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Microbialite morphology, structure and growth: a model of the Upper Jurassic reefs of the Chay Peninsula (Western France)

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Abstract

During the Early Kimmeridgian, the northern margin of the Aquitaine Basin (Western France) is characterised by a significant development of coral reefs. The reef formation of the Chay Peninsula comprises two main reefal units, in which the microbial structures can contribute up to 70% of framework. The microbial crusts, which played an important role in the stabilisation and growth of the reef body, show the characteristic clotted aspect of thrombolitic microbialites. Corals are the main skeletal components of the build-ups. The bioconstructions of the Chay area are thus classified as coral-thrombolite reefs. Four main morpho-structural types of microbial crusts are distinguished: (1) pseudostalactitic microbialites on the roof of intra-reef palaeocaves; (2) mamillated microbialites, found either on the undersides or on the flanks of the bioherms; (3) reticular microbialites in marginal parts of the reefs and between adjacent bioconstructed units; and (4) interstitial microbialites in voids of bioclastic deposits. Thrombolitic crusts developed on various substrates such as corals, bivalves, or bioclasts. The thrombolites formed a dense, clotted and/or micropeloidal microbial framework, in which macro- and micro-encrusters also occur. Variations in accumulation rate strongly influenced the reef morphology, in particular its relief above the sediment surface. The coalescence of the coral-microbialite patches created numerous intra-reef cavities of metre-scale dimensions. The direction of microbial growth, which defined the macroscopic microbialite forms, strongly depended on the position within the reef framework but was also controlled by water energy, accumulation rate and light availability.

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1. Introduction

Carbonate microbial crusts are important constituents of Upper Jurassic reefs and are known

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from various sites (e.g. Spain, Portugal, France, Morocco; cf. [Leinfelder et al., 2002](#)). Upper Jurassic reef types comprise coral, sponge and microbial reefs ([Gaillard, 1983](#); [Leinfelder et al., 1993, 1994, 1996](#); [Werner et al., 1994](#); [Schmid, 1996](#); [Insalaco et al., 1997](#); [Helm and Schülke, 1998](#); [Bertling and Insalaco, 1998](#); [Dupraz, 1999](#); [Dupraz and Strasser, 1999, 2002](#)). Microbialites can constitute the major part of the framework of such reefs, or form purely microbial bioconstructions attributed to the ‘microbial reef type’ of [Leinfelder \(1993\)](#). Microbialites are interpreted as resulting from microbial activity, mainly of cyanobacteria and other bacteria, but microencrusters such as foraminifera and small metazoans also contribute to the encrustations ([Chafetz, 1986](#); [Riding, 1991, 2000](#)). Microbialites show a strong variability in macro- and mesoscopic morphologies according to sedimentation rate and water energy ([Leinfelder et al., 1993](#); [Dromart et al., 1994](#)). While some microbialite morphologies have been previously described in reef environments ([Leinfelder et al., 1993](#); [Dromart et al., 1994](#); [Taylor and Palmer, 1994](#); [Schmid, 1996](#); [Bertling and Insalaco, 1998](#); [Insalaco, 1998](#)), their nomenclature, internal structure, and the palaeoenvironmental conditions responsible for their development are still under debate.

During the Early Kimmeridgian, reefal sedimentation occurred along the northern margin of the Aquitaine Basin (Western France) ([Fig. 1A](#)). The reefal formation of the Chay Peninsula (Charente-Maritime) represents the main reefal development occurring in the Upper Jurassic of the Aquitaine Basin ([Fig. 1B](#); [Hantzpergue and Maire, 1981](#); [Hantzpergue, 1985a](#)). A real ‘art gallery of palaeontology’, the Chay outcrop, was first illustrated by [d’Orbigny \(1852\)](#). He used the Chay section as log reference for his fourteenth geological stage, the ‘Corallian’. [Lafuste \(1953\)](#) and [Hantzpergue \(1988, 1991\)](#) give more recent stratigraphical and sedimentological descriptions. The Chay section displays marl-limestone alternations in which two major reefal units are intercalated ([Fig. 2](#)). These well-exposed bioconstructions are characterised by the exceptional diversity and preservation of calcareous microbial crusts and of numerous encrusting organisms.

Thus, the Chay Peninsula is an ideal site for the study of the morphology and structure of microbialites and coral reefs, but the reefs with their microbial crusts and faunal content have hitherto been mentioned only briefly ([Taylor and Palmer, 1994](#); [Schmid, 1996](#); [Leinfelder et al., 1996](#); [Leinfelder, 2001](#)).

This study aims to: (1) describe the microbial morpho-structures of the Chay reefs in detail; (2) propose an extended version of the microbialite nomenclature based on macroscopic features; (3) point out the influence of the sedimentary context on reef morphology and microbial morpho-structures; and (4) estimate the influence of palaeoenvironmental parameters on microbial and reefal growth.

2. Geological framework

The study area is situated in Western France (Charente-Maritime), about 10 km south of La Rochelle, at the western head of the Chay Peninsula ([Fig. 1A](#)). Marine erosion causes a continuous retreat of a 1200-m-long and 3–9-m-high cliff (several tens of metres since the beginning of the last century; [Corlieux, 1970](#)), thus providing a fresh and approachable outcrop, suitable for a detailed study.

During the Oxfordian and Kimmeridgian, two carbonate platforms developed in the La Rochelle and Angoulême regions ([Fig. 1B](#)), thus favouring the installation of coral reefs in La Rochelle and of rudist reefs in Angoulême ([Hantzpergue and Maire, 1981](#)). The development of the La Rochelle platform to the southeast is characterised by the expansion of reef facies in the direction of the Angoulême platform ([Fig. 1B](#)). The distribution of these reefs was limited to the south by Armorican faults, probably inherited from Hercynian structures ([Hantzpergue, 1985b](#)).

The reefal formation of the Chay was deposited during an important sea-level lowstand of the western European basins ([Jacquin et al., 1998](#)). It is divided into two main reefal intervals ([Lafuste, 1953](#)), which are separated by a hardground surface of regional extent (major discontinuity D4 of [Hantzpergue, 1985a](#); or D24 of [Gabilly et al.,](#)

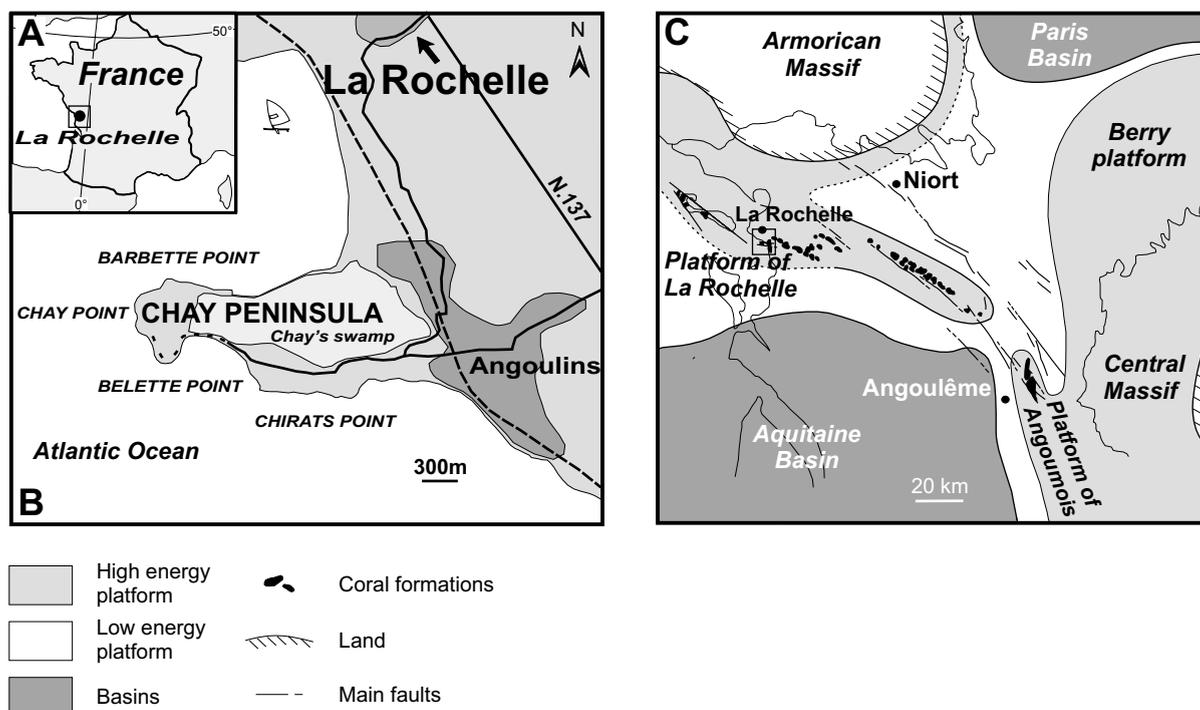


Fig. 1. (A,B) Location of the Chay Peninsula near La Rochelle, Western France. The study area is situated at the western extremity of the peninsula, between the Barquette and Belette Points. (C) Palaeogeographic setting and distribution of coral formations during the Early Kimmeridgian, modified from Enay and Mangold (1980), Hantzpergue and Maire (1981) and Hantzpergue (1985b).

1985). An additional small reef horizon occurs just above this discontinuity (Fig. 2). These reefs are intercalated in a dominantly calcareous succession and are dated to the Lower Kimmeridgian (Cymodoce Zone, Achilles Subzone; Hantzpergue, 1988, 1991).

3. Methods

Thirty-four reefal units were studied along the Chay cliff. Mapping of bioconstructions was carried out to determine their general morphology, and the importance and distribution of microbial crusts within the reefs. In order to determine the relative abundance of microbialites, reef organisms, and allochthonous and reworked sediments, a point-counting method was applied to randomly scattered squares. A 20×20-cm grid of 100 points was used on reef surfaces in order to establish the percentage of reef surface covered by the various

constituents (Gaillard, 1983). Details of the corals and microbial fabrics were studied using more than fifty large, orientated, polished-glazed slabs completed by 167 thin sections. Semi-quantitative data were acquired to establish patterns of microbial growth, and to identify the micro-encrusting organisms.

