Microbolites were indurated (“hard”) during or soon after growth as testified by the presence of synsedimentary borings and multiple overgrowths, which occurred simultaneously with various microbolite growth stages. Winnowing below crusts formed ledges that might have been encrusted on their undersides.

- Evidence of early induration of mud including laminoid stromatolite fabrics or borings, and overgrowth by cemented or firm ground-attached fauna.

- Erect to branching epibenthic organisms and, in part, digitate microbolite crusts that were capable of sediment baffling (particularly of mud and bioclastic allochems).

All of these features were strongly influenced by the rate of sedimentation; hence, it is reasonable to conclude that the sedimentary regime was probably a major control of mound formation. Examples from the Jurassic of Spain and Germany demonstrate that high faunal densities alone were insufficient to form biohermal or mound structures. The general occurrence of soft mud within the mounds, together with a generally reduced faunal abundance, suggests that allochthonous sedimentation of mud was a major prerequisite for mound formation. However, it is important to note that too much sediment would have been detrimental to overall mound development and there is evidence of periods of sediment starvation during the growth of some of the mounds examined in this study (e.g., presence of hard-ground fauna and microbolite formation). Ultimately, cessation of mound growth was, in most cases, caused by burial following increased rates of sedimentation. We therefore conclude that mound development occurred under conditions of reduced but not absent sedimentation. A particularly impressive example of this dependence of mound growth on generally reduced sedimentation rates is the Upper Jurassic Gosheim example from southern Germany. This mound complex waned through time, owing to an increase in sedimentation. Subsequent mound growth

continued only at the highest point of the mound complex, possibly because currents winnowed away fine sediment relative to the mound flanks. The entire mound was buried due to increased background (ambient) sedimentation during a transgression. In earlier papers (Leinfelder, 1993, 1994; Leinfelder and Keupp, 1995), we demonstrated that reduced rates of background sedimentation might make Jurassic mounds indicators of distinct ramp and/or shelf settings. A low slope homoclinal ramp could only have supported mud-rich mounds if they were remote enough from major sources of carbonate sediment (“carbonate factories”). Microbolite-dominated mounds could have preferentially grown on steepened slopes if sediment bypassed the mound areas via gravitational transport. On the other hand, the absence of shallow-water carbonate sediment sources may have inhibited the growth of deeper-water mounds. The sedimentation regime was modulated by sea-level changes, which shifted depositional conditions on both homoclinal and steepened ramps between favourable and unfavourable for mound development (Leinfelder, 1993; Leinfelder et al., 1994).

The faunas in both Jurassic and Mid-Palaeozoic mounds were dominated by organisms that required hard substrates (most types of siliceous sponges, corals, stromatoporoids, crinoids, brachiopods, bryozoans). Common overgrowth by “sedimentophobic” encrusters and microbolites occurring in distinct horizons as well as local gigantism of sessile forms (dish-shaped sponges in life-position up to 2 m in diameter) suggest alternations between sediment influx and sediment hiatuses. In many mounds, early lithification affected some layers and winnowing removed intercalated soft sediment from others, ultimately resulting in laminoid stromatolite-type fabrics. Mounds containing these features are interpreted to have formed through intermittent sedimentation; starvation intervals were episodically or periodically followed by accumulation of soft mud.

This interpretation of sedimentation dynamics permits categorization of our mound examples into three process-related, genetic groups (Figs. 29 and 30):

(a) Sediment-oscillation mounds: Mounds that grew during intermittent background sedimentation, which episodically changes from near-zero to moderately elevated.

