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Skeletal Development in *Acropora cervicornis*

II. Diel Patterns of Calcium Carbonate Accretion

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Abstract. Scanning electron microscopy, field studies using dyes which become incorporated into the skeleton of living corals as time markers, and petrographic and mineralogic techniques were used to describe the diel pattern of calcium carbonate accretion in the extending axial corallite of *Acropora cervicornis*. The axial corallite extends by the formation of randomly oriented fusiform crystals at the distal tip of the branch. Morphological and mineralogical characteristics suggest that these might be calcite crystals. They form a framework upon which needle-like aragonite crystals (initially small tufts) begin to grow. As the needles elongate, groups of them form well defined bundles, fasciculi, which compose the primary skeletal elements. There is a diel pattern in the deposition of the skeleton. At night (1800–0600 hours) the distal spines are pointed and composed primarily of fusiform crystals. During the day (0600–1800 hours) mineral accretion occurs on all surfaces of the skeleton, apparently by epitaxial growth on the aragonite needles of the fasciculi.

Introduction

Goreau (1959, 1963) observed that scleractinian corals which contain symbiotic dinoflagellates (= zooxanthellae) calcify faster during the day than at night. He demonstrated that light was responsible for this enhancement of mineral deposition. Subsequently, Vandermeulen et al. (1972) showed that it was photosynthesis by the zooxanthellae which had a direct effect on enhancement of calcification. Inhibition of photosynthesis reduced the rate of $^{45}Ca^{++}$ incorporation to dark levels even in the presence of light. To date no one has provided an adequate explanation for light enhanced calcification perhaps because testable hypotheses await better definition of the morphology of mineral deposition and its temporal pattern.

Barnes (1972) observed the daily pattern of the construction of the epithecal element of a coral skeleton. He found that one portion of the epitheca was deposited at night while a different portion was deposited during the day. Chalker (1977) observed a diel variation in calcification capacity (the rate of calcification at saturating light intensities) in *Acropora cervicornis*, with maxima at sunrise and sunset. The pattern persisted under constant light; it was correlated with a similar rhythm in the photosynthetic capacity of the zooxanthellae.

In previous studies, it has been assumed that calcification is a process whose rate is influenced by algal metabolism which in turn is influenced by irradiance and time of day (Chalker 1975). Recent studies (Barnes and Crossland 1980; Gladfelter 1982) suggest, however, that at least two processes might be involved in the calcification of branching species of the genus *Acropora*. In a time-lapse photographic study Barnes and Crossland (1980) demonstrated that skeletal extension along the branch axis in *A. acuminata* was more rapid at night than during the day, although calcification (as measured by incorporation of ^{14}C in skeletal carbonate) was two to three times greater in the day than at night (Barnes and Crossland 1978). Similarly, skeletal development in *A. cervicornis* (Gladfelter 1982) involves (1) deposition of a framework of micritic fusiform crystals and (2) subsequent nucleation and growth of aragonite needles on these crystals.

The purpose of the present study is to describe the temporal sequence of events in the development of the skeleton of *A. cervicornis*. Such a description may provide a basis for the formulation of a testable hypothesis to explain light enhancement of calcification. I have examined the structure of the skeleton and described the pattern of mineral accretion of the axial corallite at intervals throughout a diel cycle. The results show that there is a definite temporal and spatial pattern.

Methods

Collection and Preparation of Specimens for Scanning Electron Microscopy (SEM)

Specimens of the branching coral, *Acropora cervicornis*, were collected at a depth of 10 m in Buck Island Channel, St. Croix, US Virgin Islands at

0600, 1200, 1800, and 2400 hours. Living branch tips (4–8 cm) were removed from colonies and transported to West Indies Laboratory as described in Gladfelter (1982). Immediately after collection, some corals were fixed and prepared for skeleton and tissue examination by SEM (Gladfelter 1982); 3–5 tips were examined for each of the collection times. Other coral tips were maintained for at least 24 h in a shaded outdoor aquarium in running seawater. Samples from these specimens were then fixed at 0600, 1200, 1800, and 2400 hours.

In situ Skeletal Incorporation of Tetracycline

Coral skeletons were labelled in situ, i.e. 10 m depth in Buck Island Channel, with tetracycline, a fluorescent antibiotic which is incorporated into newly accreted calcium carbonate skeletal elements (Kobayashi and Taki 1969). A solution of tetracycline (hydrochloride crystalline, SIGMA, 2% W/V in seawater) was placed in a 5 ml syringe fitted with a 26 needle. At 0600 and 1800 hours, 10 corals were labelled by injecting 0.2 ml tetracycline solution into the gastrovascular system via a lateral polyp located ca. 8 cm from the branch tip. Previous experiments, using a different skeletal label, Alizarin Red S, had shown that an aqueous solution of a label injected 10 cm proximal to the tip was transported to and incorporated in the skeleton at the tip. Within 3 h of injection, the new skeleton at the tip appeared red due to the incorporation of the Alizarin Red S (Gladfelter unpublished). After the injection of tetracycline, in this present study, a 3 cm plastic sleeve was placed over the injected area (carefully avoiding damage to the tip) and secured with cotton string. This enclosed pocket of surrounding seawater could serve as a reservoir for label which might have leaked from the injected polyp; other lateral polyps could then take the label back into the gastrovascular system. The corals were collected 12 h after injection, transported to the laboratory, and immediately cleaned and prepared for petrographic thin sections (Gladfelter 1982). The dried skeletons were vacuum-embedded in Buhler Epoxy Resin, cut longitudinally, and petrographic thin sections (ca. 40 μm thick) were made. The labelled tips were examined by epifluorescence microscopy (Neckelmann 1982) to determine the sites of tetracycline incorporation. Unlabelled controls (20 skeletal tips collected throughout the year) were similarly prepared and examined. These controls were also used to determine the size and frequency of formation of skeletal elements.

X-Ray Diffraction of Skeletal Tips

Skeletons of *A. cervicornis* were cleaned in 5% NaOCl (Gladfelter 1982). Three undamaged tips were selected for X-ray diffraction. The distal 2 mm of an axial corallite was placed in a mortar and carefully ground with a pestle into fine dust. This dust was placed in a Phillips Norelco X-ray diffractometer. Scans were made from 25° to 30° ∅ to include the major aragonite and calcite peaks.

Electron Microprobe Analyses of Skeletal Tips

Thick and thin probe mounts were made from skeletal tips. The skeletons were oriented to expose a radial view of the axial corallite. A probe mount was then place in an electron microprobe (Applied Research Laboratories, Model EMX; 15 kV, 15 nano-amps specimen current) and transects were made across skeletal spines. Counts of Mg, Sr and Ba were made for 10 s at each point in the transect. The counts of Mg were plotted against the counts of Sr for each spine; the mean Mg count and the mean Sr count values were used to establish a new set of zero axes for each set of transect points (one set per spine).