4. Morphology and composition of reef framework

The first reefal unit (Fig. 3A) is exposed over a length of about 50 m, is 5–6 m thick, and has a massive aspect. It appears as a complex bioconstruction made up of several, more or less coalescent bioherms. Intra-reef palaeocaves up to 2–3 m high and wide, and 3–4 m long are common. However, their full extension cannot be ascertained because the cavities were infilled by sediments, which have not yet been completely eroded by recent marine erosion from the rear of the

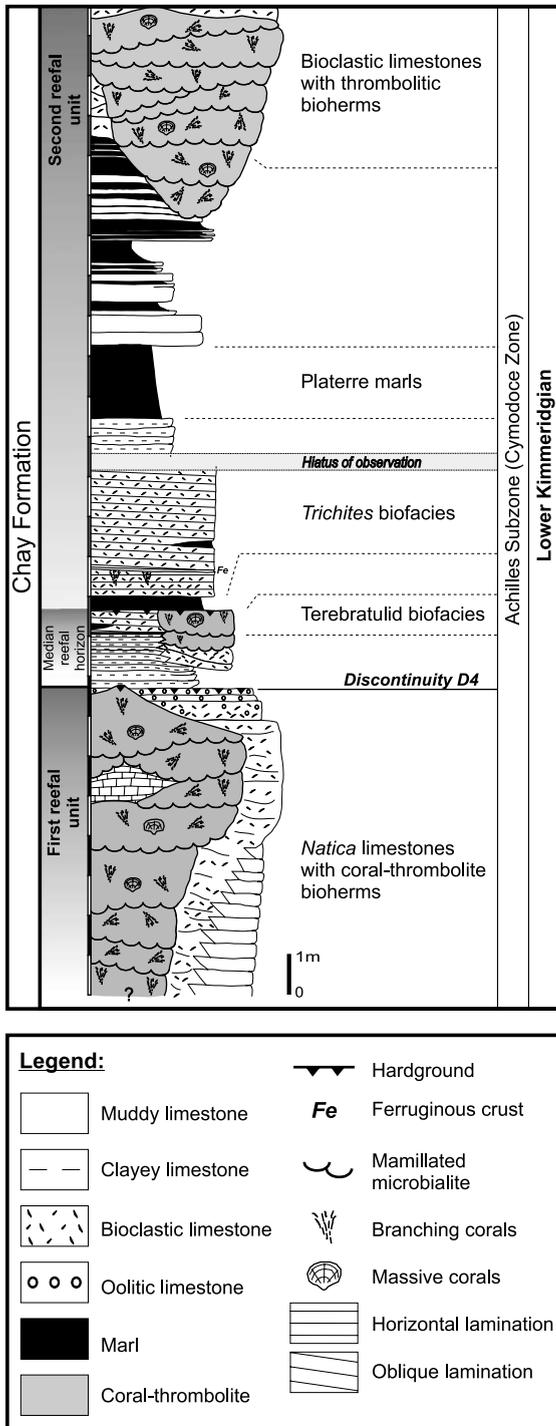


Fig. 2. Synthetic field log illustrating the stratigraphy of the section exposed along the cliff of the Chay Peninsula. Note the two main reefal units separated by the regional unconformity D4.

caves. Furthermore, recent marine erosion has caused roof collapse of four of the six observed palaeocaves. The roofs and the walls of the two other palaeocaves consist of thick microbial crusts and are covered by encrusting fauna (thecideid brachiopods, bryozoans, serpulids). There are only a few records of such cavities from the Mesozoic, which may be due to the general rarity of these structures, and/or to the difficulty of recognising them in less well exposed reefs. Only [Insalaco \(1998\)](#) and [Bertling and Insalaco \(1998\)](#) mention similar cavities from the Upper Jurassic of Northern France.

Macro- and microfaunal elements contribute in varying degrees to the framework of the reef bodies. The most conspicuous metazoans are corals, which are generally dominated by phaceloid taxa (*Calamophylliopsis*, more rarely *Stylosmia*). Massive (e.g. *Microsolena*, *Stylina*, *Heliocoenia*, thamnasteroids) and ramose corals (e.g. *Actinastrea*) occur only rarely. Other macrofaunal biota are sponges (siliceous sponges, coralline demosponges), bivalves (mainly oysters), thecideid brachiopods, cyclostome bryozoans (e.g. *Berenicea*, *Stomatopora*), serpulid worms, and echinoderms (represented by skeletal elements of crinoids and echinoids; [David, 1998](#)). The microfauna is abundant, well diversified and similar to other Upper Jurassic reefs ([Leinfelder et al., 1993](#); [Schmid, 1996](#); [Bertling and Insalaco, 1998](#); [Dupraz and Strasser, 1999, 2002](#)). The main micro-encrusters observed are annelids (*Terebella* and serpulids), foraminifera (nubeculariid, *Bullopore*, *Tolypammina*), and some problematica (*Tubiphytes*, *Koskinobullina*, *Thaumatoporella*, *Lithocodium*, *Bacinella*; [Fig. 4](#)).

The abundance of the different biota and of the allochthonous and reworked reefal sediments forming the primary reef fabrics has been evaluated. Microfossils (<1 cm), microbial micrite, and syndepositional cements are grouped together under the term ‘microframework’ ([Weidlich and Fagerstrom, 1998](#)). The analysis shows that the first reefal unit is mainly composed of microframework (>57% of the outcrop) and corals (<37%; essentially branching colonies). The other constituents (bivalves, brachiopods, sponges, bryozoans, serpulids) represent about 3% of the

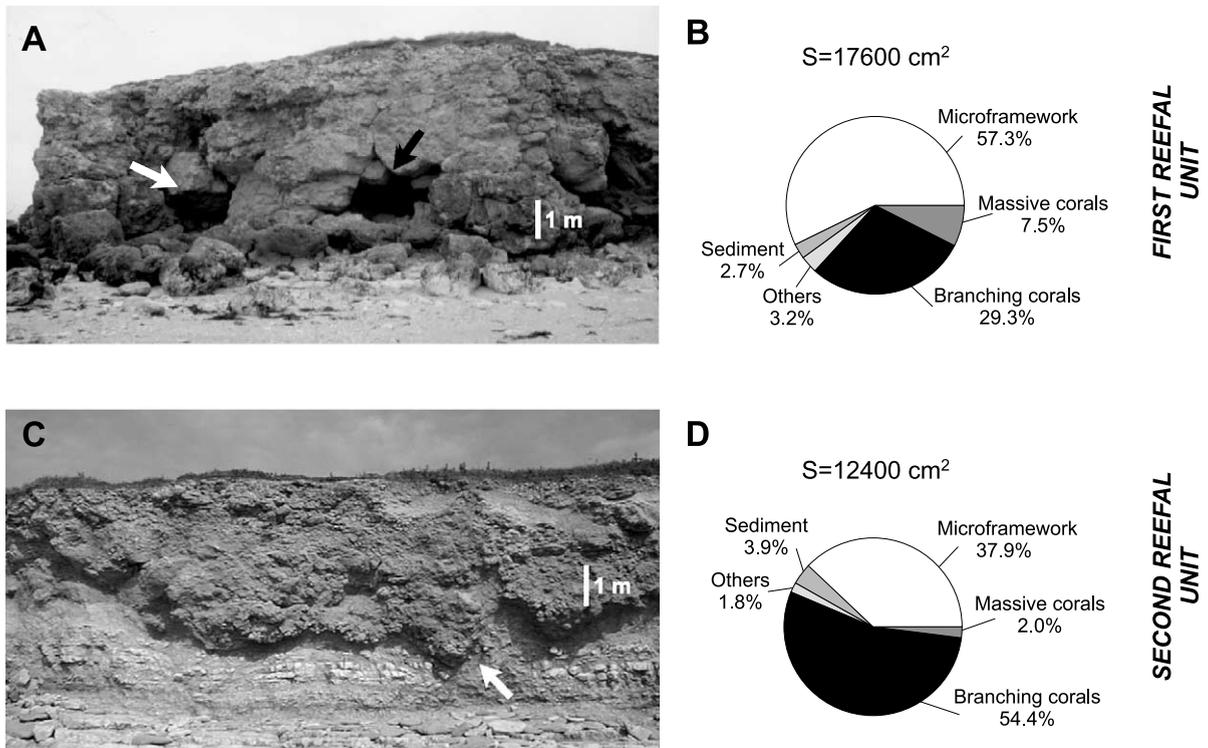


Fig. 3. (A) First reefal unit at Barbette Point showing two palaeocaves (arrows). Note that the roof of the cave marked by the white arrow has collapsed. (B) Relative abundance of biota, sediment, and microframework (microfossils, microbial micrite, and syndepositional cement) in the first reefal unit. (C) Isolated bioconstruction of the second reefal unit, showing compaction of underlying sediments (arrow). (D) Relative abundance of biota, sediment, and microframework in the second reefal unit.

reef body (Fig. 3B). Infilling sediment represents only a small part of the reef volume (about 3%).

The second reefal unit appears in the cliff as isolated patch-reefs, which have reduced dimensions, and are at the most 7–8 m long and 3–4 m high (Fig. 3C). Unlike the first reefal unit, only rare and centimetre-scale cavities are observed. The corals are almost exclusively phaceloid colonies (*Calamophylliopsis* and *Stylosmilia*), and only rarely do ramose (*Actinastrea*) and massive colonies (*Microsolena*, *Stylina*) occur. The primary reef framework is composed essentially of branching corals (>54%) and of microframework (<38%; Fig. 3D).

