

Markus Reuter · Thomas C. Brachert ·
Karsten F. Kroeger

Diagenesis of growth bands in fossil scleractinian corals: identification and modes of preservation

Received: 10 January 2005 / Accepted: 22 April 2005 / Published online: 6 September 2005
© Springer-Verlag 2005

Abstract Light and dark bands in fully recrystallized fossil hermatypic corals are generally interpreted to represent annual growth increments reflecting a photosymbiotic life style—an interpretation of far reaching significance in palaeoecology. In this paper we describe annual growth bands in the colonial coral *Porites* in a perfect (aragonite and microstructures retained) and fully recrystallized (sparry calcite mosaic) style of preservation from sediments of Late Miocene age (Crete, Greece). Analysis of a continuous spectrum of transitional preservational stages shows that in Miocene *Porites* preservation of the growth banding was controlled by preferential dissolution of the high-density band associated with cementation by drusy calcite spar during freshwater diagenesis/shallow burial diagenesis. Marine precipitates (pelletoidal Mg-calcite) preferentially accumulated along tabulate dissepiments producing an additional growth rhythmicity. Massive *Porites* had annual growth rates of ~4.0 mm, whereas in ramose branching *Porites*, a conspicuous banding is formed by concentrations of marine micropelletoidal cement along dissepiments at ~1.8 mm spacing. If taken as annual growth increments, these bands represent very low extension rates, however, they may rather reflect subannual forcing functions (i.e., lunar cycles). An identical scenario of precipitation and concentration of pelletoidal carbonate along dissepiments and dissolution-controlled documentation of growth bands can be inferred for Late Jurassic microsolenids. Therefore, growth bandings in fossil corals potentially reflect both, monthly and annual cycles. Consequently, care must be taken when using coral growth bands in palaeoecology and palaeoclimatology.

Keywords Growth bands · Coral diagenesis · Late Miocene · Jurassic · Greece · Germany

Introduction

The massive skeletons of colonial corals represent high-resolution archives of past sea surface temperatures, salinity, and productivity (Grottoli 2001). The coral record has therefore proven to be an important source of information to study seasonality and climatic oscillations on interannual to interdecadal timescales in historic and prehistoric time (Druffel 1997). However, the coral skeletons are susceptible to mineralogical and geochemical alteration, and corals older than Pleistocene are frequently recrystallized and transformed from original aragonite into secondary calcite (Constantz 1986; Dullo 1986; Dullo and Mehl 1989; McGregor and Gagan 2003). Nonetheless, conspicuous light–dark banding couplets are commonly present in many Cenozoic and Mesozoic hermatypic corals such as *Porites* and *Thamnasteria*, *Isastrea*, *Fungiastrea*, or *Microsolena*. Although fully recrystallized and cemented, general agreement exists that the banding visible in these corals reflects annual growth cyclicity. These banding patterns have been in wide use for estimates of carbonate production and reconstructions of climatic gradients during the Jurassic (Geister 1989; Insalaco 1996; Nose 1999). The presence of growth bands interpreted as annual density bands has been taken to suggest that the Triassic constructional coral *Ceriodictya variabilis* was already a photosymbiotic zooxanthellate coral (Helmle and Stanley 2003).

Paradoxically, couplets of light and dark bands interpreted to reflect annual growth increments are conspicuous in recrystallized skeletons, both visible on weathered surfaces and polished slabs, whereas in fresh materials from modern reefs, the growth bands remain mostly invisible and require radiographs for proper documentation. This circumstance raises the question of the origin and significance of the distinct bandings in fossil corals. In this paper, we describe banding patterns in colonial *Porites* from the Late Miocene of the island of Crete (Eastern Mediterranean

M. Reuter (✉) · T. C. Brachert · K. F. Kroeger
Institut für Geowissenschaften, Johannes Gutenberg-Universität
Mainz,
Becherweg 21,
55099 Mainz, Germany
e-mail: M.Reuter@geo.uni-mainz.de
Tel.: +06131-3924306
Fax: +06131-3924768

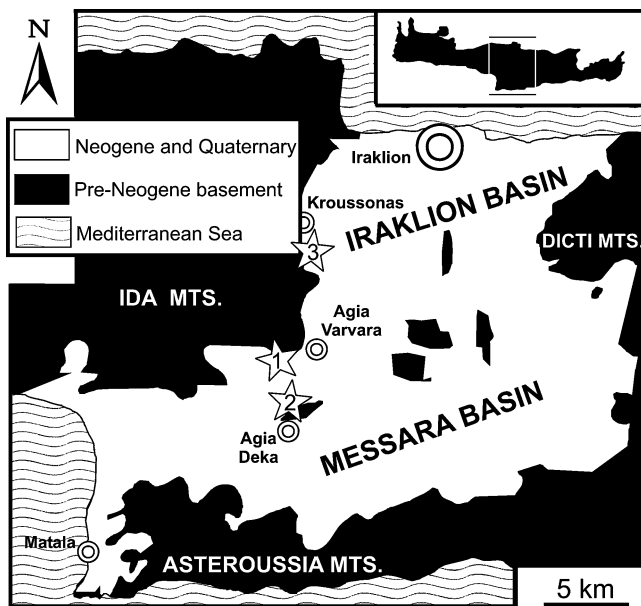


Fig. 1 Location of coral sites (asterisks) in central Crete, Greece. 1: Apomarma, 2: Psalidha, 3: Moni Gorgolaini

Sea; Fig. 1). Some of the skeletons have fully retained their original aragonite mineralogy and microstructures, whereas others are transformed into secondary calcite and fully cemented. Documentation of transitions from unchanged to altered *Porites* allows to identify annual growth bands and the mechanism of how they have been produced in recrystallized skeletons. The style of the banding, however, is not peculiar to the poritid skeletal architecture (Miocene), and exists also in microsolenid corals (Jurassic). In this paper we describe the pathway of diagenetic alteration and demonstrate two principal mechanisms of how growth bands get recorded in recrystallized skeletons. The preservation of annual growth bands strongly depends on the preferential dissolution of the high-density band during freshwater or shallow burial diagenesis. A second type of growth rhythm originates from concentrations of marine micropelletoidal cements along tabulate dissepiments. The latter potentially formed on a lunar basis, both in Cenozoic and Mesozoic hermatypic corals, and therefore give an example of the potential pitfalls when interpreting growth rates of corals for the purpose of palaeoclimatology and palaeoecology.

Material and methods

We sampled *Porites* corals with massive and branching growth forms in different stages of alteration from Upper Miocene sections in central Crete (Figs. 1, 2): corals with the original aragonite skeleton preserved derive from the top of Psalidha coral buildup (Ambelousos Formation, northwestern Messara Basin; Fig. 2a), whereas partially recrystallized massive *Porites* skeletons (coral fragments) were taken from a debris flow deposit (Varvara Formation, Western Iraklion Basin, Moni Gorgolaini locality;

Fig. 2c), and totally recrystallized massive *Porites* colonies were sampled from lower segments of Psalidha buildup and patch reef localities in the area of Kroussonas (Pirgos Member, Western Iraklion Basin; Fig. 1). Recrystallized *Porites* branches originate from a *Porites* biostrome with dense thicket framework (Ambelousos Formation, northwestern Messara Basin, Apomarma locality; Fig. 2b). Samples of microsolenid corals were taken from the Korallenolith (Oxfordian, Hainholz-Member), NW-Germany (Hainholz quarry; see Helm et al. 2003 for details of location).

Fragile aragonite coral skeletons were embedded in polyurethane foam in the field to prevent disintegration during transportation and splitting. Slabs and thin-sections were stained with Feigl's solution to reveal the distribution of aragonite and calcite. Radiographs from selected coral slabs (thickness 6 mm) were prepared at the Forschungszentrum Ozeanränder at Bremen University, Germany (T. Felis). Growth increments were measured parallel to the axis of maximum growth. In SEM view, broken and polished surfaces of the corals were analysed for ultrastructures. X-ray diffraction for the determination of aragonite and calcite was carried out at the Institut für Geowissenschaften, Mainz (H.-D. Werner) using a Seifert XRD 3000 diffractometer. Samples were scanned from 2θ of $20\text{--}60^\circ$. In all samples from aragonite corals, calcite concentrations remained below the detection limits of the method (1–2%).