Results

Diel Pattern of Mineral Accretion

An account of the morphology of the axial corallite of *Acropora cervicornis* is found in Gladfelter (1982). Briefly, the skeleton grows linearly by extension of the axial spines. These spines are connected by sclerosepta oriented radially and synapticulae oriented tangentially. To discern the diel pattern of mineral accretion at the growing tip, the axial spines and bars (Fig. 1) were selected as markers for growth.

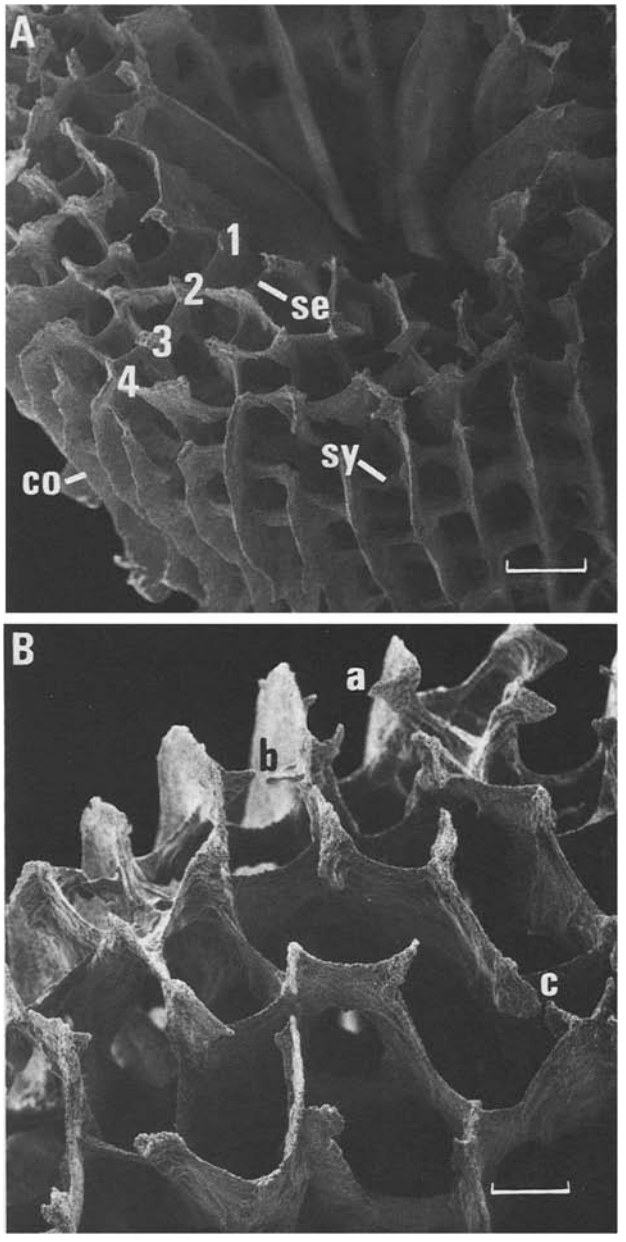

Fig. 1 A, B. SEM of the distal portion of the axial corallite of *Acropora cervicornis*. **A** The axial corallite is composed of four concentric rings of axial spines (labelled from inner to outer ring, *1–4*). The axial spines are connected by radially oriented bars, the sclerosepta (*se*) with a solid external portion, the costa (*co*) and tangentially oriented bars, the synapticulae (*sy*). Scale bar = 250 μm. **B** Higher magnification view of the axial corallite showing sclerosepta and synapticulae in various stages of development from newly forming (*a*) to partially complete (*b*) to almost entirely complete (*c*). Scale bar = 125 μm

The axial spines, the distal-most elements of the axial corallite, extend at a rate of 300 μm · d^{-1} (Gladfelter 1982). Their tips are very broad at 1200 hours (Fig. 2 A; Fig. 3 A) with numerous tufts of aragonite needles and small (ca.

