'Shingle' microstructure in scleractinian corals: a possible analogue for lamellar and microlamellar microstructure in Palaeozoic tabulate corals

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Abstract: The origin of lamellar-microlamellar microstructures in Paleozoic corals has been debated widely. Regularity and preservation with apparently well preserved fibrous microstructures suggest that the structures are biogenic, but non-fibrous, scale-like structures cannot be easily accommodated in biomineralization models of Scleractinia, the best modern analogues. However, acroporid scleractinian coral microstructure may provide an analogue for microlamellar-lamellar scales in Palaeozoic corals. We compared the microstructures of extant *Acropora* and the Mississippian tabulate coral *Michelinia meekana*. *Acropora* microstructure consists of aragonite fibers arranged in radiating trabeculae and in oblique bundles that are arranged in a low-relief, overlapping, shingle-like pattern. Individual 'shingles' range from 4–20 µm in width, 2–7 µm in thickness, and 20–150 µm in length. In ultra-thin sections *Acropora* shingles are similar in size and appearance to lamellae-microlamellae in certain Palaeozoic corals. Lamellar-microlamellar microstructure in *Michelinia meekana* consists of scales measuring 4–50 µm in diameter (in cross sections encountered in thin section) and 1.5–7 µm in thickness. The scales do not appear to be fibrous, but if the fibers in *Acropora* shingles were obscured by recrystallization, but shingles survived as recognizable units owing to the surrounding organic matrix, the resulting structures would be similar to lamellae-microlamellae. Hence, lamellar-microlamellar microstructures may have analogues in scleractinian corals, thereby supporting their fundamentally biogenic nature.

Key words: Scleractinia, Tabulata, corals, lamellar-microlamellar microstructure

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1. INTRODUCTION

Interpretation of the biogenic nature of ancient skeletal microstructures is commonly hampered by diagenetic alteration and lack of extant taxa to serve as modern analogues. Palaeozoic rugose and tabulate coral microstructures have commonly been interpreted in light of our understanding of scleractinian coral biomineralization models because modern corals are the most plausible analogues for extinct coral orders, and the trabecular microstructure of many ancient corals appears to be similar to that in the Scleractinia (e.g., HILL, 1936; SORAUF, 1993, 1996a). However, despite the rapid increase in knowledge on scleractinian biomineralization, including the important shift from physical-chemical models (e.g., BRYAN & HILL, 1941) to the matrix-mediated model (e.g., reviews in SORAUF, 1996a; CUIF et al., 1997; CUIF & SORAUF, 2001), certain microstructures in ancient corals, such as zigzag microstructure, have not been documented in scleractinian corals and are interpreted as having diagenetic origins (KATO, 1963; SORAUF, 1977; WEBB & SORAUF, 2001; SORAUF & WEBB, 2003). Differences in diagenetic behaviour resulting from different original skeletal mineralogy complicate the analogy between biomineralization models, because Rugosa had calcitic skeletons, as probably did Tabulata, compared to aragonite skeletons in scleractinians. Additionally, Mg content varies incrementally within individual low Mg-calcite skeletons of some rugose corals (SORAUF, 1996b, 1997a) and temporally within some groups of rugose corals (WEBB & SORAUF, 2002), possibly causing differing diagenetic behaviour in Rugosa and Tabulata through the Palaeozoic. Hence, specific microstructures in Palaeozoic corals may be: 1) biogenic and original; 2) consistent (i.e., reproducible) and recognizable diagenetic alterations of biogenic structures; or 3) diagenetic alterations that mask original biogenic structures. A better understanding of ancient skeletal microstructures is critical because of the general paucity of taxonomic characters in ancient corals (e.g., WEBB, 1993), taxonomic utility of coral microstructures (e.g., WANG, 1950; KATO, 1963; WANG et al., 1989), and the possibility of using diagenetic behaviour as a proxy for changing seawater chemistry (WEBB & SORAUF, 2002).