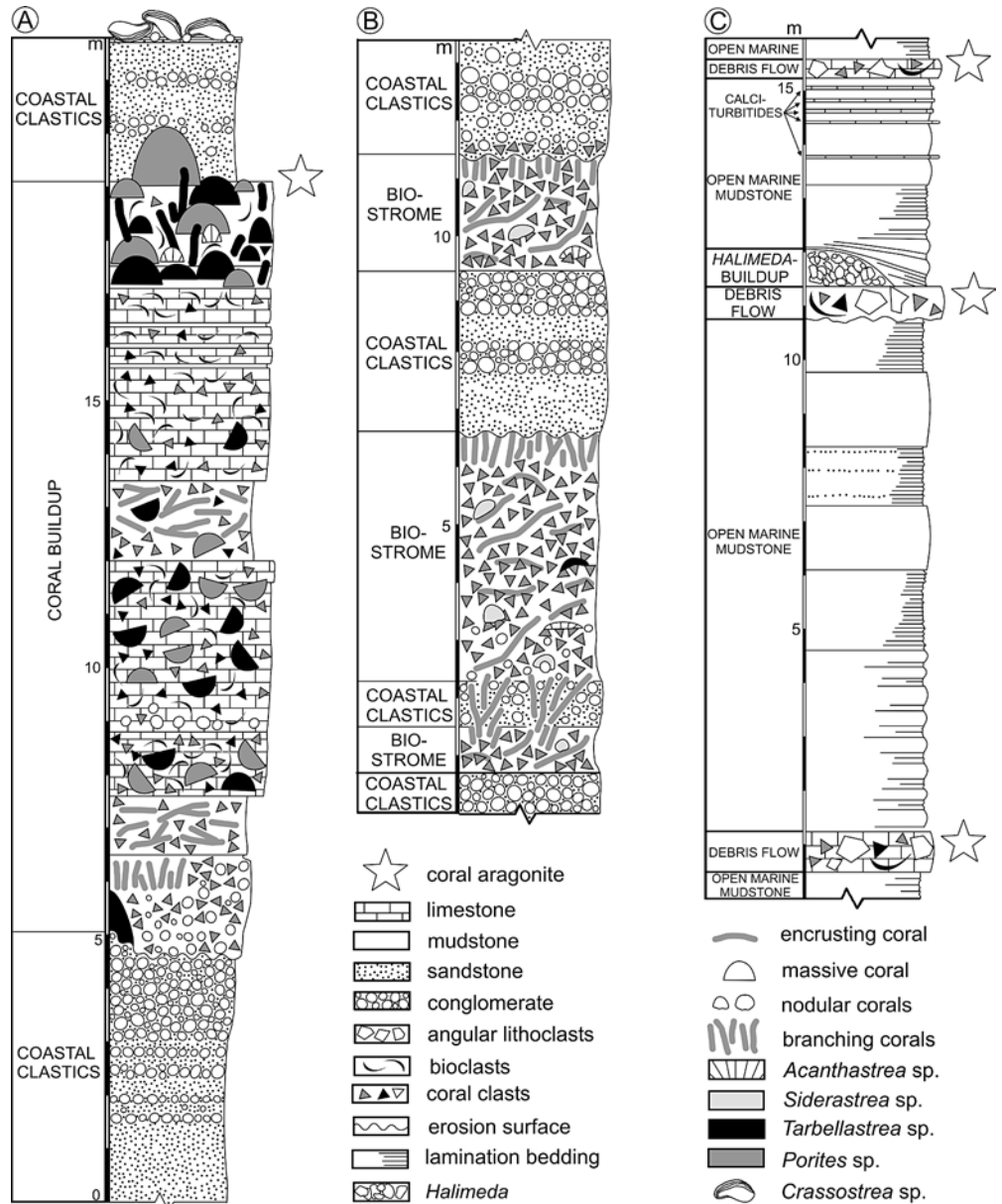
One aragonite coral specimen was selected according to visibility and thickness of the growth bands for stable isotope analysis (sample P1). Sampling was performed along a continuous transect following the growth axes of the colony. Stable isotope analysis was performed by M.M. Joachimski (Erlangen University, Germany). Carbonate powders were reacted with 100% phosphoric acid at 75°C using a Kiel III online carbonate preparation line connected to a ThermoFinnigan 252 mass spectrometer. All values are reported in per mil relative to V-PDB by assigning a $\delta^{13}\text{C}$ value of +1.95‰ and a $\delta^{18}\text{O}$ value of -2.20‰ to NBS19. Reproducibility was checked by replicate analysis of laboratory standards and is better than $\pm 0.03\%$ (1σ).

Results

Palaeogeographical setting of the island of Crete

The Late Miocene palaeogeography of the Mediterranean Sea was similar to the present-day situation: it formed a marginal sea of the Atlantic Ocean, which was not connected with the Indopacific. A sea strait temporally linked the eastern Mediterranean via the Aegean with the Paratethys epicontinental sea to the north of the Alpine orogen system (Rögl and Steininger 1984). In contrast to the present, extensive coral reef growth occurred almost everywhere in the Mediterranean area. This biogeographic pattern and the remarkably low diversity of reef corals is generally believed to reflect a warmer-than-present climate

Fig. 2 Geological sections of **a** Psalidha (N 35.08424°, E 024.96094°), Early Tortonian. **b** Apomarma (N 35.11252°, E 024.96398°), Early Tortonian. **c** Moni Gorgolaini (N 35.20535°, E 024.98190°), Early Messinian.



and a position of the Mediterranean area at the northern margin of the global coral reef belt (Brachert et al. 1996; Esteban 1996; Kroeger 2004).

The Late Miocene section of central Crete: distribution and preservation of corals

The Late Miocene section of central Crete starts with clastics of the Ambelousos Formation of Tortonian age (Meulenkamp et al. 1979). Depositional environments range from brackish lagoons to marginal marine environments. Coarse clastics formed along the coastline and were intermittently colonised by laterally extensive coral biostromes and patch reefs. Coral biostromes composed of large massive colonies of *Porites* and *Tarbellastrea* with minor contributions of *Acanthastrea* (Fig. 3a, d) developed during episodes of low terrigenous input, whereas thicket-like

coral biostromes constructed by ramose branching *Porites* formed during episodes of high siliciclastic influx (Fig. 3b). At a single locality in northwestern Messara Basin, a stack of biostromes (autobiostromes and parabiostromes, *sensu* Kershaw, 1994), constructed either by massive or by ramose branching corals form a coral buildup 15 m thick (Fig. 2A; Psalidha locality).

The sediments of the Ambelousos Formation are covered by marl and finely bedded calcareous mudstone of the Varvara Formation of Late Tortonian–Early Messinian age (Meulenkamp et al. 1979; Moissette et al. 1993). At the basin margin and on uplifted fault blocks, the Varvara Formation sediments grade into coralline algal/bryozoan bioclastic limestone of the Pirgos Member. Locally, the Pirgos Member is formed by small patch reefs formed by massive corals (*Porites*, *Tarbellastrea*) with minor contributions of branching *Porites*. In more distal settings, the

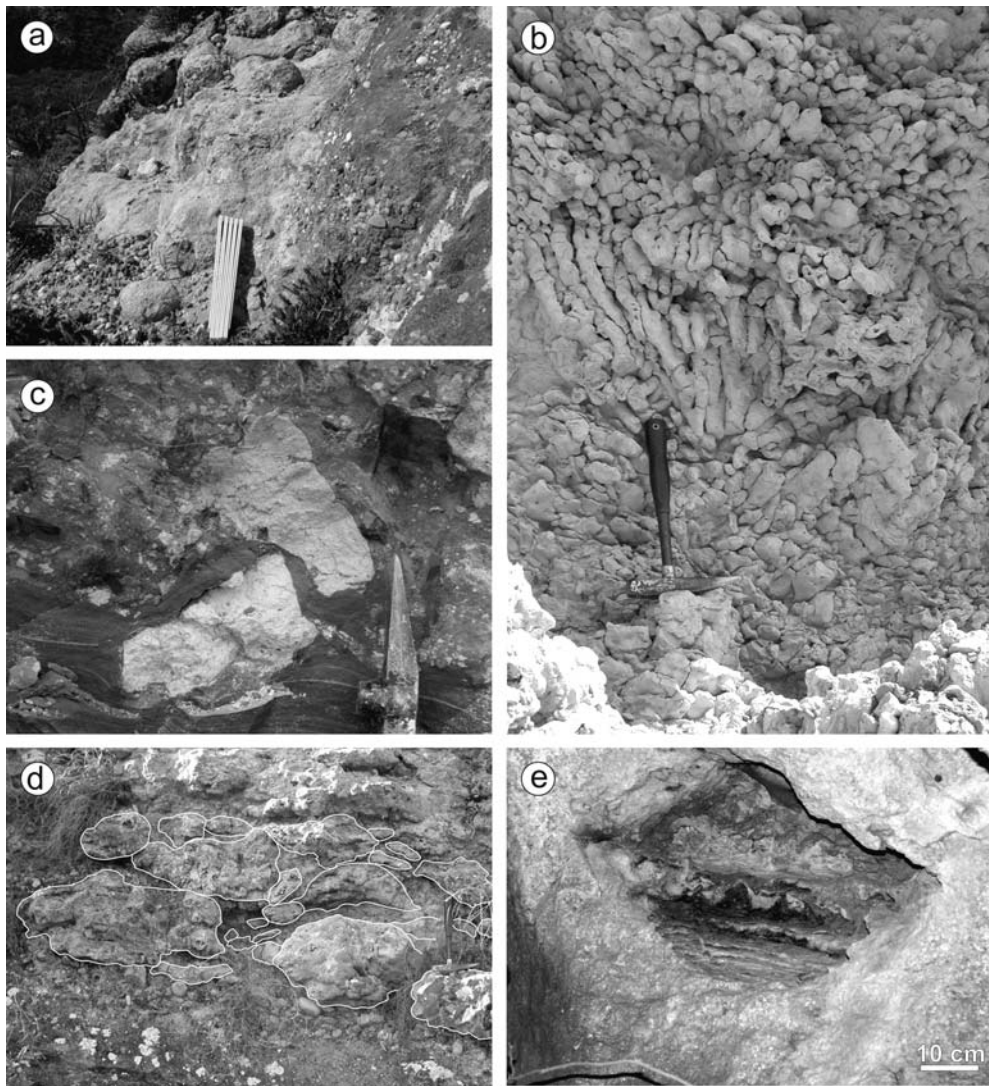


Fig. 3 Weathering aspect of massive and branching *Porites*, Late Miocene, central Crete. **a** The growth topography of the buildup is perfectly preserved by a drape of poorly classified sandstone and conglomerates. Psalidha, Early Tortonian. **b** Weathering aspect of a coral biostrome formed by interlocking branches of *Porites*. Psalidha, Early Tortonian. **c** Debris flow deposit with angular coral blocks (*Porites*).