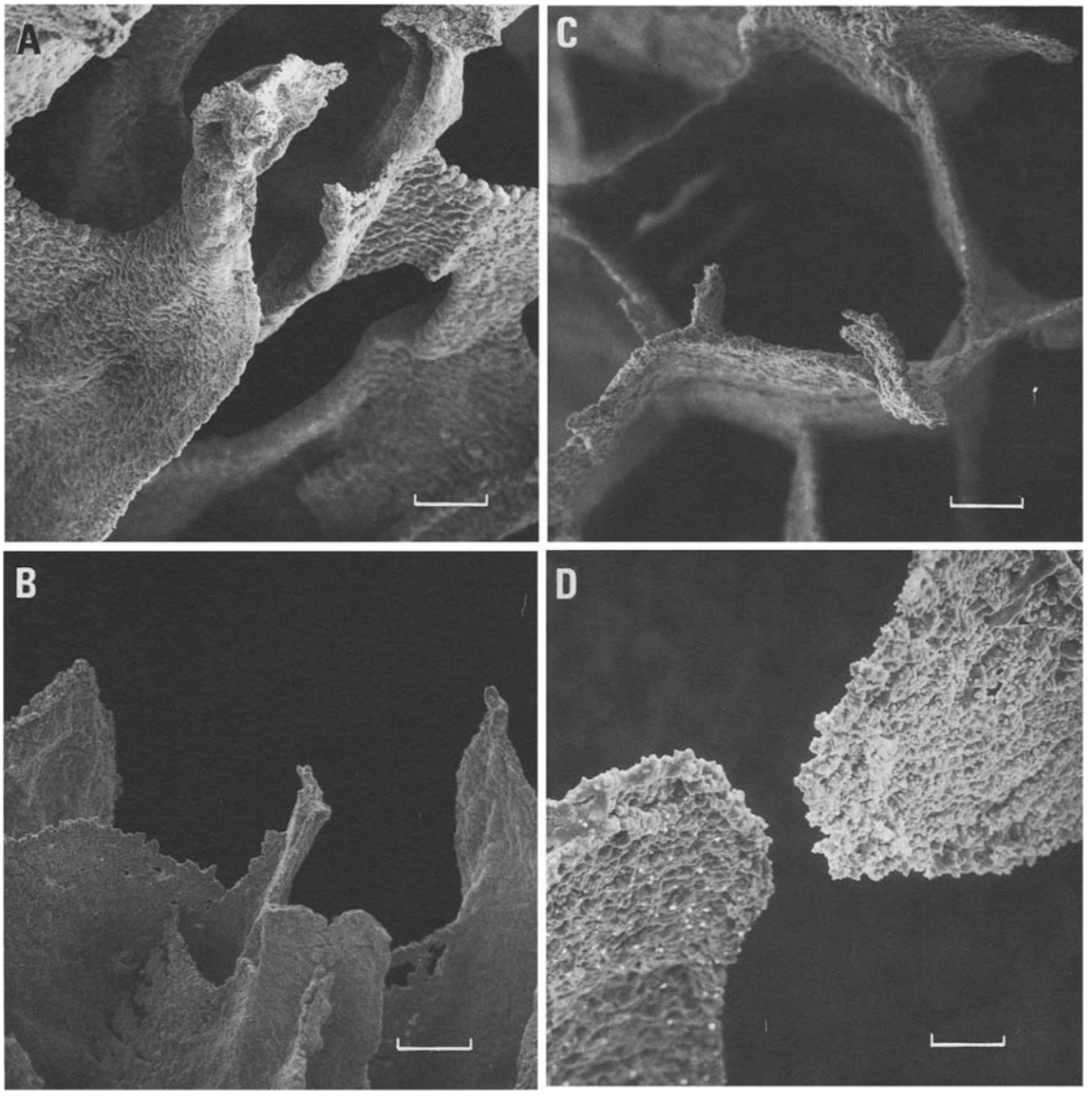

Fig. 2 A–D. SEMs of the axial corallite at different points of the diel cycle. **A** 1200 hours. Note the blunt, broad tip of the axial spine. The distal-most edges of the bars have a pebble-like appearance, characteristic of the fasciculi. Scale bar = 50 μm. **B** 1800 hours. Note the acute shape of the axial spines, the porous nature of the connecting bars and the thin, ragged distal edges of the connecting bars, indicating the hasty erection of the framework. Scale bar = 50 μm. **C** 2400 hours. Note the acute shape and the fragile appearance of the axial spine which is primarily composed of fusiform crystals and the initial tufts of aragonite. Scale bar = 50 μm. **D** 0600 hours. A bar in an intermediate stage of development. Note the numerous fusiform crystals on the leading edges of the bar. The bar is still very thin and composed primarily of fusiform crystals and tufts of aragonite. Scale bar = 12.5 μm

1 μm) randomly oriented fusiform crystals. This is in contrast to the spines at 0600, 1800 and 2400 hours (Fig. 2 B, C; Fig. 3 C) which are more narrow at the apex, with the almost exclusive presence of fusiform crystals. The fusiform crystals present on the growing surfaces of the skeleton at 1800, 2400 and 0600 hours appear to be somewhat larger (ca. 2–3 μm) than those present at 1200 hours. Corals maintained for 24 h in an aquarium with flowing seawater show the same pattern of development as the freshly collected specimens.

Connecting bars, the sclerosepta and the synapticulae form on an average of ca. $10 \cdot mo^{-1}$. These can be found in all stages of development at any hour of the day (Fig. 1 B; Fig. 2). The formation of a bar involves the same sequence of depositional events as seen in the extension of a spine: fusiform crystal deposition (Fig. 2 B, D; Fig. 3 B, D) with subsequent formation and growth of tufts of aragonite needles, and then elongation of needles organized in discrete bundles, the fasciculi. At 1800, 2400 and 0600 hours the distal edges of bars are very narrow, composed almost entirely of fusiform crystals (Fig. 2 B, D; Fig. 3 B, D; Fig. 5 B). At 1200 h this distal edge is much broader; it is now composed of the initial elements of the fasciculi, tufts of needle-like crystals (Fig. 2 A; Fig. 5 B). Often large gaping holes are left in the framework of a bar due to the rapid rate of axial construction (Fig. 2 B; Fig. 3 B). These holes are filled in within the day by accretion of mineral on the aragonite needles framing the holes.