One important class of microstructures with possible taxonomic importance in Palaeozoic corals includes lamellar-microlamellar microstructures (e.g., WANG, 1950; LAFUSTE & PLUSQUELLEC, 1976, 1985; LAFUSTE, 1980; RODRIGUEZ, 1989; WANG & CHEN, 1989). However, such microstructures have generated much controversy because similar microstructures have not been documented in living Scleractinia (CHEVALIER, 1987) and the means of producing them by scleractinian biomineralization models has been difficult to envision (SORAUF, 1993, 1996a). Regardless, various lamellar and microlamellar microstructures are abundant in tabulate corals (e.g., LAFUSTE & PLUSQUELLEC, 1976, 1985, 1987; LAFUSTE, 1978, 1980, 1983; TOURNEUR et al., 1989; LAFUSTE et al., 1993) and rugose corals (e.g., SEMENOFF-TIAN-CHANSKY, 1984; RODRIGUEZ, 1989; WANG et al., 1989). The his-

tory of the lamellar-microlamellar controversy has been reviewed in detail by RODRIGUEZ (1989) and SORAUF (1993, 1996a). In general, RODRIGUEZ (1989) favoured a biogenic origin for the microstructure because of its regularity within specific taxa, even where specimens are from different diagenetic backgrounds, occurrence with fibrous microstructure (e.g., LAFUSTE, 1983; LAFUSTE et al., 1993), and lack of other evidence for recrystallization. SORAUF (1993, 1996a) took an opposing view, noting that some lamellar microstructures are demonstrably diagenetic (e.g., SORAUF, 1996b, 1997b; OEKENTORP, 2001) and that specimens of the same species of rugose coral that had been described as having either fibrous or lamellar microstructure (e.g., *Siphonodendron* from Algeria; SEMENOFF-TIAN-CHANSKY, 1984) were also likely to differ owing to different diagenetic histories rather than different biomineralization processes occurring in the same species. SORAUF's (1993, 1996a) primary objection to a biogenic origin for lamellar microstructure was the absence of a mechanism by which biomineralizing corals that otherwise produce fibers could produce single scale-like crystals parallel to the growing surface. Important in SORAUF's (1996a) argument is the lack of a scleractinian analogue for lamellar-microlamellar microstructure.

Recent investigation of organic matrix-controlled biomineralization in corals has provided evidence supporting the existence of such an analogue. Although scleractinian microstructure is generally characterized by radiating aragonite fibers arranged into trabeculae or fibro-normal sheets, fibers also occur in individual bundles that lie nearly parallel to the surface in *Fungia* (SORAUF, 1972, Pl. 11, Fig. 2 and Pl. 14, Figs. 4, 5, & 6; JELL, 1977, Fig. 8b), *Acropora* (GLADFELTER, 1983, Fig. 8b; LOWENSTAM & WEINER, 1989, Fig. 5.3; CUIF et al., 1997, Pl. 1, Figs. 3, 4; GAUTRET et al., 2000, Fig. 2a-c), and *Flabellum* (SORAUF & PODOFF, 1977; STOLARSKI, 2003, Fig. 5a). SORAUF (1972) used the term 'shingles' to describe such clusters of obliquely oriented aragonite needles on the septal flanks in *Fungia* and described them as resembling overlapping fish 'scales'. The term 'fish scales' was again used to describe *Flabellum* by SORAUF & PODOFF (1977), and subsequent variations have included 'scale-like' as used by GAUTRET et al. (2000) in *Acropora* and by STOLARSKI (2003) in *Flabellum* and *Galaxea*. CUIF et al. (1997) called the bundles in *Acropora* 'elongate sclerodermites' to distinguish them from other microstructural elements. GAUTRET et al. (2000, Fig. 1c) illustrated ultra-thin sections of fiber bundles in *Acropora*, which they called 'scale-like' microstructure, and there the bundles bear a close resemblance to lamellae and microlamellae as seen in ultra-thin sections of tabulate corals (Pl. 1, A-B). If such bundles were recrystallized into single crystals, they would form a microstructure almost identical to microlamellae-lamellae in tabulate corals. Hence, SORAUF (1993, 1996a) may have been correct when he suggested that at least some lamellar microstructure in Palaeozoic corals may have resulted from the very low angle oblique growth of fibers on the growing surface. The purpose of this paper is to: 1) describe microstructural elements in acroporid scleractinian corals that are similar in some regards to lamellar-microlamellar microstructure in Palaeozoic tabulates; and 2) directly compare the microstructures of extant *Acropora* and the Mississippian tabulate coral, *Michelinia meekana* GIRTY from Arkansas, using the same analytical techniques (i.e., ultra-thin section and scanning electron microscopy – SEM). The 'shingle' microstructure ('scale-like' microstructure of GAUTRET et al., 2000) of *Acropora* and other scleractinian corals may provide an analogue for lamellae/microlamellae, and thereby provide the basis for interpreting some ancient microstructures in light of scleractinian biomineralization models.