Moni Gorgolaini, Early Messinian. **d** Coral carpet composed of massive colonies of *Porites* and *Tarbellastrea* with minor contribution of *Acanthastrea*; all fully recrystallized. Apomarma, Tortonian. **e** Mold formed after massive *Porites* colony in skeletal limestone, Agios Thomas, Late Tortonian

reefs are replaced by non-framework coral communities formed by large (> 1 m) massive *Porites* and *Tarbellastrea* colonies that are preserved as empty molds (Fig. 3e). The Pirgos Member is compositionally identical with calciturbidites and debrites with coral blocks intercalated with the laminated marl of the lower Varvara Formation (Fig. 3c). Some down-slope carbonate buildups formed by the green alga *Halimeda* vermetid gastropods and bryozoans exist in the Varvara Formation. The Late Miocene sequence ends with laminated gypsum that interfingers with the Varvara Formation mudstone and was deposited in distal parts of the basin only.

Rhythmic banding in Late Miocene *Porites* corals

Although preserved at various stages of transformation from aragonite into calcite, cementation, and recrystallization, all corals analysed show a rhythmic banding. In massive “aragonite corals” this banding is a representation of the annual growth bands, whereas in recrystallized corals the banding is either due to preferential dissolution of the high-density band (annual rhythmicity) or is an effect of micropelletoidal marine carbonate cement concentrated along tabulate dissepiments (monthly rhythmicity).

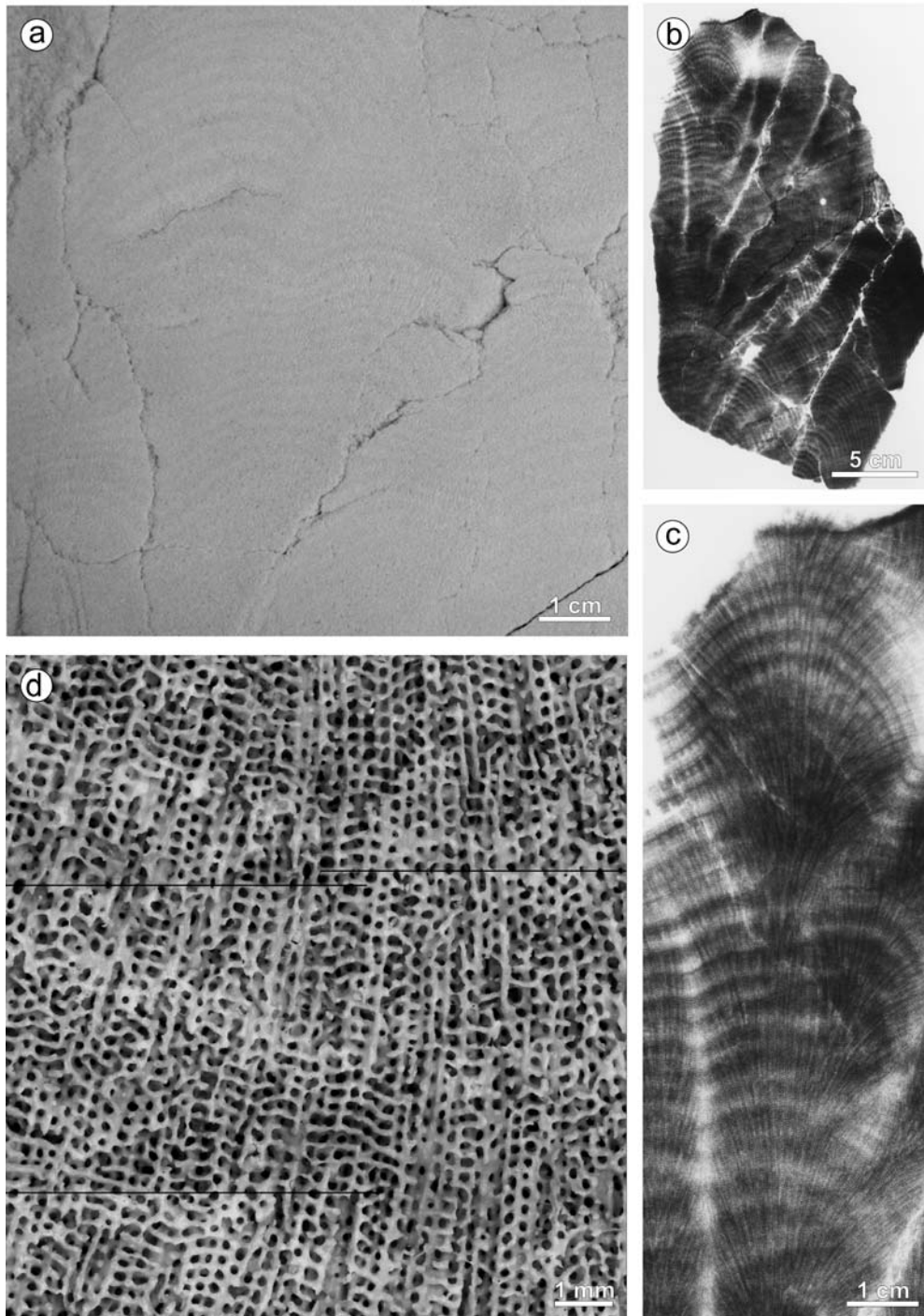


Fig. 4 Polished surfaces and X-ray radiographs from “aragonite *Porites*”. Psalidha, Early Tortonian. **a** Large fragment of a massive *Porites* showing couplets of “light” and “dark” bands. **b** X-ray radiograph (positive print) showing density bands and abundant fractures. Microcrystalline calcite in fractures appears dark in the radiograph. The skeleton immediately adjacent to the calcite veins remains un-

changed. A second system of fractures is still open and unfilled (white). **c** Close-up from **b** showing density banding. Contact zone of individual convex upward growth zones is X-ray transparent, which reflects reduced skeletonisation. Positive print. **d** Detailed view of coral slab showing couplets of “light” and “dark” bands

Banding in “aragonite corals”

The aragonitic coral skeletons were easily identified in the field by their conspicuous white color and very low weight due to retention of the original porosity. Slabs of

the massive aragonite *Porites* exhibit a faint banding on a millimeter scale (~ 4.0 mm). It is formed by alternating “light” (1–2 mm thickness), and thick “dark” laminae (2–5 mm thickness; Fig. 4a, d). The laminations reflect growth of the colony formed by laterally linked convex

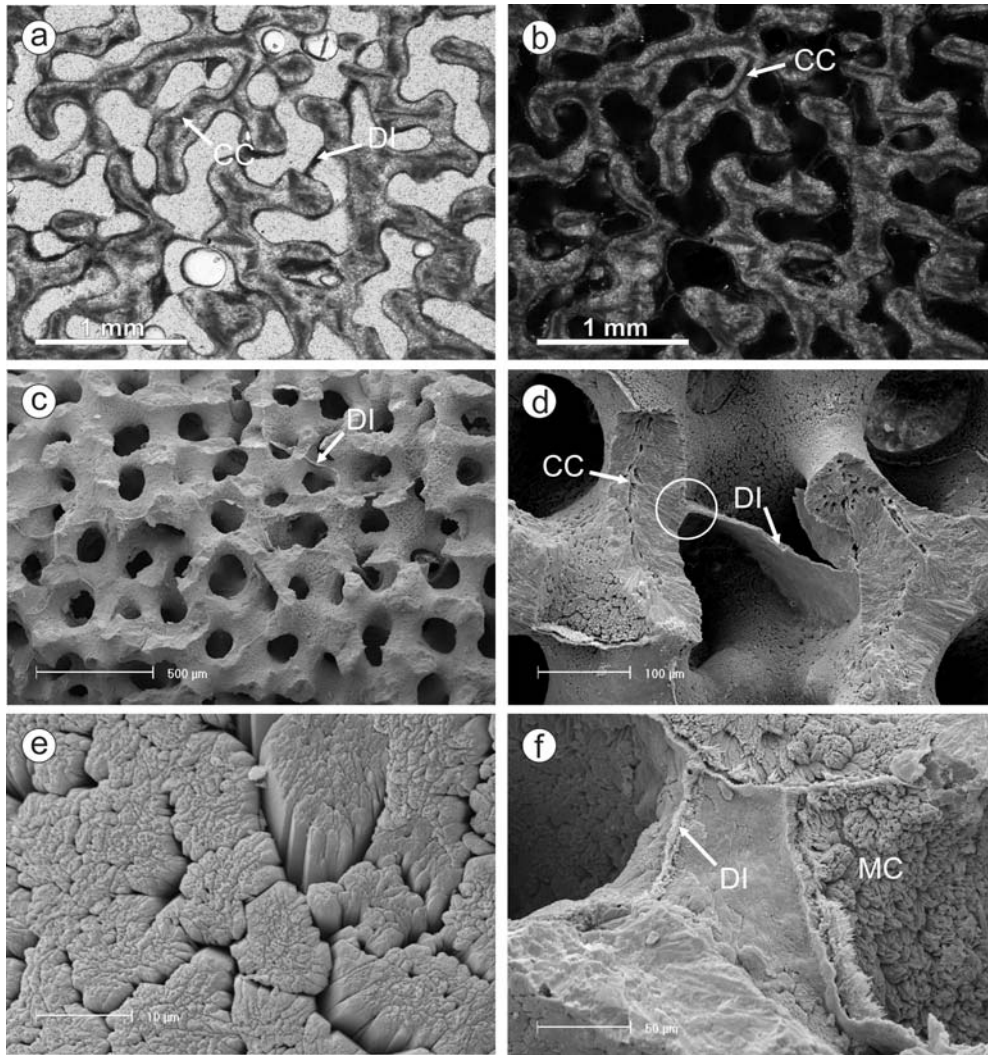


Fig. 5 Microscopic aspect of “aragonite corals”. Psalidha, Early Tortonian. **a** Thin-section view of the coral skeleton. Dissepiments (DI) forming meniscate bridges and the centers of calcification (CC) are clearly visible. Micrite envelopes cover most of the skeleton, but diagenetic overgrowths are volumetrically not significant. Bright circles represent air bubbles within epoxy resin. Plane light. **b** Same picture as in **a**, crossed nicols. **c** Overview of the pristine aragonite texture with well-preserved dissepiments (DI), SEM micrograph

