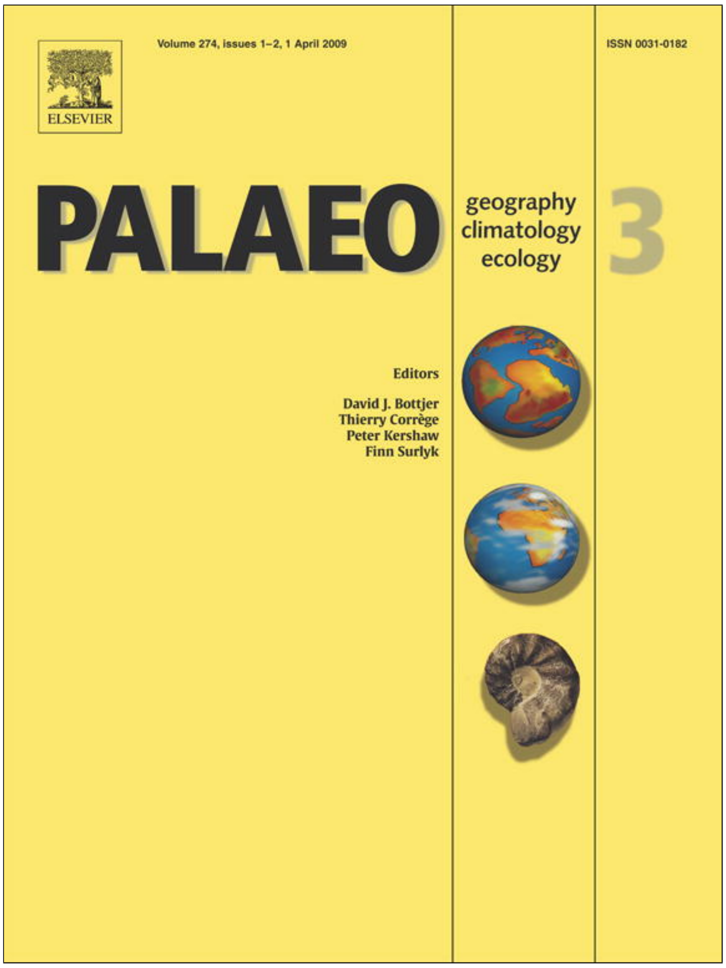
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The first microbialite - coral mounds in the Cenozoic (Uppermost Paleocene) from the Northern Tethys (Slovenia): Environmentally-triggered phase shifts preceding the PETM?

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ABSTRACT

Upper Thanetian microbialite-coral mounds from the Adriatic Carbonate Platform (SW Slovenia) are described herein for the first time, representing an important case study of extensively microbially-cemented boundstones in the Early Paleogene. The mounds are constructed primarily by microbialites associated to small-sized coral colonies, forming metric bioconstructions in a mid-ramp setting.

Detailed macroscopic and microscopic studies show that microbes are the major framework builders, playing a prominent role in the stabilization and growth of the mounds, with corals being the second most important component. Microbial carbonates represent up to 70% of the mounds, forming centimetric-thick crusts alternating with coral colonies. The microbial nature of the crusts is demonstrated by their growth form and internal microfabrics, showing accretionary, binding, and encrusting growth fabrics, often with gravity-defying geometries. Thin sections and polished slabs reveal a broad range of mesofabrics, with dense, structureless micrite (leiolite), laminated crusts (stromatolites), and clotted micritic masses (thrombolites). A first layer of micro-encrusters, including leiolites and thrombolites, occurs in cryptic habitats, whereas discontinuous stromatolites encrust the upper surface of corals. A second encrustation, the major mound construction phase, follows and is dominated by thrombolites, encrusting corals and other micro-encrusters. This sequence represents the basic constructional unit horizontally and vertically interlocked, in an irregular pattern, to form the mounds. The processes, which favored the deposition of these microbial carbonates, were mainly related to *in situ* precipitation, with minor evidences for grain agglutination and trapping processes.

Scleractinian corals comprise moderately diversified community of small (centimetric) colonial, massive, platy encrusting, and branching forms. Coral colonies are distributed uniformly throughout the mounds without developing any ecological zonation. These features indicate that coral development remained at the pioneer stage throughout the mound growth.

The spatial relationships between corals and microbialites, as well as the characteristics of microbial crusts and coral colonies, indicate a strong ecological competition between corals and microbes. A model for the evolution of the trophic structures during the mound growth is proposed, with changes in the paleoecology of the main bioconstructors triggered by frequent environmental perturbations. Turbidity and nutrient pressure, interpreted here as related to frequent recurrences of wet phases during the warm, humid climate of the Uppermost Thanetian, might have promoted temporary dominance of microbes over corals, causing rapid environmentally-driven “phase shifts” in the dominant biota.

1. Introduction

Microbial carbonates have waxed and waned in the Earth History (Webb, 2001). Especially the Cenozoic was characterized by a drastic decline of microbialites. No microbial-dominated reefs were so far reported from the Early Paleogene (e.g., Perrin, 2002) and only few examples were described for the Neogene (Late Miocene, SE Spain; Riding et al., 1991; Braga et al., 1995). Thus, the study of the microbialite-coral mounds, object of this work, provides insights into the development of patch reef facies in the Late Thanetian, including previously unexpected microbially-cemented facies.

Starting from the ‘mid’ Danian, environmental conditions in (sub) tropical zones of the Tethys and Atlantic coasts were favorable for the expansion of coralgal communities to form buildups, for example in the Pyrenean basin (Baceta et al., 2005), in the Majella platform

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(Vecsei and Moussavian, 1997), and Egypt (Schuster, 1996). During the Thanetian smaller bioconstructions, mainly composed of calcareous algae associated with moderately diversified communities of small corals, were developed especially in mid-latitude settings both in the Tethys (Terry and Williams, 1969; Bebout and Pedexter, 1975; Vecsei and Moussavian, 1997) and in the Atlantic realm (Bryan, 1991; Baceta et al., 2005). Within these Paleocene bioconstructions, the occurrences of microbialites were until now neglected. However, a number of these studies reported the occurrence of micritic and peloids fabrics without attributing it specifically to a microbial origin (Bebout and Pedexter, 1975; Bryan, 1991; Vecsei and Moussavian, 1997). This holds true also for the Adriatic Carbonate Platform (AdCP, Vlahovič et al., 2005) where small Danian and Thanetian coral–algal buildups (SW Slovenia) were described, but no microbial-related structures were reported (Drobne et al., 1988; Turnšek and Drobne, 1998). Only reworked clasts, likely Thanetian in age and described as “mud-mound” type buildups, were found (Turnšek and Košir, 2004).

The microbialite-coral mounds described here represent the first *in situ*, microbially-cemented bioconstructions described from the AdCP, and hitherto from the Tethyan realm. Located on the southern part of the Kras region, some road-cuts near to Divača village (SW Slovenia) reveal the existence of meter-size microbialite-coral mounds, latest Paleocene (Latest Thanetian) in age. These well-exposed bioconstructions are characterized by an exceptional development and preservation of microbial crusts, associated with a diverse coral community. Objectives of this work are: (1) describe for the first time these Upper Paleocene microbialite-coral mounds and their variety of fabrics, through field observations and petrographic analysis; (2) propose a model for the development of these microbial-coral mounds, interpreting the factors which determined the settlement, morphology, growth, and ecological relationships of microbial and coral communities.

2. Stratigraphical and geological settings

The carbonate succession investigated in this study crops out in the southern part of the Kras Plateau in SW Slovenia (Fig. 1). This area during the latest Cretaceous to Early Paleogene was characterized by

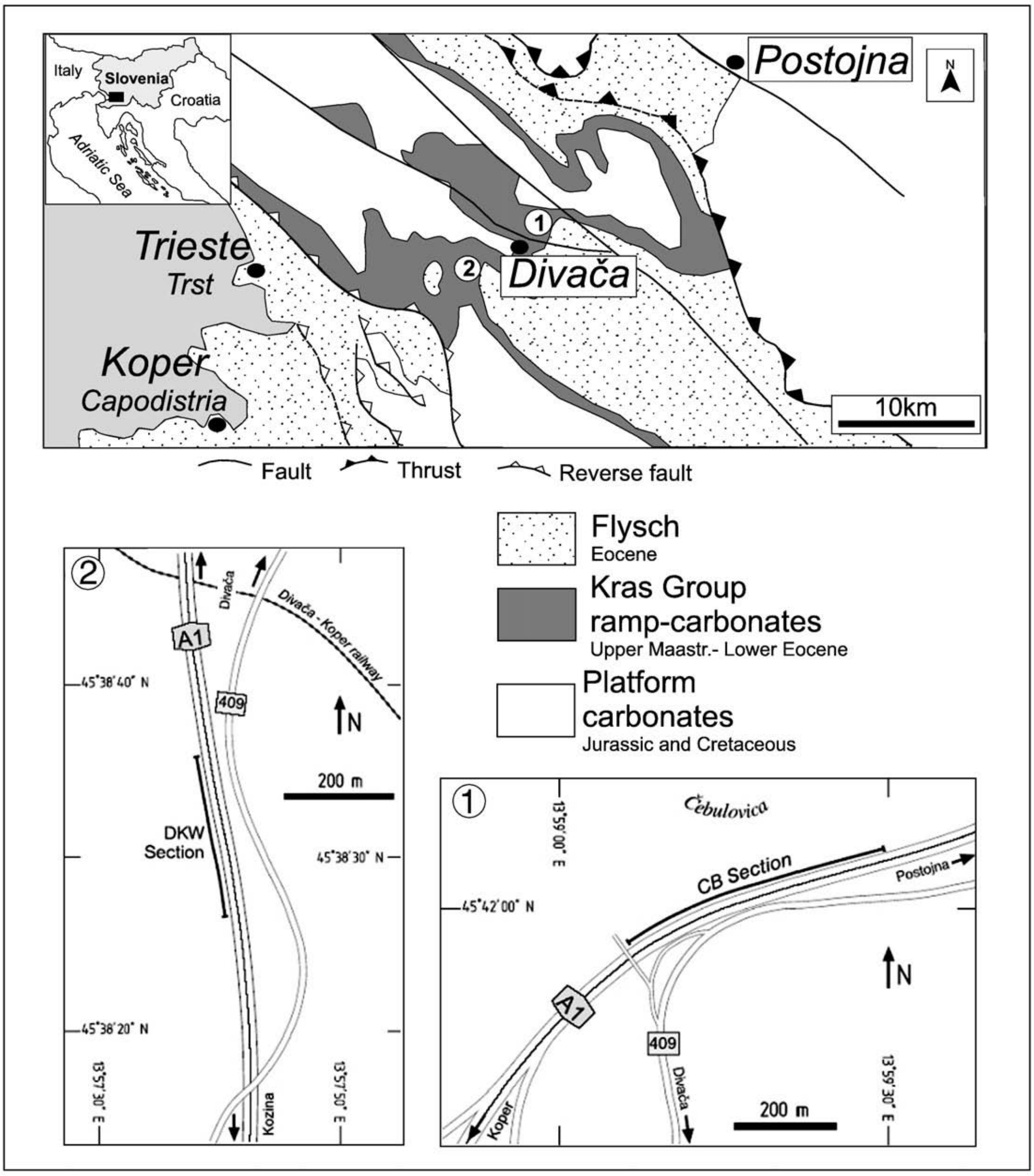


Fig. 1. Simplified geological map of the Kras region (SW Slovenia) modified from Košir (2003), with location of the studied sections: (1) Divača; (2) Čebulovica.

shallow-water depositional environments, developed on the marginal parts of the formerly extensive Mesozoic Adriatic Carbonate Platform (AdCP). Towards the north/northeast, a deep-water basin was forming in a foreland basin associated with the growing southwestward-verging Dinarides orogenic wedge (Otoničar, 2007 and references therein). Vertical facies successions of Paleocene and Lower Eocene shallow-marine carbonates generally exhibit a retrogradational pattern, reflecting a deepening trend and final drowning of the carbonate platform by pelagic and hemipelagic deposits (Košir, 1997).