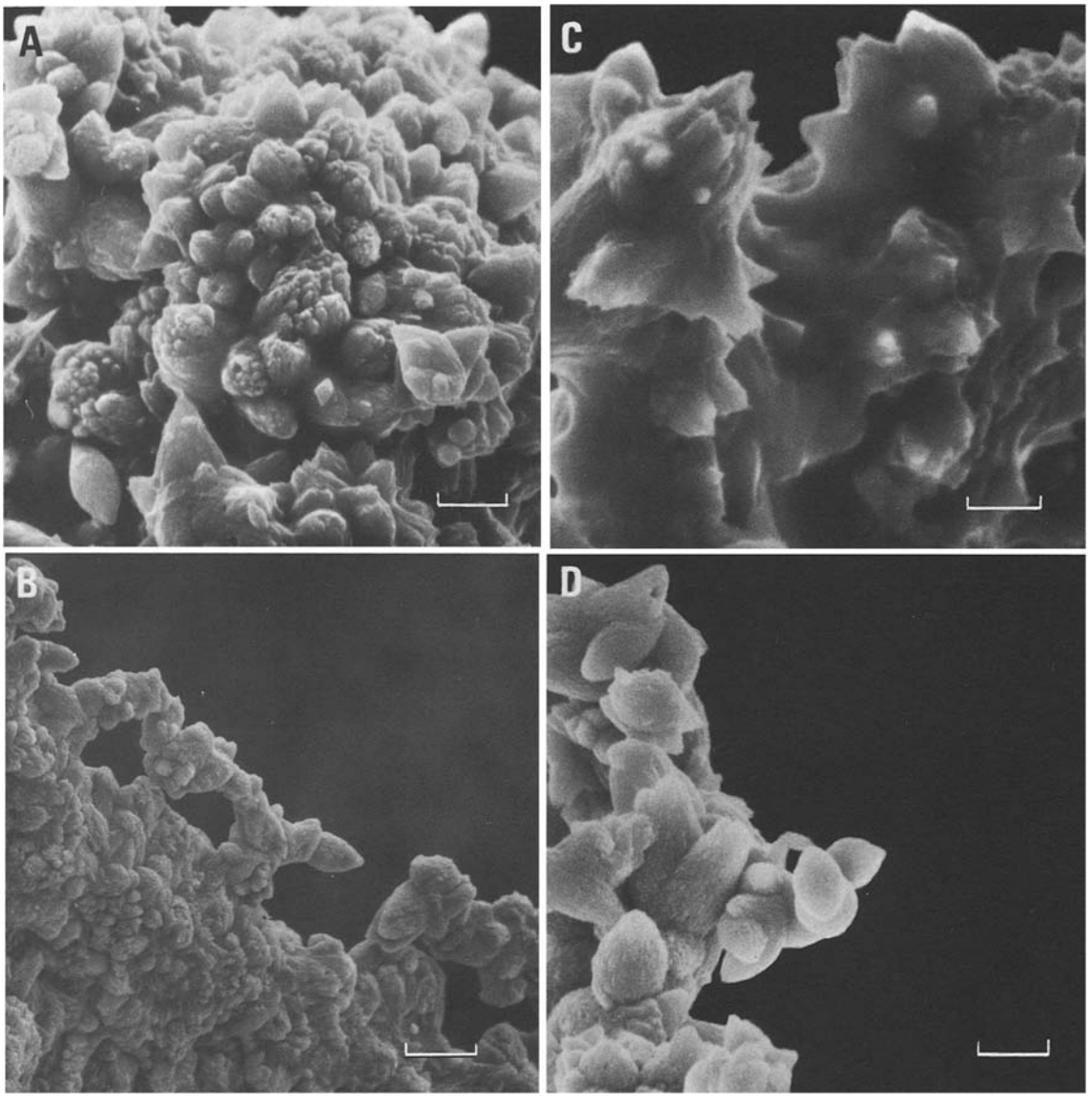

Fig. 3 A–D. SEMS of the leading edges of skeletal elements at different points during the diel cycle. **A** 1200 hours. View of the distal tip of the axial spine. Note the broad tip composed of numerous tufts of aragonite along with scattered randomly oriented fusiform crystals. Scale bar = 1.3 μm. **B** 1800 hours. Distal-most portion of a bar. Note the fusiform crystals, gaps left in the bar by the hasty erection of the framework, and tufts of aragonite on the surface of the bar just below the edge. Scale bar = 5 μm. **C** 2400 hours. View of the tip of an axial spine. Note the numerous, large, randomly, oriented fusiform crystals. Scale bar = 1.3 μm. **D** 0600 hours. View of the leading edge of a partially developed bar. Note the extensive but fragile development of a framework of fusiform crystals. Also note the fishscale-like texture of these crystals. Scale bar = 1.3 μm

The bars have a length (parallel to the axis of the corallite) ranging from less than 200 μm to greater than 1,000 μm. Initially the width of the bars is less than 50 μm, composed of the inner framework of fusiform crystals and tufts of aragonite needles, the initial elements of the fasciculi. After several months, these bars become much wider, eventually occluding the spaces between them (Gladfelter 1982).

Diel Pattern of Tetracycline Labelling

To determine if the site of mineral deposition varied with time of deposition, I labelled corals in situ at 0600 and 1800 hours with tetracycline, a fluorescent stain which is incorporated into developing skeleton. I found that the in situ pattern of deposition of tetracycline varied with time of day (Fig. 4). Corals labelled in the early morning (0600 hours) had the most intense labelling just proximal to the branch tips and on all surfaces of the skeleton below the tip (to a maximum observed distance of 2 cm proximal to the tip). The most intense labelling at night (i.e. in those branches injected with label at 1800 hours) occurred in the tips of the spines of the axial and lateral corallites, portions of the sclerosepta projecting into the calyx and the distal-most set of bars. Both labelled and control corals had a dim autofluorescence on all portions of the skeleton.

The results of the observations on the diel pattern of mineral accretion and the diel pattern of tetracycline label-

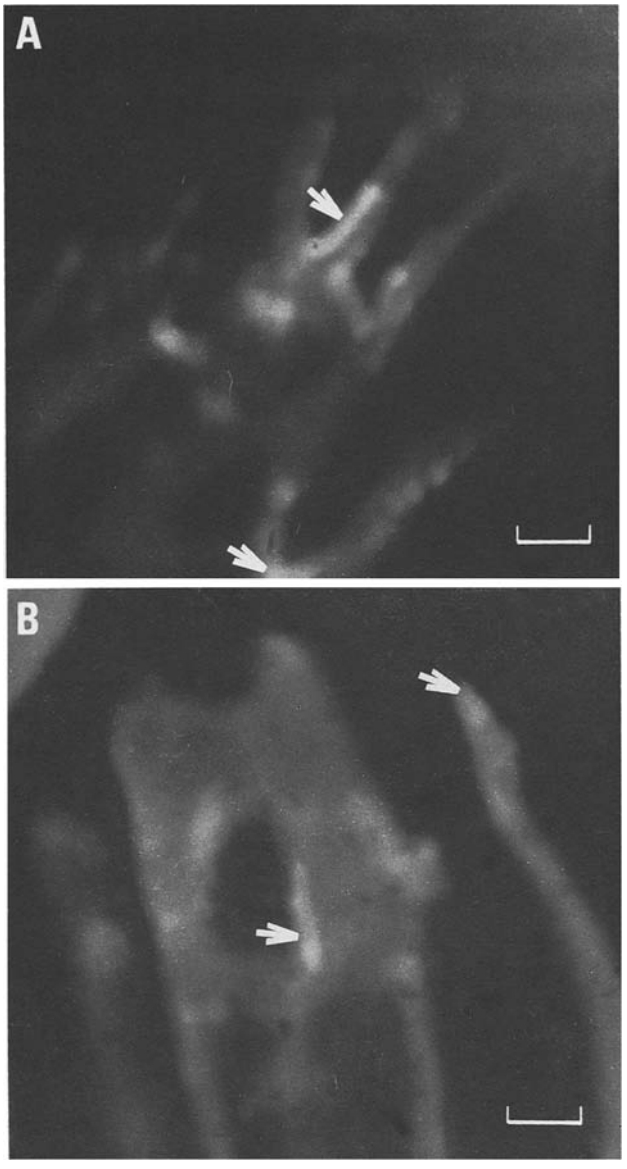

Fig. 4. In situ incorporation of tetracycline into the skeleton during the day (**A**) and at night (**B**). These are fluorescence photomicrographs of petrographic thin sections of labelled coral. Scale bar = 100 μm. **A** Lateral corallite of a coral labelled at 0600 hour. *Arrows* indicate most intense labelling on spines proximal to the tip and on all surfaces of the skeleton below the tip. **B** Axial corallite of a coral labelled at 1800 hour. *Arrows* indicate intense labelling on the tips of the spines and on the bar just proximal to the distal most bar. There was very little labelling in the skeletal region proximal to the view shown in this figure