from fresh fracture. **d** The skeleton formed of trabecular fans is well preserved; the centers of calcification (CC) are affected by some dissolution. The dissepiments (DI) form diaphragms in continuity with trabecular fans (circle). **e** SEM micrograph. **e** Smooth surface of the skeleton formed by blunt crystal terminations. **f** Dissepiments (DI) mark the boundary of smooth skeletal surfaces and surfaces covered by early marine cement (MC)

upward laminations. X-ray radiographs from coral slabs show a very prominent wavy banding, that is fully equivalent with density bands described from modern *Porites* (Knutson et al. 1972; Figs. 4b, c). Between individual areas of convex upward growth of the colony, a narrow zone of low X-ray density exists (Figs. 4b, c). Such a zone of low skeletonisation also exists in modern corals (Grigg 1982; Felis et al. 2004), which can be taken as an indication of the pristine state of preservation of the skeleton, because no later dissolution has occurred. The zone of low density is where most late fractures have formed. Some of the fractures have been filled with cryptocrystalline carbonate, whereas a second generation has remained open (Fig. 4b). However, the X-ray radiographs clearly show, that carbonate infills of fractures or weathering crusts do not extend into the skeleton.

In thin-section, the banding is hardly visible, however, as shown by (Pätzold 1984), the coral skeleton of the coenosteum and calyces is more massive in the high-density bands as compared to the low-density bands. In addition, the trabecular fans appear darker (i.e., more fine) in the “light” bands (“light” in reflected light) and tend to have central micritic linings and clots composed of smaller crystallites than within the “dark” bands (in reflected light; Fig. 5a, b). For the sake of consistency the terms “light” and “dark” bands always refers to the aspect of the corals in reflected light, although in thin-section the “light bands” appear dark, the “dark” bands light (Table 1). The micritic lining and clots represent the centers of calcification, however, according to their unusual large size in some bands, they must have been affected by recrystallization or dissolution (McGregor and Gagan 2003). Thus, the conspicuous banding visible

Table 1 Terminology used in this paper for growth bands in “aragonite corals”

Descriptive terminology	Aspect in reflected light	Aspect in transmitted light	Aspect on x-ray radiographs (positive)	Stable isotope composition	Interpretation
“light” band	high reflection (light)	dark	dark	positive $\delta^{18}\text{O}$, negative $\delta^{13}\text{C}$	“high-density band” cool and/or dry season
“dark” band	low reflection (dark)	light	light (X-ray transparent)	negative $\delta^{18}\text{O}$, positive $\delta^{13}\text{C}$	“low-density band” warm and/or wet season

in slabs and some thin-sections reflects incipient diagenetic alteration, which preferentially affected the bands appearing “light” in reflected light.

In SEM view, the radial trabecular fibers do not show significant signs of dissolution nor recrystallization (Figs. 5c–f). The surface of the skeleton is either smooth and formed by crystal aggregates with blunt crystal terminations (Fig. 5e), or ragged due to acute tips of trabecular fans and crystal aggregates (Fig. 5f). Both surface types have been found in a close spatial relationship and normally separated by thin meniscate bridges within the skeleton (Figs. 5d, f). In growth direction, the meniscate bridges exhibit a smooth upper and ragged lower surface due to tiny crystals (Fig. 5f). In direct contact with the coenosteum and calyces, the crystals of the meniscate bridges are in a clear structural continuity with trabecular fans (Fig. 5d). The microstructure of the meniscate bridges, therefore, reflects an original growth fabric (the dissepiment) and is not a secondary cement. In living corals, the dissepiments form along the lower surface of the calcioblastic tissue. We further conclude that smooth surfaces of the skeleton formed in contact with the calcioblastic tissue of the coral, and were not overgrown later by cement (Figs. 5e, f). However, syntaxial early marine cement overgrowths formed deeper in the coral, after withdrawal of the calcioblastic tissue from the skeleton during growth, forming the ragged undersides of the dissepiments and syntaxial cements of the deeper skeleton (Fig. 5f). All in all, these observations rule out the possibility of significant structural modifications of these skeletons during diagenesis.

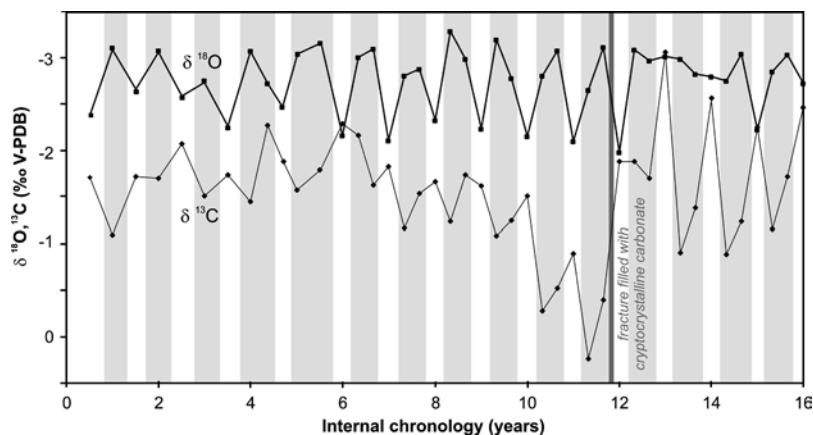
Stable isotopes of oxygen ($\delta^{18}\text{O}$ V-PDB) and carbon ($\delta^{13}\text{C}$ V-PDB) exhibit a mean composition of -2.76% and

-1.54% respectively. Both isotope systems exhibit a cyclic signal, which systematically reflects the growth bands. In $\delta^{18}\text{O}$, the high-density bands are more positive, at -2.0 to -2.5% , whereas the low-density bands are at -3% . The cyclic carbon isotope signatures ($\delta^{13}\text{C}$) are phase-shifted relative to $\delta^{18}\text{O}$: minima in (-2.0%) coincide with the high-density bands, whereas the maxima (0 to -1.0%) coincide with the low-density bands of the couplets. A sharp decrease in $\delta^{13}\text{C}$ occurs at ~ 13 years and synchronous with a distinct plateau in $\delta^{18}\text{O}$ (Fig. 6). From a compatible rhythmic $\delta^{18}\text{O}$ pattern in modern corals we infer that the thin high-density bands formed during the suboptimal season (winter), whereas the thick high-density bands during the optimal season (summer). Rosenfeld et al. (2003) also found that the phase shift of the carbon and oxygen isotope cycles common to many modern corals can be referred to seasonal changes in photosynthesis, i.e., less photosynthesis in winter. The highly consistent relationship of growth banding and isotope variations documents seasonal growth and is evidence of a pristine state of preservation, because diagenesis tends to homogenize isotopic compositions (McGregor and Gagan 2003). Consequently, the marked decrease in $\delta^{13}\text{C}$ at ~ 13 years (internal chronology) and the rather negative plateau in $\delta^{18}\text{O}$ can be considered the expression of diagenetic alteration of the skeleton related to a small fracture.

Banding in recrystallized corals

The vast majority of corals from the Ambelousos and Varvara Formations are leached (Fig. 3e) or transformed into

Fig. 6 Stable isotope record ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, V-PDB) resolved for the density bands of a massive *Porites*. The oxygen isotope signal shows a pronounced plateau at 13–15 years related to diagenetic alteration of the skeleton extending from a small fracture. Grey bars mark the “dark” bands (= summer) of the annual couplets. Sample P1, Psalidha locality, Early Tortonian



coarse blocky calcite (Fig. 3b, d). This is the typical state of preservation of zooxanthellate corals from Neogene sediments (Martín et al. 1989; Brachert et al. 2001). In the aragonite corals from the Psalidha outcrop, skeletons with a perfectly preserved outer zone (50–100 cm) may coexist with a fully recrystallized nucleus along a narrow chalky zone (10 mm). Beyond this zone, the original aragonite textures of the coral skeleton have been entirely transformed into calcite spar and/or empty voids. Adjacent to the chalky zone, original intraskeletal void space of the coral skeleton is filled with coarse blocky calcite spar (size 100–150 μm). Thin-sections stained with Feigl's solution reveal that fiber-shaped aragonite relicts of the skeleton (trabecular fibers) may be present preferentially along the periphery of the skeletal elements, whereas centers represent open voids formed by dissolution (Fig. 7a). Leaching, therefore, started along the centers of calcification and continued to form a hollow canal system within the skeleton (Figs. 7b, c). However, in a submillimetric spatial relationship, no aragonite may be left over from dissolution leaving irregular empty skeletal molds with no documentation of the skeleton. These voids are elongate bands (1–2 mm thickness) being a perfect reflection of the growth fabrics, where the skeleton has been preferentially destroyed by dissolution (Fig. 8). The pattern of centrifugal dissolution observed in thin-section has been confirmed by SEM observation. In specimens impregnated with epoxy resin, some skeletal void space has been cemented by sparry calcite spar prior to final dissolution of the last aragonite relicts (Figs. 7b, c). In this instance, collapse of the skeleton weakened by dissolution (Fig. 7b) implies that both, skeletal molds and intraskeletal porosity remained unfilled prior to cementation by blocky spar. In a last stage after cementation, residual aragonite fibers were dissolved (Figs. 7b, c). However, the skeleton is not uniformly preserved or documented as ghost in calcite spar.