Corals are always strongly encrusted in the reefs of the Chay Peninsula, and the crusts were previously interpreted as being formed by red algae (Lafuste, 1953; Hantzpergue, 1988). By comparison with the microbial crusts of Iberia (Lein-

felder et al., 1993), Taylor and Palmer (1994) have emphasised the importance of microbial participation in the bioframework. Microbialites vary strongly in abundance and constitute between 30% and 70% of the analysed reefs. These microbial crusts exhibit a mainly thrombolitic macroscopic fabric, recognisable by its clotted aspect (Aitken, 1967). The bioconstructions of the Chay Peninsula are thus classified as coral-thrombolite reefs (Taylor and Palmer, 1994).

5. Microbialite morpho-structures

Microbialites generally dominate the outcrop, covering nearly all of the original palaeosurfaces visible today. They are associated with corals of different morphologies (e.g. branching, massive) and, in some cases, bivalves (oysters) or other

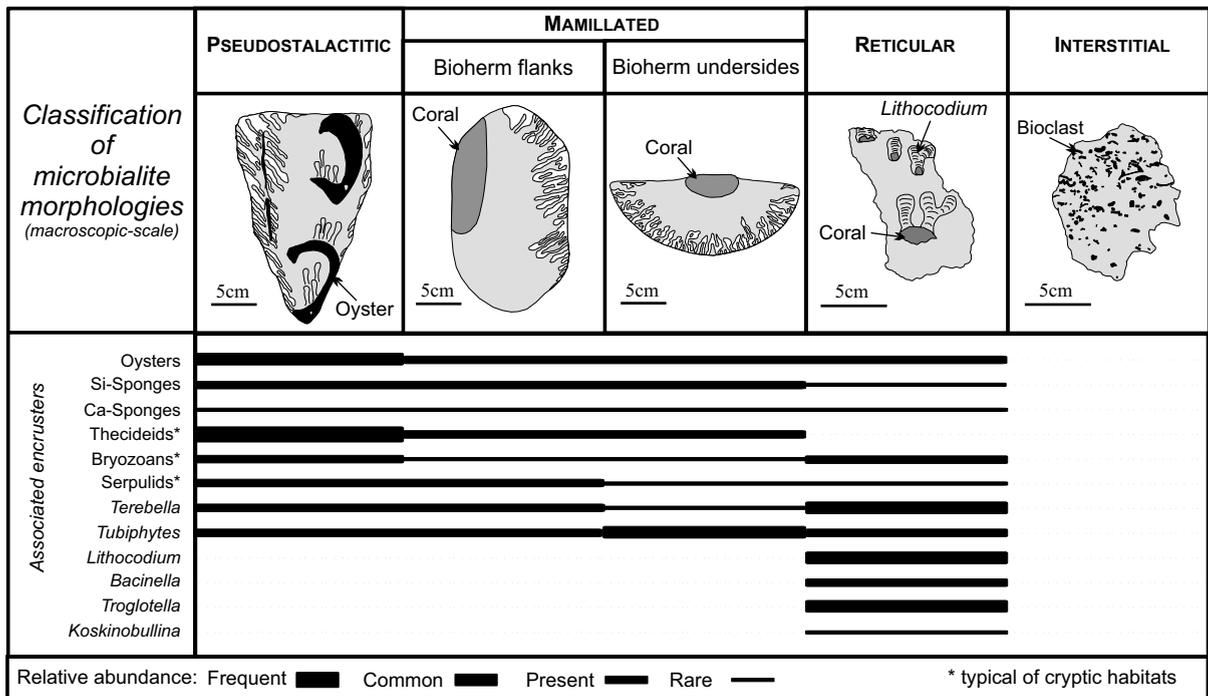


Fig. 4. Classification of the macroscopic morphologies of microbial crusts observed at the Chay Peninsula; relative abundance of the principal associated macro- and micro-encrusters. Allomicrite in white; microbialites in grey. Abbreviations: Si-sponges, siliceous sponges; Ca-sponges, calcareous sponges.

skeletal organisms that serve as substrate for their growth.

The identification of the different microbialite types poses the difficult problem of the scale of observation (Shapiro, 2000). The classification proposed here (Fig. 4) is based on macroscopic (i.e. 'gross form of the microbialite bodies with typical dimensions in tens of centimetres to metres'; Shapiro, 2000, p. 166) and mesoscopic observations (i.e. 'internal textures of macrostructural elements that are visible to naked eyes'; Shapiro, 2000, p. 166), and on their position within the bioconstructions (Fig. 5). Microbialites mostly display a dense mesoscopically clotted crust fabric (i.e. 'mesoclots'; Kennard and James, 1986; Shapiro, 2000). This fabric is typical of thrombolites (Aitken, 1967; Kennard and James, 1986), but some structureless leiolithic mesofabrics (Braga et al., 1995) are also observed.

In the central part of the reef bodies, the massive aspect of the framework makes it difficult to

distinguish microbialite morphologies. At the periphery of the reef masses, four types of microbialite morpho-structures have been distinguished (Figs. 5 and 6). Some of these forms have already been figured in recent works (Leinfelder et al., 1993, 1996; Schmid, 1996; Bertling and Insalaco, 1998), but their exact location in the reef framework and their structure has been only partly described as yet.

5.1. Pseudostalactitic microbialites

The most spectacular type of microbial crust are certainly the pseudostalactitic microbialites (Fig. 6A). Macintyre and Videtich (1979) introduced the term 'pseudostalactite' to describe projections of serpulid tubes and magnesium calcite on the ceiling of recent submarine caves in the northwest of Columbus Cay (Belize). In the Chay Peninsula, these stalactitic forms are essentially composed of microbial carbonates associ-

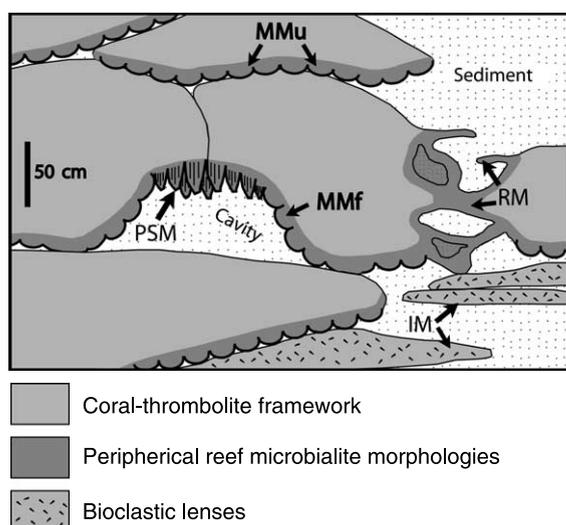
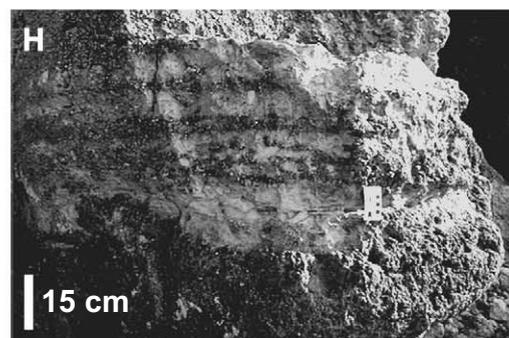
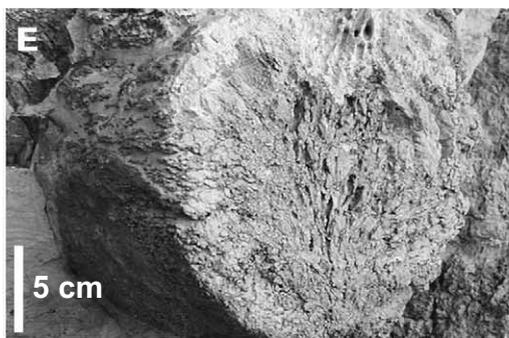
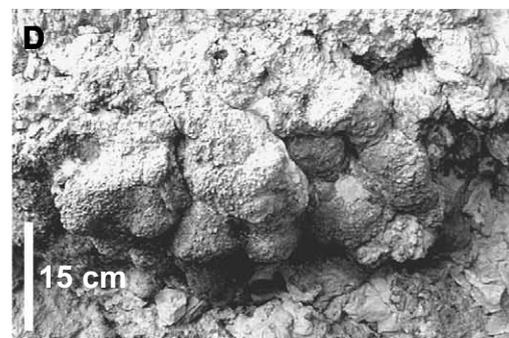
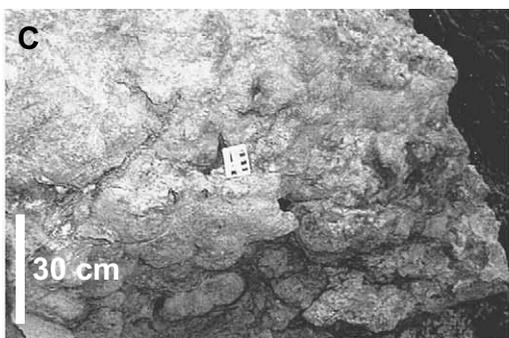
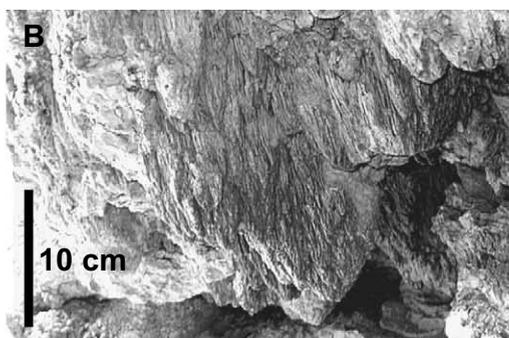
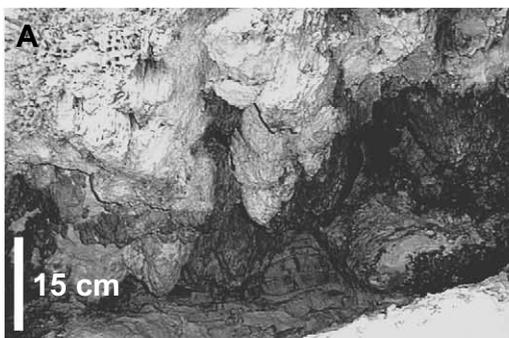