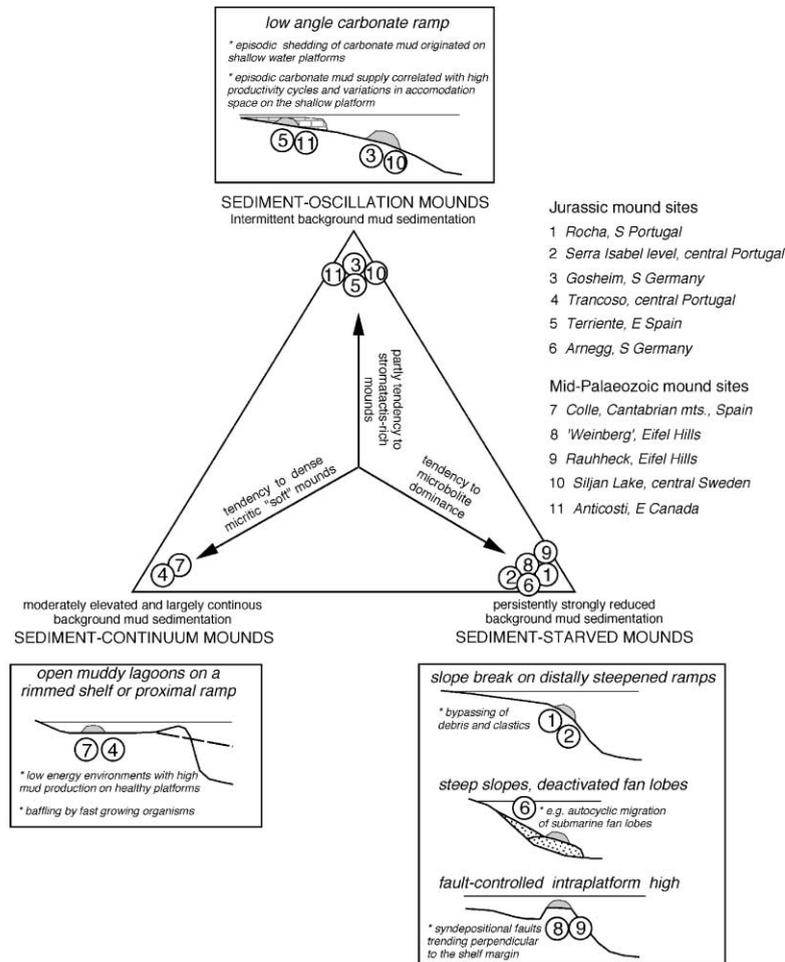


Fig. 29. Background sedimentation model of mound formation in the Jurassic and Mid-Palaeozoic. The development of microbrites, stromatactis cavity systems and 'soft' mounds appears to have been intimately controlled by the intensity and dynamics of allochthonous mud sedimentation involved in mound formation. Mud sedimentation is largely linked to shelf configuration and the productivity of existing shallow-water carbonate platforms, with export events probably being related to increased productivity episodes and/or accommodation problems (e.g., during late highstand).

(b) Sediment-starved mounds: Mounds growing under persistently strongly reduced background sedimentation.

(c) Sediment-continuum mounds: Mounds that grew during a continuous period of moderate background sedimentation.

6.1. Sediment-oscillation mounds

The periodic or episodic changes in background sedimentation within these mound types are high-

lighted by alternating features diagnostic of indurated and unconsolidated soft sediments. They comprise such morphologically and compositionally different mound types such as muddy sponge–microbrite mounds, stromatactis mounds and some coral microbial mud-mounds. This group appears to be the most prominent mound group during both the Mid-Palaeozoic and Late Jurassic, and frequently included very large mound complexes. Jurassic mounds were mostly enriched in microbrites, whereas stromatactis features were more prominent in the Mid-Palaeozoic

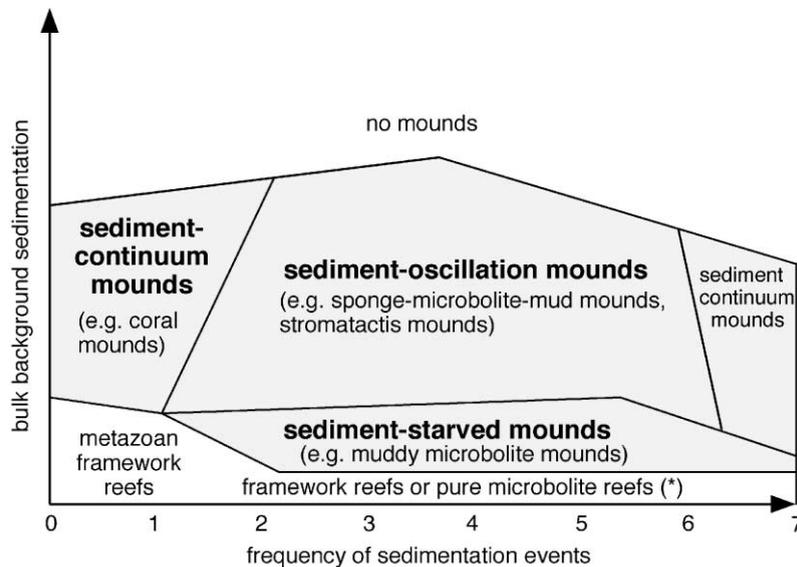


Fig. 30. Conceptual model of the interplay of muddy background bulk sedimentation rate and frequency of sedimentation episodes. Metazoan framework reefs or pure microbolite reefs (which developed in settings hostile to metazoans), grew under conditions of near-zero sedimentation. During continuous, slightly elevated sedimentation, coral mounds may have substituted for framework reefs, if fast growing baffling organisms were present. Generally elevated, but oscillating sedimentation resulted in development of large sponge–microbolite mud-mounds or stromatactis mounds. Elevated sedimentation rates would not have permitted mound formation. The rate of bulk sedimentation that regulated episodes of mound growth was probably controlled by the frequency of sedimentary oscillations. 0–1: continuous sedimentation; 1–6: different frequencies of episodic sedimentation; 6–7: near-continuous sedimentation owing to high-frequency episodic sedimentation.