Ramose corals show additional, alternative growth rhythms. Polished slabs exhibit stacks of convex upward light and dark bands formed of micrite and sparry calcite, or crescent-shaped empty voids. The micritic bands peripherally merge with an outer micritic envelope (few millimetres wide) which reflects the general growth form of the colonies. The convex micritic bands are laterally discontinuous and tend to become progressively thinner toward the centre of the colonies, which may be formed entirely of sparry calcite, or may even exhibit an open void lined by blocky calcite cement (Figs. 9a–d). Although, according to staining experiments of thin-sections with Feigl's solution, no original aragonite is left, the architecture of the skeleton is clearly visible in the outer zones, because it is fully encased in micrite (Figs. 9c–e). The clear banding results from intercalations of micrite and micro-pelletoidal carbonate, which show a clear cut base and an irregular top (Figs. 9a–b). The pelletoidal layers tend to become thinner inward (Figs. 9a, c), because the fine-grained carbonate may have filtered into the skeleton as a sediment (Fig. 9e) or may have formed as a micropelletoidal cement (Fig. 9b; cf. Macintyre 1977; Lighty 1985; Macintyre 1985). The structure of the skeleton may be enhanced

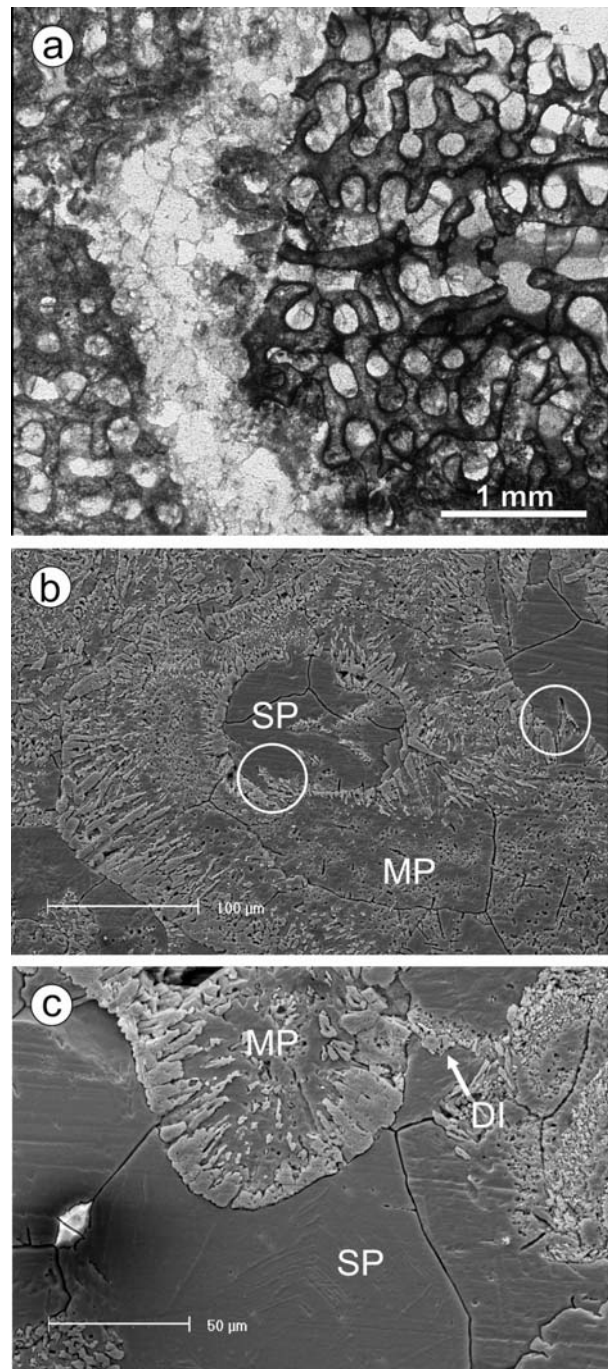


Fig. 7 Microscopic aspect of recrystallized massive *Porites*. Psalidha, Early Tortonian. **a** Thin-section micrograph. To the left of a veinlet, the skeleton is fully transformed into blocky calcite spar. Intraskeletal porosity is sealed by blocky calcite cement leaving ghost structures of the original skeleton. To the right of the veinlet, the skeleton shows the same type of preservation, however, relicts of the original aragonite exist at the periphery of the skeleton as visible by the black stain of Feigl's solution. Crossed nicols. **b–c** SEM micrograph of recrystallized skeleton impregnated with epoxy resin (polished surface etched with dilute HCl). Blocky calcite spar seals skeletal porosity (SP) and molds (MP) formed by solution enlargement of the centers of calcification. Light grey fibrous elements tracing relicts of the skeleton and dissepiments (DI) represent molds filled by epoxy resin. Mechanical compaction of the skeleton took place prior to cementation by calcite cement (white circles)

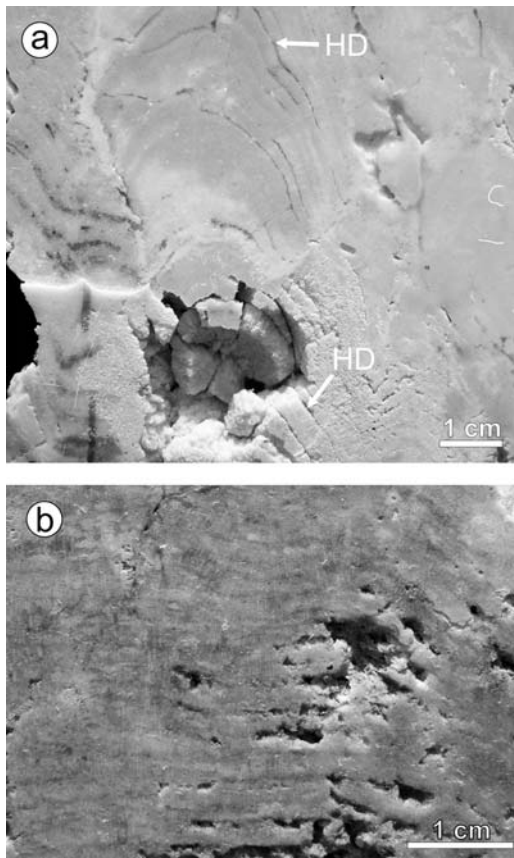


Fig. 8 Polished slabs of massive *Porites*. **a** Narrow, sheet-like empty voids (HD) resulting from preferential dissolution of the “light” bands. Moni Gorgolaini area, Late Tortonian–Messinian. **b** Ghost structures of growth bands in a fully recrystallized *Porites* result from preferential dissolution and cementation of elongate void spaces interpreted to represent the original high-density bands. Agios Antonios reef, Kroussonas area, Tortonian

by thin micrite envelopes separating drusy granular spar formed within intraskeletal pore space and skeletal molds (Fig. 9b).

Discussion

Retention of the original aragonite

The “aragonite corals” show some conspicuous banding, which is clearly visible on radiographs from coral slabs (Fig. 4), and in stable isotope signatures (Fig. 6). It is identical to annual density bands known from modern *Porites* (Knutson et al. 1972). According to the isotopic composition of unaltered specimens (Fig. 6), these bands represent the high-density bands (Rosenfeld et al. 2003). “Aragonite *Porites*” were found to occur in two specific geological settings: (1) blocks in debris flow deposits embedded in marl (Moni Gorgolaini), or (2) along the top surface of Psalidha buildup. In the latter situation, corals protruding into poorly classified sandstone has retained the original aragonite mineralogy, whereas all aragonite fauna has been

dissolved and recrystallized in the well-drained carbonate mass below. From these observations we infer an inactive “stagnant” meteoric to shallow burial diagenetic environment with little/no pore water movement (*sensu* Longman 1980) for the zone of aragonite preservation (no dissolution and cementation). Isolated fragments of aragonite corals encased in gypsum have been described from the Fortuna Basin (SE-Spain). In this case, preservation of the original aragonite skeleton was suggested to result from its inclusion in evaporite minerals (Santisteban and Taberner 1983).

Origin of the banding in recrystallized *Porites*

Relicts of the original aragonite skeleton encased in calcite cement at various stages of destruction by dissolution imply that preservation of the skeleton must have been a function of a high rate of cementation versus a lower rate of dissolution of the original skeleton, and that dissolution and cementation took place largely at the same time. We will show that retention of growth bands in the overall recrystallized skeleton is controlled by two independent processes: (1) dissolution processes dominating over cementation in the freshwater phreatic diagenetic/shallow burial environment (Fig. 10) and/or (2) growth rhythms expressed by tabulate dissepiments and cryptocrystalline marine cements.