Fig. 5. Location of the different types of microbialite morphologies in the reefs of the Chay Peninsula. Abbreviations: PSM, pseudostalactite microbialites; MMu, mamillated microbialites of bioherm undersides; MMf, mamillated microbialites of bioherm flanks; RM, reticular microbialites; IM, interstitial microbialites.

ated with encrusted organisms. Taylor and Palmer (1994) mentioned this microbialite morphology of the Chay outcrop, and Bertling and Insalaco (1998) from the northern Paris Basin, but these authors did not detail their internal structure. Pseudostalactitic microbialites are found mainly on the roofs of intra-reef palaeocaves. They exhibit a cone-shaped morphology, pointing downward (Fig. 6B). The dimension of the caves limits their size. The biggest specimens are 25 cm high and 15 cm wide. The pseudostalactite surface shows vertical and parallel flutes divided at the top into two or three lobes (Fig. 7A). These columns are up to 5 cm long and have a diameter of about 2 cm. They display a dendritic form comparable to that of modern freshwater microbialites (Laval et al., 2000). The encrusters at the surface of pseudostalactitic microbialites are abundant thecideid brachiopods (up to ten individuals per cm²; cf. Taylor and Palmer, 1994), oysters, bryozoans, and serpulid worms. These encrusters are considered to be characteristic faunal elements of cryptic environments (Taylor and Palmer, 1994; Wilson, 1998). Bivalve fragments

are locally trapped between microbialite columns. The analysis of polished slabs shows that the microbialites are mainly composed of encrusting oysters associated with thrombolites (Fig. 8A,B). The oysters serve as a substrate for microbial colonies that, according to the cross-section, exhibit coalescent vertical columns (Fig. 8A,B) or dendroid forms (Fig. 8C,D; Schmid, 1996; Helm and Schülke, 1998). Sedimentary particles infill available space between the thrombolitic columns. In thin sections, microbial crusts that are darker than the micritic matrix are formed by a dense, clotted to peloidal micrite, in which sparitic or micritic cements fill the remaining porosity (Fig. 7B). They display various characteristics suggesting a microbial origin, such as microscopic, locally laminated columns or domes, which are typical of thrombolitic textures (Leinfelder et al., 1993). Crust accretion also incorporates some bioclasts and silt-size quartz. Internally as well as externally, the crusts exhibit some encrusting microorganisms that are dominated by polychaetes (*Terebella*, serpulids), foraminifera (nubeculariids and *Tubiphytes morronensis* Crescenti), and cyclostome bryozoans (*Berenicea*). These encrusters are comparable to those recorded from Kimmeridgian coral reefs of Spain (Leinfelder et al., 1993) and the Oxfordian coral reefs of the Swiss Jura (Dupraz and Strasser, 1999).

In contrast to the generally downward and slightly laterally extending growth direction of the pseudostalactite as a whole, the single thrombolitic growth increments composing this structure show a generally upward growth direction (Fig. 8A,B). Cemented oysters commonly developed upon cavity roofs, allowing such upward growing crusts (stage 1; Fig. 9A). Only parts of the cemented, left valves are observed in pseudostalactite development, indicating a post mortem encrustation by the microbes. Corals and downward-facing protuberances of the pre-existing lithified microbialite roof may also have provided favourable surfaces for initial stages of pseudostalactite growth. The thrombolitic columns developed on the entire surface of the oyster shells grew vertically upward and locally, at a first stage, also laterally outward (stage 2; Fig. 9A). Hence, these columns are either vertical, or first horizon-



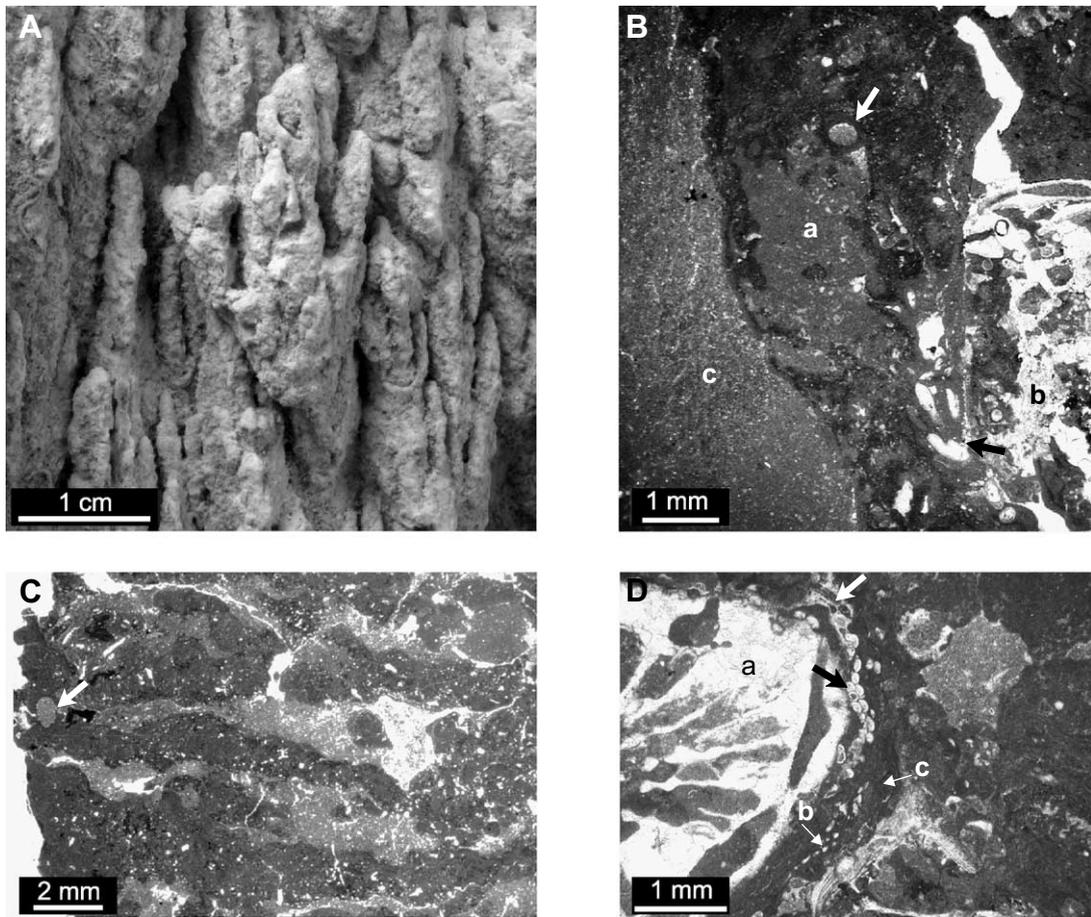
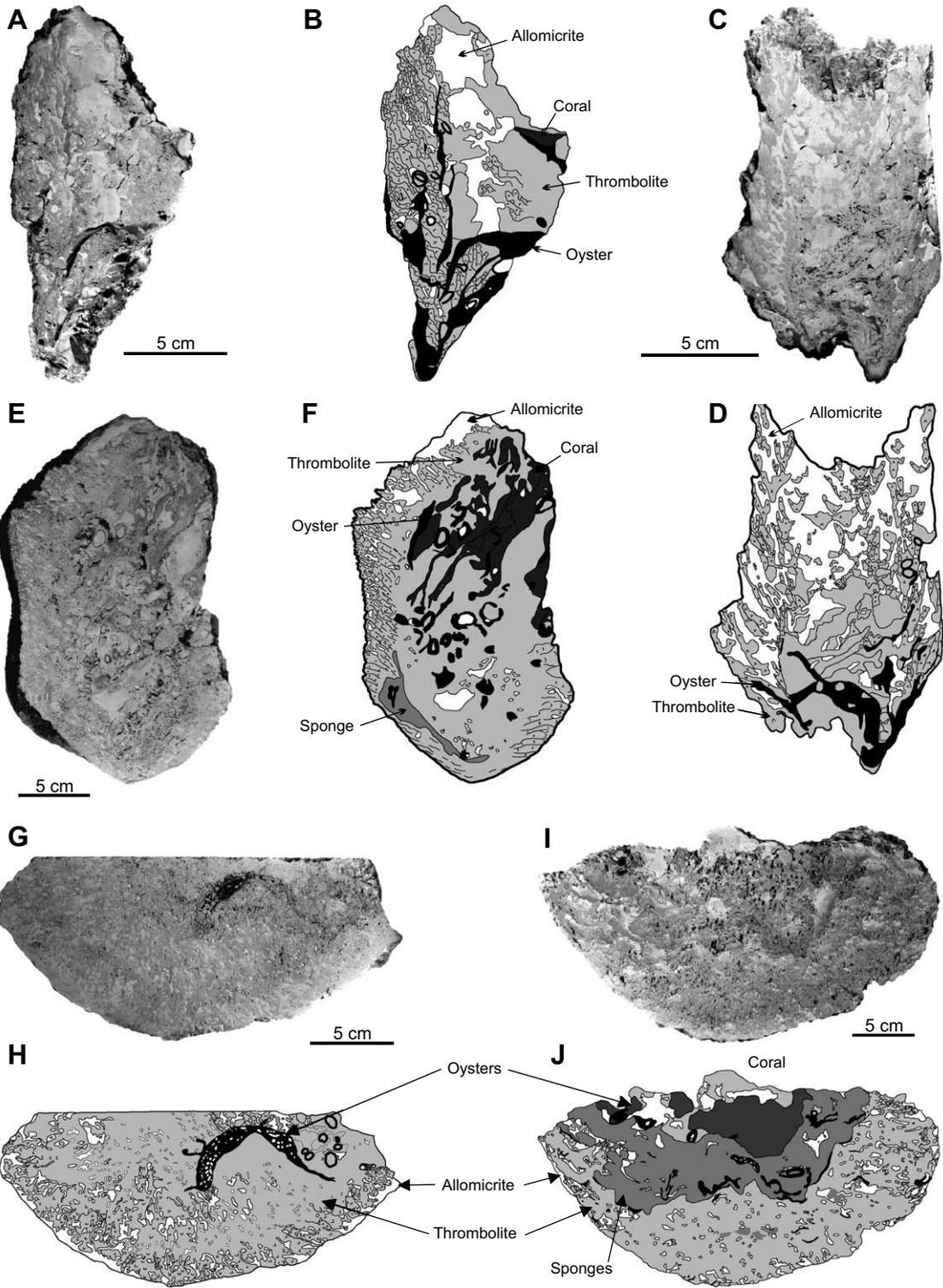


Fig. 7. (A) Surface of pseudostalactitic microbialites showing vertical, parallel flutes, which may be divided at their top into two or three lobes. (B) Thin section of an equivalent microbial structure showing upward growth (a), which develops on a coral substrate (b). This microbial flute is encrusted by numerous nubeculariids (black arrow) and a serpulid (white arrow), before being covered by allochthonous particles (c). (C) Thrombolitic columns with a sparse fauna (*Terebella*, white arrow) showing a lateral growth direction; flank microbialites; medium reefal horizon. (D) *Calamophylliopsis* (a) encrusted by *Koskinobullina* (black arrow), bryozoan (white arrow), nubeculariids (b) and inner thrombolitic layer (c). See text for more detailed explanations.

