STRUCTURE AND INCREMENTAL GROWTH IN THE AHERMATYPIC CORAL *DESMOPHYLLUM CRISTAGALLI* FROM THE NORTH ATLANTIC

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ABSTRACT. *Desmophyllum cristagalli* has some characteristics in common with other ahermatypic corals living in deep water (2000 m for our specimens). This weakly colonial species is characterized by a theca greatly thickened by deposition of stereome, also forming massive deposits within the corallite and sometimes completely filling it. Septal trabeculae are uniformly small in diameter in this species, and tend to blend into a fine-grained septal 'dark line' when seen in transverse thin section. These characteristics are seen elsewhere in the family Caryophylliidae and also are noted in some other deep-water-dwelling ahermatypic corals. Incremental, perhaps periodic, growth of exoskeleton is noted in these specimens of *D. cristagalli*, although they originated in a deep, apparently stable environment.

BASIC microstructural and architectural features of the ubiquitous deep-water ahermatypic coral *Desmophyllum cristagalli* Milne Edwards and Haime, 1848, are similar but not identical to those described for shallow-water hermatypic corals (Sorauf 1970, 1972; Wise 1970; Jell 1974; Jell and Hill 1974). Even in their dark and cold-water environment, these corals exhibit incremental growth which may be periodic. Structural details of this species, together with data on ahermatypic corals from the families Caryophylliidae, Flabellidae, and Dendrophylliidae (Sorauf 1970; Sorauf and Podoff, in press), should eventually be of aid in interpreting fossil corals and their palaeoenvironments. These details are also judged of interest for the understanding of the mode of calcification in scleractinian corals and especially in determining the effect of algal symbionts (zooxanthellae) which are apparently of great importance in the calcification processes of reef-dwelling corals.

This study included optical and scanning electron microscopy of the micro-structure of specimens of *D. cristagalli* from a depth of 2000 m in the North Atlantic Ocean. This structure has been ascertained from study of external surfaces, broken transverse and longitudinal sections, thin sections, and polished and etched sections. This allows consideration of the mode of formation of theca and the lateral thickening of the septa by stereome, sometimes with the resultant total filling of the interseptal spaces, and also allows speculation on incremental growth of skeletal elements.

MATERIAL AND METHODS

Specimens of *D. cristagalli* were kindly made available for this study by Dr. J. R. Cann, Department of Environmental Sciences, University of East Anglia, Norwich, England. They are fresh-appearing specimens dredged from 2000 m at latitude 36° 34′ N., longitude 11° 46′ W. in the North Atlantic Ocean (Station 056 of the *Shackleton* 1972 cruise). The material has been deposited in the British Museum

(Natural History), London, and catalogue numbers refer to the coral register of the Palaeontology Department.

Material for scanning electron microscopy was prepared in a manner similar to that outlined by Sorauf (1972). Scanning electron microscopy was done on the AMR model 900 S.E.M. in the Department of Geological Sciences, State University of New York at Binghamton, and on the Cambridge Stereoscan S.E.M. model 1a, housed and operated by the University of Queensland Electron Microscope Centre, Brisbane.

Genus DESMOPHYLLUM Ehrenberg, 1836

Type species. D. cristagalli Milne Edwards and Haime, 1848, Holocene, from off Cape Breton.

The genus includes sessile, essentially solitary, trochoid forms, although loosely colonial forms consisting of many cornate corallites budding irregularly are known (Squires 1959, figs. 8, 10). The corallites are usually taller than wide, flaring upwards from a narrow cylindrical base and often fixed to the substrate by lateral cementation of the proximal parts. The septa are numerous, closely spaced, exsert, and extend to the axis. The genus is marked by a somewhat thick, dense wall composed largely of stereome; no epitheca is distinguishable. Costae are well developed near the calice but are obsolete and covered by stereome elsewhere in most species. Sparse endothecal dissepiments are developed in some of our specimens. Columella and pali are absent.

Desmophyllum is the nominate genus of an entirely ahermatypic subfamily of the family Caryophylliidae, itself largely composed of ahermatypic genera. The genus is widely distributed in all major oceans and in water as deep as 2000 m, with a fossil record dating back to the Middle Cretaceous (Wells 1956, p. F426).

Desmophyllum cristagalli Milne Edwards and Haime, 1848, p. 253

D. cristagalli is at present broadly interpreted, allowing a large amount of variation in this cosmopolitan coral. The microstructure of this species, or of any other species of *Desmophyllum*, has not been established previously.

Description of material. The two specimens studied are both broken basally so that the attachments are missing (Pl. 1, figs. 1–3); they are 35 and 40 mm in height with

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EXPLANATION OF PLATE 1

Figs. 1-6. *Desmophyllum cristagalli*, Recent, Atlantic Ocean. 1, transverse calicinal view of single corallite illustrating exsert septa (BMNH 1975.10.20.1), ×2. 2, longitudinal view of budded specimen to show costal ridges in the calicinal part of the individual and the granulose surface of the thick theca (BMNH 1975.10.20.2), ×2. 3, calicinal view of specimen in fig. 2 illustrating small individuals of *Trochocyathus* on skeleton. Note that sample has been rotated so that broken bud at base is that seen in fig. 2 (BMNH 1975.10.20.2), ×2. 4, photomicrograph of transverse thin section through exsert septa at calicinal margin showing central dark lines in septa and crystal orientation approaching perpendicularity to septal flanks (BMNH 1975.10.20.3), crossed nicols, ×25. 5, transverse thin section through immature portion of corallite with development of thick stereome on outside of small diameter corallite (BMNH 1975.10.20.3), crossed nicols, ×25. 6, transverse thin section through older portion of corallite with biogenic aragonite filling interseptal spaces to form solid massive cross-section (BMNH 1975.10.20.3), crossed nicols, ×25.