A reliable, detailed reconstruction of the architecture and size of the Early Paleogene carbonate platform is difficult due to the complex thrust-nappe structure of NW Dinarides. However, the platform geometry inferred from regional facies relationships (Drobne, 1977; Jurkovšek et al., 1996, 1997) corresponds to a carbonate ramp depositional system characterized by roughly parallel NW–SE trending facies belts. The width of the carbonate ramp, only inferred from a rough palinspastic restoration (Placer, 1981), probably did not exceed 50 km, while the maximum width of the contemporaneous fore-deep basin was probably less than 200 km. It is important to note, however, that the position of the front of the orogenic wedge during the Early Paleogene cannot be established with precision.

A general stratigraphic column of the Upper Cretaceous, Paleocene, and Eocene deposits in the Kras region is shown in Fig. 2. The Cretaceous and Early Paleogene carbonate successions, together with the overlying siliciclastic successions, exhibit a stratigraphic pattern typical for underfilled foreland basins (Sinclair, 1997). This pattern reflects deposition during major tectonic events when the AdCP was subaerially exposed, subsequently re-established with deposition of the Uppermost Cretaceous — Early Paleogene carbonate sequence, then drowned, and finally buried by prograding deep-water clastics (flysch) (Otoničar, 2007). The Uppermost Cretaceous — Early Paleogene succession is composed by a lower unit (the Kras Group; Košir, 2003), that overlies the forebulge unconformity (Otoničar, 2007 and references therein), and comprises three formations: 1) Liburnian Formation (Upper Maastrichtian to Lower Paleocene) characterized by restricted, marginal marine, paralic and palustrine carbonates (Ogorelec et al., 2001); 2) Trstelj Formation (Upper Paleocene) composed of a lower member dominated by foraminiferal limestones and an upper member with foralgal limestones and buildups (Zamagni et al., 2008), deposited in shallow-water setting; and 3) *Alveolina-Nummulites* Limestone (Lower Eocene) dominated by larger benthic foraminifera (Drobne, 1977; Jurkovšek et al., 1996; Zamagni et al., 2008).

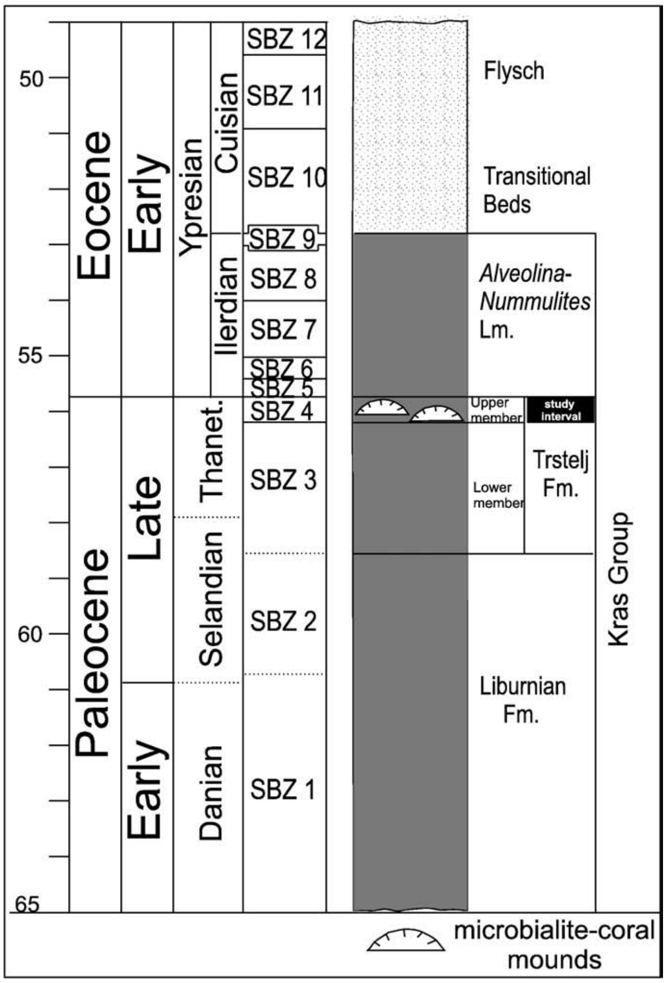


Fig. 2. Stratigraphic framework for the Kras region during the Early Paleogene. Shallow marine biozonation (Shallow Benthic Zone, SBZ) and time scale based on Serra-Kiel et al. (1998), with the Paleocene–Eocene boundary placed at the SBZ 4 – SBZ 5 limit.

The mounds, object of this work, belong to the upper member of the Trstelj Formation (Fig. 2), covering the SBZ 4 (Upper Thanetian, according to the zonal scheme of Serra-Kiel et al., 1998). In the studied area this member, which contains the microbialite-coral mounds, consists of middle-ramp facies (Zamagni et al., 2008). This interpretation is supported by the presence in the mounds of corals with platy morphologies, typical for low light environments, the presence of thin foralgal crusts of corallines and peyssonneliaceans, the absence of lagoonal and very shallow-water biota, and the dominance of fine-grained wackestones and packstones associated to the mounds, indicating deposition under low energy regime.

Turnšek and Drobne (1998) described coral assemblages from several localities in the Kras regions, occurring in different levels of Paleocene carbonates from the Selandian (SBZ 2) up to the latest Thanetian (SBZ 4). These coral-bearing limestones were interpreted as small coral-algal patch-reefs (Drobne et al., 1988; Turnšek and Drobne, 1998), but no microbially-cemented frameworks were described so far.

3. Materials and methods

The microbialite-coral mounds are exposed in road-cuts between Postojna and Koper (Fig. 1). Two localities have been studied in detail, Čebulovica and Divača (Fig. 1). In the case of the Divača mound a two-dimensional reconstruction of component distribution has been performed based on a combination of field observations, macroscopic study on slabs, and microscopic data from thin sections (Fig. 3A–B). In the case of the Čebulovica, difficult accessibility and the intense fracturing, limited a detailed mapping of the mounds. Nonetheless, the combined study of the Čebulovica and Divača mounds permits to understand the relationship between the bioconstructed facies and the associated bioclastic deposits.

The Divača mound has a lenticular shape and it is exposed over a length of about 240 m, and a maximum thickness of 10 m (Fig. 3A–B). The base of the mound is not exposed; therefore these thicknesses measured must to be considered as minimum values. For the high-resolution paleoecological and sedimentological analysis a total of 165 samples were collected along the mound and vertical transects covering the whole exposed bioconstruction and the overlying deposits. In the Čebulovica section the microbial carbonates form massive metric-thick mounds (up to 6 m thick) exposed over a length of 70 m, alternated with foralgal packstones and wackestones (Fig. 3C) (Foralgal Facies, *Assilina*-dominated assemblage and Orthophragminids-dominated assemblage, cf. Zamagni et al., 2008). In total 100 samples were collected from the Čebulovica mounds.

Samples have been studied on polished, etched slabs, and in thin sections to investigate the patterns of microbialite growth and relation with other skeletal (mainly corals) and encrusting components. For optical-microscope analysis about 80 large thin sections (5.0×7.5 cm) and 50 small thin sections (2.8×4.6 cm) from the Divača mound and

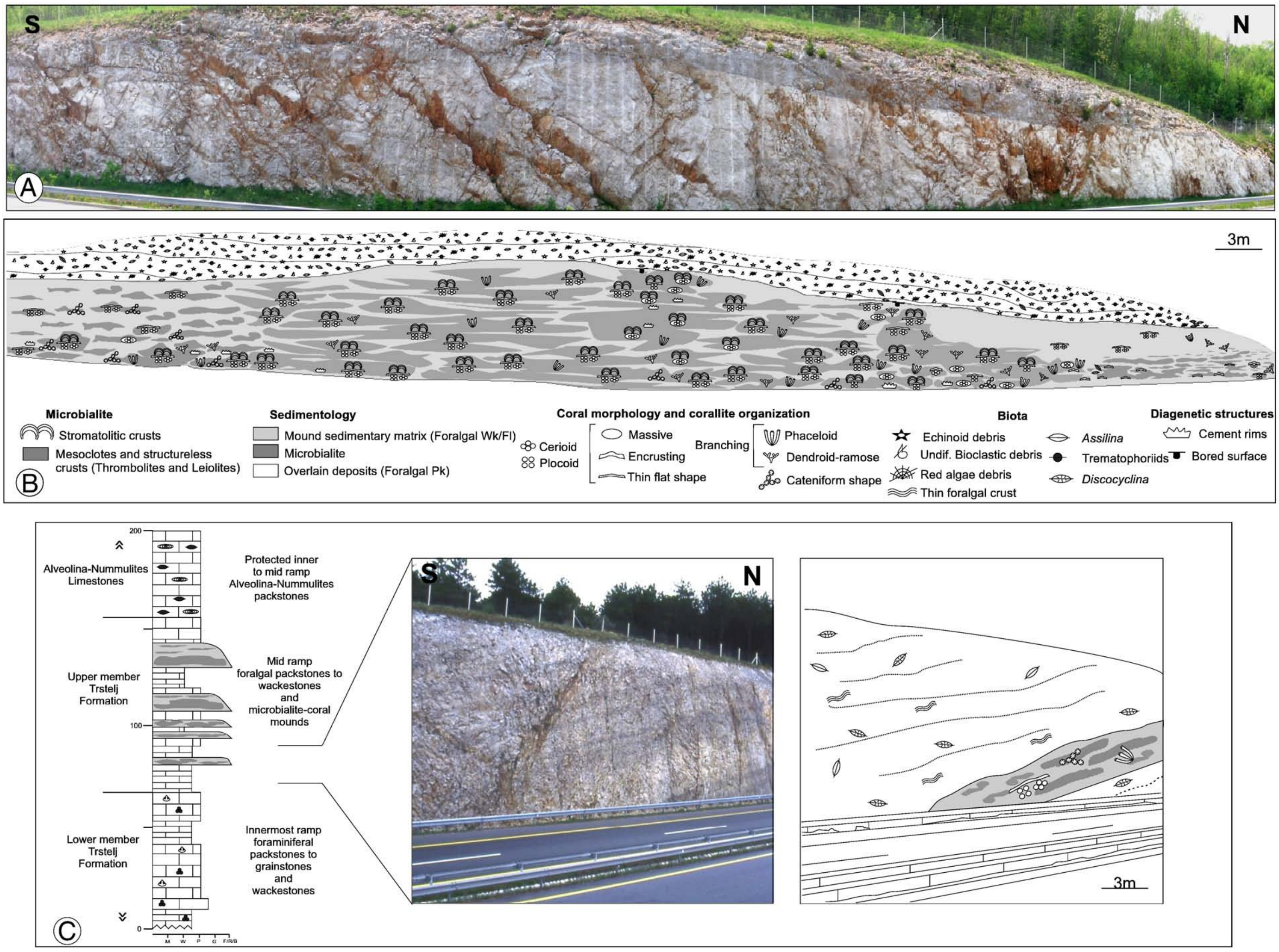


Fig. 3. (A) First part of the Divača mound. (B) General distribution of the microbial carbonates and coral morphologies compared to the mound matrix. The foralgal packstones overlay the bioconstruction. (C) Stratigraphy of the Late Paleocene–Ilerdian (Eocene) Čebulovica section and outcrop photo of one of the mounds.