Fig. 6. (A) Microbial crusts with a pseudostalactite form on the roof of a palaeocave in the first reefal unit. Note the coral (*Calamophylliopsis*) in the top left-hand corner, which serves as a support for the microbial development. The draped cave-filling sediments are still present at the base of the cave. (B) Detail of pseudostalactitic microbialites from the cavity shown in (A). (C,D) Underside surface of bioherms showing the mamillated microbialite forms in the second reefal unit. (E) Microbialites of bioherm flanks. A phaceloid scleractinian form (*Calamophylliopsis*) in growth position serves as a support for considerable microbial development; first reefal unit. (F) Thick microbialites on bioherm flank; first reefal unit. (G) Reticular development of microbialites between two adjacent coral-thrombolitic bioherms in the first reefal unit. (H) Bioclastic deposits cemented by interstitial microbialites; first reefal unit.



tal and then vertical, thus forming a bend. The subsequent downward and lateral growth of pseudostalactites were favoured by the settlement and cementation of new oysters either directly onto former generations of oysters, or on the microbialites (stages 3 and 5; Fig. 9A). Thus, they provided again surface and space for the development of successive upward growing thrombolitic layers (stages 4 and 6; Fig. 9A). The encrustations by bryozoans, serpulids, and oysters, which need hard substrates for the settlement of their larvae, indicate interruptions of the microbialite growth or, at least, partially microbe-free surfaces. Later on, the microbialite growth continued without significant structural change. The pseudostalactite development is thus the result of alternately downward growing oysters and dominantly upward growing microbialites. This complex growth sequence contrasts with the interpretation given by Bertling and Insalaco (1998) for similar structures in the Oxfordian of the Ardennes. The column-like microbialite increments, which were described as ‘torpedo-shaped’ and termed ‘microbial pendants’ by these authors, were interpreted as being formed gravitationally, suggesting a downward growth direction of the microbialites. However, our study shows that these structures did not result from ‘gravitational forces pulling down on the free growing microbial films’ (Bertling and Insalaco, 1998, p. 145), but indicate an essentially upward microbial growth. The upward growth direction of the increments is clearly indicated by their convex-up, partly layered microstructure (Fig. 7B). Downward and laterally directed microbialite growth occurs only very rarely in the pseudostalactites and is only a temporary growth stage.

5.2. Mamillated microbialites

The mamillated microbialites occur in both reefal units, predominantly on the undersides of the bioherms (Fig. 6C,D) and on the bioherm flanks (Fig. 6E,F). The underside microbialites of the Chay Peninsula are similar to those described by Leinfelder et al. (1994) from Spain (Tormon reef) and by Bertling and Insalaco (1998) from Oxfordian bioherms of the Paris Basin. They correspond to the ‘downward facing hemispheroids’ of Leinfelder et al. (1993, 1996). Bertling and Insalaco (1998) described these hemispherical shapes as ‘pillows’ of thrombolites. The term ‘mamillated’, introduced by Taylor and Palmer (1994) for this morphology in the Chay Peninsula, is preferred here because it is essentially descriptive, whereas ‘pillow’ does not typically represent a microbial structure and the term ‘downward facing hemispheroids’ implies a microbial growth direction. The underside microbialites measure 8–40 cm in diameter. Like the flank microbialites, they generally show smooth or bumped surfaces, locally colonised by numerous encrusters (oysters, sponges, bryozoans, serpulids, thecideid brachiopods). However, in contrast to the pseudostalactite surfaces, the abundance of cryptic fauna (e.g. thecideids) is significantly reduced. The analysis of polished slabs shows a radiated microbialite growth direction from various nuclei, generally branching corals or encrusting oysters (Fig. 8G–J). The central part of this type of microbialites generally consists of a massive thrombolitic crust that grew directly on the nucleus (Fig. 8G,H). The peripheral part is commonly made of small (1–2-cm-high) thrombolitic columns, displaying either a lateral or a down-

Fig. 8. (A,B) Internal structure of pseudostalactitic microbialites in longitudinal section, showing vertical microbial columns. (C,D) Longitudinal section of pseudostalactitic microbialites, perpendicular to (A), showing a microbial dendroid form resulting from the division of the microbial column into two or three lobes (see Fig. 7). Note the importance of the oysters, which are responsible for the cone-shaped morphology of this pseudostalactite and serve as a substrate for microbial growth. (E,F) Polished slab of microbialites of a bioherm flank in the median reef unit. Note the two layers in the microbial crust. The first layer is composed of a massive microbial crust with various encrusters (sponges, bivalves); the second layer with thrombolitic columns shows lateral and upward growth. (G,H) Mamillated microbialites of bioherm undersides in the first reefal unit. The massive thrombolitic crust in central position developed directly on a bivalve. In the peripheral part, thrombolitic columns show a radial microbial growth. (I,J) Underside microbialite morphology, in which abundant siliceous sponges (lithistids) developed on a coral nucleus. In this case, the thrombolitic columns have a reduced development but their growth is still radial. First reefal unit.

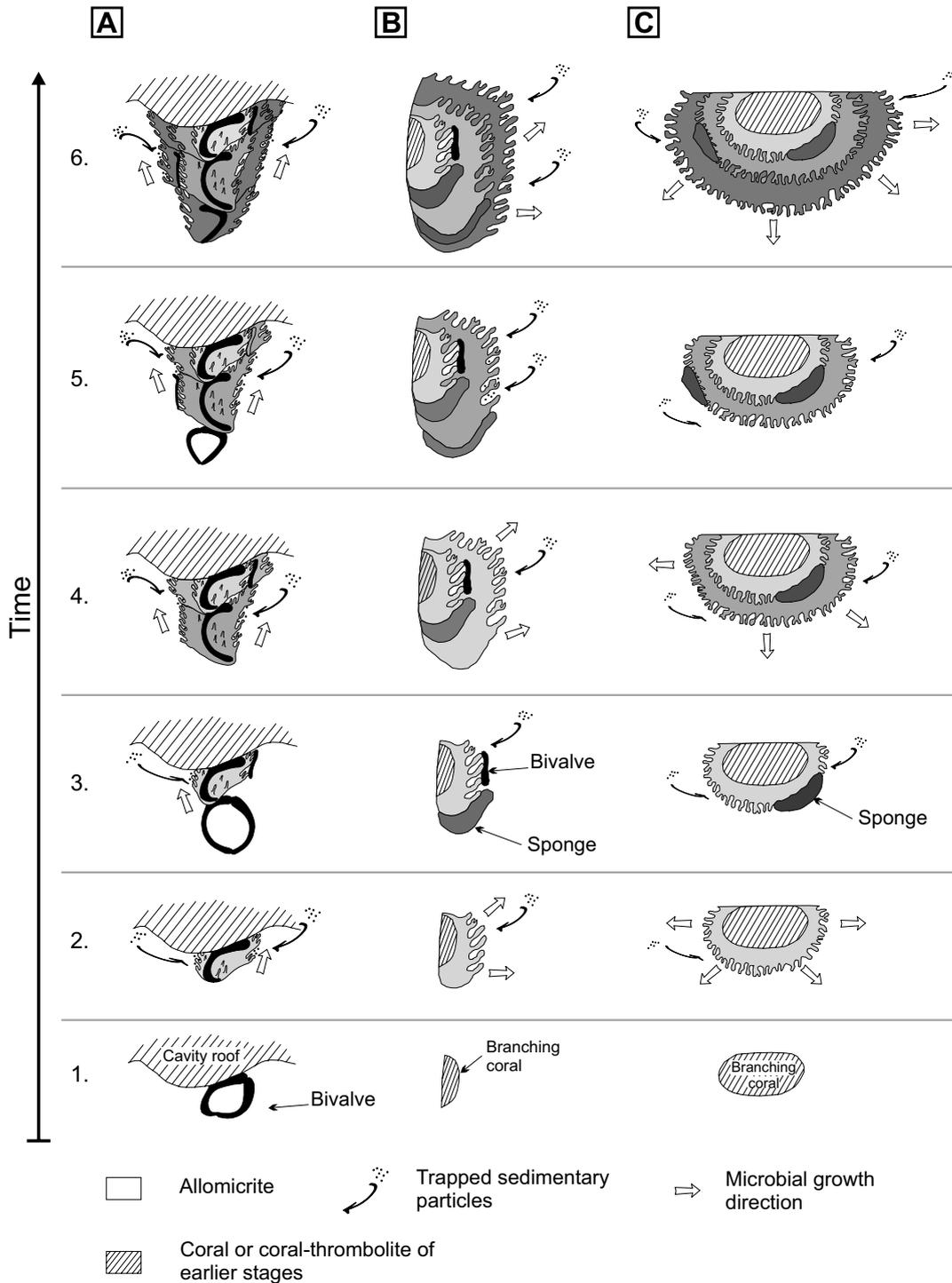


Fig. 9. Growth models for pseudostalactitic microbialites (A), mamillated microbialites of bioherm flanks (B), and bioherm undersides (C). Note that flank microbialites display intermediate directions of microbial growth between those of underside and pseudostalactitic microbialites. The preponderant role played by oysters in the creation of relief is essential for the upward microbial growth observed in pseudostalactites. Sedimentary particles (allomicrite) are trapped between the thrombolitic columns.