PLATE 1
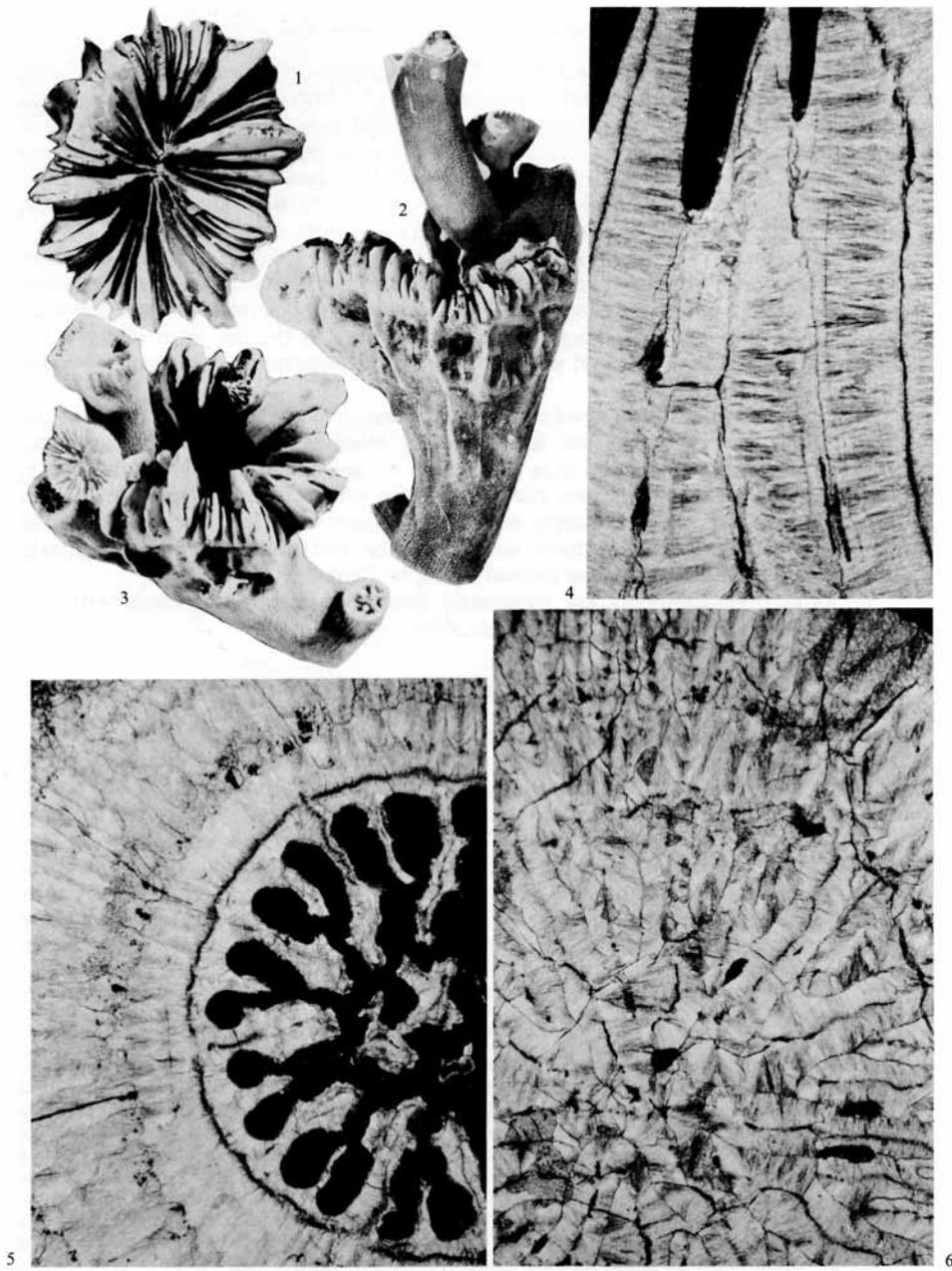
SORAUF and JELL, *Desmophyllum*

calical diameters of 18–25 mm and 19–25 mm respectively. Corallites are trochoid, flaring distally from slightly curved tubular bases (5–7 mm diameter) with the calices crowned by a series of prominent exsert septa. The walls of the basal parts of the corallites are thick and dense; the surface here is even but finely granulose whereas the upper 20 mm shows twelve well-developed costal ridges with the most prominent corresponding to the first cycle of septa (Pl. 1, figs. 1, 2). Both specimens show the basal attachments of juvenile corallites arising from these corallites.

Both specimens show the loosely colonial corallum (Pl. 1, figs. 2, 3). Some juveniles have developed by budding off from the parent while others have developed from planulae settling on an abandoned part of the corallum. The latter is most certainly the case for the small *Trochocyathus* individual seen at the left edge of fig. 3 on Plate 1. The coralla are coated with a fine layer of manganese oxide and the outer margin is deeply bored.

Septa in four cycles with nearly complete insertion of the fifth cycle, reach to the axis. Below the calice they are fine, flexuose, relatively smooth with occasional granulations and meet at the axis. They may be geniculate axially. In the calice, the septa thicken, especially over the calicinal rim where the exert septa are smooth and rounded. They descend steeply to the calical floor with their free axial portions showing prominent growth lines paralleling the proximal edge with regularly developed granulations likewise present on septal flanks.

Endothecal dissepiments are irregularly developed at varying levels with the first encountered immediately below the calice.

MICROSTRUCTURE

Septal structure. The septa of *D. cristagalli* have a tendency to break along a central zone within the septum (axial 'plane' of the septum), with the resultant exposure of this surface as seen in the scanning electron micrograph forming fig. 1 of Plate 2. Broken interfering clusters of aragonite crystallites (Pl. 2, fig. 2) are noted forming lateral additions to the axial zone. This thickening layer has crystallite clusters showing true physical interference with the growth of neighbouring clusters to form the septal flank material as noted here. This is somewhat different from septal flanks seen in many modern corals in that we note here a tendency for clusters to continue growth as somewhat coherent units, instead of forming crystallites oriented more

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EXPLANATION OF PLATE 2

Figs. 1–6. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, septum broken along axial plane with resultant wrinkled surface, gently curved crystals bending out from axial plane to form palisade at upper right, and crystal growth in interfering clusters which thicken septa, ×50. 2, enlargement of upper-right portion of fig. 1 showing bending crystal clusters and divergence of crystals within cluster, ×200. 3, axial surface with crystals bending out from central zone to thicken septum, and with a prominent plane of discontinuity within the palisade where one cluster of crystallites overgrows another, ×100. 4, view of broken surface of axial 'plane' of septum with apparent wrinkles, ×200. 5, broken crystallite clusters from 'growth wrinkle' shown in fig. 4, illustrating how crystal cluster growth deviates from axial plane, ×1000. 6, enlargement of another broken crystallite cluster showing tufting of crystallites along ridges, ×2000.