30 large thin sections from the Čebulovica mounds have been prepared.

The taxonomic study of corals is based on randomly oriented thin-sections of cemented carbonate rocks. The taxonomic framework used to identify species is based on the work of Turnšek and Drobne (1998), and revision of Baron-Szabo (2006). All the samples used for systematic study of the corals are stored in the Institute of Geosciences at the University of Potsdam.

The biostratigraphic scheme used in this work follows the shallow benthic foraminifera biozones (SBZ) of Serra-Kiel et al. (1998; Fig. 3). The Paleocene–Eocene boundary is located in this study between SBZ 4 and SBZ 5. The absolute time scale is adopted from Berggren et al. (1995).

4. General patterns of encrustation within the mounds

The mounds are complex bioconstructions, mainly composed by sheetstone facies (dominated by sheet-like massive corals, based on classification of Insalaco, 1998) associated with bafflestones, and rudstones. They are composed by microbialites, colonial corals, micro-encrusters, macrofauna, mound matrix, and cements. The distribution of the components within the mounds is quite heterogeneous (Fig. 3). An overview of the relationship between these components indicates that in a first phase corals and micro-encrusters, including discontinuous stromatolitic crusts on top of coral surfaces and cryptic microbialites form a first loose, microbially-cemented framework. In a second phase benthic thrombolites, occurring as centimetric-thick crusts, become the dominant constructors excluding other encrusting biota. This pattern represents, in a simplified reconstruction, the basic constructional unit horizontally and vertically interlocked, in an irregular pattern, to form the mounds. No isochronous surfaces dominated either by corals or microbialites can be traced within the mounds.

In the following section the diagnostic features of the microbialites are treated in detail, and the other components are described in the Section 6.

5. Microbialite morphologies and fabrics

The microbialites volumetrically dominate the mounds, being the major framework constructor and stabilizer. The term “microbialite” is used according to the broad definition of Burne and Moore (1987, p. 241–242) as organosedimentary deposits that have accreted by combination of trapping and binding of detrital sediments by a benthic microbial community and/or mineral precipitation. Microbial carbonates form up to 70% of the Divača mound and around 50% in the Čebulovica mounds and are characterized by a range of mesofabrics (scale of description according to Shapiro, 2000) that can be attributed to: stromatolites, thrombolites, and leiolites (definitions according to Riding, 2000). Often the three types grade into one another even

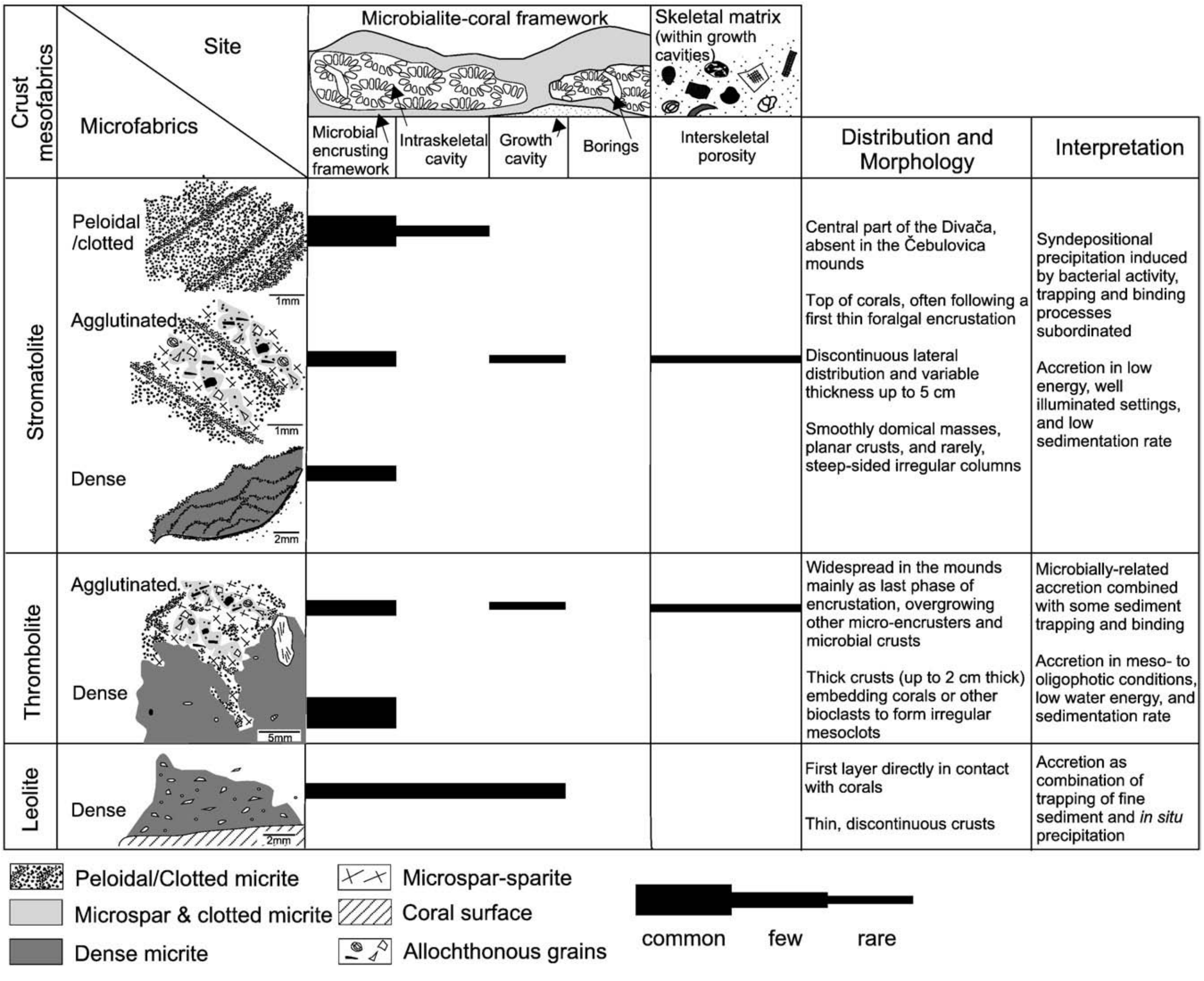


Fig. 4. Types of microbial carbonate fabrics distributed in different microenvironments of the mounds, main features, and interpretation.

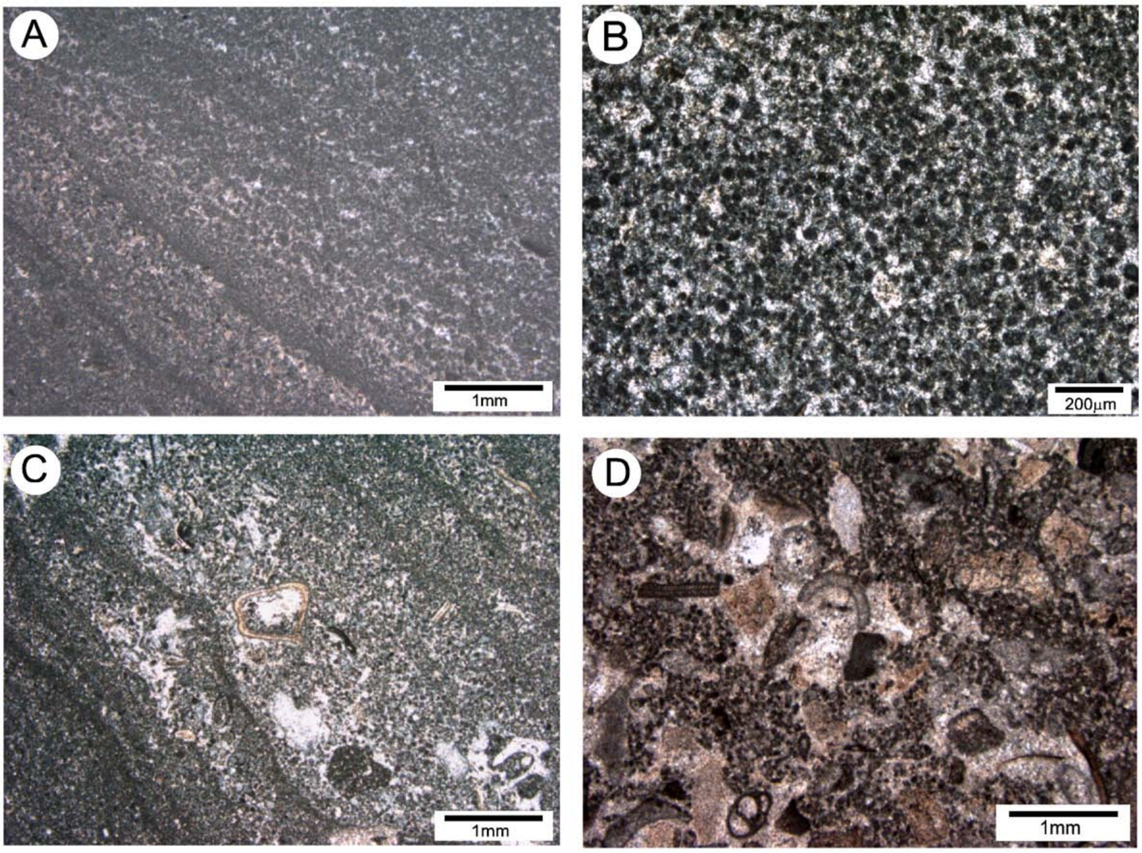


Fig. 5. Microfabrics. (A) Lamination with darker layers produced by fine-grained closely packed peloids alternated with laminae with coarser, less-compacted peloids within microsparite. (B) Peloidal microfabric. (C–D) Detail of agglutinated microfabrics. (C) Peloidal grainstone with crude lamination. Lamination with coarsening upward sequence due to agglutination of allochthonous material embedded into spar and microspar, alternated with clotted/dense layers. (D) Agglutinated fabric with the bioclasts embedded into sparry calcite with patches of peloids, forming a peloidal grainstone.

within the same thin section, indicating a complex construction of the framework. Macroscopically, the microbialites have a structureless, massive aspect, which makes difficult to distinguish the different morphotypes in the field. As a coarse rule, usually the microbialites are darker than the adjacent cavity-filling sediment. Microscopically, a range of fabrics has been observed and described in detail in the following paragraphs. For an overview, a simplified sketch of the meso-/microfabrics spatial distribution within the mound micro-environments together with a qualitative evaluation of their abundances, their major morphological features, and interpretation are illustrated and summarized in Fig. 4.