Growth banding in massive Porites related to dissolution processes

The skeleton of massive and branching *Porites* from coral buildups in central Crete are generally recrystallized and transformed into calcite. Preservation of the growth banding in these corals appears to follow a basic scheme related to dissolution. Dissolution started at centers of calcification within the trabecular network. Corals that are only moderately affected by diagenesis document a preferential dissolution of the light band, i.e., the high-density band (Fig. 8a). Elevated dissolution rates in the high-density bands as compared to the low-density bands is interpreted to be a consequence of the smaller crystal forming the “light” high-density band. Upon continual dissolution, many of the corals, therefore, display open, elongate voids left over from dissolution, which are parallel to the growth bands and more or less filled with calcite cement (Fig. 8b). The presence of a banding formed by dissolution loss of the high-density bands implies, that the first generation of micrite rims/micropelletoidal carbonate was not pervasive over the whole skeleton, and preservation of skeletal molds is a function of relative dissolution rates versus relative cementation rates in the marine and freshwater diagenetic environment (Fig. 10). Depending on the relative rate of cementation, the skeleton may be encased as a whole in a mosaic of sparry calcite (high relative cementation rate) or may be documented by stack of alternating couplets of voids skeletal

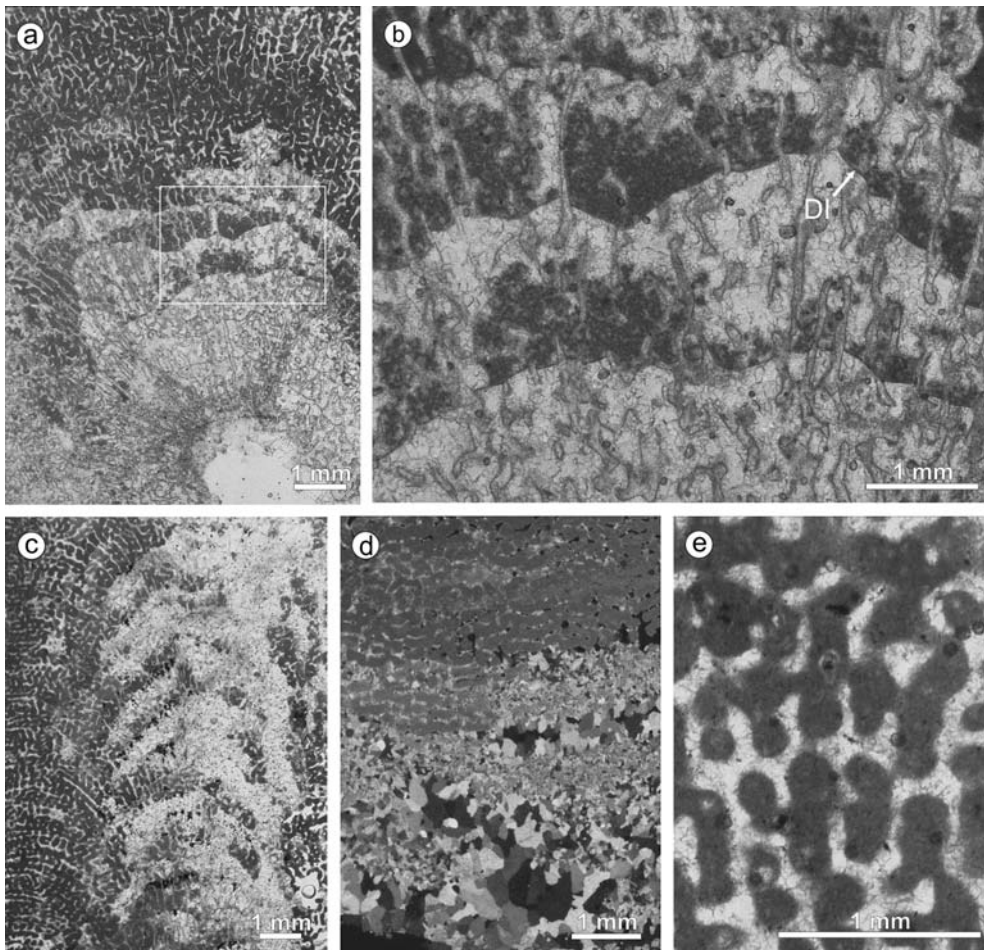


Fig. 9 Growth banding in recrystallized branching *Porites*. Apoparma outcrop, Tortonian. **a** Thin-section micrograph showing growth banding produced by alternating micropelletoidal micrite and sparry calcite cement. Intraskelatal void space at the periphery of the branch is filled with micrite (*upper margin of photograph*). The centre of the branch is formed by open void space (*lower margin of micrograph*). Plane light. **b** Close-up from Fig. 9a showing concentrations of micropelletoidal carbonate along tabulate dissepiments (DI). Thin section micrograph, plane light. **c** Longitudinal section of a branching *Porites* colony. Conspicuous ghost structures of growth banding are present within the centre of a branch. The growth bands

merge at the periphery of the branch to form a homogeneous layer. Thin-section micrograph, plane light. **d** Detail from peripheral zone of a *Porites* branch. Micrite occurs within the marginal intraskelatal void spaces only. Some segments of the skeleton are open void space (moldic porosity), preferentially along the outer surface of the colony (*upper margin of picture*). The centre of the branch (*lower half of picture*) is formed by a mosaic of anhedral calcite cement increasing in size toward the centre of the stick (drusy cement). Thin-section micrograph, crossed nicols. **e** Thin-section micrograph from peripheral zone of *Porites* branch. Skeleton replaced by drusy calcite spar. Plane light

layers filled by sparry calcite (Fig. 8b). The recrystallized corals exhibit ghost structures of the original skeleton (low relative rate of precipitation of calcite) formed by drusy calcite cement formed within molds of the original skeleton. Dissolution occurred through enlargement of the centers of calcification as evident from various stages of dissolution of aragonite and subsequent precipitation of blocky calcite. Prior to dissolution, the skeleton was encased in micrite envelopes or drusy calcite cement or a mixture of both to be preserved. In this scenario, the bands with ghosts represent the high-density bands. According to the type of cement formed (equant blocky spar), cementation took place in a freshwater phreatic/shallow burial environment (cf. Folk 1974; Longman 1980).

Central parts of coral colonies tend to be empty voids, because no fine-grained carbonate reached/formed in the

central segments of the colonies nor did any fibrous or blocky cements form within this zone before dissolution. Some segments of the moldic porosities were subsequently filled by blocky cement (Figs. 9a, d, 10).

Growth banding in ramose Porites controlled by dissepiments

In the more marginal zones of the colonies, infiltration of fine-grained sediment into the skeleton, or precipitation of pelletoidal cement was controlled and dammed by the presence of laterally continuous dissepiments (Figs. 9a–b). Marine microcrystalline carbonate occurs preferentially along the outer rims of the corals (Fig. 9c) or peripheral to bor-

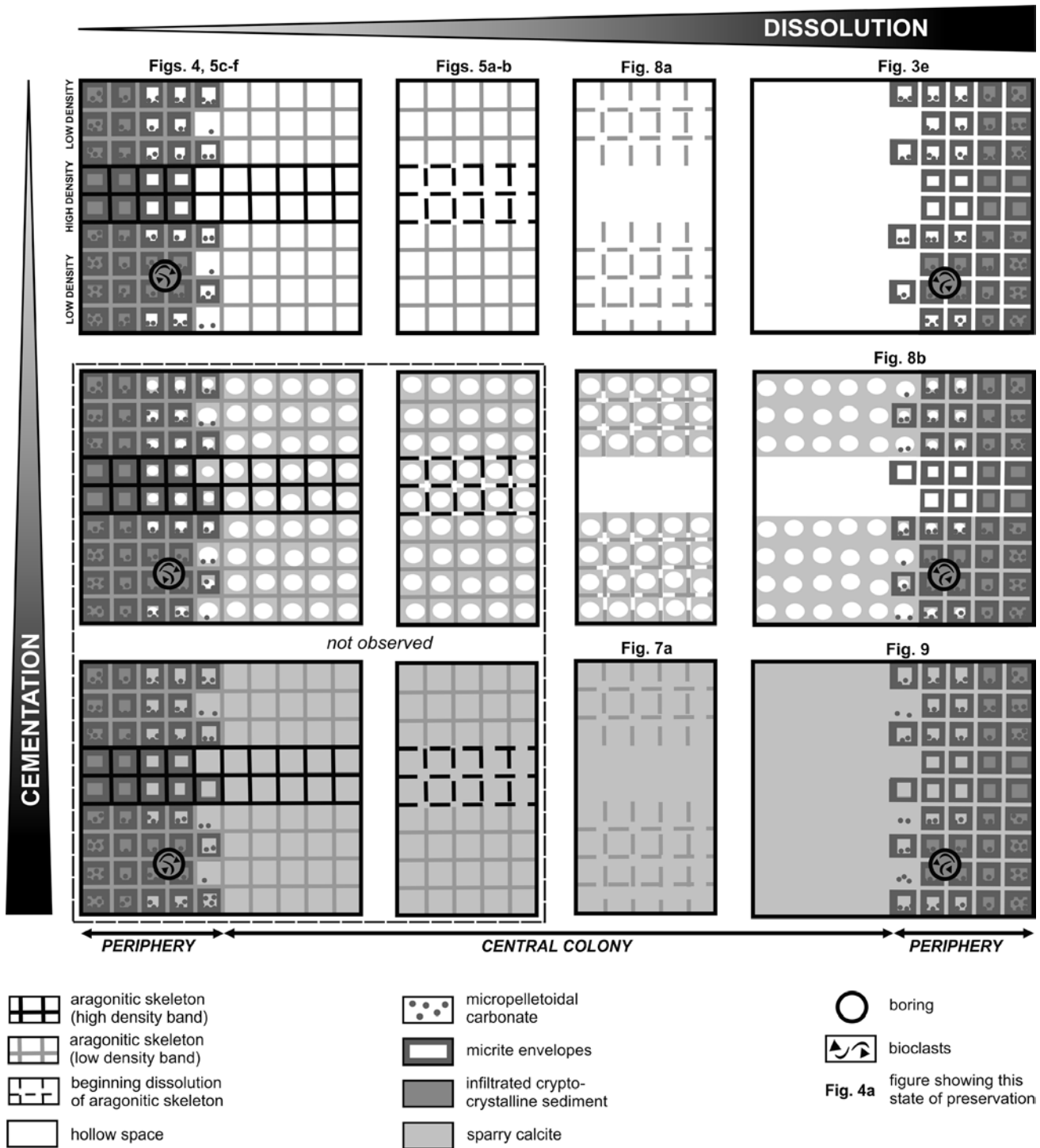


Fig. 10 Schematic representation of diagenetic pathways in *Porites* skeletons controlled by relative rates of dissolution and cementation in a freshwater/shallow burial environment. Marine sediment and