ward growth direction and producing a bumped surface. Columns that grew directly on the nucleus are rarely observed. Montaggioni and Camoin (1993) have described such a two-layer structure of microbial crusts in Holocene reefs of French Polynesia. The second, outer layer of these Holocene microbialites shows thrombolitic columns similar to those observed in the underside microbialites of the Chay. However, the first, inner layer differs from that of the Chay because it has a laminated structure that did not develop in the Chay microbialites (Fig. 7D). Various organisms (bivalves, sponges) encrusted the Chay underside microbialite surfaces. In some samples, siliceous sponges are very common and may have played an important role in microbialite development (Fig. 8I,J), carbonate precipitation being favoured by the decay of sponge tissues (Reitner, 1993; Delecat et al., 2001). The flank microbialites exhibit a radial growth, which results in the formation of hemispheroid morphologies (Fig. 6E,F; cf. Bertling and Insalaco, 1998). In polished slabs, the flank microbialites present similar structures to those at the undersides. A massive thrombolitic crust is associated with various encrusting organisms in the internal part, whereas microbialite columns with a sparse fauna are observed in the external part (Fig. 8E,F). The nuclei generally are branching corals. Sedimentary particles and rare bivalves are trapped between the thrombolitic columns. The microfabric and the encruster fauna in mamillated microbialites are the same as in pseudostalactitic morphology (Figs. 4 and 7C).

The growth structures are similar for the underside and the flank microbialites. However, the direction of microbial growth in these two structures is different. The microbial crusts generally became established on coral branches or fixed oysters (stages 1; Fig. 9B,C). Starting from these nuclei, microbial growth continued both laterally and downward for the underside microbialites, and both laterally and vertically (essentially upward) for the flank microbialites (stages 2; Fig. 9B,C). The first increment of microbial growth was constituted by thrombolitic columns, which were progressively bound by successive generations of microbialites, associated organisms, and trapped particles that developed the charac-

teristic massive aspect of the central part of the mamillated microbialites (Fig. 8F,H,J). Various organisms (sponges, oysters, bryozoans) also participated in the formation of mamillated microbialites (stages 3 and 5; Fig. 9B,C). They contributed to the lateral and downward development of the underside microbialites and were mainly responsible for occasional downward growth of the flank microbialites. New thrombolitic layers (stages 4 and 6; Fig. 9B,C) eventually covered them. There is a remarkable relationship between the density of encrusters and the development of microbial crusts. When the encrusters are abundant, the crusts are characterised by limited column development (Fig. 8J). On the contrary, the microbial columns can reach several centimetres (Fig. 8H) when these organisms are rare. However, the thickness of the mamillated microbialites seems to be independent of encruster abundance but is controlled by the available space on the flanks or on the undersides of the bioherms. Concerning the internal structure of the mamillated microbialites, both massive (dense) and ‘dendritic’ structures (such as in Fig. 9) occur within the equivalent ‘downward-facing hemispheroids’ described from the Upper Jurassic of Spain (Celtiberian Basin) by Leinfelder et al. (1993) and Schmid (1996). These authors interpreted this ‘dendritic’ structure as indicating higher input of allochthonous carbonate mud.

5.3. *Reticular microbialites*

The reticular microbialites are commonly observed at the periphery of the bioherms. Microbialites thus extended the surface of the bioherms, and formed bridges between coral colonies and bioconstructions. This type of microbialites built relatively thin crusts (5–15 cm) that developed over several tens of centimetres between two bioherms (Fig. 6G). The microbial crusts commonly were coalescent, producing a 3-D meshwork. The gaps between the reticular crusts generally were filled by allomicrite. The single reticular microbialite elements usually have a hard, encrusted (e.g. oysters) and perforated upper surface, whereas the lower surface occasionally displays small pseudostalactitic microbialite development. In sec-

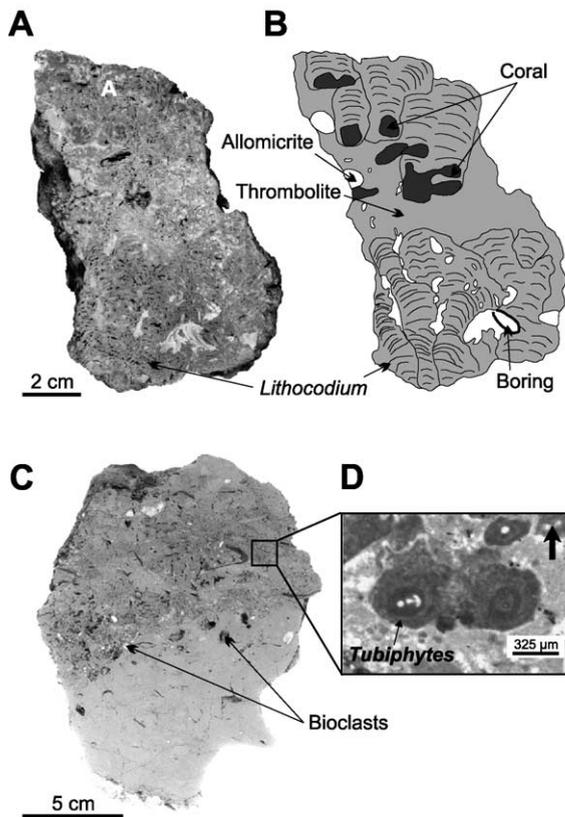


Fig. 10. (A,B) Detail of reticular microbialite internal structure. Note the columns essentially composed of *Lithocodium aggregatum*; first reefal unit. (C) Detail of the internal structure of interstitial microbialites; first reefal unit. (D) Thin section of the sample shown in (C): two *Tubiphytes* serve as a substrate for upward growth of the microbial colonies. The black arrow indicates the top of the sample.

tions, the reticular microbialites exhibit the characteristic clotted mesostructure of thrombolites (Fig. 10A,B). These thrombolitic crusts are associated with corals and the columns of the micro-encruster *Lithocodium aggregatum* Elliott, 1956.

As far as can be observed, the nuclei generally are colonies of phaceloid corals where the microbes successively encrusted and filled the space between the branches (stage 5; Fig. 11). In other cases, the coral branches were at first colonised by a more diverse micro-encruster fauna (mainly *Lithocodium*), which was subsequently encrusted by the microbialites. The *Lithocodium* colonies generally display a columnar upward growth

(Fig. 10). Microbial crusts also filled the spaces between the *Lithocodium* columns and exhibited a pronounced upward growth up to the height of the *Lithocodium* colonies. The microbialites then formed lateral spurs, bridge-like structures between single coral colonies, and finally coalescent microbialite elements resulting in a reticular meshwork. Rapid lithification created partially free-hanging bridges, as indicated by very small pseudostalactitic growth on the lower surfaces of the reticular crusts (stage 6b; Fig. 11). Once this stage was achieved, two scenarios can be envisaged: (1) the bridges were covered by sediment and constituted the reticular microbialites observed today (stage 6a; Fig. 11); (2) the microbialites continued to develop in association with new reef builders and encrusters to form a compact mass similar to that observed in the central part of the reef bodies (stages 6b and 7; Fig. 11).

5.4. Interstitial microbialites

Atypical microbialites are observed in the bioclastic sediments deposited laterally or at the base of the bioherms and are described as interstitial microbialites (Fig. 6H). This type is only observed in the first reefal unit, where bioclastic lenses are 2–3 m wide and 5–40 cm thick. The interstitial microbialites bound various bioclasts such as bivalves, corals, brachiopods, serpulids, gastropods, and micro-encruster fragments (*Lithocodium*, *Terebella*, *Tubiphytes*; Fig. 10C). Microbialites exhibit a thrombolitic mesostructure but can also display a structureless mesofabric characteristic of leiolites. The clotted microstructure and domal morphologies indicating vertical growth (Fig. 10D) suggest the microbial origin. No micro-encrusters are observed within this microbial microstructure.