5.1. Stromatolitic fabric

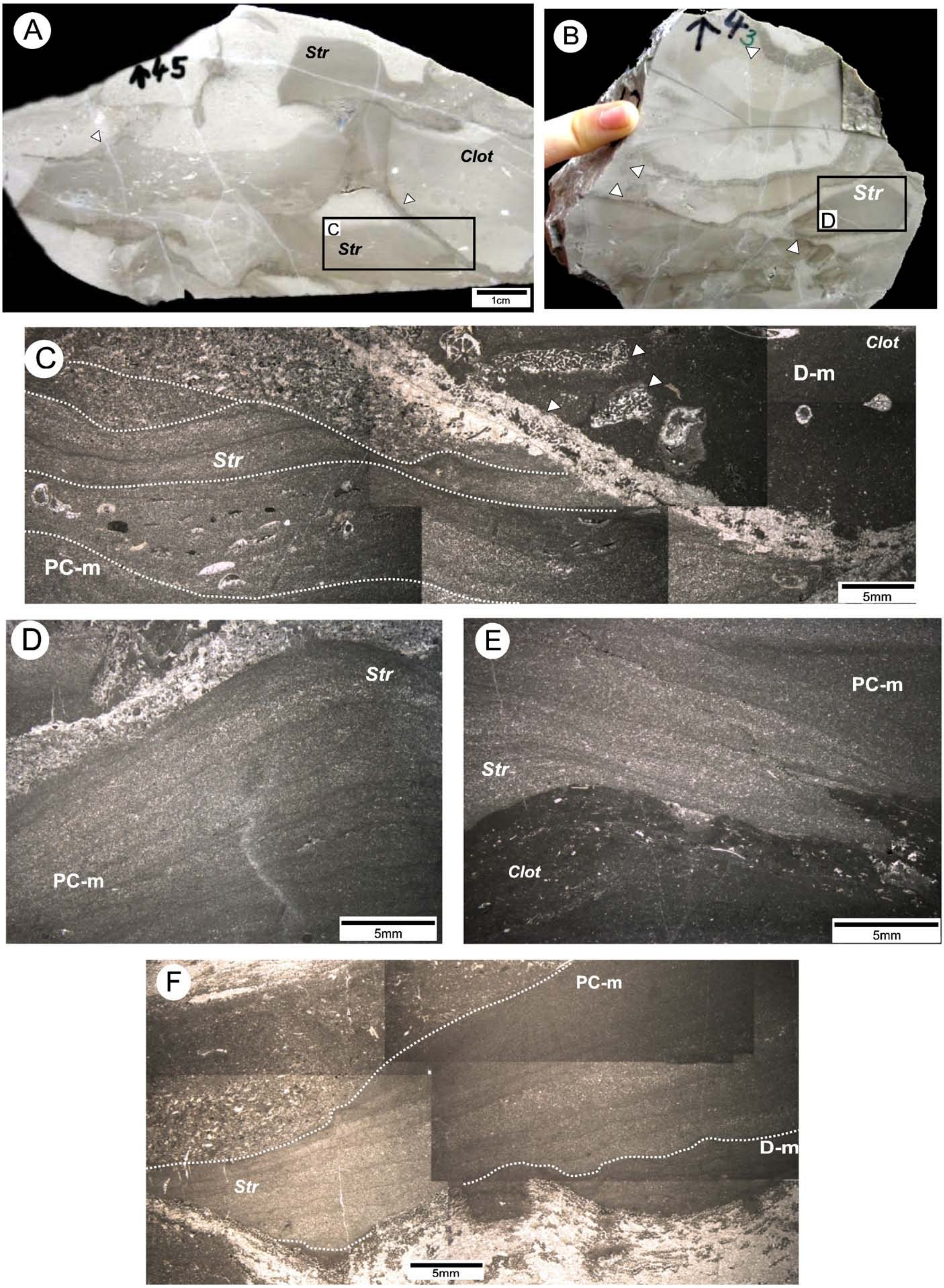
5.1.1. Characteristics

Stromatolitic fabrics are best developed in the central part of the Divača mound; whereas they are almost absent in the Čebulovica mounds.

Typically they occur on top of corals, often following a first thin foralgal encrustation, showing discontinuous lateral distribution and a variable thickness up to 5 cm. They form smoothly domal masses, planar crusts, and rarely, steep-sided irregular columns. The stromatolitic fabric consists of dense to peloidal/clotted micrite, commonly with scarce fine-grained allochthonous material embedded. The lamination is largely defined by changes in peloidal packing and differential compaction (Fig. 5A–B). The peloids in the stromatolites have a wide range of size but often they are ~50 μm wide, with margins both well-defined with simple outlines and more irregular to form aggregates creating a clotted fabric. In both cases, the remaining cavities between peloids and aggregates are filled by sparry calcite (Fig. 5C). A third fabric occurs, the agglutinated fabric, that can be described as peloidal packstone to grainstone with fine sand to silt-sized bioclasts (mainly small foraminifera and angular algal fragments, both micritized) and patches of silt-sized peloids floating in a sparry calcite (Fig. 5D).

In thin section, lamination ranges from wavy to smooth and it is usually best developed on planar and low domal crusts (Fig. 6), instead it is more irregular and poorly developed on steep-side crusts. Where sediment supply increases, laminae are weakly developed or absent and gradually pass to agglutinated microbialites or to detrital carbonate sediment. The stromatolites show both abrupt and gradual contacts with the detrital carbonate sediment, acting as matrix in the mound. When detrital sediment becomes more abundant, the matrix can be incorporated into the crust, coarsening the texture, or forming distinct separated laminae. Locally, stromatolites overlay the dense thrombolitic mesoclots (Fig. 6E).

Fig. 6. Divača mound. Stromatolitic mesofabric. Arrows indicate upward direction. (A–B) Polished surface with corals indicated by white arrows. (C) Thin-section photomicrograph detail of panel A (rectangle). Laminated crust on the left side of the coral colony (white arrows) with wavy accretionary style. The crust is composed of clotted micrite, passing abruptly to sedimentary matrix. Dense structureless micritic mass on the right side, with embedded coral fragments (white arrows). (D) Thin-section photomicrograph detail of panel B (rectangles) with domical, laminated microbial crust. (E) Stromatolite with crude lamination overlain dense mesoclot. (F) Thin-section photomicrograph of a crust with domal shape on top of coral, with crude lamination. The crust follows a first discontinuous layer of dense, irregularly laminated stromatolite and passes upward to fine detrital wackestone. *Str*: Stromatolite. PC-m: Peloidal/Clotted micrite; D-m: Dense micrite.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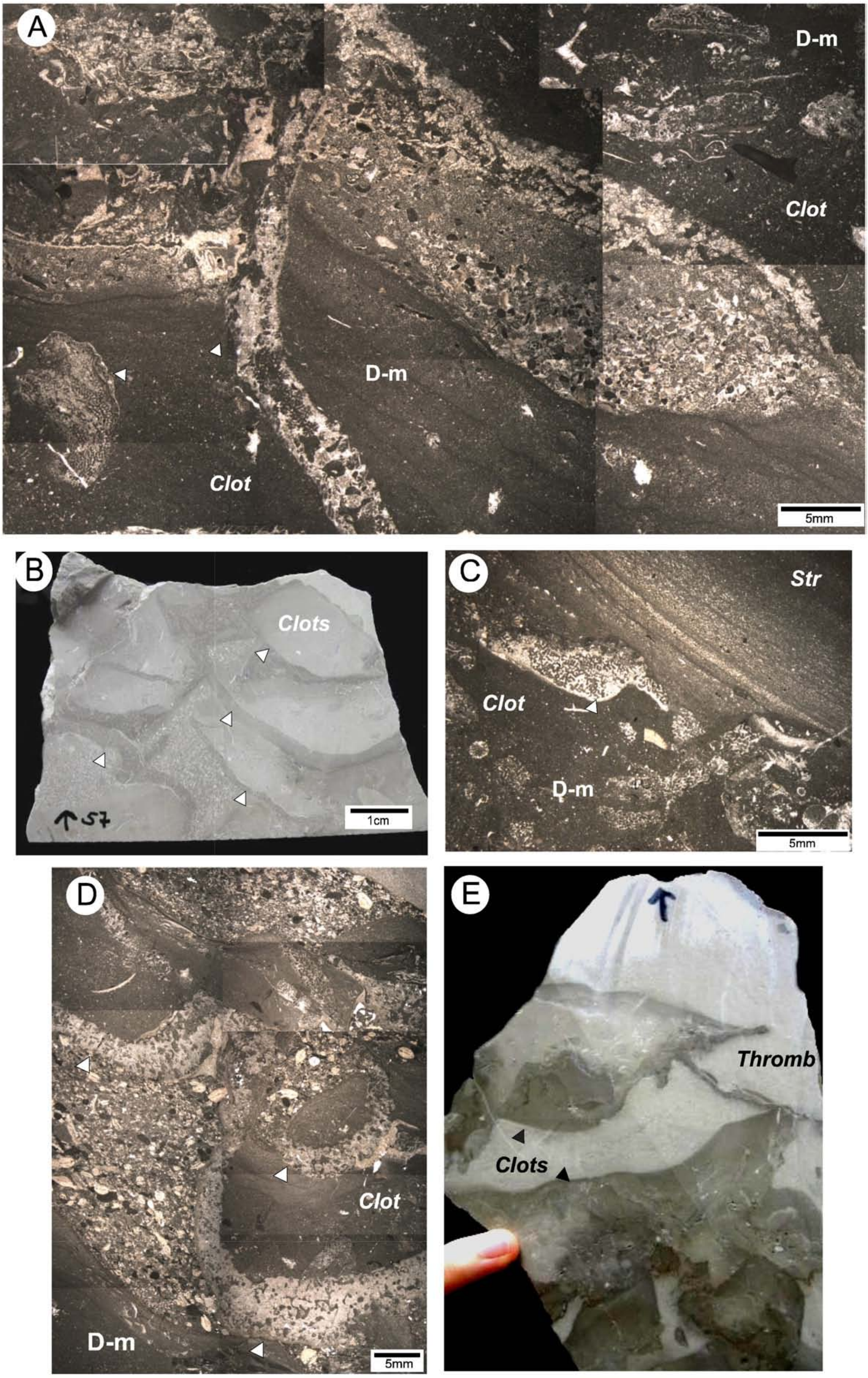
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D-m
5mm
E
Thromb
Clots

Crusts composed by dense micrite with a crude lamination can be observed as first layer directly on top of corals, to form a discontinuous, thin (<1 mm) layer (Fig. 6F).

5.1.2. Interpretation

The stromatolitic fabric is clearly a syndepositionally lithified feature, as indicated by the gravity-independent accretion and the nature of the lamination, with discontinuous and reduced lateral persistence. Additionally, the floating habit of peloids and peloidal clusters within the sparry cement indicates an early mechanical stabilization and a biologically-induced accretion of the crusts. These microfabrics are widely distributed in modern (e.g., Dupraz et al., 2004) and fossil stromatolites (e.g., Riding and Tomás, 2006), where they have been interpreted as produced by the micrite nucleation within biofilms embedding microbial communities (e.g., Sprachta et al., 2001; Dupraz et al., 2004).