PLATE 2
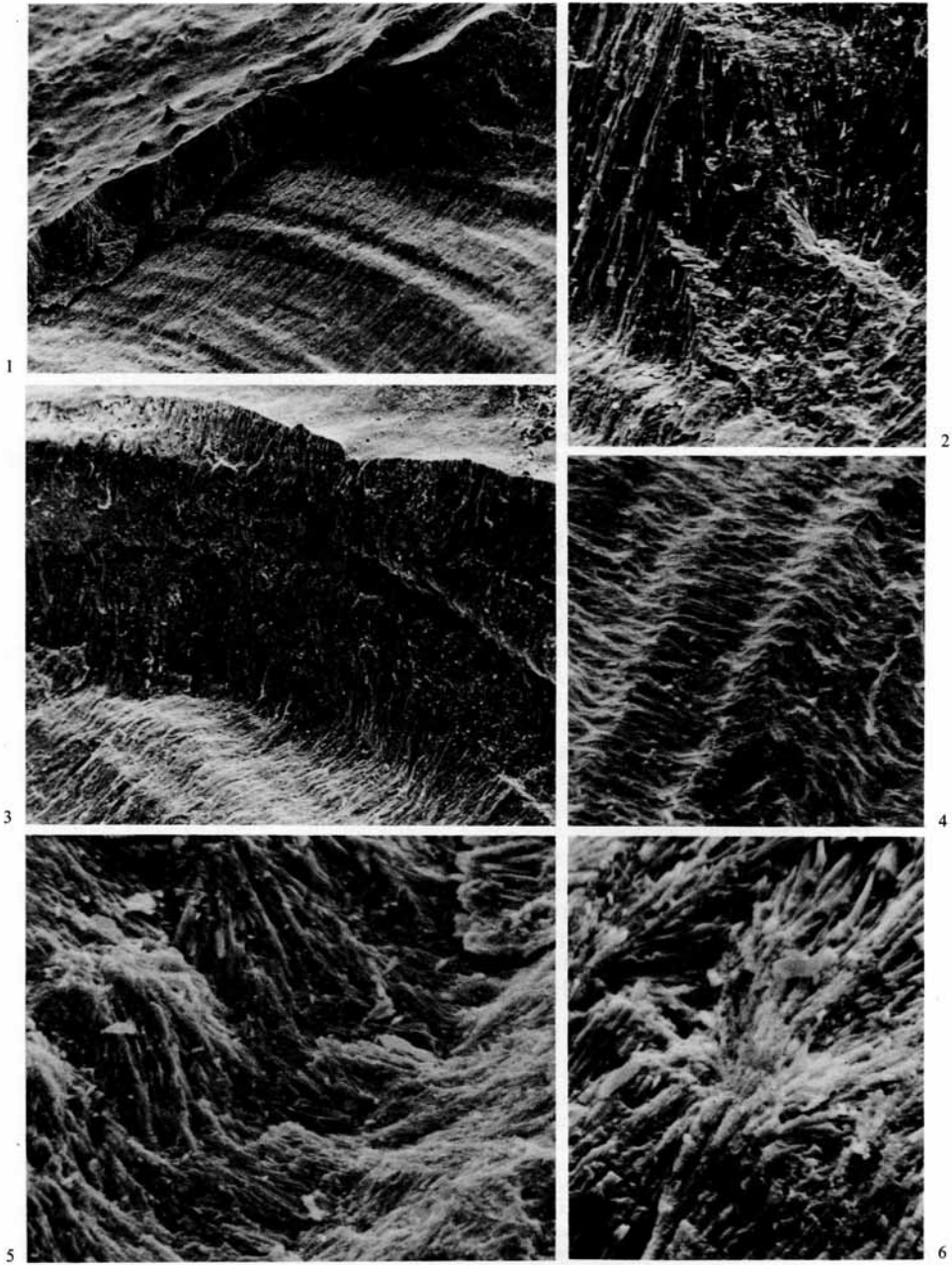
SORAUF and JELL, *Desmophyllum*

or less parallel to one another and perpendicular to the outer surface of the skeletal element. It should here also be noted that *Desmophyllum*, unlike other corals studied in detail (to date), has a very different aspect in sections broken parallel to the axial zone of the septum (as in Pl. 2, fig. 2), and sections broken perpendicular to the long axis, along incremental growth lines (Pl. 2, figs. 1, 3). In the latter case, crystallites are close to parallel as they bend out from a growth 'ridge', contrasting with the interfering clusters noted previously in sections with the orientation parallel to the axial zone (Pl. 2, fig. 2). The relationship between crystallite growth clusters, each cluster expanding rapidly, is a relationship of competition for space and mutual interference. There are definite victorious clusters in each interfering pair, with resultant overgrowth. One such line of overgrowth is shown in fig. 3 of Plate 2.
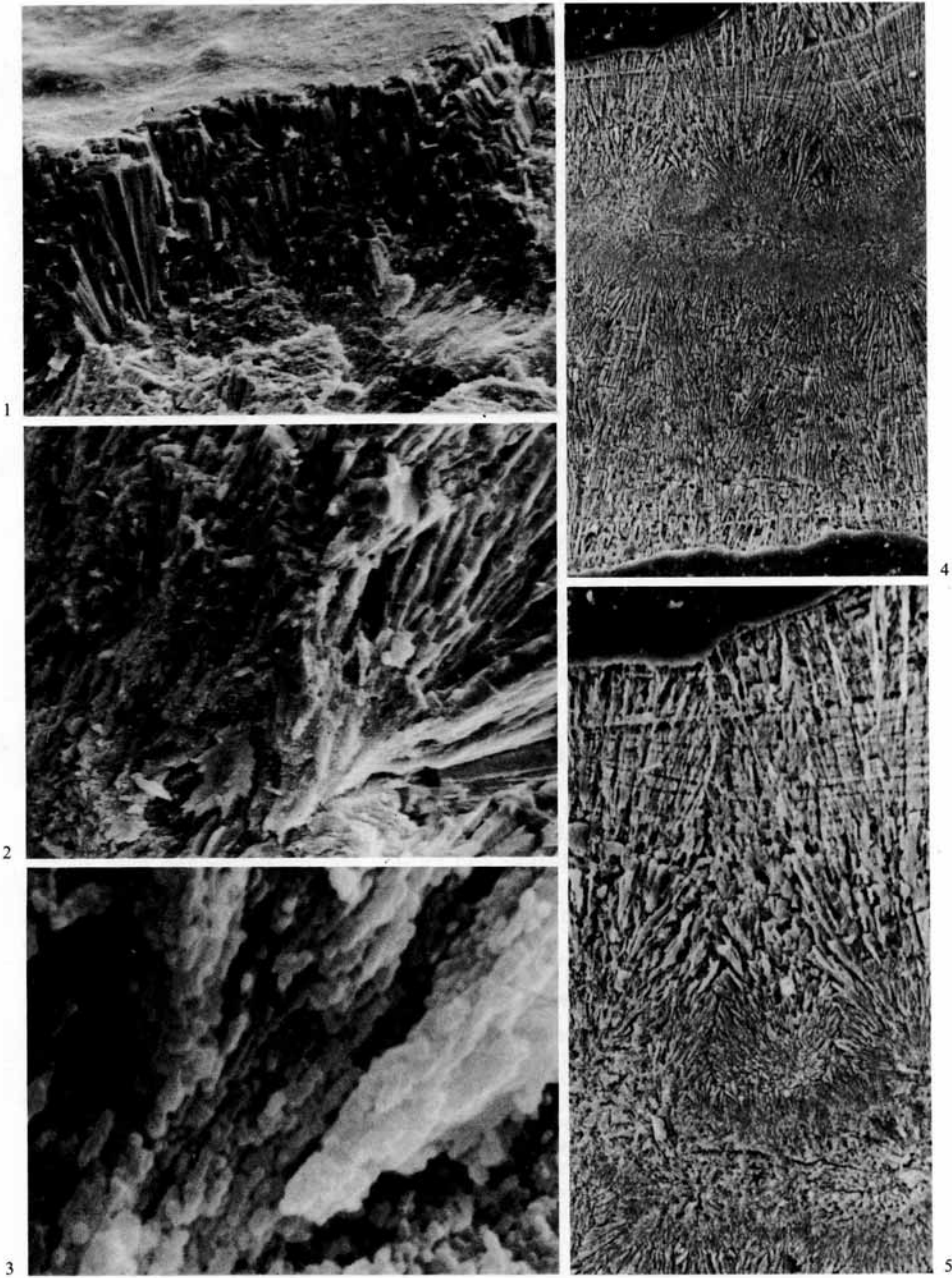
The broken surface of the axial region of the septum is wrinkled (Pl. 2, fig. 4) by ridges formed by broken crystallite clusters which diverge from the axial plane of the septum (Pl. 2, fig. 5). Upon close inspection, one notes broken tufts of crystallites (Pl. 2, fig. 6) where calcification has apparently been rapid and crystals diverging greatly. These clusters then form the palisaded thickening of the septa (Pl. 3, fig. 1). Within individual clusters (Pl. 3, fig. 2) a difference in perfection of crystallites is noted, with sub-rounded crystal forms common at the apex and broad, dense, large crystallites forming further out from the apex (Pl. 3, figs. 2, 3). The latter are most likely compound, but fracture as single crystal units.

Thin sections transverse to septa near the calicinal rim show the development of lateral crystallites approximately perpendicular to the flank surface of the septum, and diverging from a thin central row of very fine trabeculae (Pl. 1, fig. 4), which appears as a 'central dark line' in low-power photomicrographs (Pl. 1, fig. 4). The laterally contiguous trabeculae are of small diameter and composed of extremely fine crystallites (Pl. 3, figs. 4, 5). At these higher magnifications, it is also clear that the outer flanks of the septa are formed by mutually interfering radiating clusters of crystals, here with growth lines etched into prominence (Pl. 3, figs. 4, 5). In these last figures, the surprisingly cohesive nature of the clusters is also well shown.