2. MATERIAL AND METHODS

Four specimens of *Acropora* sp., including two live-collected and two dead Holocene specimens from reefrock, were collected from Heron Reef, Great Barrier Reef, Australia. Live-collected samples were emersed in sodium hypochlorite (NaOCl) for 8 to 12 hours to remove organic matter prior to analysis. A single *Michelinia meekana* GIRTY corallum from a black shale bed near the base of the upper Mississippian Pitkin Limestone in Madison County, Arkansas (location MS462 of WEBB, 1987) was chosen for comparison, because PLUSQUELLEC & SANDO (1987) documented typical tabulate lamellar microstructure in the species.

Observations were performed with a FEI QUANTA 200 scanning electron microscope (SEM) operating at high vacuum and 15 kV using both secondary and backscattered electron images, and energy dispersive x-ray analysis (EDX). Secondary electron imaging was used on broken and external surfaces, with some specimens etched with dilute formic acid (2%) for 20 seconds prior to being coated with carbon. One-half of each polished section was etched, as above, prior to being carbon coated; the other half was not etched. Non-etched parts of polished sections were viewed using the backscatter and EDX detector fitted to the SEM allowing easy comparison of secondary and backscattered electron images. Transverse and longitudinal ultra-thin sections (lame à faces polies or "LFP" of LAFUSTE, 1970) were prepared to observe microstructures with petrographic microscopy.

3. RESULTS

3.1. *Acropora* microstructure

Observations from SEM and ultra-thin sections support the contention of CUIF et al. (1997) that *Acropora* microstructure consists of aragonite fibres arranged in 1) typical radiating trabeculae and 2) layers composed of bundles that are arranged in a low-relief, overlapping, shingle-like pattern (Pl. 1, A, C, D and Pl. 2, A-E). Individual fibres in trabecular regions are arranged roughly perpendicular to the growth surface and show signs of preferentially etched 'growth bands' as previously illustrated by CUIF & SORAUF (2001). Because the fibers radiate away from the growth centers, the growth bands are more or less parallel to the accreting surface.

Shingle microstructure consists of individual 'shingles' that are 4–50 μm in width and 2–7 μm in thickness (as measured in thin section and in SEM). The length of the shingles varies between 20 and 150 μm. However, individual shingles have variable and curving growth directions that are commonly oblique to the plane of the ultra-thin or polished section. Consequently, it is difficult to observe shingles completely from their point of nucleation to their termination. Hence, the greatest length attained by shingles is unknown. Fibers within shingles are roughly parallel to the surface of underlying shingles and radiate laterally at angles between 6–45° with low angles being dominant (Pl. 2, E). Where fibers are roughly parallel (i.e., low angle of divergence), they may not be apparent in ultra-thin sections, and in many cases, shingles appear to be single crystals

in cross-polarized light despite their clearly fibrous origin. Petrographic observation using a gypsum plate suggests that crystallographic axes of aragonite fibers are consistent. Shingle growth is directed mostly distally within corallites, although growth directions are non-parallel on surfaces with complicated relief. On etched surfaces, preferential etching causes thin dissolution growth bands similar to those in the trabeculae regions (e.g., CUIF & SORAUF, 2001). Some shingles appear to originate from the distal edges of trabeculae where they are continuous with bundles within the trabeculae, but many occur against trabeculae with distinct discontinuity (Pl. 1, C-D and Pl. 2, C). In many cases it is unclear exactly where the shingles nucleated, but layers of shingles commonly fill relatively large spaces between trabeculae, and in some cases they occur more than 25 layers deep. In ultra-thin sections *Acropora* shingles are similar in size and appearance to lamellae-microlamellae in Paleozoic corals, commonly having roughly crescent-shaped cross-sections.

In polished and etched sections, the outermost edges of shingles are more resistant to acid etching than the inner aragonite emphasizing the shingle structure in SEM images (Pl. 2, C). A similar pattern was shown on the septal flanks of *Fungia* where skeletal carbonate was removed to leave organic matrix surrounding the original 'scales' (SORAUF, 1972). CUIF et al. (1997) suggested that the etching pattern results from an intra-crystalline organic coating on the fringes of the 'sclerodermites' that was protected from the oxidising agent (NaOCl) used to remove organic matter. That interpretation was subsequently confirmed by the correlation of acridine orange staining to the regions that stand in relief by GAUTRET et al. (2000).