Hence, the stromatolitic fabrics in the studied mounds are interpreted as having formed by syndepositional precipitation induced by bacterial activity, with additional trapping and binding playing a minor role. Nevertheless, the local occurrence of stromatolites with agglutinated fabrics and crude lamination points to episodes of higher bioclastic input, probably due to storms and bottom currents, with enhanced trapping and binding of allochthonous grains by the microbial mats. The agglutinated stromatolites likely were produced by microbial colonization of the interskeletal space, stabilizing the sediment and producing the peloidal packstone and grainstone fabrics.

The distribution of stromatolitic crusts mainly on the upper surface of corals points to a prominent role of photophile microbes, responsible for their accretion. The discontinuous distribution of these crusts on the coral surfaces might be related to a development confined to dead part of coral colonies. Moreover, this accretion was probably quite fast and continuous as testified by the almost complete absence of any other micro-encrusters associated with these crusts. The dominance of planar and low domal morphologies over columnar structures and the general development of well-defined lamination are interpreted as linked to a generally low to moderate sedimentation rate (Dupraz et al., 2006).

5.2. Thrombolitic fabric

5.2.1. Characteristics

Microbialitic crusts showing clotted mesostructure characteristic of thrombolites (Aitken, 1967; Kennard and James, 1986; Shapiro, 2000) are commonly present in the mounds. Thrombolites have been observed within cavities, but they mainly occur as the last phase of encrustation, overgrowing other micro-encrusters and microbial crusts, filling the growth cavities, and encrusting the first coral-microbialite framework. Thick thrombolitic crusts (up to 2 cm thick) develop on the upper surface of corals as well as embedding them or other bioclasts to form an irregular clotted fabric (Fig. 7). Macro- and mesoscopically, these microbialites show a clotted aspect (Fig. 7B–E) and consist of millimeter to centimeter-sized dark, dense micritic clots passing to lighter areas enriched in allochthonous grains. The clots have an irregular shape with sharp as well as “fuzzier” margins grading to agglutinated microbialites or sedimentary matrix. Thrombolites have been also observed associated with clasts of stromatolitic crusts and coral debris to form a chaotic, breccia-like fabric (Fig. 8A–B), which hints for a complex growth history of the mounds.

5.2.2. Interpretation

The thrombolites show some of the typical features described by Kennard and James (1986), with dense mesoclots with little debris inside separated by patches of micrite, sediments and cements. The dense to peloidal/clotted nature of the microfabrics has been interpreted as the result of carbonate precipitation induced by the metabolic activity of heterotrophic coccoid or coccoid-dominated microbial communities (e.g., Kennard and James, 1986; Leinfelder et al., 1996; Dupraz and Strasser, 1999).

The studied thrombolites have a broad distribution irrespective of exposure to light, forming encrustations on both sides of corals and in cryptic habitats. This points to a formation linked to the activity of sciaphile bacteria, using heterotrophic metabolisms, in settings with low energy and low sedimentation rate (e.g., Leinfelder et al., 1993; Camoin and Montaggioni, 1994; Leinfelder et al., 1996; Camoin et al., 1997; Camoin et al., 1999; Dupraz and Strasser, 1999, 2002).

Apart from *in-situ* precipitation and trapping and binding, the major processes leading to the development of thrombolites, other processes also might have played a role in the formation of the thrombolitic mesofabric. The common presence of borings in the thrombolites as well as the co-occurrence and transition to stromatolite crusts, forming locally chaotic texture resembling a breccia, seem to point to syndepositional reworking (e.g., storms and bioturbation) responsible for enhancing the clotted fabric. Braga et al. (1995) described Miocene thrombolites from Spain, produced by multiple processes with the calcification of microfossils associated with a complex interaction of irregular agglutination, skeletal encrustation, erosional processes and bioturbation.

5.3. Leiolitic fabric

5.3.1. Description

Leiolitic fabric occurs in both the Divača and the Čebulovica bioconstructions, but is better developed in the first, where it is widespread throughout the mound even volumetrically quite subordinated compared to thrombolites and stromatolites. Macroscopically, leiolites are difficult to distinguish due to the general aphanitic aspect of the mound limestones. They form thin discontinuous crusts. In the thin section, they are usually composed of dense micrite with well-sorted, very fine-grained debris embedded. The contact with the surrounding deposits is usually sharp and their crustose nature is inferred from the development of knobs and protuberances (Fig. 8C–D). Commonly these crusts form a first layer directly in contact with corals as well as in interskeletal and growth cavities, being followed by stromatolite and/or thrombolite crusts, and the mound matrix.

5.3.2. Interpretation

The common presence of allochthonous fine sand-sized debris embedded in the leiolitic crusts seems to indicate accretion resulting from the combination of trapping of fine sediment and microbially-induced precipitation of micrite. Their occurrence on the upper surface of corals as well as cryptic habitats points to an origin from microbial communities with variable light requirements.

6. Other components of the microbialite-coral mounds

6.1. Coral assemblage

The coral colonies occur in the mounds without a clear growth direction and without a defined ecological zonation throughout the bioconstructions, showing a heterogeneous distribution of morphotypes. They do not form coral-dominated levels within the mounds, rather they are randomly distributed. The corals and associated micro-encrusters are usually welded by thick microbial crusts (stromatolites and to a less extend leiolites) and surrounded by thrombolites. The

Fig. 7. Divača mound. Thrombolitic mesofabrics. Arrow indicates upward direction. (A) Thrombolite with dark micritic clots embedding corals (white arrows). (B–D) Polished surface and thin-section photomicrograph with thick crusts of structureless micrite as clots on top of corals (white arrows), passing to bioclastic deposits filling the inter-clot space. (C) Passage from thrombolitic dense crust with embedded coral debris to laminated stromatolite overlying the mesoclot. (E) Polished surface. Mesoclots with darker aspect and irregular shape (black arrows), passing abruptly to lighter areas. *Thromb*: Thrombolite; *Str*: Stromatolite. D-m: Dense micrite.

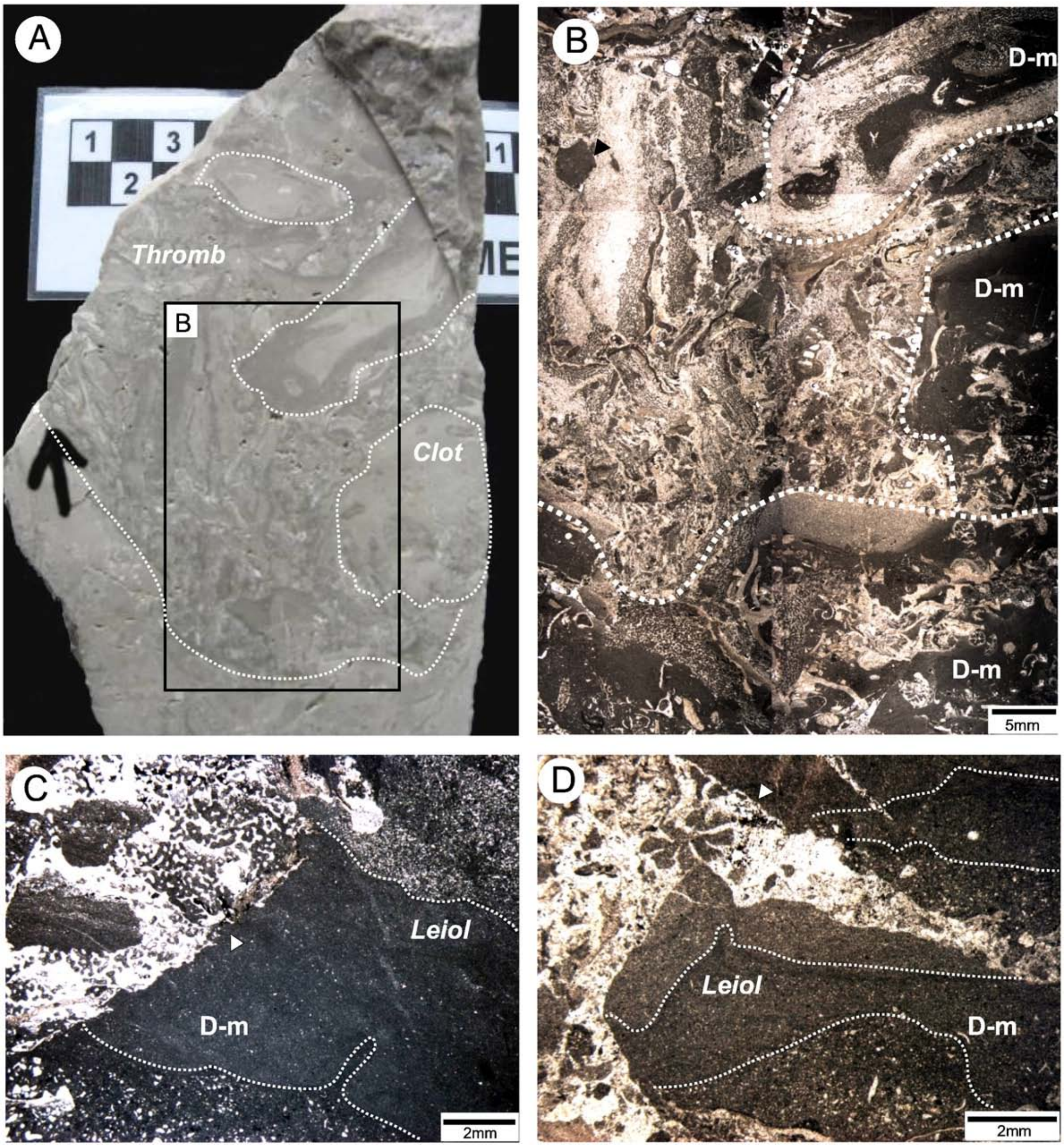

Fig. 8. Divača mound. Thrombolitic meso- and microfabrics. (A–B) Polished surface and thin-section photomicrographs. Clotted mesofabric with chaotic association of coral debris and dense clots. Leiolites. (C–D) Corals (white arrows) encrusted by thin dense micrite with fine debris inside passing to dense, debris-free micritic crusts. *Thromb*: Thrombolite; *Leiol*: Leiolite. D-m: Dense micrite; PC-m: Peloidal/Clotted micrite.

microbial crusts develop over corals in growth position and coral clasts. Alternations between encrusting coral and microbial crusts are observed at centimetric scale to form a first loose framework (sheetstone growth fabric). Coral skeletons are commonly affected by bioerosion.