The microbial colonies colonised and filled the interstices between the various bioclastic storm deposits, which were present close to the bioconstructions (stage 1; Fig. 11). The bioclasts are angular, suggesting a limited reworking and rapid stabilisation by the development of microbial films within the interstitial porosity (stage 2; Fig. 11). In conditions of low accumulation rates, microbially lithified bioclastic deposits provided a

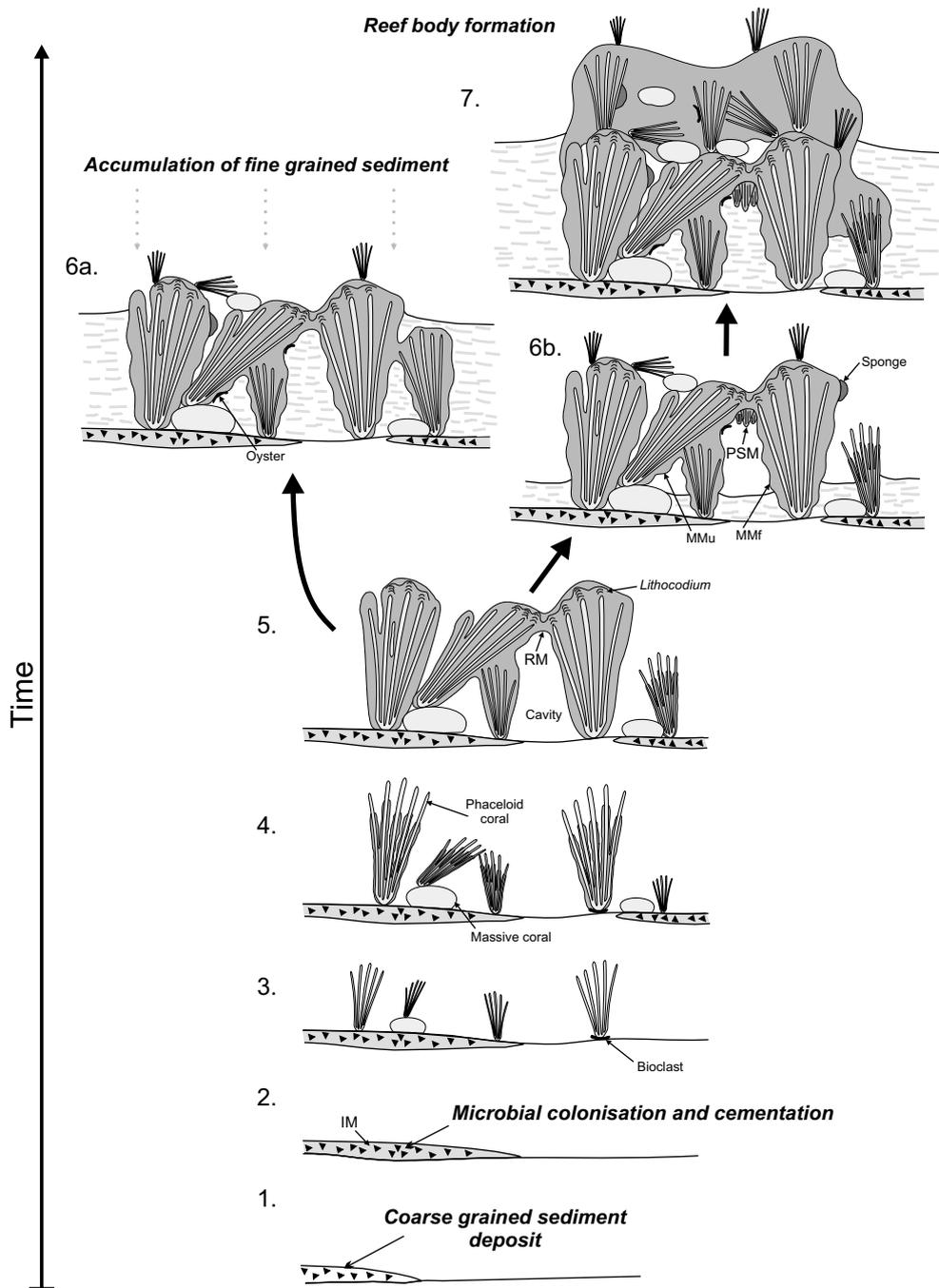


Fig. 11. Schematic sketch showing the genetic-temporal relationship between the four types of microbialite morphologies and a simplified model of reef body formation. Legend in Fig. 5. See text for explanations.

suitable substrate for coral colonisation (stage 3; Fig. 11). In the over cases, fine-grained sediments covered the bioclastic deposits including the interstitial microbialites.

6. Interpretation

6.1. Microbialite growth history

The growth history of the four main microbialite types is strongly related to their specific position within the reefs. Despite the complex growth pattern of the single reef bodies and transitions between the different microbialite morphologies, it is possible to reconstruct the genetic and functional relationships between the main microbialite types. There exist genetic–temporal relationships in such a way that the most conspicuous microbialites in the outcrop (pseudostalactitic microbialites) represent the latest structures within a genetic sequence. Based on these general genetic relationships, a very simplified model of development of the different microbialite morphologies and of the reef bodies at the Chay can be given (Fig. 11). However, it only represents a first step in the reconstruction of the Chay reefs and does not take into account the more complex internal structures. The chronological sequence is as follows:

(1) Interstitial microbialites filled the voids within bioclastic sediment layers and bound the particles (stages 1 and 2; Fig. 11). Such stabilised firm substrates favoured the establishment of coral colonies (e.g. phaceloid, more rarely massive corals), and may principally represent the initial stage of reef development (stage 3; Fig. 11). The phaceloid *Calamophylliopsis* may also have colonised less firm substrates (Werner, 1986; Leinfelder et al., 1996).

(2) As the growth of the coral branches advanced, microbial films covered parts of the coral branches out of reach of the polyps living at the end of the branch and thus produced initial crusts (stage 4; Fig. 11). At this stage, the lower parts of the corals including the interstices between the branches may have been completely covered and filled with microbialites. Unevenly growing micro-

bialites and episodic storms caused the coral colonies to topple over, which explains the relatively high percentage of corals not preserved in life position (about 60%). The growth of the reticular microbialites generally began on branches of phaceloid corals, from which they extended laterally to form bridges (stage 5; Fig. 11). In this way, they could connect neighbouring coral colonies and contributed to the development of a rigid framework. In a more advanced stage, reticular microbialites could connect neighbouring bioherms, thus initiating the formation of reef cavities.

(3) Further growth of mamillated microbialites on the flanks of the bioherms, and new settlement of corals on the top, as well as lateral growth of reticular microbialites, enlarged the height and the lateral extension of the bioherms (stage 6; Fig. 11). A pre-existing positive relief, which was provided by a relatively rigid coral-microbialite framework, allowed mamillated microbialites to grow. Encrustations at their base (e.g. oysters) clearly show that no direct contact existed between the underside microbialites and the sea floor.

(4) The coalescence of crust structures as well as the tilting of reef bodies led to roofing-over between neighbouring bioherms and the formation of reef caves (Garrett et al., 1971). Then, pseudostalactitic microbialites developed from the cave roofs, filling in the cavities (stages 6b and 7; Fig. 11). In some cases, an increase in the accumulation rate of allochthonous sediment led to the filling of the cavities and stopped pseudostalactitic microbialite development (stage 6a; Fig. 11).

6.2. Microbialite growth rate

The cryptic cave microbialites of Lizard Island (Reitner, 1993) exhibit very low net growth rates of 10–15 mm/1000 yr. However, relatively fast microbialite growth has been postulated for shallow-water coral-thrombolite reefs where it can be deduced from established coral growth rates (Nose and Leinfelder, 1997). The close inter-growth of corals and microbial crusts in these reefs makes it very probable that the microbialites

grew nearly as fast as the corals, some 1–2 mm/year (Schmid, 1996; Schmid et al., 2001). In the Chay Peninsula, corals and microbialites show a similar complex growth pattern. Nevertheless, if we take into consideration both a microbial encrustation that stayed below the living coral top (Dupraz and Strasser, 1999, 2002) and the time it took for the surrounding sediment to cover the primary bioherm relief, it appears more probable that the growth rate of the microbialite morpho-structures was lower than the coral growth rate.

6.3. *Microbialite roles in reef development*

As it is known from the Oxfordian reefs of Switzerland (Dupraz and Strasser, 1999) and Miocene reefs (Riding et al., 1991; Saint Martin et al., 1996, 2000), microbialite growth generally followed the growth of corals and other metazoans. The repetitive occurrence of this metazoan–microbialite association resulted in a complex pattern in the Chay reefs. This pattern clearly indicates that the microbialites were not only acting as binding structures in stabilising the reef body (Fagerstrom, 1991), but also contributed essentially to the volume and the morphology of the reefs (Fig. 6A–F). This kind of microbial development was also partly responsible for the development of reef caves. Therefore, the microbialites can be considered as part of the constructor guild (Leinfelder et al., 1996).

6.4. *Main factors controlling microbial growth*

The bioconstructions of the two reefal units differ in microbialite composition, faunal content, and lateral facies, pointing to differences in palaeoenvironmental parameters. The most complete spectrum of microbialite morpho-structures is developed in the first reefal unit. There, all four morpho-structure types occur repeatedly within the reef, each type being characteristic of a special position in the bioherms. It can be assumed that the growth pattern of the microbialite types and their relation to certain positions within the reef bodies are not due to chance causes but mirror distinct palaeoenvironmental factors, which were stable for some time during reef growth.

It is generally admitted that water energy and accumulation rate are the two main factors controlling macroscopic and mesoscopic growth forms of microbialites (Braga et al., 1995; Schmid, 1996). Microbialite growth is favoured by a very low accumulation rate, because microbial communities are not able to survive high sediment input (Sun and Wright, 1989; Dromart, 1992; Keupp et al., 1993). Mesoscopic dendroid forms, which are comparable to the thrombolitic increments observed in pseudostalactitic microbialites, have been considered characteristic of low water energy and low to moderate accumulation rates (Fig. 8C,D; Schmid, 1996). This author also mentions that mamillated microbialites (his ‘hemispheroid’ form) occurred in conditions of low accumulation rates and low to moderate water energy. This is in good accordance with our palaeoenvironmental interpretation prevailing in the internal parts of the Chay reefs. In the outer, exposed zones of the reef body, water energy is higher, and abrupt sediment supply is more frequent. These were possible factors limiting the upward microbial growth of reticular microbialites, and can explain why this morphology preferentially shows microbial crust infilling the available space between micro-encruster columns or coral branches (Fig. 12).