micropelletoidal cements preferentially occur at the margins of the colonies

ings and within discrete levels because connectivity of the intraskeletal porosity is partitioned by laterally continuous dissepiments (basal plates). Rhythmic changes of micropelletoidal carbonate and sparry calcite controlled by the presence of dissepiments must therefore mimic original growth increments. In modern *Porites* dissepiments form accord-

ing to lunar cycles (Barnes and Lough 1993; Cohen and Sohn 2004), which helps to explain the narrow spacings at ~1.8 mm. Nonetheless, the annual growth rates in ramose *Porites* remain difficult to reconstruct, because coral growth may have been strongly seasonal and, therefore, subannual, lunar cycles may have an incomplete record.

Banding in microsolenid corals (Jurassic)

Couplets of light and dark bands in Mesozoic corals are interpreted to represent annual growth bands described from various taxa, including the Triassic *Cerriostella* and the Jurassic genera *Microsolena*, *Isastrea*, and *Thamnasteria* (Ali 1984; Geister 1989; Insalaco 1996; Nose 1999). We have chosen microsolenid corals for comparison with *Porites*, because the complex 3D skeletal network of the microsolenids formed by confluent and porous septa, synapticulothecate corallites, and tabulate dissepiments has some general similarity with the poritid skeleton (Fig. 11).

The corals investigated form massive, head-like colonies. Polished slabs show conspicuous black, grey, and light grey patches and bands, which represent an almost perfect, but smaller, representation of the outer surface of the colonies (Fig. 11a). The conspicuous banding visible in polished slabs results from losses of skeletal documentation (black bands formed by mosaics of coarse calcite spar, no micrite linings present), from ghosts of the skeleton encased in fine drusy calcite spar (grey bands), and from elongate patches or bands made of micropelletoidal carbonate caught in the intraskeletal network along tabulate dissepiments (light grey bands; Fig. 11a). The thickness of individual light/dark couplets (<5 mm) and their lateral continuity, however, is highly variable, and tends to decrease outward. In thin-section view (Figs. 11b–c), the coral skeleton turns out to be fully transformed into calcite and no original aragonite is left. Thin micritic envelopes almost entirely cover the former skeleton, giving a perfect representation of skeletal architecture, including septa, synapticles, and dissepiments, whereas the skeleton itself is replaced by drusy equant spar. This calcite cement nucleated along both sides of the micrite envelope as a cement, on the outer surfaces and in voids left from dissolution of the entire skeleton. Wherever the linings are not present, no trace of the original skeleton is left in an overall mosaic of coarse blocky calcite, which appears black in polished slabs (Fig. 11a). Patches of cryptocrystalline carbonate preferentially occur along the outer margin of the colony and along borings or other discontinuities. They may fuse laterally to form bands parallel to the growth fabrics of the skeleton, which show a clear cut base and an irregular top, because the micropelletoidal carbonate accumulated along tabulate dissepiments (Figs. 11b–c). The cryptocrystalline carbonate accumulations represent early diagenetic precipitates of peloidal Mg-calcite (marine), because they do not contain any bioclasts and are fully equivalent with those described from modern scleractinian corals in terms of fabric and dimension (Lighty 1985; Macintyre 1985). In the microsolenid skeleton, we observed the most continuous accumulations of pelletoidal carbonate to occur immediately above bands formed of coarse blocky spar without traces of the skeleton (interpreted to represent the high-density band removed by dissolution) which further enhances the prominence of the banding. The reason for this rhythmic precipitation of marine cement remains obscure, however, it is tentatively suggested that it may correspond with a warmer water temperature during summer. In analogy to

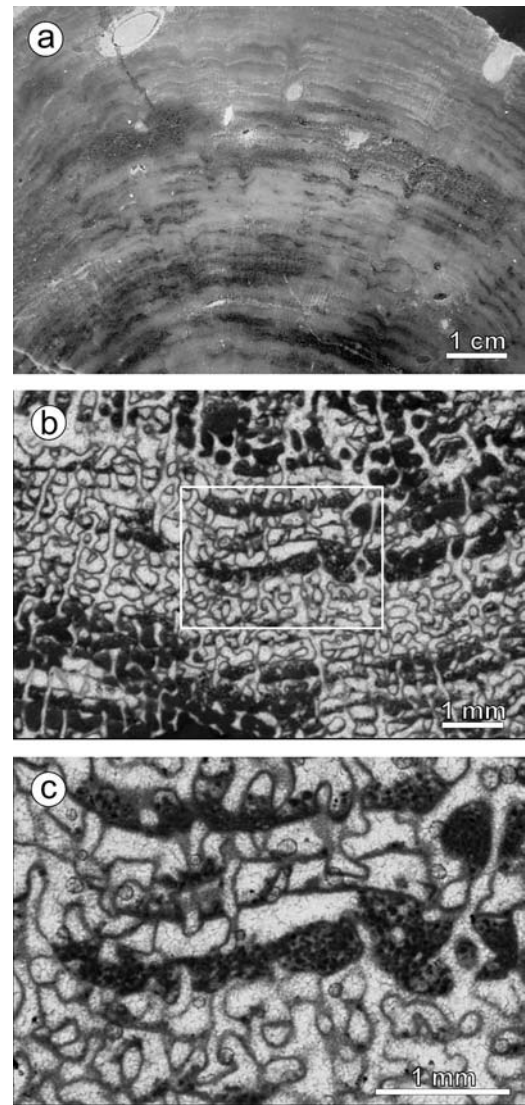


Fig. 11 Banding in a Late Jurassic microsolenid coral. Oxfordian, Hainholz Quarry, NW-Germany (see Helm et al. 2003 for location). **a** Polished slab. Dark bands with white spots are coarse blocky calcite. Ghost structures of the skeleton exist in the medium grey bands (fine blocky spar) and light grey bands (micropelletoidal carbonate). **b** Thin-section view (plane light) of a microsolenid coral. Subsequent to the formation of a micrite envelope, the original skeleton has been leached and replaced by equant spar. Micropelletoidal carbonate settled or formed within skeletal cavities; it preferentially accumulated along tabulate dissepiments. Thin-section micrograph, plane light. **c** Detail of **b**. Thin-section micrograph, plane light

the diagenetic scenario developed for Miocene *Porites*, the dark bands (reflected light) formed through preferential dissolution along discrete layers and subsequent cementation by coarse sparry calcite (no ghost structures preserved) represent the high-density band.

In other Jurassic corals (*Thamnasteria concinna*, *Fungiasrea arachnoides*, *Isastrea explanata*) Ali (1984) found that the banding results from alternating regions with thicker and more numerous skeletal elements (septa, dissepiments = high-density band), and regions of a thinner and less well-developed skeleton (septa, dissepiments

= low-density band). This vertical variation in skeletonization was suggested to have been enhanced by differential diagenesis leading to more intense recrystallization in high-density bands and less recrystallization in low-density bands, where relicts of the original skeleton are preferentially preserved in cryptocrystalline carbonate infilling intraskeletal void spaces (Ali 1984; Insalaco 1996). Although our study supports the earlier identifications of high and low-density bands, our observations obtained from various stages of diagenetic alteration in *Porites* show, that the banding is not an effect of more intense recrystallization of the high-density bands. We suggest, the high-density bands to have little preservation potential, because dissolution rate of the skeleton is enhanced when compared to the low-density band. Upon subsequent cementation, the skeleton may represent stacks of elongate dissolution voids (representing the high-density bands) filled by coarse blocky spar and bands formed by relicts of the skeleton encased in calcite spar (representing the low-density band).