In the Divača mound corals might represent up to ~30% of the bioconstruction. Colonies are small, centimetric in width (less than 10 cm) and corals have moderate generic/low specific diversities (13 genera, 15 species) (Fig. 9). The dominant morphologies are represented by plocoid and cerioid encrusting, thin platy and massive low-relief colonies. Dendroid and phaceloid forms are less abundant but widespread throughout the bioconstruction. Some of the most common species are the massive *Goniopora elegans* (Leymerie, 1846) and *Astrocoenia gibbosa* Duncan 1880, the encrusting *Astreopora esperanzae* Frost and Langenheim 1974, *Stylocoenia neutra* Barta-Calmus 1973, and *Actinacis cognata* Oppenheim 1901. Other very common encrusting forms include the tiny, cateniform *Bacarella vipavica* Turnšek 2004, described for the first time in Turnšek and Košir (2004), and the reptoid *Rhizangia padricensis* Turnšek 1998, described for the first time in Turnšek and Drobne (1998). Dendroid and phaceloid colonies are mainly represented by *Dendrophyllia candelabrum* Hennig 1899, and *Oculina conferta* Milne Edwards and Haime 1850. Colonies and fragments of *Madracis sp.* Milne Edwards and Haime 1849, *Oculina becki* (Nielsen, 1922), *Pachygyra savii* (d'Achiardi, 1866), *Plocophyllia carstica* Turnšek 1988, and *Litharaea sp.* Milne Edwards and Haime 1851 have been also observed.

In the Čebulovica mounds corals seem to be less abundant, and less diverse, compared to the Divača mound, even if these features might be artifacts due to a more spaced sampling. Corals represent ~20% of the mounds and are mainly represented by the *Actinacis cognata, Astreopora esperanzae, Bacarella vipavica, Rhizangia padricensis*, and *Stylocoenia neutra* associated with *Dendrophyllia* spp., and *Oculina conferta*.

6.2. Micro-encrusters

Micro-encrusters, mainly foraminifera, directly encrust the coral surfaces forming discontinuous coatings, up to 2 cm thick, complex

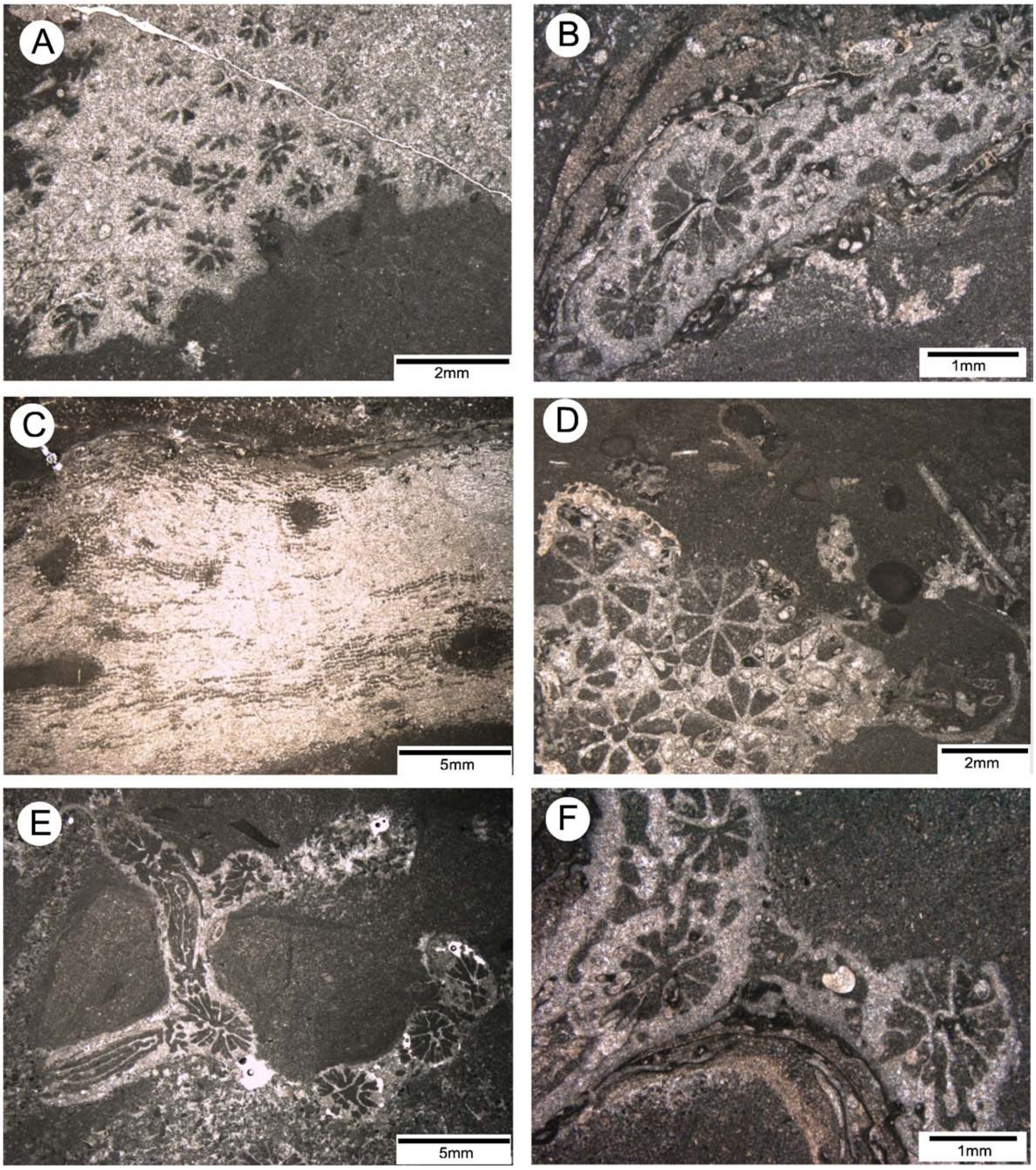

Fig. 9. Coral assemblage. (A) *Stylocoenia neutra* Barta-Calmus 1973. (B) *Astreopora esperanzae* Frost and Langenheim 1974. Note the acervulinid encrustation. (C) *Actinacis cognata* Oppenheim, 1901. Note macroborings. (D) *Astrocoenia gibbosa* Duncan, 1880. *Planorbulina* specimen on the top left of the coral colony. (E) *Oculina becki* (Nielsen, 1922). (F) *Rhizangia padricensis* Tunšek, 1998.

encrustations, with *Acervulina* and *Haddonia* associated with *Miniacina, Planorbulina*, and nubeculariids as the most common forms (Fig. 9B–D–F). Calcareous red algae, subordinated compared to the foraminifera, are represented by melobesioids, which form very thin (less than 500 μm), discontinuous veneer around corals. These encrustations are usually not bored pointing to a rapid overgrowth by microbialites. Other, less frequent micro-encrusters are bryozoans, calcareous sponges and serpulids. Encrusters are generally excluded during the prominent microbialite growth.

6.3. Macrofauna

The macrofaunal biota (excluded corals) is generally a subordinated component (an average of ~10%) represented by small calcareous sponges, delicate branching bryozoans, thin shelled bivalves, small gastropods, and echinoderms (rare skeletal elements of crinoids and more commonly echinoid spines and fragments). Locally, tiny spicules of sponges have been observed. Small benthic foraminifera are few and represented by rotaliids associated with very rare miliolids and textulariids. Larger benthic foraminifera are scarce and represented by small, flattened specimens of *Discocyclina* and *Assilina*.

6.4. Mound matrix

The microbialites, corals, and micro-encrusters together contribute to form a sort of mound framework. Primary growth cavities in the mounds are filled, together with microbialites, by allochthonous and reworked sediments forming the mound matrix. This matrix is represented by wackestones to packstones with fine, abraded

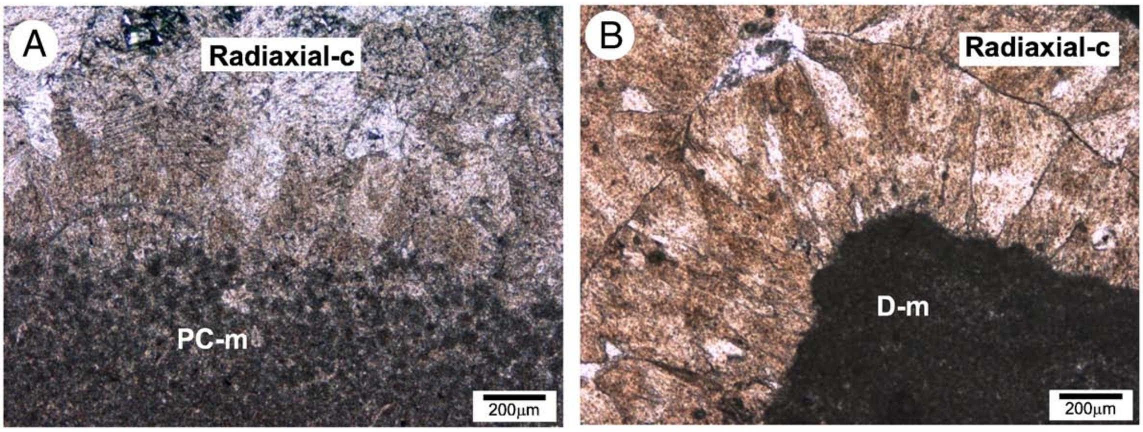

Fig. 10. (A) Radiaxial-fibrous calcite embedding peloids and nucleated directly on the microbial substrate with peloidal microfabric. (B) Isopachous rim of radiaxial-fibrous calcite nucleated directly on dense microbial substrate. D-m: Dense micrite; PC-m: Peloidal/Clotted micrite; Radiaxial-c; radiaxial calcite.

fragments of calcareous red algae (corallines, peyssonneliaceans and fragments of *Distichoplax biseralis* (Dietrich) Pia), micritized grains, small foraminifera, and fine debris. Locally larger benthic foraminifera (*Assilina azilensis* Tambareau, *Assilina yvettae* Schaub, and *Discocyclina seunesi* Douvillé) and other small benthic foraminifera can be also accumulated (Fig. 7D). This mound matrix passes to the microbial crusts through sharp contacts, although often it seems to grade and be incorporated into the microbial crusts, forming agglutinated fabrics.

6.5. Cements

Locally, millimetric to centimetric-thick, isopachous rims of brownish, inclusion-rich radiaxial-fibrous calcite have been observed to fill cavities of irregular shape, growth cavities or to alternate with microbial crusts. The transition from the peloidal micrite of the microbialites to the radiaxial-fibrous calcite rims can be gradual, with peloids embedded in the calcite crystals (Fig. 10A) or sharp, marked by an undulate surface (Fig. 10B). This relationship provides a further argument for the early lithification of the microbialites.

7. Lateral and overlying skeletal deposits associated with the mounds

The Divača mound grades laterally into wackestones/floatstones. These are characterized by fine bioclastic debris and thin foralgal crusts, mainly of peyssonneliacean algae *Polystrata alba* (Pfender) Denizot associated with acervulinids and bryozoans. Coral fragments can occur, often encrusted by acervulinids. Small benthic foraminifera (mainly rotaliids) and rare larger foraminifera (small/flattened *Discocyclina* specimens) form an assemblage comparable to the Orthophragminids-dominated assemblage in the Čebulovica section (cf. Zamagni et al., 2008). Locally, angular fragments of microbial crusts are resedimented.