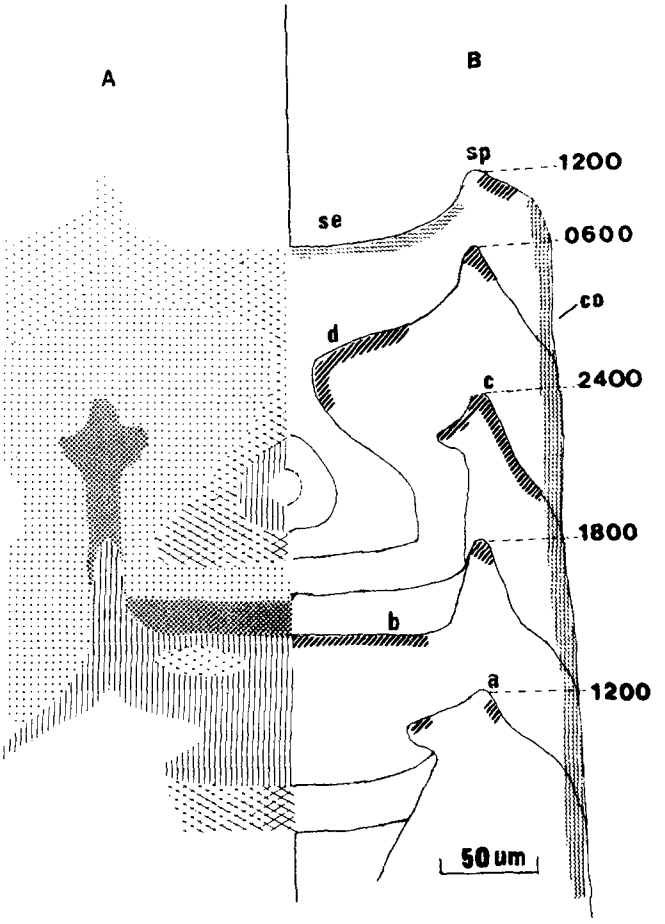

Fig. 5A, B. Summary of diel pattern of calcium carbonate accretion in the axial corallite of *Acropora cervicornis*. The two outermost spines (*sp*) connected by a bar, the scleroseptum (*se*) which terminates in a solid ridge, the costa (*co*) are depicted in this view. **A** This view portrays the extent of skeletal construction which occurs during each 6 h interval. Note the process of infilling in holes in the bar, left after rapid growth of the bar. 1200–1800 hours; 1800–2400 hours; 2400–0600 hours; 0600–1200 hours. **B** This view shows the linear extension of the spines during each 6 h interval (see text for details). The site of fasciculi and the site of predominantly fusiform crystals are indicated. The sites of the SEMs of Fig. 3 are designated: A: 1200 hours, B: 1800 hours, C: 2400 hours, D: 0600 hours

ling are combined in Fig. 5. A radial view of the two outermost spines with a connecting bar (a scleroseptum) is depicted. The portion of the skeleton deposited during each 6 h interval of the day is shown in Fig. 5. The relative linear extension during each time interval was not determined in this study. It is based on the proportion of the total daily extension deposited in a 6 h interval reported by Barnes and Crossland (1980) for rapidly extending tips of another staghorn coral. The axial spines and connecting bars have a similar diel pattern of development. Micritic fusiform crystals form a framework on the distal edges of the spines and bars at 1800, 2400 and 0600 hours. At 1200 hours, the apex of the spines and the distal surfaces of the bars are broad due to the development of the initial stages of the fasciculi. At all times of the day, fully developed fasciculi are found on the costa, ca. 150 μm from the tip.

Diel Pattern of Calicoblastic Tissue Morphology

To determine if the configuration of the calicoblastic ectoderm adjacent to the tips of the axial spines (Fig. 6) changes over a diel cycle I examined cryofracture preparations of decalcified axial polyps exposing the calicoblastic tissue surface at the tip. The results (shown in Fig. 6) indi-