3.2. *Michelinia* microstructure

Lamellar-microlamellar microstructure in *Michelinia meekana* consists of roughly parallel scales measuring 1.5–7 µm in thickness and 4–50 µm in diameter, although the smaller diameters may represent the edges of larger scales, as all measurements were made in thin sections. The scales do not appear to be fibrous, and each seems to be composed of a single calcite crystal (Pl. 2, H). The measured dimensions are consistent with those from previous observations of the species by PLUSQUELLEC & SANDO (1987), who calculated an average thickness of 5 µm and length of 40–50 µm for their lamellar calcite crystals. Analysis with a gypsum plate suggests that neighbouring crystals have roughly similar crystallographic orientations. The scales are generally more or less parallel to the median dark line in both longitudinal and transverse section, with no significant differences in dimensions between section orientations. A common feature is the draping or deflection of lamellar microstructures around septal spines (Pl. 1, B and Pl. 2, G). Where spines are truncated transversely in section (sections tangential to the wall), surrounding lamellae display a circular pattern (Pl. 2, I). Etched polished sections reveal the same structures when viewed with SEM, but in that case the etching process exposes lamellae microstructures by preferentially removing calcite at the scale margins (Pl. 2, F & G). Backscatter images and EDX analyses do not reveal any subtle compositional variation between lamellae.

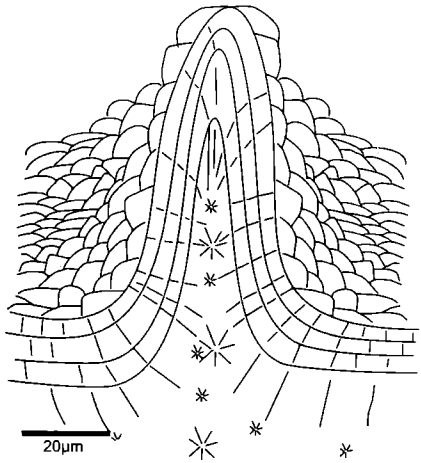

Fig. 1:
Typical microstructure of acroporid corals showing fibrous trabecula with growth banding developed from centers of calcification with subsequent shingle microstructure growth.

4. DISCUSSION

4.1. *Acropora* skeleton growth model

Microstructural observations confirm that the growth of the *Acropora* skeleton is a two-stage process as proposed by Cuif et al. (1997). The initial phase of growth involves fibrous aragonite crystals radiating from seed crystal nuclei forming trabeculae, followed

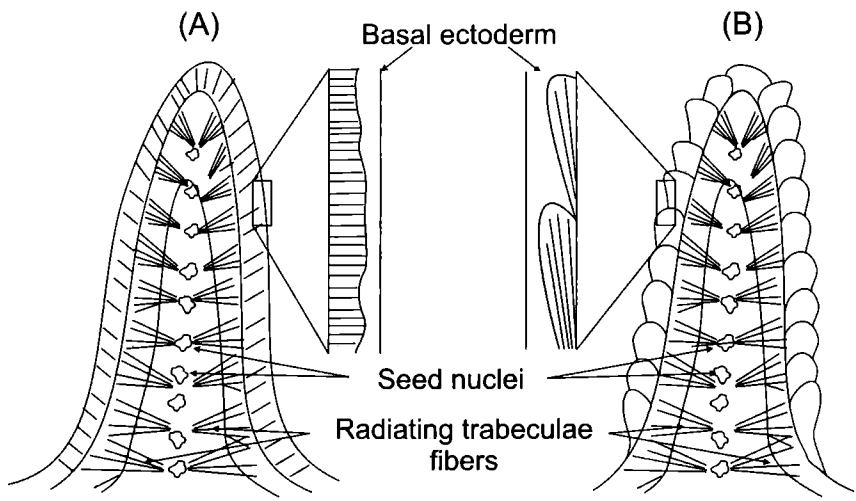

Fig. 2: Schematic growth model for coral skeleton.
(A) represents model where growth of aragonite fibers is perpendicular to the basal ectoderm.
(B) represents the proposed growth model in acroporid corals where coral fiber growth can be parallel to the surface of the ectoderm in pockets, which results in shingle like growth (e.g., Cuif et al., 1997).

by infilling of spaces between trabeculae and coating of surfaces by the growth of bundles of aragonite fibers that occur at an oblique, low angle to the basal ectoderm resulting in the shingle microstructure (Figs. 1, 2). The conventional model for coral skeletal development involves growth of aragonite fibers perpendicular to the basal ectoderm (see summary in SORAUF, 1996a) as opposed to the oblique fiber growth at a low angle to the ectoderm that forms the shingle microstructure, but both types of growth are constructed by aragonite needles that contain preferentially etched bands that presumably reflect control to a similar degree by the distribution of organic matrix.