Sediment accumulation rate and water energy alone, however, are not sufficient to explain all aspects of growth morphologies. Based on their microbial growth directions, continuity between the different morpho-structures is emphasised by the study of the palaeocaves in the first reefal unit (Fig. 13). The different morphologies of microbialites consist of small thrombolite columns (Fig. 9). On the undersides of the bioconstructions, the columns of mamillated microbialites had a lateral and downward growth. A transition to flank microbialites (lateral and vertical growth, mainly upward) is observed passing from the bioherm undersides to the bioherm flanks that form the walls of the palaeocaves. Transitional forms between flank to pseudostalactitic microbialites are also seen. Interestingly, microbialites in the various morpho-structures always tend to grow vertically when space was available. The development of the columnar morphology for the pseudosta-

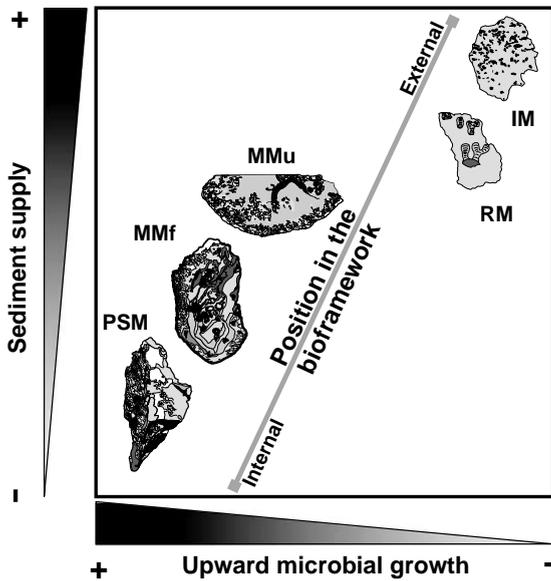


Fig. 12. Relationships between morphology of microbialites, position in the bioconstruction, upward microbial growth, and sediment supply. See text for explanations. Legend in Fig. 5.

lactic and the mamillated microbialites can be explained by allochthonous sediment input, which led to a complete filling of the intercolumn space (Reitner, 1993). Nevertheless, this explanation fails for the underside microbialite type where downward microbial growth is observed. This latter morphology is located close to the sediment surface and was probably more influenced by accumulation rate and water energy. However, its internal structure (i.e. columnar growth) does not really differ from that of the flank microbialites, which could be well projected above the sea floor. This suggests that accumulation rate and water energy had only a weak influence on the direction of microbial growth. Thus, upward growth structures of microbialites cannot be interpreted only in terms of high accumulation rate, as commonly inferred in the literature (Gaillard, 1983; Dromart et al., 1994; Schmid, 1996).

The fundamental upward growth may indicate a certain dependence of the microbial organisms on light penetrating into the palaeocaves, as observed in Recent cryptic habitats of Caribbean reefs (Zankl, 1993). However, in the modern example, the crusts grow laterally towards the cave entrance where the light comes from, whereas in

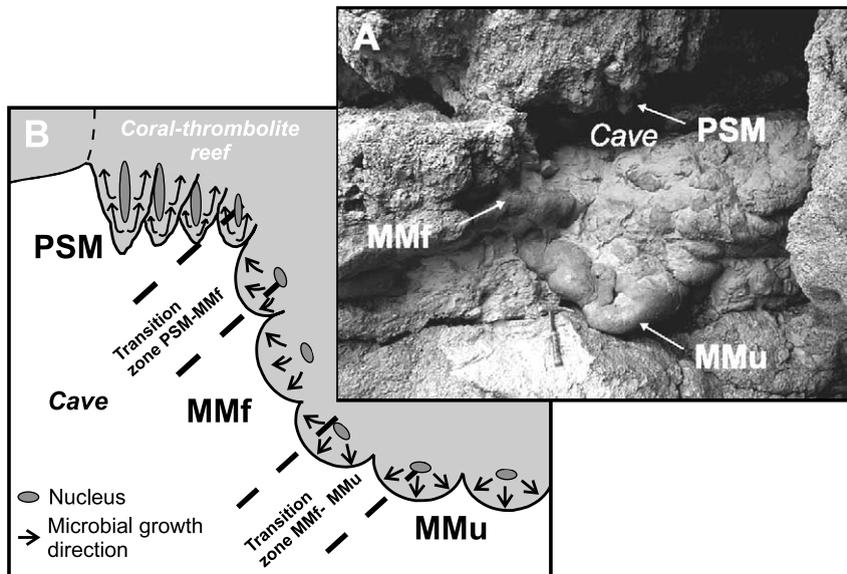


Fig. 13. (A) Palaeocave in the first reefal unit showing the position of pseudostalactitic, flank and underside microbialite morphologies. Hammer for scale. (B) Inferred microbial growth direction of the different microbialite forms observed in a palaeocave. Legend in Fig. 5.

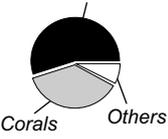
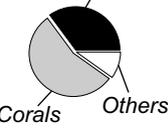
	Major composition	Accumulation rate	Coral growth fabrics	Cavity	Microbialite morpho-structures
First reefal unit	 <p>Microbialites Corals Others</p>	Low	Superstratal	Large-scale cavities	Pseudostalactite Mamillated bioherm underside bioherm flank Reticulate Interstitial
Second reefal unit	 <p>Microbialites Corals Others</p>	Moderate	Slightly superstratal to constratal	Few or no cavities	Mamillated bioherm underside

Fig. 14. Microbialite morpho-structures of the first and second reefal units in relation to reef composition, coral growth fabric, presence/absence of cavities, and accumulation rate.

the Chay Peninsula the pseudostalactites always show a predominantly vertical growth. If the vertical growth direction of the pseudostalactites was light-influenced, one has to postulate chimney-like openings in the cave roof as mentioned from Recent caves (Reitner, 1993). Through such openings came a little light and fine-grained sediment, which together could have controlled both the positive phototropism and the columnar structure of the microbialite growth.

6.5. Palaeoenvironmental conditions and the formation of the two reefal units

The coral-thrombolites occurred in two units that are separated by a major discontinuity represented by a hardground of regional importance (Fig. 2). The reefs of the two units share a general coral-thrombolitic fabric but differ markedly in the dimensions of the reef bodies, the composition of the microbialites, and the faunal content (Fig. 14). The first unit is characterised by a very complex bioconstruction consisting of several coalescent bioherms and exhibiting all four microbialite types. Reef caves are very well developed. In contrast, the second reefal unit consists of more or less isolated bioherms with reduced dimensions (7–8 m long, 3–4 m high). Only rare and centimetre-scale cavities are developed here.

Laterally to the reefs of the first unit, dominantly muddy limestones (wackestones) were deposited. These sediments are interstratified with fine-grained storm deposits, several centimetres thick, showing hummocky cross stratification, indicating that the coral-thrombolitic reefs developed in relatively deep water (tens of metres) but above the storm wave base. Only short-lived high-energy events interrupted the generally low-energy conditions. The first reefal unit forms a vast bioconstruction that displayed a superstratal growth type with coalescent patch reefs (Gili et al., 1995; Insalaco, 1998). The superstratal growth fabric was the result of the interaction of corals and binding microbialites, forming small patches as a first step. A relatively low accumulation rate was responsible for a pronounced upward growth. The elevation of the small bioherms above the sea floor and roofing-over processes led to the coalescence of patches and, in later stages, the formation of cavities of widely varying geometry and size (Garrett et al., 1971; Scoffin, 1972; Zankl and Schroeder, 1972; Insalaco, 1998). These large cavities, especially when their vertical dimensions were considerable (decimetres to metres), exhibit microbialite morpho-structures on their roofs (Fig. 13).

The sediments surrounding the reefs of the second unit consist of bioclastic wackestones to

packstones. Higher water-energy conditions and a probably shallower bathymetry than in the first reefal unit are inferred. A limited positive relief (0.5–1 m) of the bioherms surrounded by considerable bioclastic deposits resulted in a more con-stratal coral growth fabric (Gili et al., 1995; In-salaco, 1998). This implies that reef growth rate and accumulation rate were comparable, or that the latter was only slightly lower. The phaceloid *Calamophylliopsis* corals, which are the main skeletal constituents in the second reefal unit, are considered as being well adapted to conditions of high sedimentation rate (Leinfelder et al., 1996). Thus, the development of these corals produced low-relief (tens of decimetres) morphologies above the sediment surface. Bioclastic sediments were deposited on the reef flanks and infilled the majority of the inter-colony spaces. Only small cavities at the undersides of branching colonies of *Calamophylliopsis* have been observed. They are located in the most internal parts of the build-ups, which were relatively well protected from sediment supply. Consequently, mamillated microbialites of reduced dimension developed at the undersides of the bioherms, whereas morpho-structures of intra-reef cavities (pseudostalactites and flank microbialites) and reticular microbialites between two bioherms are absent.

7. Conclusions

(1) Bioconstructions are mainly formed by the phaceloid coral *Calamophylliopsis* and thrombolitic microbialites, which can constitute up to 70% of the framework. The microbial deposits played an important role in the stabilisation and growth of the bioconstruction.

(2) Four macroscopic morpho-structures of microbialites are located at diverse positions in the bioherms: mamillated microbialites on the flanks or at the undersides of the bioherms; pseudostalactitic microbialites on the roof of palaeocaves; reticular microbialites in the area between bioconstructions; and interstitial microbialites infilling the interstices of bioclastic deposits.

(3) Accumulation rate and water energy con-

trolled the reef morphologies and their growth type. A low accumulation rate enabled the bioconstructions to develop a superstratal growth type. The framework presents numerous large intra-reef cavities, and mamillated, pseudostalactitic and reticular microbialites developed. Low relief growth types occurred under conditions of moderate to high accumulation rate, and cavities were very rare and small. Only mamillated microbialites at the undersides of the bioherms developed, and were located in the most internal part of the bioconstructions where they were protected from sediment input.

(4) Macroscopic microbialite morphologies and their mesofabrics can be characterised by the direction of microbial growth. Microbial deposits show various directions of development such as upward, lateral, and downward, but where space was available, thrombolitic columns grew essentially upwards. A link to light penetration into the palaeocaves rather than a direct influence of water energy and accumulation rate is suggested for microbialite growth.

(5) These results allow a better understanding of the development of microbialites in Kimmeridgian coral reefs and emphasise the role of microbialites in reef building. A pre-existent coral framework was needed for the development of certain microbial morphologies. Microbialites with particular growth forms clearly suggest that they did not only play a binding role in the reef body but can also clearly be assigned to the constructor guild.

Acknowledgements

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