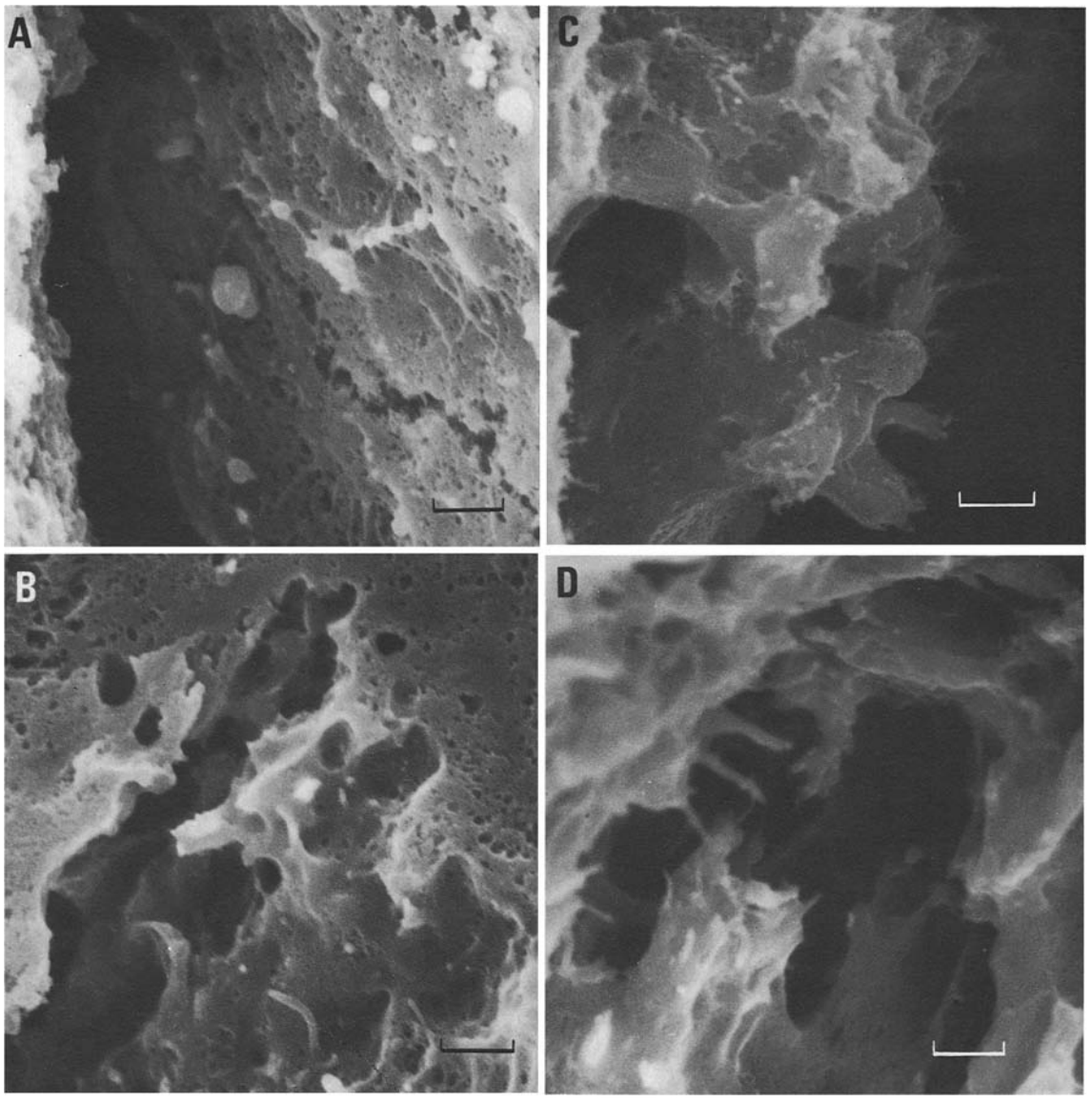

Fig. 6 A–D. SEMs of the calicoblastic membrane surfaces at the tip of the extending spines at different points during the diel cycle. Compare with comparable magnification SEMs of the axial spines (Fig. 3 A, C). Scale bar = 1.3 μm. **A** 1200 hours. Calicoblastic membrane is relatively smooth, with the presence of a few cell processes ca. 0.1 μm in width. **B** 1800 hours. Membrane has large pockets, 1–2.5 μm in width, with numerable cell processes ca. 1 μm long and 0.1 μm wide. **C** 2400 hours. Membrane similar to view **B** with several pockets and numerous cell processes. **D** 0600 hours. Cell membrane surface similar in appearance to that seen at 1800 and 2400 hours (**B, C**)

cate that the membrane at 1800, 2400 and 0600 hours (Fig. 6 B, C, D) has numerous pockets whose dimensions are the same order of magnitude as the fusiform crystals (ca. 1–2.5 μm) observed at the tips of the axial spines at those times of day. There are in addition numerous small projections (ca. 0.1 μm in width and up to ca. 1 μm in length) from the surfaces of the cells at these times. The effect of the projections is to greatly increase the surface of tissue adjacent to the skeleton. The surface of the calicoblastic ectodermal cells at 1200 hours, in contrast, is relatively smooth, having no large pockets and relatively few projections (Fig. 6 A).

The characteristic cell membrane surface at the tips of the spines at 1200 hours (Fig. 6 A) is also present proximal to the axial spines and is adjacent to skeletal surfaces composed of fasciculi at all times of the day (Fig. 7 A, B). The skeleton and the calicoblastic cell membrane surface are mirror image surfaces (Fig. 8 A, B). There are characteristic indentations in the tissue surface (Fig. 8 A) with the same dimensions at the surface features of the fasciculi (Fig. 8 B).

Mineralogy of the Skeleton

To identify the mineral of the crystals composing the skeleton of *A. cervicornis*, I examined ground samples of the axial corallite with the X-ray diffraction technique. The X-ray diffraction of the distal 2 mm of the axial corallite ($n = 3$) showed a predominance of aragonite (>98.5%),

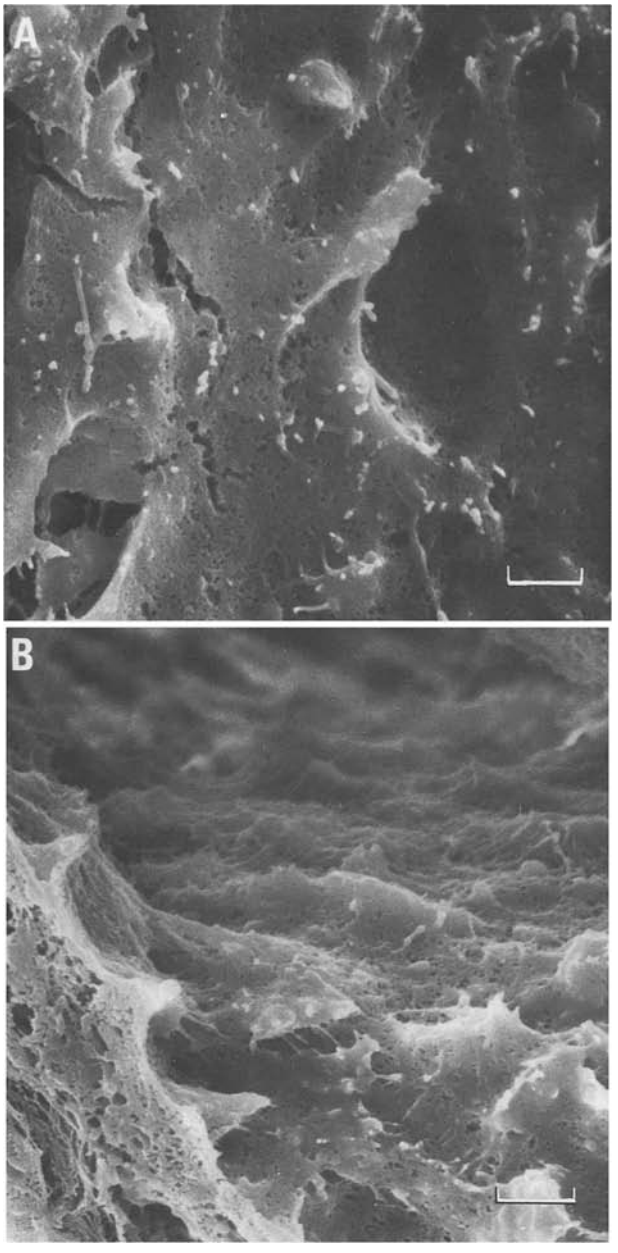

Fig. 7 A, B. SEMs of the calicoblastic membrane proximal to the tip, adjacent to a skeleton which has fully developed fasciculi. **A** 1200 hours. Calicoblastic cell membrane has a smooth appearance with a few small cell processes, and two folds about 10 μm apart. Scale bar = 2.5 μm. **B** 1800 hours. Calicoblastic cell membrane surface similar to that seen in **A**. Folds conforming to the shape of the ends of the fasciculi (ca. 5 μm) seen in cross section. Scale bar = 5 μm