4.2. Lamellar-microlamellar microstructure – a modern analogue?

An important reason for controversy regarding the biogenicity of lamellar-microlamellar microstructures has been the lack of a modern analogue for their formation in organisms that otherwise have fibrous microstructure (SORAUF, 1993, 1996a). The controversy has been complicated by the fact that lamellar-microlamellar microstructures have generally been studied in ultra-thin section (e.g., LAFUSTE, 1970), a technique that has rarely been utilized in scleractinian studies (e.g., GAUTRET et al., 2000; PERRIN & CUIF, 2001). Regardless, it has become apparent that the physical-chemical trabecular model for coral skeleton growth wherein radiating aragonite fiber growth is perpendicular to the basal ectoderm (e.g., BRYAN & HILL, 1941; SORAUF, 1972) can only be partly applied to many scleractinian corals (e.g., the Triassic *Pachythecalis major*, CUIF, 1975; acroporids, CUIF et al., 1997). The recognition that organic matrix controls aragonite fiber orientation and distribution (CHEVALIER, 1987; CUIF et al., 1997, GAUTRET et al., 2000; CUIF & SORAUF, 2001) and the recognition of shingle-like 'sclerodermites' in scleractinian coral skeletons (CUIF et al., 1997) allows for scleractinian corals to be re-evaluated in terms of biomineralization analogues for lamellar-microlamellar microstructures.

Investigations of shingle microstructure in scleractinian corals using ultra-thin sections and polished and etched sections produced 5 key observations: 1) The size of *Acropora* shingles observed in thin section (4–50 μm diameter, 2–7 μm thick) is in the same range as lamellae-microlamellae previously described in Palaeozoic corals. Scales in Palaeozoic tabulate corals generally range between 10 and 50 μm in diameter and 2 and 8 μm in thickness (RODRIGUEZ, 1989; PLUSQUELLEC & TOURNEUR, 1998). 2) The outlines of shingles in thin section are commonly somewhat crescent-shaped (GAUTRET et al., 2000) with the concavity towards the growth surface as is common in microlamellar microstructures of some tabulate corals (RODRIGUEZ, 1989; PLUSQUELLEC & TOURNEUR, 1998). 3) The near parallel orientation of the C-axes of aragonite fibers within shingles makes fibers difficult to differentiate in most ultra-thin sections, although sweeping extinction can be seen where shingles are cut roughly tangential to the overall accreting surface. 4) Crystallographic axes of aragonite fibers in adjacent shingles are generally fairly consistent, because most shingles grew in a similar direction. 5) Organic matter appears to occur preferentially around the margins of shingles, thereby possibly isolating them somewhat from each other as suggested by GAUTRET et al. (2000).

For shingle microstructure in *Acropora* to serve as an analogue for lamellar-microlamellar microstructures in Palaeozoic coral skeletons four criteria must be met. 1) Fibrous shingles must have been produced in the tabulate corals at very low angles to the acc-