In transverse thin sections of septa in a branch corallite, it can likewise be noted that the 'dark line' is not uniformly developed as an axial plane that is apparent in all septa (Pl. 4, fig. 1), as commonly the trabecular centres are only weakly developed. However, when the trace of a septal axis is followed back into the theca, well-defined and well-rounded trabecular centres can be seen clearly developed, but of extremely small diameter (Pl. 4, fig. 2). This is the position of maximal septal growth, where septa are exsert, and additionally, in this position the cross-section is perpendicular

PLATE 3

SORAUF and JELL, *Desmophyllum*

to the trace of the trabecular axes. Orientation is thus playing an important role in allowing visual definition of the septal trabeculae.

Transverse thin sections in the stock of a budded corallite show that at first glance (Pl. 1, fig. 6; Pl. 4, fig. 3) it is difficult to distinguish septa from infilled interseptal spaces. The central portions of the corallite, where stereome is abundant, show crystallites filling the interseptal areas that are the same size and have the same orientation as those in the lateral part of the septum (Pl. 4, figs. 4, 5). They most simply represent continued crystallite growth into the interseptal spaces until all available space is occupied.

Longitudinal sections of the septa of *Desmophyllum* differ somewhat depending on whether the section passes close to the axial zone of the septum or the septal flank. In the latter case, the view is virtually indistinguishable from longitudinal sections through the theca.

The simplest geometrical arrangement of the very small diameter trabeculae (or trabecula-like bundles) is seen in longitudinal sections which pass close to but not directly along the axial zone of the septum. A section here (Pl. 5, fig. 1) shows several rows of trabeculae diverging from the general axial zone (right side), with small diameter trabeculae seen almost in longitudinal section here to the left of the laterally directed rows of trabeculae. Those trabeculae seen in longitudinal section are regarded as showing the main growth direction of the septa and forming the 'dark line', seen in photomicrographs (Pl. 5, fig. 2). The trabeculae seen in longitudinal section gradually bend or branch so that some crystallites grow perpendicular to the septal flank and form stereome indistinguishable from that infilling interseptal spaces and forming theca (Pl. 5, fig. 4). Where micrographs include a portion of the septal flank material, the 'dark line' of fine trabeculae is interrupted by the presence of larger, parallel crystallites with growth lines within them (Pl. 5, fig. 3). In these sections, it should be noted that there is only an important and easily visible growth line between trabeculae and septal stereome. This is as noted previously in transverse sections (Pl. 4, figs. 4, 5). This is also shown (Pl. 5, figs. 1 and 4; Pl. 6, fig. 3) where trabeculae are seen grading into bundles of larger crystallites which in turn grade into stereome with ill-defined trabecular centres.