Conclusions and implications

Coral limestone of Late Miocene age from the island of Crete (Greece) exhibits the typical pattern of preservation of the hermatypic coral skeleton: moldic porosity related to leaching of the original aragonite skeleton and partial or full replacement by sparry calcite cement. In some marl deposits and poorly classified sandstone/conglomerate, however, coral skeletons underwent no significant nonmarine diagenesis and, correspondingly, have fully retained their original mineralogy, microstructures, and porosity (stagnant diagenetic environment). Conspicuous couplets of “light” and “dark” bands in coral slabs represent annual growth increments because they are fully compatible with prominent density bands detected in X-ray photographs and stable isotope variations ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$). The conspicuous “light” and “dark” annual bands corals result from slight variations in skeletonisation and crystal size of the skeleton. In the active diagenetic environment, alteration and dissolution of the skeletons starts at the centers of calcification, however, at higher rates in the “light” bands (the high-density bands) because of the reduced crystal size. This process favors the formation of sheet-like voids, that reflect the growth bands. Where dissolution rates do not fully overcome cementation rates leading to formation of a large mold, annual banding in massive, recrystallized *Porites* may be preserved in the freshwater/shallow burial diagenetic environment. Thickness of the banding is equivalent to the “aragonite *Porites*” (~4 mm), which demonstrates the potential use of growth bands in palaeoclimatology and palaeoecology. For instance, vertical extension rates of few mm per year in massive *Porites* are known from high latitude reefs in modern oceans only, and appear to be typical for the periphery of the present global tropical reef belt (Grigg 1982; Lough and Barnes 2000). In terms of the Late Miocene palaeogeography, the Mediterranean area can be considered the outpost of the global coral reef

belt in the Northern Hemisphere (Esteban 1996). Branching *Porites* exhibit growth banding formed by concentrations of pelletoidal micrite along tabulate dissepiments. The narrow spacing of this type of banding (~1.8 mm) and its association with dissepiments implies the possibility of reflecting a subannual, lunar rhythmicity (Lough and Barnes 2000; Cohen and Sohn 2004). Estimates of vertical extension rates in fossil corals, therefore, require proper documentation of the high and low-density bands, whereas the existence of rhythmic growth bands alone is insufficient as to detect annual growth and a photosymbiotic lifestyle. Conspicuous, millimetric couplets of light and dark bands are also present in Mesozoic corals. In the microsolenid skeleton, we observed continuous accumulations of pelletoidal carbonate along dissepiments immediately above bands formed of coarse blocky spar (interpreted to represent the high-density band removed by dissolution). The prominent banding present in these massive corals results, therefore, from the superposition of monthly and annual growth rhythms. This interpretation agrees with the reconstructed high latitude position for the sampled Jurassic (Oxfordian) coral reef from NW-Germany (Lower Saxony basin), located at a transitional position between the warm Tethys and the temperate boreal faunal provinces during the Oxfordian (Helm et al. 2001).

Acknowledgements G. Fassoulas (Jraklion, Crete) and the Gergeri administration in central Crete (Rouvas) are thanked for their generous support during the recovery of the samples and for providing the working and export permits. K.-H. Münk (Mainz, Germany) facilitated the preparation of the coral slabs. Radiographs from coral slabs were prepared by T. Felis and his team (Bremen, Germany). X-ray diffraction analyses were carried out by H.-D. Werner (Mainz, Germany) and Thomas Griebemer (Mainz, Germany) supported the SEM work. Thomas Steuber (Bochum, Germany) and an anonymous reviewer helped to clarify our ideas. This work was funded by the Deutsche Forschungsgemeinschaft (DFG, Germany) through grant no. Br 1153/7.

References

- Ali OE (1984) Sclerochronology and carbonate production in some Upper Jurassic reef corals. *Palaeontology* 27:537–548
- Barnes DJ, Lough JM (1993) On the nature and causes of density banding in massive coral skeleton. *J Exp Mar Biol Ecol* 167:91–108
- Brachert TC, Betzler C, Braga JC, Martín JM (1996) Record of climatic change in neritic carbonates: Turnovers in biogenic associations and depositional modes (Upper Miocene, southern Spain). *Geol Rundsch* 85:327–337
- Brachert TC, Hultsch N, Knoerich AC, Krautworst UMR, Stückrad O (2001) Climatic signatures in shallow water carbonates: high-resolution stratigraphic correlation in structurally controlled carbonate buildups (Late Miocene, S-Spain). *Palaeogeogr Palaeoclimatol Palaeoecol* 175:211–237
- Cohen AL, Sohn RA (2004) Tidal modulation of Sr/Ca ratios in a Pacific coral. *Geophys Res Lett* 31:4
- Constantz BR (1986) The primary surface area of corals and variations in their susceptibility to diagenesis. In: Schroeder JH, Purser BH (eds) *Reef Diagenesis*. Springer, New York, pp 53–76
- Druffel ERM (1997) Geochemistry of corals: Proxies of past ocean chemistry, ocean circulation, and climate. *Proc Nat Acad Sci USA* 94:8354–8361

- Dullo W-Chr (1986) Variations in diagenetic sequences: and example from Pleistocene coral reefs, Red Sea, Saudi Arabia. In: Schroeder JH, Purser BH (eds) Reef Diagenesis. Springer, New York, pp 77–90
- Dullo W, Mehl J (1989) Seasonal growth lines in Pleistocene scleractinians from Barbados: record potential and diagenesis. *Paläont Z* 63:207–214
- Esteban M (1996) An overview of Miocene reefs from Mediterranean areas: General trends and facies models. In: Franseen EK, Esteban M, Ward WC, Rouchy J-M (eds) Models for carbonate stratigraphy from the Miocene reef complexes of Mediterranean regions. *SEPM, Concepts Sedimentol Paleontol* 5:3–54
- Felis T, Lohmann G, Kuhnert H, Lorenz SJ, Scholz D, Al-Rousan SA, Al-Moghabi SM (2004) Increased seasonality in Middle Eastern temperatures during the last interglacial period. *Nature* 429:164–168
- Folk RL (1974) The natural history of crystalline calcium carbonate: effect of magnesium content and salinity. *J Sediment Petrol* 44:40–53
- Geister J (1989) Quantitative aspects of coral growth and carbonate production in a Middle Jurassic reef. In: Jell PA, Pickett JW (eds) *Fossil Cnidaria* 5. *Ass Aust Paleont Mem* 8:425–432
- Grigg RW (1982) Darwin Point: a threshold for atoll formation. *Coral Reefs* 1:29–34
- Grottoli A (2001) Past climate from corals. In: Steele J, Thorpe S, Turekian K (eds) *Encyclopedia of ocean sciences*. University of Pennsylvania, Department of, Earth and Environment Science Philadelphia, pp 2098–2107
- Helm C, Schülke I, Fischer R (2001) Paläogeographie des Korallenooliths (Mittleres Oxfordium–Unteres Kimmeridgium): Tethyale Faunen- und Florenelemente auf höherer Paläobreite (Niedersächsisches Becken, NW-Deutschland). *Geor Beitr Hannover* 2:51–64
- Helm C, Reuter M, Schülke I (2003) Der Korallenoolith (Oberjura) im Osterwald (NW-Deutschland, Niedersächsisches Becken): fazielle Entwicklung und Ablagerungsdynamik. *Z Dt Geol Ges* 153:159–186
- Helmle KP, Stanley GD (2003) Oldest coral bands in the Triassic of North America and the evolution of photosynthesis. 9th Int Symp Fossil Cnidaria Porifera, pp 1–6
- Insalaco E (1996) The use of Late Jurassic coral growth bands as palaeoenvironmental indicators. *Palaeontology* 39:413–431
- Kershaw S (1994) Classification and geological significance of biostromes. *Facies* 31:81–92
- Knutson DW, Buddmeier RW, Smith SV (1972) Coral chronometers: seasonal growth bands in reef corals. *Science* 177:270–272
- Kroeger KF (2004) Sedimentary environments and climate change: a case study (late Miocene, central Crete). *Inst Geowiss, Johannes Gutenberg-Univ Mainz*
- Lighty RG (1985) Preservation of internal reef porosity and diagenetic sealing of submerged early Holocene barrier reef, southeast Florida shelf. *SEPM Spec Publ* 36:123–151
- Longman MA (1980) Carbonate diagenetic textures from nearsurface diagenetic environments. *AAPG Bull* 64:461–487
- Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *J Exp Mar Biol Ecol* 245:225–243
- Macintyre IG (1977) Distribution of submarine cements in a modern Caribbean fringing reef, Galeta Point, Panama. *J Sediment Petrol* 47:503–516
- Macintyre IG (1985) Submarine cements—the peloidal question. *SEPM Spec Publ* 36:109–116
- Martín JM, Braga JC, Rivas P (1989) Coral successions in Upper Tortonian reefs in SE Spain. *Lethaia* 22:271–286
- McGregor HV, Gagan MK (2003) Diagenesis and geochemistry of *Porites* corals from Papua New Guinea: implications for paleoclimate reconstruction. *Geochim Cosmochim Acta* 67:2147–2156
- Meulenkamp JE, Dermitzakis M, Georgiadou-Dikeoulia E, Jonkers HA, Böger H (1979) Field guide to the Neogene of Crete. *Publ Dept Geol Palaeont Univ Athens*
- Moisette P, Delrieu B, Tsagaris S (1993) Bryozoaires du bassin néogène d'Héraklion (Crète centrale, Grèce). *Le Miocène Supérieur: premiers résultats*. *N Jb Geol Paläont Abh* 190:75–123
- Nose M (1999) Environmental control on the morphology and the linear growth rate of *Microsolena agariciformis* Étallon (Scleractinia) from the Upper Jurassic of Portugal. *Profil* 16:125–133
- Pätzold J (1984) Growth rhythms recorded in stable isotopes and density bands in the reef coral *Porites lobata* (Cebu, Philippines). *Coral Reefs* 3:87–90
- Rögl F, Steininger F (1984) Neogene Paratethys, Mediterranean and Indo-Pacific seaways: Implications for the paleobiogeography of marine and terrestrial biotas. In: Brenchley P (ed) *Fossils and Climate*. Wiley, New York, pp 171–179
- Rosenfeld M, Yam R, Shemesh A, Loya Y (2003) Implication of water depth on stable isotope composition and skeletal density patterns in a *Porites lutea* colony: results from a long-term translocation experiment. *Coral Reefs* 22:337–345
- Santisteban C, Taberner C (1983) Shallow marine and continental conglomerates derived from coral reef complexes after desiccation of a deep marine basin: the Tortonian-Messinian deposits of the Fortuna basin, southeast Spain. *J Geol Soc Lond* 140:401–411