The Divača mound is abruptly overlain by stratified foralgal packstones (Fig. 3A–B), which rest over a hardground surface marking the top of the mound. This surface is characterized by borings filled by the overlying deposits, indicating an early lithification for the mound. These deposits belong to the upper member of the Trstelj Fm. (Foralgal Facies, *Assilina*-dominated assemblage, cf. Zamagni et al., 2008), Latest Thanetian in age (SBZ 4). The packstones are dominated by perforate foraminifera, mainly *Assilina*, associated with less common small/ovate *Discocyclina* and rare big miliolids. Calcareous red algae occur as fragments, crusts and nodules with melobesioids and peyssonneliaceans as dominant forms. Echinoid fragments are abundant.

The Čebulovica mounds are vertically alternated with the packstones and wackestones of the Foralgal Facies of the Trstelj Fm. (Zamagni et al., 2008) (Fig. 3C). The comparison with the Divača mound suggests that the Čebulovica mounds represent either a superposition of several incipient mounds overlain by the foralgal facies or a lateral mound facies representing a transition between the mound core and the lateral deposits. The packstones and wackestones alternating with the incipient mound facies contain bioclasts that are generally angular and associated with abundant and irregularly distributed micrite. The bioclasts show widespread micritization and the development of constructive micrite envelopes (see Perry, 1999) pointing to an intense colonization by microbial organisms, promoting the stabilization of these sediments (Hillgärtner et al., 2001). Locally, the isoorientation of the foraminiferal tests and their distribution resemble tubular tempestites (see Tedesco and Wanless, 1991). These structures have been observed especially in the bioclastic packstones dominated by *Assilina*.

These features would suggest that the skeletal deposits overlying the Divača mound and the packstones alternating in the Čebulovica mounds accumulated under the influence of periodical storms or bottom currents affecting the mid-ramp and redistributing material from the inner/upper–mid-ramp towards the distal part of the ramp (Zamagni et al., 2008).

8. Discussion

8.1. Coral and microbialite growth rates and their roles in the mound development

Microbial growth rates are relatively low in comparison to that of Recent colonial corals, with microbialite largely restricted to cryptic habitats in modern reefs (e.g. Webb, 2001). Microbial precipitates can become prominent components of a bioconstruction where environmental conditions produce a slower coral growth rate, like in the case of deep-water reef mounds (e.g., Sun and Wright, 1989). Considering the microbial carbonate accretion rates reported in literature from marine settings, it is possible to establish a range from 1–2 mm/yr for the stromatolite/thrombolite complex on Stocking Island, Bahamas (Macintyre et al., 1996) up to 8 mm/yr calculated by Montaggioni and Camoin (1993) for stromatolitic crusts within a coralgal reef in Tahiti. These accretion rate estimates slightly overlap the growth rate of scleractinians living in moderately deep waters, even if they are on average slower. Growth rates of some modern zooxanthellate scleractinian corals from the Caribbean, reported by Dullo (2005), clearly show a decrease with increasing water depth. The Caribbean *Porites* shows an annual growth rate in the order of 10 mm/yr in shallow-water regions, dropping to 4 mm/y in deeper-water settings and 2.3 mm/yr at 30 m depth in Jamaica. *Montastrea* from deep water (45 m depth) of Jamaica is characterized by a very slow growth rate of 1.6 mm/yr.

In addition to water depth, changes in water quality may further decrease coral growth rates. Episodic increases of nutrient/turbidity levels might reduce the coral growth rates and directly or indirectly favoring partial to complete mortality by bacterial infestation, disease and suffocation (Hallock, 1987; Thacker and Paul, 2001; Hallock, 2005; Ritson-Williams et al., 2005; Smith et al., 2006, 2008). The development of discontinuous stromatolitic crusts on the upper surface of platy corals might be an indication for the presence of local bacterial infestation affecting living corals; alternatively microbes could have used only dead part of the colonies as substrate. In both cases the deterioration of water quality in terms of coral requirements might have been the cause of coral demise with the microbe spreading as consequence. This change of dominant bioconstructors from corals to microbes could be interpreted in terms of “phase shift” (see Done, 1992 for definition) related to environmental degradation. Today the rapid overgrowth of degraded reef corals by algae (e.g., McCook, 1999) and other cnidarians (e.g., Work et al., 2008) is a phenomenon observed in regions where a combination of factors related to human activity (e.g., overfishing, eutrophication) strongly reduces the cover of living corals. Nonetheless, it remains an intriguing issue whether the new invaders are responsible for coral death or if they just colonize dead coral surface. In the case of the studied mounds, the widespread bioerosion affecting coral skeleton, prior to major thrombolite encrustation points to nutrient pressure (e.g., Hallock, 1988) already affecting corals, and likely limiting their growth capacity.

The widespread development of microbialitic crusts in open, not confined environments, associated with complex intergrowth with corals, indicates that the microbialites and corals might have had comparable growth rates, thus competing for space. The dominance of encrusting, flat forms and low-relief massive coral colonies suggests the necessity to optimize light catchment. This would point to growth in the oligophotic zone, implying a general slow coral growth rate due to a less vigorous photosynthetic activity. Additionally, the coral assemblage shows features which indicate a general tolerance to turbidity pressure with small corallites and plocoid- (e.g. *Actinacis*) cerioid (e.g., *Goniopora*) colonies common (Sanders and Baron-Szabo, 2005). Nonetheless, episodic increases in turbidity/nutrient levels might have affected these corals strongly reducing their growth rates, and promoting the thrombolite development.

Further observations suggest that environmental “disturbances” were rather episodic than continuous. Based on the dimensions of the coral colonies (max. 6/7 cm) we can speculate that their growth periods might have duration of few decades assuming slow growth rate of 1–2 mm/yr. This would explain the pioneer stage of the coral community in these mounds. They occur as disoriented and more-or-less fragmented colonies, with any ecological zonation within the bioconstructions, possibly as consequence of a shorter time interval of disturbance compared to the time needed for full community recovery. Actually, both in fossil and recent records frequently disturbed coral communities appear as rubble piles and/or mounds instead of coral reefs (Sanders and Baron-Szabo, 2005 and therein references).

8.2. Micro-encruster assemblage and macrofauna

The study of the encruster assemblages combined with their association to specific microbialite types has been used largely and successfully applied for paleoenvironmental reconstructions (e.g., Upper Jurassic reefs: Leinfelder et al., 1993; Dupraz and Strasser, 1999). Two major groups of encrusters provide useful hints for a general discussion: encrusting foraminifera and coralline algae. Both encrusting foraminifera, and to a less extend red algae, are common in the coral-microbial phases and absent in the thrombolite-dominated growth phases.

Foraminifera include common opportunist forms with acervulinids and nubeculariids dominant, often overgrown by *Haddonia*. Modern counterparts of these encrusters are not associated with photosymbiotic endosymbionts (Reiss and Hottinger, 1984). Recent acervulinids are common in very shallow water, as cryptobionts, up to lower limit of the photic zone, likely due to the disappearance with depth of benthic diatoms, their food source (Reiss and Hottinger, 1984). Their constructional role is enhanced where light conditions reduce competition for substrate encrustation (Perrin, 1992). Modern species of the genus *Haddonia* live in shaded areas, indicating a sciaphile affinity (Matteucci, 1996). The widespread occurrence of these heterotrophic encrusters indicates suitable conditions in terms of food availability. The exclusion of encrusting foraminifera from the benthic thrombolites would suggest that conditions promoting fast microbial growth were preventing the development of other encrusters.

Coralline algae are present but clearly were not successful with respect to corals, microbialites, and encrusting foraminifera with a minimal binding function of in the framework construction. Coralline algae were important framework bioconstructors during the Late Paleocene (e.g. in the Pyrenees, Baceta et al., 2005) and experienced a diversification at that time (Aguirre et al., 2000). These facts exclude the possibility that the reduced presence of coralline algae was related to evolutionary processes. The presence of organisms adapted to normal marine-water conditions, first of all corals, precludes the possibility that the environment had not normal salinity or oxygen levels. Therefore, the reasons for the development of microbial and foraminiferal encrustations instead of corallines need to be further investigated. A similar, enigmatic situation occurred also in Upper Miocene coral-microbialite reefs from Southern Spain (e.g. Riding et al., 1991), where corallines have been excluded from the frame building and substituted by thick microbial crusts.

Among the macrofaunal components, the larger benthic foraminifera are few and represented by *Assilina* and *Discocyclina* genera. At present, *Assilina* thrives in the lower photic zone on soft, muddy sediments, with *Assilina ammonoides* able to tolerate eutrophication events (e.g. Lacadive Islands; Langer and Hottinger, 2000). Macrofaunal elements other than larger foraminifera and corals are represented by grazers and filter-feeders (echinoids, gastropods, bivalves, bryozoans, and calcareous sponges). Their presence indicates adequate nutrient concentrations to sustain this fauna. Bioerosion is quite well developed as testified by the widespread occurrence of macroborings in coral skeletons.

Based on the weight of these evidences it is possible to reconstruct environmental conditions, during the growth of micro-encrusters and macrofauna, as characterized by oligophotic and mesotrophic nature. Thus, the exclusion of micro-encrusters during the massive growth of thrombolites might indicate enhanced concentration of nutrients to high mesotrophic to eutrophic levels promoting the fast microbial bloom.

8.3. Microbialite growth history

Repeated episodes of shifts from corals to microbialites produced the vertical superposition of several microbialite-coral growth units. The microbial crusts were lithified early, as revealed by the common occurrence of encrusting corals using microbialites as stable substrates, the presence in the lateral deposits of resedimented fragments of microbial crusts and the bored surface of the Divača mound at the contact with the overlain foralgal packstones. The presence of macroborings in thrombolites, further confirms an early lithification. The shift from one microbialite morphotype to another could have resulted from episodes of enhanced microbial calcification, changes in the morphology of microorganisms, fluctuations in the relative importance of microbial calcification respect to trapping of sediment. Furthermore, environmental changes related to nutrient/turbidity pressure might have promote changes in the trophic structure, leading to a shift from phototrophic to heterotrophic nutritional modes