In longitudinal sections paralleling and closely approximating the path of the axial plane of the septum, much more divergence of rows of trabeculae is seen. As was noted previously, in broken sections regular rows of trabeculae diverge from


EXPLANATION OF PLATE 4

Figs. 1–5. Photomicrographs (1, 3) and scanning electron micrographs (2, 4, 5) of *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, photomicrograph of septa and theca in immature portion of corallite with central dark line in septa and also with dark line of divergence outlining centre of early septotheca, crossed nicols, ×63. 2, transverse section within theca showing clear development of septal trabeculae, ×1000. 3, transverse thin section of stock of budded corallite showing complete filling by crystallite growth, with interseptal spaces difficult to differentiate from septa, crossed nicols, ×63. 4, overview of septum in transverse section with continued crystal growth over prominent growth line into interseptal space, ×500. 5, enlarged portion of fig. 4 showing that crystal orientation and position does not change from septum (on right) into lumen. Margin of septum is marked by prominent growth line, ×2000.
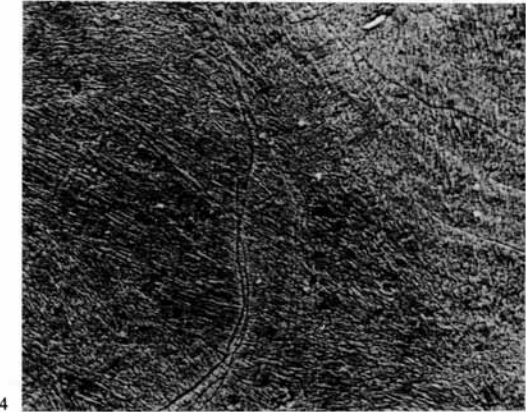
PLATE 4
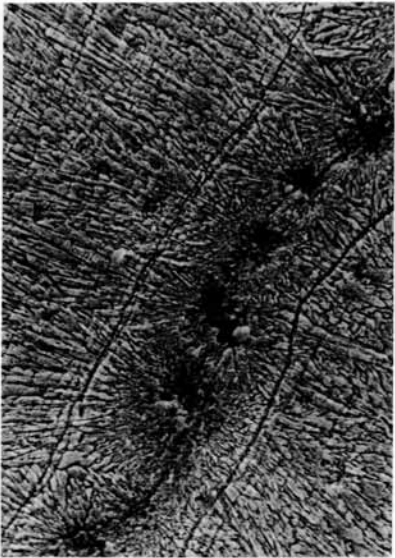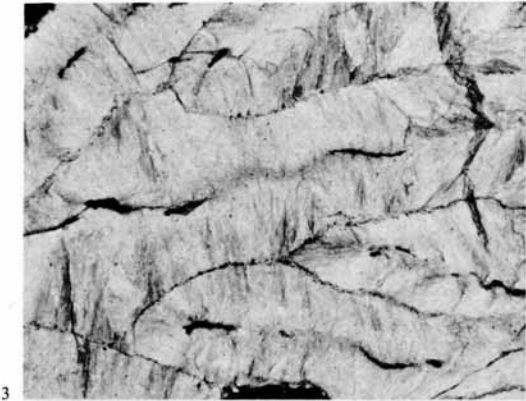
SORAUF and JELL, *Desmophyllum*

the axial zone and bend outward toward the septal flank. These lateral outgrowths are in the form of diverging clusters and interfere with each other within the same generation, as well as with other rows of clusters (commonly overgrown).

Two types of growth lines are seen, one a line occurring on individual crystallites (Pl. 8, fig. 1), in which etching exaggerates a crystal discontinuity, and a second type formed by rows of diverging trabeculae. This bending of trabeculae out of the axial plane of the septum produces striking and informative polished and etched sections.

Growth parallel to the axial zone, with large crystallites, is common (Pl. 6, fig. 2) with growth punctuated by easily identifiable growth lines. At the top of this sequence can be seen a breaking down of large crystallites into smaller branching crystallites. This row of branching crystallites is then followed by one or more rows of trabeculae which diverge at a high angle from the axial plane forming a striking visual discontinuity with pre-existing crystal clusters (Pl. 6, figs. 2–4). This may well be the type of discordance where the row of tufted crystallites is seen overgrown by the overlying trabeculae (Pl. 6, fig. 4) or there can be a bending of the row of tufted crystallites to form trabeculae (Pl. 7, fig. 1). The discordant arrangement is commoner in our material with layers of trabeculae and overgrown crystallites (Pl. 6, fig. 4). Crystal sizes generally present at the corners of junctions of trabeculae are generally slightly larger than usual, perhaps an indication of additional space for growth. In this figure, the approach towards stereome at the left of the micrograph is shown by the presence of larger crystal sizes at the side of the micrograph.

In the inner septal stereome of the flank, there is a rapid increase in the diffuseness of the trabecular centres as distance from the axial plane increases (Pl. 7, figs. 2, 3).

Stereome, thecal. One of the striking characteristics noted in the subfamily Desmophyllinae (especially in *Desmophyllum* and *Lophelia*) is the presence of a wall and septa thickened by deposition of stereome (secondary biogenic aragonite). This section deals with the thick outer wall, characterized by dense stereome.

In thin sections of young individuals, it can be seen (Pl. 1, fig. 5; Pl. 4, fig. 1) that a dark line surrounds the calice and is apparently identical to and in places contiguous with the dark line of septa. The dark line in the theca results from the intersection of the plane of the thin section with a cylindrical zone of divergence of growing crystallites. This line, referred to here as the calicinal dark line, may be analogous to the septal 'dark line' (or axial zone), but it is apparently not trabecular in nature.