examples. Stromatactis mounds tend to be more regularly cyclic compared to mounds of Jurassic age possibly because of the irregular, often digitate growth of microbolite crusts formed during sediment-starved intervals. Mound growth was usually terminated by increased background sedimentation.

6.2. *Sediment-starved mounds*

During long periods of strongly reduced sedimentation, provided that lateral growth was restricted by sediment by-pass or tectonic uplift, prolific microbolite growth might have built up in suitable depositional environments. Microbolites were accompanied by hard-bottom epibenthic fauna, except during times of hypersalinity or oxygen depletion (e.g., Rocha example). The tendency of microbolites to develop rugged, irregular surfaces permitted limited deposition of detrital mud in pockets and cavities, without interrupting thrombolitic microbolite development. Sediment influx might have even triggered even more pronounced digitate growth of microbolites, whose

growth form in subtidal areas largely depends on background sedimentation rate and water energy (Schmid, 1996; see also discussions in Logan et al., 1964; Pratt and James, 1982). Sediment-starved mound growth was probably terminated by increased sedimentation. Alternatively, if the mound managed to grow up into shallow water (e.g., the wave-washed zone), microbial intervals might have passed upward into coral-framework reefs.

6.3. *Sediment-continuum mounds*

This mound group displays little evidence of early lithification. Instead, faunal characteristics such as partially buried corals (progressively buried during growth), lack of microbial and other encrustations on epibenthic fauna, epibenthic soft-bottom dwellers such as certain sponge, coral and crinoid taxa, and semi-infaunal to infaunal mollusks or burrows, all suggest mound growth during nearly continuous periods of sedimentation. Microbial films were probably important in stabilising and hardening the sediment,

but owing to the constant rain of sediment, it could not calcify into a typical thrombolitic fabric (Leinfelder and Keupp, 1995). Early stabilisation and, possibly, induration is, however, indicated by undeformed burrows as well as by the occurrence of firm-bottom-dependent fauna. Mounds of this category were generally small, short-lived and rare because they formed close to the upper limits of tolerable sedimentation.

6.4. *Structural setting of general mound groups*

Our sediment-dynamic model is based on mound examples whose environmental and palaeogeographic setting is well constrained. All of the examples of sediment-oscillation mounds discussed in this paper developed on gentle, homoclinal ramp settings of variable water depth (Fig. 29). Large, and presumably long-lived mound complexes only developed in mid to outer ramp settings a considerable distance from shallow-water "carbonate factories" that would have shed fine sediment toward them. The Gosheim example suggests that sedimentary oscillations necessary for mound growth can be related to sea-level changes, which in turn might correspond to changes in shallow-water productivity and transport. Within the mounds, the actual sites of sediment-deposition were increasingly modulated by development of irregular mound morphologies. Shallow-water mounds of this category are short-lived and strongly dependent on a considerably lowered rates of sedimentation. This too might have been influenced by sea level change, particularly dramatic sea level rises.

The examples of sediment-starved mounds discussed in this paper were largely related to the existence of regionally or locally steepened slopes, or settings on isolated topographic highs (Fig. 29). These environments facilitated gravitational bypass of sediments around the structures and winnowing of fine sediment from mounds by currents. Steepened slope or elevated mounds could have been very large. Sediment-starved mounds that are postulated to have developed on homoclinal ramps probably formed during episodes of very pronounced sea-level rise. Such mounds were usually quite small.

Sediment-continuum mounds (Fig. 29), which were relatively short-lived and generally small, grew just below the upper sediment threshold of tolerable sedi-

mentation for mound development. They also required fast-growing baffling organisms that could keep up with continuous sedimentation. Since these organisms were largely restricted to shallow-water environments, this mound group might be diagnostic of low-energy shallow platform or upper ramp areas. Especially coral mounds being dominated by corals adapted to elevated sedimentation (cf. Hubbard and Pocock, 1972; Leinfelder, 1986) fall into this category.