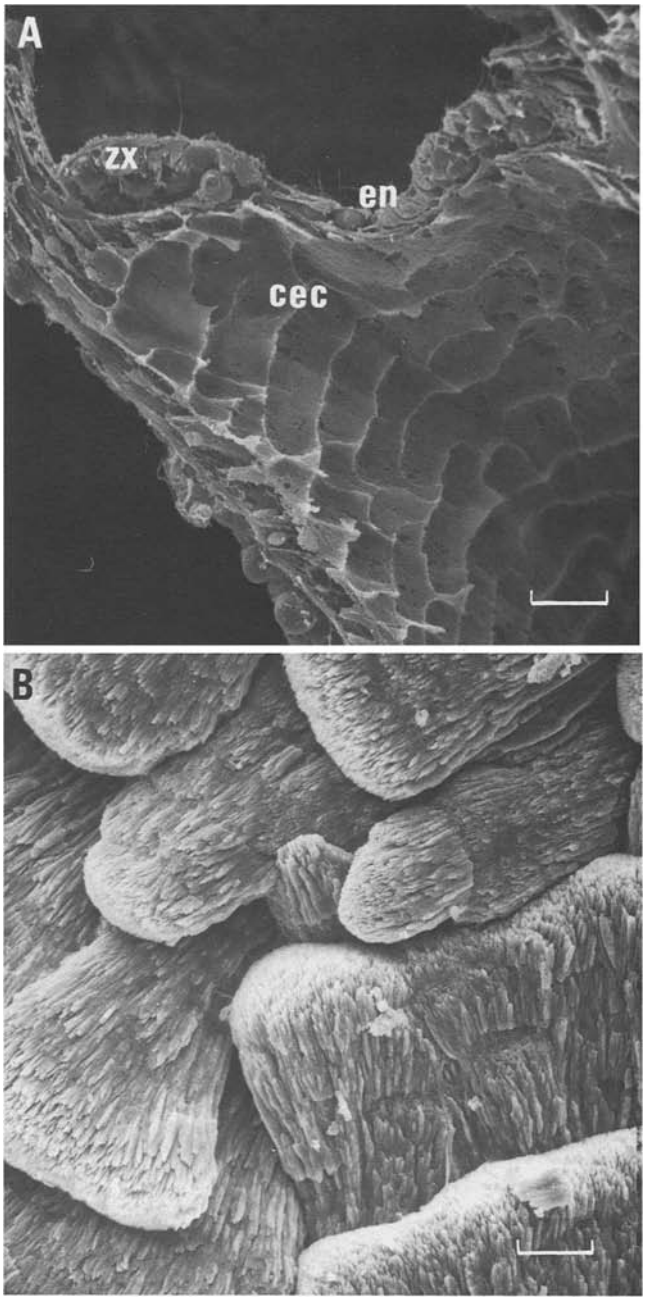

Fig. 8 A, B. SEM of the surface of the calicoblastic tissue and underlying skeleton of fully developed portions of the coral. **A** Calicoblastic ectoderm (*cec*) with folds corresponding to underlying fasciculi. Indentations in the tissue surface mirror the outer faces (ca. 10–15 μm wide) of fascicular bundles of aragonite needles: many fasciculi lie adjacent to one another, making parallel folds. The flagellated endoderm (*en*) contains zooxanthellae (*zx*); it is separated from the calicoblastic ectoderm by thin mesoglea. Scale bar = 12.5 μm. **B** Fasciculi composed of bundles of parallel aragonite needles. Scale bar = 5 μm

but a possible trace of calcite. Since calcite tends to incorporate Mg and discriminate against Sr and Ba, while aragonite has the opposite tendency (Milliman 1974), I examined the skeletal spines with an electron microprobe which can quantify the presence of trace amounts of elements. The center of skeletal spines are relatively enriched in the fusiform crystals of the framework. I found that the plots of Mg versus Sr counts from the electron microprobe revealed differences in the interior portions of some spines. Spines sampled had either a random distribution of points in all four quadrats or a distribution with a preponderance of points falling in the lower right (i.e. enriched in Mg, poor in Sr) and upper left (i.e. poor in Mg, enriched in Sr) quadrats. The points enriched in Mg were clustered towards the center

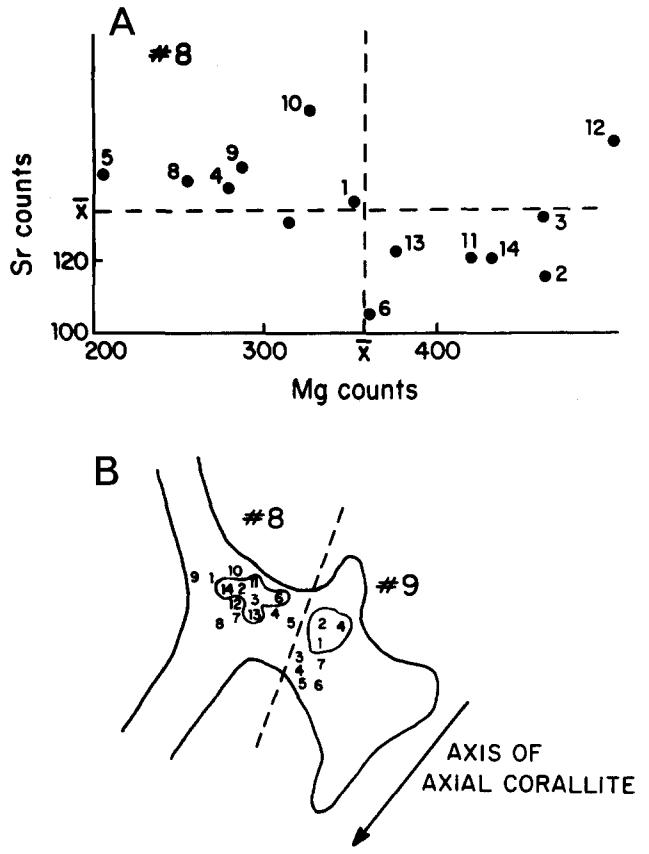

Fig. 9 A, B. An example of the results of electron microprobe analysis of a longitudinal section of the axial corallite. **A** Strontium and magnesium counts for one spine (No. 8) plotted against one another. The mean values of each set of counts forms a new set of zero axes. (Mg, $\bar{x}=360$; Sr, $\bar{x}=134$). Numbers on points refer to position sampled on spine (see **B**). Note that the points fall primarily in the upper left quadrat (indicating enrichment in Sr and less Mg than average) and the lower right quadrat (indicating enrichment in Mg, and less Sr than average). **B** Drawing of a skeletal element in which a portion of a spine (No. 8) and a portion of a bar (No. 9) have been analyzed with the electron microprobe. The points enclosed within the contour lines (i.e. 2, 3, 6, 11, 13, 14 for No. 8; 1, 2, 4 for No. 9) are all enriched with respect to Mg, and fall in the lower left quadrat of their respective graphs

of the skeletal element, while those enriched in Sr were found towards the outer boundary (Fig. 9). The counts of Ba were too similar to background controls to be useful.