EXPLANATION OF PLATE 5

Figs. 1–4. Photomicrograph (2) and scanning electron micrographs (1, 3, 4), *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, longitudinal section close to axial plane of septum with individual trabeculae easily distinguishable where they diverge from the axial plane (at right) and more difficult to isolate where they more closely parallel the septal plane, ×1000. 2, somewhat oblique longitudinal thin section illustrating somewhat smeared out central dark line (arrow), crossed nicols, ×63. 3, longitudinal section showing coarser crystallites developed parallel to, but away from axial plane where plane is wrinkled (thus more distant at this position), ×1000. 4, longitudinal section showing trabeculae paralleling axial plane at right centre and gradually bending out to form stereome (at left) without trabecular centres, ×1000.

PLATE 5
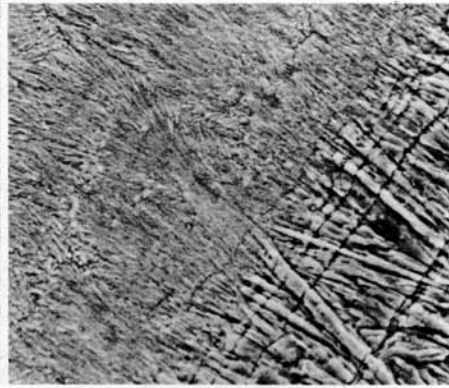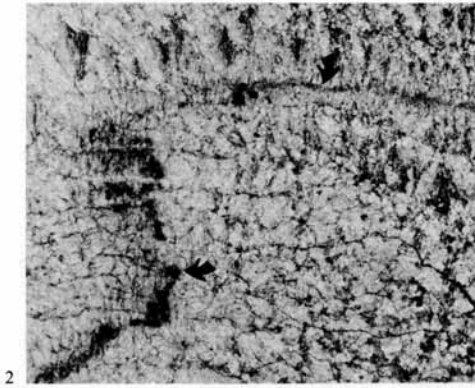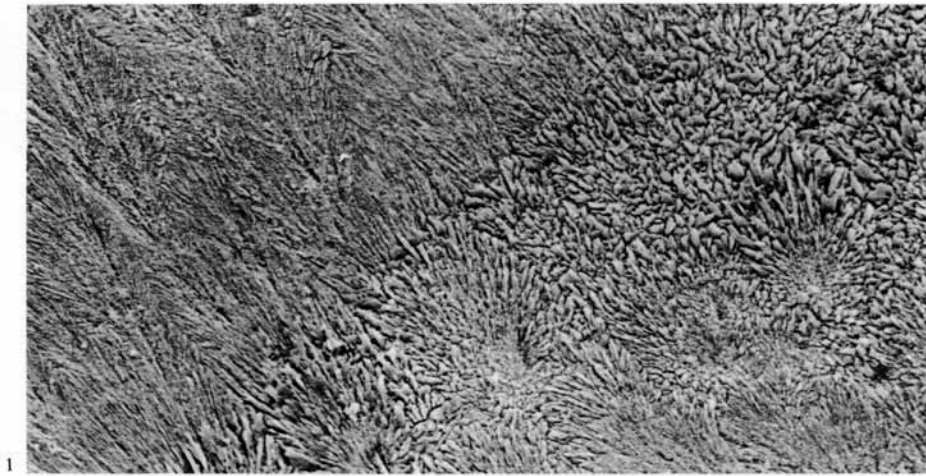
SORAUF and JELL, *Desmophyllum*

It can be seen that where septa and theca intersect (Pl. 4, fig. 2) septal trabeculae are readily distinguished from the 'dark line' in the theca resulting from divergence of crystallites.

Photomicrographs (Pl. 1, fig. 5; Pl. 4, fig. 1) show a definite discontinuity exterior to the calicinal dark ring. This discontinuity is apparently the result of contrast between inner, more ordered, dense aragonite crystallite clusters, and an outer, less orderly secondary biogenic stereome added to the maturing corallite. As can be seen in photomicrographs (Pl. 1, fig. 5), the outer wall is totally composed of semi-continuous crystallite clusters with axes of calcification perpendicular to the surface of the theca and divergence of crystallites from the axes. These differ from septal trabeculae mainly in their lack of discrete centres of finer crystallites. The stereome is composed of crystal clusters growing in subparallel arrangement, as in septal thickening (Pl. 7, fig. 3) and it is only in the interior portions of the wall that axes of divergence are clearly noted (Pl. 7, fig. 4) and a short distance from the axial plane one is hard put to identify such organization in tangential section.

The outer surface of the wall of *Desmophyllum* is granulated but with a smooth microarchitecture (Pl. 7, fig. 5) and normally no individual crystallite ends can be seen even at magnifications of several thousand times natural size. However, in the area between the septal ridges at the top of corallites, crystallite growth edges are readily apparent (Pl. 8, figs. 1, 2). This area is occupied by the edge zone of the coral (according to Squires 1959, p. 19), and is obviously where continuing calcification and thickening of theca is occurring.

Stereome, calicinal filling. Our specimens of *Desmophyllum* are characterized at least partially by infilling of interseptal spaces, presenting the aspect of having the entire lumen filled with stereome in earlier stages (Pl. 1, fig. 6; Pl. 4, fig. 3). It may be that this characteristic is a basal support method at times alternative to development of tabular dissepiments such as seen occasionally in adult *Desmophyllum* and as described previously in *Lophelia* (Sorauf 1970, p. 11). Such complete infilling is also seen in the solitary genera *Flabellum*, *Caryophyllia*, *Balanophyllia*, and *Thecopsammia* (Sorauf and Podoff, in press).

Septal thickening is due to continued growth of aragonite crystallites which lose their well-defined centres of calcification as distance from the axial zone increases (Pl. 7, figs. 2, 3). In a polished and etched section of a stereome-filled corallite (Pl. 4,

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EXPLANATION OF PLATE 6

Figs. 1–4. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, longitudinal micrograph with marked growth lines (exaggerated by etching) cutting straight across crystal growth direction, ×1000. 2, longitudinal section showing growth lines as in fig. 1, but also illustrating growth discontinuity by overgrowth of trabeculae at top that have diverged greatly from the axial plane and the apparent increased number of smaller crystals at the top of the growth cycle below the discontinuity, ×1000. 3, longitudinal section parallel to but at a distance from the axial zone of the septum, with trabecular centres not distinguishable within septal stereome at left, ×1000. 4, longitudinal section showing trabeculae, changing orientation angles, and rather sharp discontinuity with overlying crystal clusters, ×2000.