reting surface. 2) The C-axes of the fibers must have been nearly parallel to ease recrystallization into single crystals and thereby maintain some aspects of biogenic shape. 3) The shingles must have been isolated more or less during diagenesis by organic matrix. 4) The fibers must have been subject to diagenetic recrystallization. Criterion 1 is supported by the similarity in dimensions and orientations of *Michelinia* scales and *Acropora* shingles. The biomineral fibers of *Acropora* shingles clearly grew at low angles to the surface upon which they grew. Criterion 2 is supported by petrographic analysis using a gypsum plate because the crystallographic axes of adjacent *Michelinia* scales are generally similar, thereby being consistent with inherited original orientation of biocrystal fibers that controlled the crystallographic orientation of subsequent diagenetic recrystallization. Criterion 3 is supported by the enhanced etching around the edges of *Michelinia* scales. Whereas Recent and Holocene *Acropora* skeletons retain adequate organic matter at the edges of shingles to retard etching, ancient carbonates are likely to have lost any original organic matter to oxidation leaving, if anything, microporous zones more subject to etching (e.g., SORAUF & CUIF, 2001). Criterion 4 is supported by a likely original high-Mg calcite skeletal mineralogy in tabulate corals, at least during some time intervals. WEBB & SORAUF (2001) and SORAUF & WEBB (2002) showed that Mg-calcite rugose coral skeletons underwent minor recrystallization during early diagenesis wherein fibrous microstructures were transformed to zigzag lamellar microstructures with the loss of Mg from the lattice. A similar process in tabulate corals, provided it was constrained by the distribution of organic matter as in modern shingle microstructure, might produce scales. Hence, scales may represent diagenetic features in general, but each scale may reflect the morphology of a biogenic shingle.

One possible objection to the proposed analogue model is the co-occurrence of both fibrous and lamellar-microlamellar microstructure in some corals (RODRIGUEZ, 1989). If the fibers in lamellae recrystallized to form apparent monocrystalline scales, why did the other fibrous microstructure survive? The co-occurring fibrous and lamellar microstructures illustrated by RODRIGUEZ (1989, Fig. 1) suggest that the layers of fibronormal microstructure were recrystallized to a more or less similar degree to the microlamellae. Individual biomineral fibers are not preserved in the fibrous layers, but the layers consist of coarser calcite with a coarse, but oriented, fibrous structure. Individual crystals within the fibrous sections are in many cases as thick as single crystals that make up scales. Hence, the original fibers may be equally recrystallized in both regions and the major differences in preservation may reflect differences in the relative amounts, and distribution, of organic matrix. The relatively small scales were possibly completely enclosed by organic matrix thereby isolating them, whereas the larger layers of fibers perpendicular to the surface may have contained relatively less internal matrix as in trabecular fibrous structure of *Acropora*. In *Ohiopora cylindrica* presumably originally fibrous spines are clearly very coarsely recrystallised amidst lamellae that appear well preserved (LAFUSTE & PLUSQUELLEC, 1987).

5. CONCLUSIONS

Interpretation of the biogenicity of lamellar-microlamellar microstructures in Palaeozoic corals has been hampered by the lack of an extant analogue.

However, certain microstructures in acroporid scleractinian corals are similar in appearance to lamellar-microlamellar structure in tabulate corals. *Acropora* sp. skeletal growth appears to be a two-stage process involving primary fibrous trabeculae followed by shingle microstructure. If the fibers in *Acropora* shingles were obscured by recrystallization, but shingles survived as recognizable units owing to the surrounding organic matrix, the resulting structures would be similar to lamellae-microlamellae. Hence, Sorauf's (1993; 1996a) possible mechanism for lamellar-microlamellar microstructure formation (i.e., low-angle oblique fiber growth on surfaces) may have a direct analogue in the Scleractinia. Therefore, although some lamellar-microlamellar microstructures are entirely diagenetic in origin, at least some lamellar-microlamellar microstructures may be fundamentally biogenic in nature, although reflecting slight recrystallization, and hence, their use in systematics may be supported (e.g., Lafuste & Plusquellec, 1976; Rodriguez, 1989).

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Plate 1

Ultra-thin sections of *Acropora* sp. and *Michelinia meekana* GIRTY.

A: Transverse ultra-thin section of live-collected *Acropora* sp. showing shingle microstructure draped around trabecula, which has similar appearance and dimensions to microstructure in *Michelinia* shown in B.

B: Longitudinal ultra-thin section of *M. meekana* showing lamellae deflected around septal spine. Note that A and B are shown at the same scale.

C, D: Sections of Holocene *Acropora* sp. showing clear demarcation between fibrous trabecular and shingle microstructure (arrows). Note apparent sinuous appearance of some of the shingles. All scale bars are 50 μm.