The influence of sedimentation on mound development in conjunction with generally high stands of sea level explains the success of mounds during the Mid-Palaeozoic and Late Jurassic. High sea level ensured widespread development of gently sloping shelf areas and isolation of carbonate mound areas from sites of rapid carbonate sedimentation. Changing productivity on the shallow shelf and oscillations in shallow-water accommodation space, which were induced by sea-level changes, were responsible for variable sedimentation rates of fine detritus in distal shelf areas.

6.5. *Biological variability of mound groups*

We have concluded that the three mound groups described above (Figs. 29 and 30) were mainly governed by sedimentation. Other factors which have been shown to influence modern biohermal growth such as salinity, water energy and light, cannot explain the differences that we observed in Mid-Palaeozoic and Jurassic mound composition, as our examples generally occurred in deeper subtidal settings where these factors show only minor fluctuations. This is not to say that these variables were insignificant in mound development. Indeed, shallow-water mounds were likely to have been additionally influenced by factors other than sedimentation rate. For example, the style of microbial calcification that led to different fabrics, such as stromatactis or thrombolites, comprise a specific microbial association that were influenced by qualities such as intensity of light, water quality, turbulence and nutrient content. Upper Jurassic mounds situated within a mixed carbonate mud-terrigenous clay setting, such as Kimmeridgian examples from Iberia or Oxfordian examples from southern Germany, exhibit pronounced microbolite development that has been attributed in part, to elevated nutrient influx as a side effect of mild terrigenous contamination (cf. Schmid, 1996).

7. Conclusions

- We propose a new classification of mound types based on main constituents in order to facilitate comparisons between Jurassic and Mid-Palaeozoic mounds.

- Tropical to subtropical shelf deposits in Late Jurassic and Mid-Palaeozoic times were characterised by both pervasive growth of shallow-water framework reefs and mud-mounds.

- All of the mounds examined in this study possess direct or indirect evidence of microbial activity, early induration, and, in many cases, sediment winnowing (e.g., stromatactis features). Microbolite crusts were more abundant in Jurassic complexes, while stromatactis was much more common in Mid-Palaeozoic mounds.

- In the Late Jurassic, siliceous sponge mounds were mostly situated in moderately deep settings on near-horizontal to very gently sloping ramps on the northern Tethys shelf, whereas local to regional slope breaks were the sites for microbolite mound growth. Coral-dominated mounds were rare features that developed atop muddy shallow-water carbonate platforms.

- The largest, and probably most widespread mounds of the Mid-Palaeozoic were stromatactis mounds. They contained variable proportions of crinoids, stromatoporoids and corals, as well as microbolite crusts. As in the Jurassic, mounds were positioned on distal, gently sloping shelves. Coral mounds or microbolite-dominated mounds were uncommon. As in the Jurassic, they were related to muddy lagoons and tectonically induced slope breaks. Mixed mound types seem to have been more common during this interval of time than in the Jurassic.

- The dependence of mound formation on both accumulation of allochthonous mud and microbial stabilisation indicates that mounds only grew within specific ranges of reduced, frequently oscillating, allochthonous sedimentation. This is documented by stacked successions in the Jurassic, repetitive patterns of mud accumulation, and early hardening and winnowing in stromatactis mounds. Stromatactis cavities were commonly inhabited by abundant cryptic ostracodes, which probably grazed on microbial matter, thus helping to shape stromatactis cavities. The sedimentation and growth pattern of such 'sediment-oscillation mounds' contrasted with more continuous growth pat-

terns displayed by microbolite-dominated 'sediment-starved mounds', and mud-dominated 'sediment-continuum mounds'. The dependence on stable sedimentary conditions throughout their growth kept most of the latter variety very small. Sediment-oscillation mounds were generally larger and much more widespread.

- High biostratigraphic resolution in some Jurassic mound examples and additional faunal criteria permits the estimation of mound growth rates and correlation of mound development with sea level changes. This approach yielded growth rates of microbolite crusts as high as 1–2 mm/year and episodes of mound growth 100 to 500 ka for a 30-m-thick mound. This is consistent with a 4th to 5th order cyclicity for the growth of large mound structures.

- The dependence of mound development on reduced and often oscillating allochthonous sedimentation explains the success of mounds during the Mid-Palaeozoic and Late Jurassic. In both time periods, suitable conditions were provided by changing productivity on the shallow shelf and fluctuating sedimentation rates of fines in distal shelf areas.

- The extant lithoherms in the Florida Strait might serve as a model for stromatactis mounds (cf. Neumann et al., 1977; Messing et al., 1990; Paull et al., 2000).

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