PLATE 6
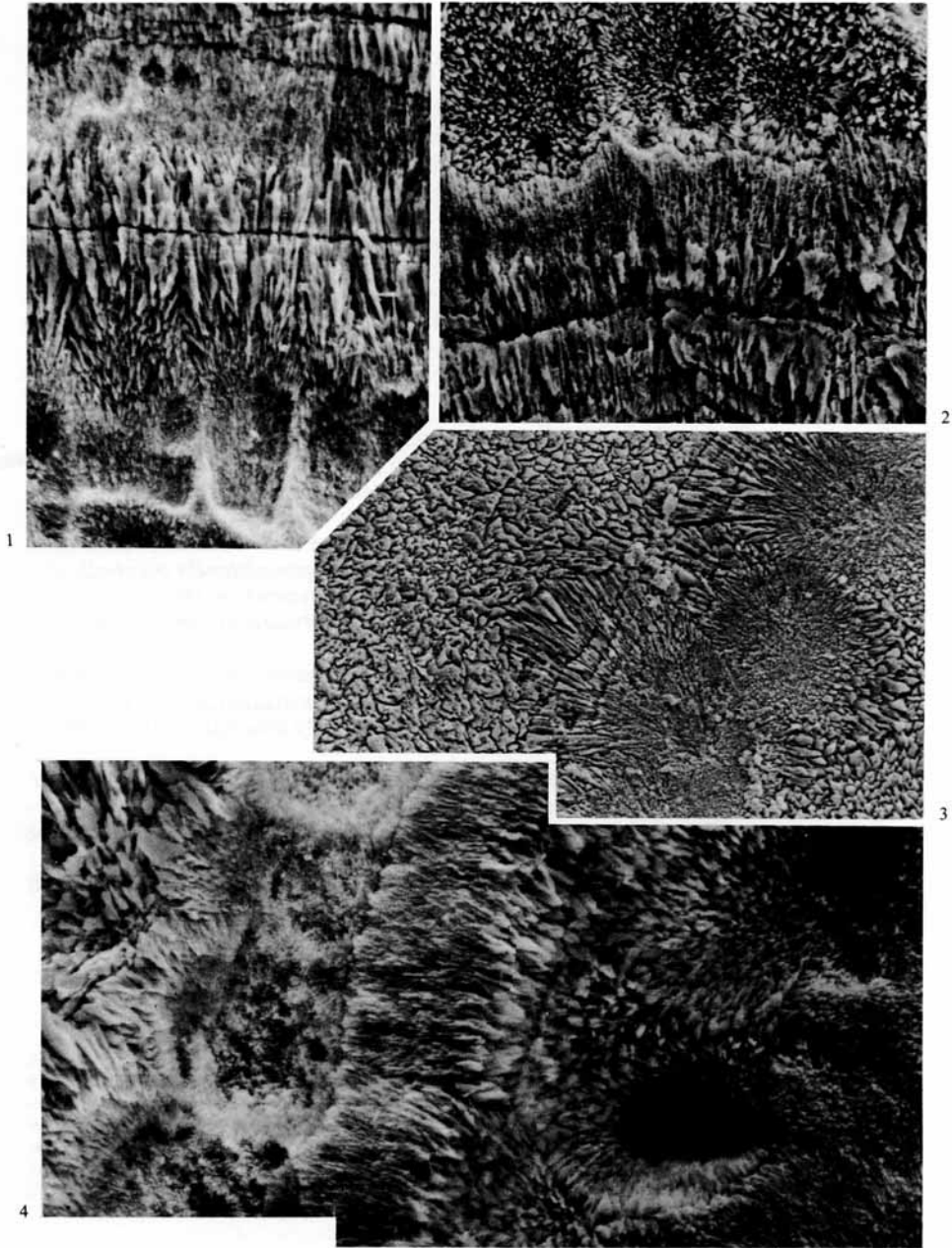
SORAUF and JELL, *Desmophyllum*

figs. 4, 5) the interseptal stereome is seen formed by continued epitaxial crystal growth out from septal flanks. Growing crystallites join at a midline with those growing out from a neighbouring septum. Thus, the mass of infilling crystals is distinguished in crystallite size and habit from those in septal flanks only by the presence of more prominent growth lines in the latter. There is apparently a halt in crystal growth when the septum is completed, with later overgrowth occurring with the same size, shape, crystallographic orientation, and position as those crystals forming the septal flanks.

This form of crystal growth and the characteristic of forming a continuous floor to the calice is shared with *Lophelia* and other members of the family group that are characterized by tabular dissepiments. As previously noted (Sorauf 1970), the dissepiments in *Lophelia* are formed of a sheet of crystallites that are continuous with those sheets that thicken septa. In *Desmophyllum* dissepiments with a continuous blanket of crystallites occur occasionally, as well as the complete infilling by stereome in early stages.

Dissepiments. Dissepiments are sparse but present in each of the large corallites in our sample. The dissepiments are very similar to those of the *L. prolifera* described by Sorauf (1970, p. 11). As seen in scanning micrographs, the dissepiments completely fill the interseptal spaces (Pl. 8, fig. 3), thus are referred to as tabular dissepiments. As seen from the upper or distal side, the surface is more or less featureless, and is composed of a carpet of small crystallites growing approximately perpendicular to this surface (Pl. 8, fig. 4). The septal thickening (stereome) on the flanks of the septa appears to be continuous with the upper layer of crystals on the dissepiments, just as in *L. prolifera*.

The under surface (proximal) is characterized by a prominent central junction groove, and weak growth lines (Pl. 8, fig. 5), and at higher magnifications, this under surface is seen to be formed by laterally growing, centrally directed, weakly bundled crystallites (Pl. 8, fig. 6).