Discussion

There is a diel temporal and structural pattern in the construction of the skeleton of *Acropora cervicornis*. Morphology of the crystal (fusiform or needle) and the site of deposition (axial spines, axial extension of bars or thickening of skeletal elements) vary systematically through the day. These observations lend support to the suggestion by Barnes and Crossland (1980) that "the symbiotic association [of zooxanthellae and coral] permits rapid growth because the coral can invest in flimsy scaffolding at night with certainty that the bricks and mortar will be available in the morning." Coral physiologists who are attempting to determine factors influencing light enhancement of calcification should note that two depositional processes are probably occurring. Calcium carbonate accretion during the day is primarily epitaxial growth on aragonite needles. These had been nucleated on the surface of a previously deposited fusiform crystal framework. Light enhancement of calcification, therefore, is likely to be a result of an increased rate of deposition on the aragonite needles (i.e., epitaxial growth). Peaks in "calcification capacity" (dawn and dusk) correspond to periods with much newly deposited framework material on the connecting bars between the spines (0600 and 1800 hours). These periods are times when the extending axial corallite has many new tufts of aragonite, i.e., the initial stages of the fasciculi deposited in the distal most portions of the skeleton. The many aragonite needles exposed on the surface of fasciculi provide an extensive surface area for rapid epitaxial growth. However, still unanswered are the questions: what conditions favor rapid epitaxial growth on aragonite needles, and how does light through the photosynthetic response of the algae enhance calcification?

Morphological and geochemical data suggest that the two types of crystals deposited in the skeleton of *Acropora cervicornis* might be different minerals. The first type, deposited as small (1–3 μm) fusiform crystals having a fish-scale-like surface texture, are similar in SEM appearance and size to high magnesium calcite crystals found precipitated in inorganic marine cements (Towe and Malone 1970; L.S. Land, personal communication). The microprobe data support the hypothesis that these might be calcite crystals because the center of some skeletal elements (presumably those in which the probe section exposed the central framework which is composed of fusiform crystals) show an increased Mg content and a decreased Sr content. There have been other reports of calcite occurring in scleractinian corals. Wainwright (1964) suggested its presence as a 1–2 μm thick initial deposit in the basal plate of *Pocillopora damicornis*; Vandermeulen and Watabe (1973) confirmed the presence of some calcite in the larval skeleton of *P. damicornis*. Barnes (1970) postulated that the initial mineral deposition in all larval scleractinian skeletons might be calcite. The only previous report of calcite in adult coral skeletons was made by Houck et al. (1975) on a sample of *Porites lobata* but this claim was later disputed by MacIntyre and Towe (1975) who suggested that the calcite might well have been deposited by boring organisms and not by the coral itself.

X-ray diffraction confirms that *Acropora cervicornis*, as other scleractinian corals, is predominantly composed of aragonite. The formation of spherulitic growths of aragonite needles is the beginning of the second kind of crystal deposition in the skeleton of *A. cervicornis* (Gladfelter 1982). The spherulitic growth form is typical of inorganically precipitated aragonite (Bryan and Hill 1941); the

constraint of adjoining crystals and calicoblastic tissue leads to the development of bundles of parallel aragonitic needles called fasciculi (Barnes 1970; Gladfelter 1982).

It is known that type of mineral, rate of nucleation and rate of crystal growth is influenced by the ionic and or organic content of the fluid from which the crystals precipitate (Kitano and Hood 1965; Kitano et al. 1976). With typical levels of Mg ions in the seawater (i.e. $1.2\ g \cdot l^{-1}$; Sverdrup et al. 1942), aragonite is the preferred precipitate of calcium carbonate (Milliman 1974). However, the presence of organic solutes such as citrate favors the deposition of high magnesium calcite; the greater the concentration of citrate, the greater the percentage of high magnesium calcite (Kitano et al. 1976). Similaly lower pH or the presence of sulfate or ammonium ions also favors the precipitation of calcite over aragonite (Milliman 1974). Once nucleated calcite has a slower rate of precipitation than does aragonite. The micritic fusiform crystals of the framework appear to serve as a surface for nucleation of aragonite needles. Nucleation on a foreign particle (i.e. in this case, the surface of the fusiform crystal) requires significantly lower supersaturation and free energy change than nucleation in the absence of a solid interface (Garside 1982). Epitaxic growth on the aragonite needles requires an even lower level of supersaturation. Thus, at sites in the skeleton where crystals are nucleated, the degree of supersaturation of the fluid between the tissue and the skeleton must be higher than at sites where only epitaxic growth occurs.

The high surface area of the calicoblastic membrane at the site and time of the most extensive fusiform crystal development and growth (i.e. the apex of the axial spines at 1800, 2400 and 0600 hours) might imply a regulation of the exchange of ions and soluble organic molecules between the interior and exterior of the calicoblastic cell. Ionic and organic content of a fluid exerts an important influence on the type of mineral which forms. The relatively low surface area of the calicoblastic membrane over the axial spine at 1200 hours, and at all sites adjacent to fasciculi at all times of the day could reflect the fact that continued epitaxial growth on extant crystals requires (1) a relatively low degree of supersaturation (see above) and (2) less control on the chemical composition of the fluid above the crystals, because aragonite is the most likely mineral to be deposited in a solution of tropical seawater (Milliman 1974; Kitano et al. 1976; Garside 1982).

Once the framework of fusiform crystals is deposited, the basic plan of the skeleton is complete. The axial spines are more acute in shape and almost entirely formed of fusiform crystals at 1800, 2400 and 0600 hours. At 1200 hours, presumably after a period of less rapid extension, the spines are much blunter in appearance with numerous tufts of aragonite. There are also numerous fusiform crystals present at 1200 hours, but these are generally smaller than those seen at other times during the day. Fewer and smaller fusiform crystals at 1200 hours may indicate that conditions favoring their nucleation and growth may not be as good at that time than at other times during the diel cycle. Yet, conditions favoring epitaxial growth on aragonite needles are at their best.

To summarize, there is a diel pattern in the development of the axial corallite of *Acropora cervicornis*. During the night (1800–0600 hours), the axial spines are pointed and composed primarily of fusiform crystals. During the day (0600–1800 hours) calcium carbonate accretion occurs on all surfaces of the distal portion of the skeleton, apparently by epitaxial growth on the aragonite needles composing the fasciculi. The axial spines then appear broad at their apices at noon and display numerous tufts of aragonite as well as scattered small fusiform crystals. Bars connecting the spines can be formed at any hour of the diel cycle, by the deposition of a fusiform framework, but thickening of the bars as well as the axial spines by addition of the aragonite needles takes place primarily in the light of day (0600–1800 hours). These patterns persist under laboratory conditions.

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