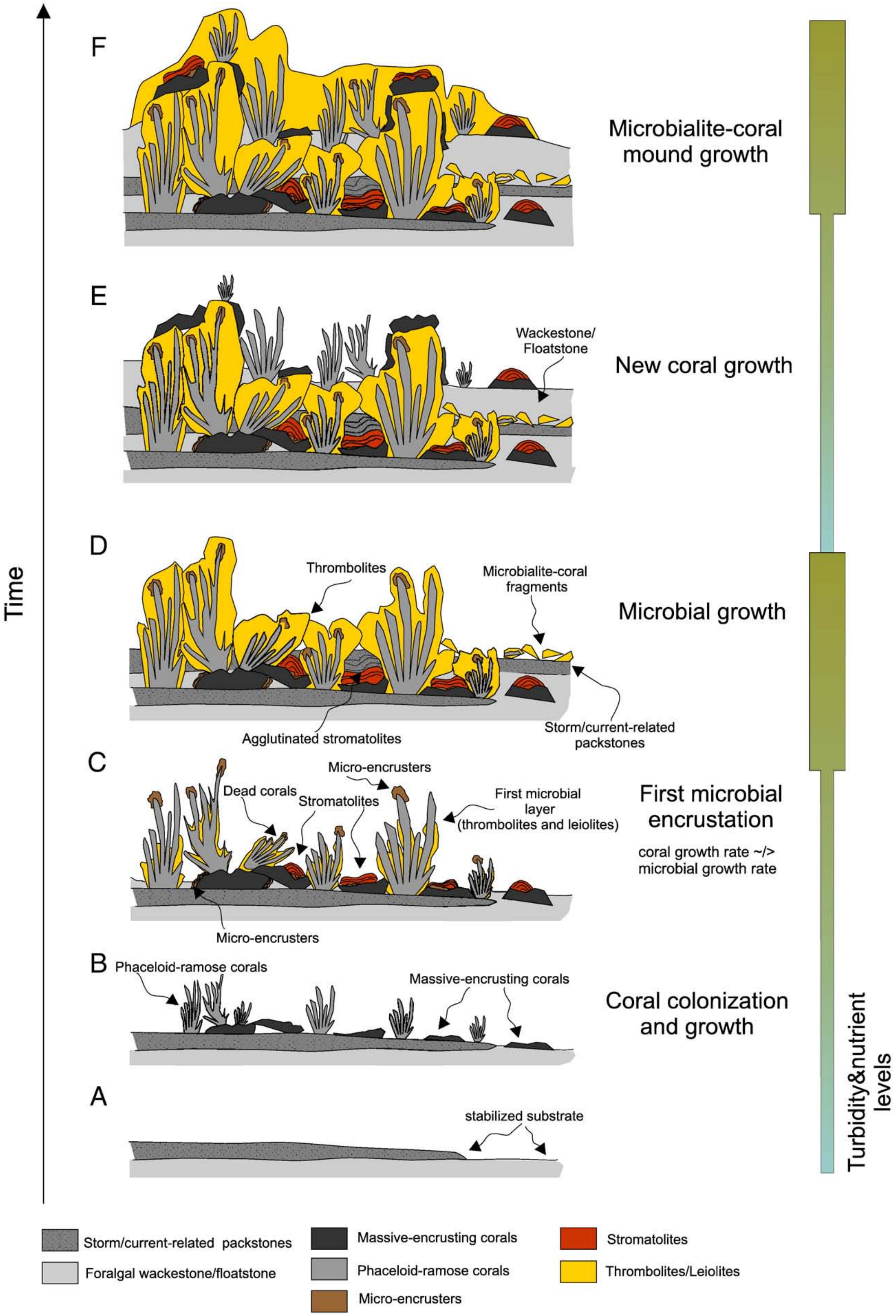

Fig. 11. Simplified model for the evolution in time of the mounds. See text for explanation.

(Hallock and Schlager, 1986; Dupraz and Strasser, 2002; Mutti and Hallock, 2003), associated with a change in microbe community and, thus microbialite fabrics.

Based on the geometric relationship between corals, microbial crusts, mound matrix, and bioclastic deposits associated with the mounds, and despite the complex growth pattern and transition between the different microbialite morphologies, a simplified model of development for the microbial crusts and for the mound bodies is tentatively reconstructed (Fig. 11):

(1) A first stage for the mound evolution was the development of a stable substrate. The bioclastic sediments occurring laterally to the Divača mound and vertically alternated with the Čebulovica mounds were deposited in the distal mid ramp under the periodical influence of storms and bottom currents. The widespread micritization of the bioclasts and the development of constructive micrite envelopes suggest an intense activity of microendolithic organisms immediately after deposition of the bioclastic deposits. In conditions of low accumulation rate, as likely was during the deposition of these limestones, this process could have initiated the stabilization of the bioclastic deposits (Hillgärtner et al., 2001), thus proving an initial substrate for coral colonization (Fig. 11A).

(2) After the early stabilization of the substrate, the mound growth initiated with coral colonization and a first generation of micro-encrusters. During this phase, first structureless, cryptic microbialites (leiolitic and thrombolitic crusts) and planar to domal stromatolites were growing. The growth of these crusts probably started on platy corals, from which they extend laterally to connect coral colonies contributing to the formation of a first framework (Fig. 11B–C). At this time the coral and microbialite growth rates were comparable, with corals being slightly faster. The development of the microbial crusts during this phase was confined to cavities within the framework and likely dead part of the coral colonies, as suggested by the later discontinuity of the stromatolitic crusts. The environmental conditions at this time were of low–moderate turbidity, low mesotrophic condition and low sedimentation rate, as inferred by stromatolite crust morphologies, mainly planar and domal, with steep-sided form almost absent (Dupraz et al., 2006) and flat encrusting and low-surface relief massive coral colonies dominant (Sanders and Baron-Szabo, 2005).

(3) Changes in the environmental parameters, with temporal increase of nutrient availability and turbidity caused a shift to high mesotrophic–eutrophic conditions, with thrombolites taking on the building role (Fig. 11D). The sediment accumulation was probably still low, and did not prevent the thrombolite growth, with sediments likely by-passing the mounds (Larcombe et al., 2001), but still causing increase of nutrient levels and high turbidity. The state of preservation of the corals, with widespread macroborings, and common coral fragments embedded into thrombolites, indicates a shift to heterotrophic nutritional mode, with high bioerosion rate, coupled with reduced coral growth rates in highly turbiditic conditions, which favored the thrombolite growth. Thus, the blooming of microbialites was probably not the cause of the coral demise, but the consequence, with corals likely dead at the time of thrombolitic encrustation. The shift from corals to thrombolites was therefore an environmentally-driven process, resulting in change of the trophic structure at micro- and macroscale from phototrophic to heterotrophic, with demise of corals and stromatolites substituted by thrombolites.

(4) After a period of recovery with lowering of turbidity/nutrient levels, during which bioeroders are still active producing macroborings on the thrombolites, a new colonization of the lithified microbialite substrate by corals and micro-encrusters occurred (Fig. 11E) leading to the further growth of the mound (Fig. 11F).

8.4. Main factors controlling microbialite-coral growth and mound development as related to local and global climatic events

Physico-chemical properties of the environment control and eventually promote microbial accretion processes (e.g., Neuweiler, 1993; Riding, 2000). Thus, climate, paleogeographic configuration, and their impact on water physico-chemical features such as alkalinity, pO_2, salinity, nutrient/terrigenous influx, and sedimentation rate are the most important extrinsic factors controlling the development of microbially-induced precipitates. The studied carbonates were deposited along the marginal areas of the large, isolated Adriatic Carbonate Platform (paleolatitudes ~32°N), locally subaerially exposed since the Late Cretaceous (Vlahovič et al., 2005). During the Thanetian, the Tethyan realm was affected by a general warm, humid, subtropical climate (Bolle and Adatte, 2001; Lourens et al., 2005; Pearson et al., 2007). At mid-latitudes, a more pronounced seasonality was developed, with warm climate characterized by alternation of wet and dry seasons (Bolle et al., 2000; Schmitz and Andreasson, 2001; Egger et al., 2002; Schmitz and Pujalte, 2007). Durn et al. (2003) have reported from this area of Istria bauxites as well as paleokarsts indicating prevailing humid conditions which favored laterization processes.

Repeated brackish incursions are characteristic throughout the Thanetian in NW AdCP as testified by the presence of levels rich in ostracods, gastropods, characeans, and locally coal, alternated with fully marine deposits (Bignot, 1972). These evidences suggest the occurrence of wet periods, with increased runoff and development of brackish conditions. Dissolved compounds from rivers and groundwater discharges were likely mechanisms of nutrient delivery to the ramp during this time. The nutrients and particulates might have been redistributed along the ramp by currents promoting high mesotrophic conditions also at intermediate depths (mid ramp). Locally, intense phosphatization in the more proximal ramp was described (Jurkovšek et al., 1996).

Thus, fluctuating runoff due to repeated wet seasons could have been responsible for creating environmental instability inducing periodic changes in the nutrient pressure, turbidity level and delivery of alkaline waters (from the weathered AdCP). These conditions might have favored the growth of small coral colonies alternated to that of benthic microbialites, causing a shift in the nutritional mode from phototrophic to heterotrophic and thus favoring a phase shift of dominant mound biota.

The inferred intensification of wet periods during the Late Thanetian, based on the study of these microbialite-coral mounds, would fit with the general climatic evolution in the Tethys. In fact, based on clay mineral studies (e.g., Bolle et al., 2000), seasonal and drier conditions during the Early Paleocene shifted to extreme humid and warm climate at the Paleocene-Eocene boundary, concomitant with the Paleocene-Eocene Thermal Maximum event (PETM, Zachos et al., 2001). A global eutrophication of surface waters in marginal seas, close to this event was recognized (e.g., Crouch et al., 2001), with the *Apectodinium* dinoflagellate acme coinciding with the PETM (Crouch et al., 2003), and occasional *Apectodinium* pulses just before the PETM (Sluijs et al., 2007). Geochemical proxies further sustain an increase of sea-surface productivity (sapropelitic sediments and biogenic barium, Schmitz et al., 1997; Speijer et al., 1997; Bains et al., 2000; Gavrilov et al., 2003). Concerning the northern margin of Tethys, Egger et al. (2002) suggested that well before the Paleocene–Eocene boundary, the high rates of precipitation caused an increase in continental runoff and associated nutrients delivery favoring enhanced productivity in surface waters.

The growth of these microbially-cemented bioconstructions, considered until now to be virtually absent during the Early Paleogene (Webb, 1996), shed new light for the interpretation of paleoenvironmental conditions in shallow-water realms, during a time of rapidly changing climate, leading to the extreme, super-greenhouse conditions of the PETM.

9. Conclusions

- The study of the microbialite-coral mounds, from the NE margin of the AdCP (SW Slovenia, 32°N paleolatitudes), offers a unique opportunity to document extensive microbially-cemented bioconstructions, developed during the Latest Thanetian (Latest Paleocene).
- The mounds are mainly composed of: (a) microbially-precipitated micrite, sparite and microsparite forming early lithified crusts with accretionary, binding and encrusting growth forms, and gravity-defying morphologies (up to 70% of the mounds); (b) moderately diversified coral community (15 species; usually small plate-shaped colonies); (c) micro-encrusters (especially encrusting foraminifera); (d) mound matrix composed by foralgal wackestones to packstones.
- Microbialites show different mesofabric types with common, centimetric-thick stromatolites, usually occurring on top of platy corals; and leiolites forming discontinuous veneers on top of corals and cryptic sites and thrombolites encrusting coral colonies and other mound components. Corals and micro-encrusters, including cryptic leiolite/thrombolites and stromatolites on top of corals, form the first framework. A second encrustation with the development of thick thrombolites marks the phase shift in dominant biota, from phototrophic to heterotrophic dominated nutritional mode. This shift is interpreted as environmentally-driven, with increase of nutrient pressure and turbidity weakening the coral growth and turning microbes as main bioconstructors.
- Combination of extrinsic parameters (favorable physico–chemical properties of the seawater related to warm, subtropical climate), worked together with intrinsic factors, (coral autoecology and biostrategic interrelationship between the microbial and coral communities), to form these microbialite-coral mounds. Repeated increases of nutrients/turbidity, and input of alkaline waters linked to enhanced weathering and runoff during the wet periods generated environmental instability reducing the growth rate of corals and turning microbial accretion as the prominent process responsible for the mound construction and stabilization. The occurrence of repeated wet periods during the Late Thanetian in this part of the Tethys might have represented the prelude to the extremely humid and warm conditions developed during the super-greenhouse PETM event.

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