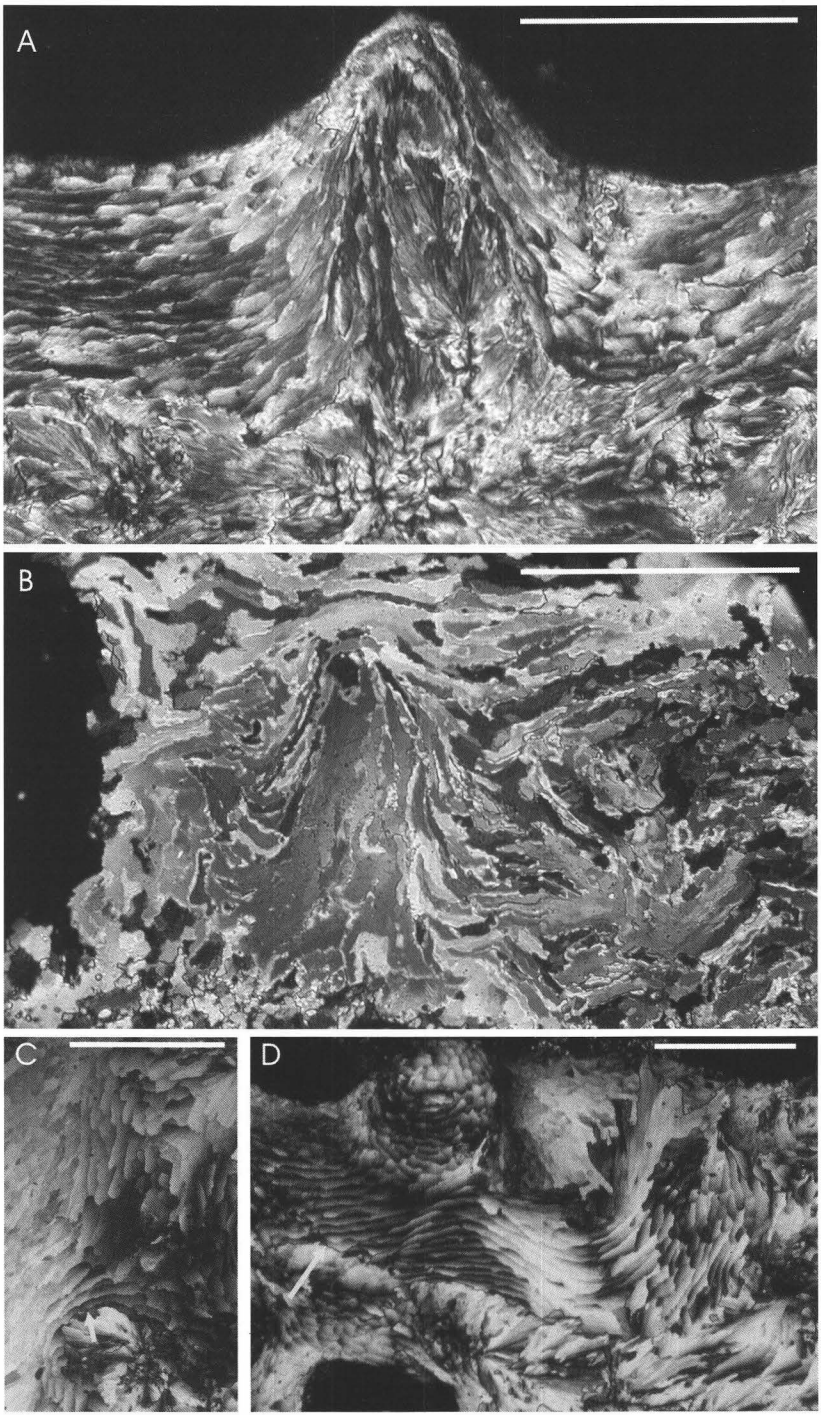

A
B
C
D

Plate 2

A: SEM image of live-collected *Acropora* sp. illustrating stacking pattern of shingles and growth banding within shingles. Scale bar equals 50 µm.

B: SEM image showing end-on view of shingles on the surface of a live-collected *Acropora*. If the individual shingles were recrystallised, each as a single unit, they would have a similar appearance to scales displayed in *Michelinia meekana* seen in F. Scale bar equals 20 µm.

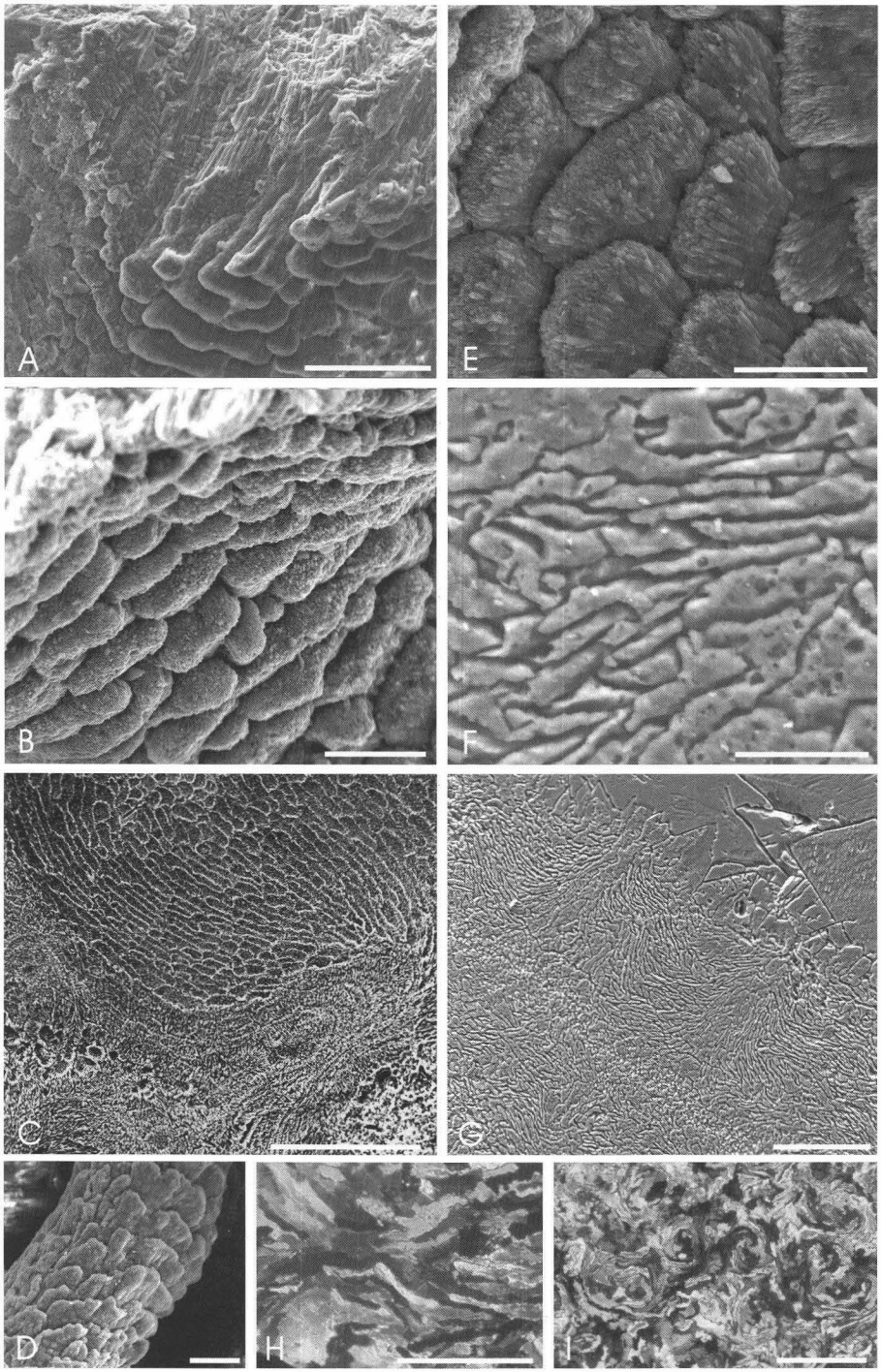
C: Prominent trabecula and enveloping shingle microstructure in a polished and etched section of Holocene *Acropora*. Scale bar in C equals 100 µm.

D, E: SEM images of surface of live-collected *Acropora* illustrating low relief, overlapping shingle like microstructure and slight radiation of aragonite fibres within each bundle. Scale bar in D and E equals 20 µm.

F: Polished and etched section of *Michelinia meekana* showing preferential etching of the margins of the lamellae. Scale bar equals 20 µm.

G: Lamellar-microlamellar microstructures have a similar appearance to shingles seen in C, in a polished and etched longitudinal section of *Michelinia meekana* showing scales deflected around septal spines. Scale bar G equals 100 µm.

H, I: Ultra-thin sections of *Michelinia meekana*. H shows lamellae parellel to the median dark line whereas I shows transversely truncated septal spines with lamellae forming circular patterns. Scale bar in H and I equals 50 µm.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