Thus, in all major aspects these dissepiments are similar to those of *Lophelia*, colonial ahermatype closely related to *Desmophyllum* and also found in deep waters of the Atlantic. The main variation between the two is the occurrence of stereome infilling the calices of small diameter, budded corallites in *Desmophyllum*; tabular dissepiments are more sparse in *Desmophyllum*, and apparently restricted to adult corallites.

EXPLANATION OF PLATE 7

Figs. 1-5. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, somewhat oblique longitudinal section to illustrate appearance of trabeculae which are parallel to the axial plane at the lower left, but are above bent out at a considerable angle of deflection, × 1000. 2, longitudinal section showing transition into septal stereome in which trabecular centres are still discernible, × 500. 3, longitudinal section of crystallites in septum growing in subparallel fashion perpendicular to plane of etched section, × 500. 4, transverse view of early part of theca to illustrate one single row of crystal clusters growing towards former margin, here with manganese (?) crust not etched by EDTA, × 300. 5, individual granulation on outer flank of theca, × 2000.

PLATE 7
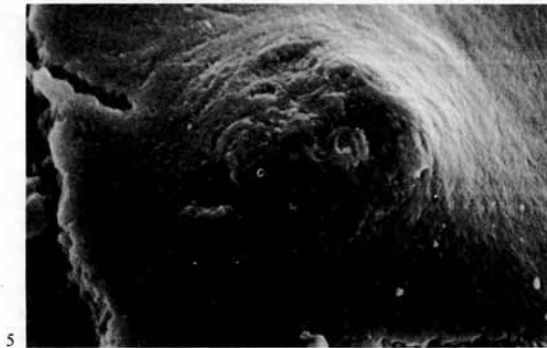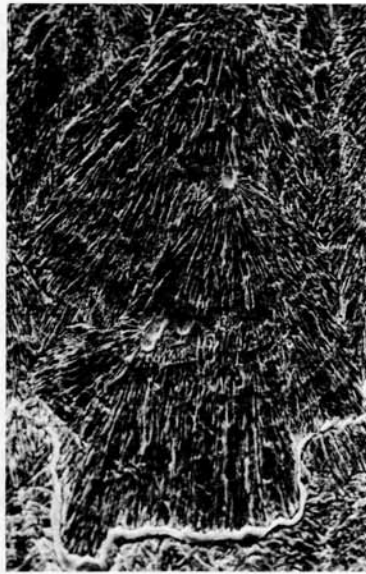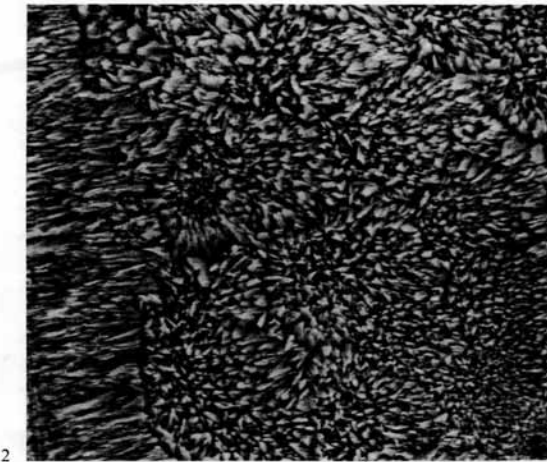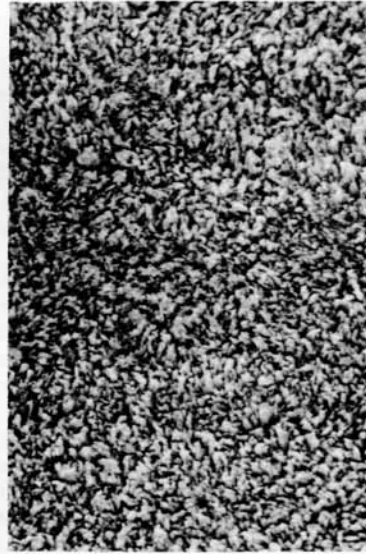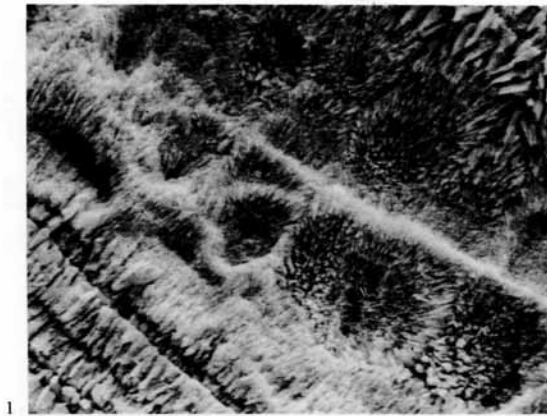
SORAUF and JELL, *Desmophyllum*

INCREMENTAL GROWTH

Apparent wrinkling in the axial zone of septa has been shown to be an artifact of breaking rows of rapidly expanding (laterally diverging) crystallite clusters. It seems apparent that the coral exoskeleton is being formed at varying rates, and that an increase in crystallization rate causes a lateral expansion of a crystallite cluster system, with very fine trabeculae formed. These most commonly overgrow pre-existing trabecular groups with an apparent discontinuity (Pl. 2, figs. 2, 3; Pl. 6, figs. 1, 2, 4). This lateral growth then reflects times of more rapid calcification, alternating with times of slower accretion represented by lesser developed clusters.

Such incremental growth is also noted in trabeculae, dissepiments, and stereome. Growth lines (as opposed to the septal wrinkling) are also noted within the crystals forming flanks of septa (Pl. 3, figs. 4, 5) and growth 'rings' are seen in the thecal stereome (Pl. 1, figs. 5, 6). These growth increments are at the least episodic and apparently periodic, since the size of increments is rather uniform for any single skeletal element.

Periodic incremental growth in hermatypic, shallow-water corals is strongly influenced by the presence of symbiotic zooxanthellae (Goreau 1959). However, Goreau also found that calcification in hermatypic corals did continue during periods of darkness, although at a lesser rate apparently connected to inactivity of the zooxanthellae, and was able to conclude that the secretion of the enzyme carbo-anhydrase is important in the calcification of the hermatypic skeleton. It should perhaps also be supposed that deep-water-dwelling ahermatypic corals, forming skeleton under adverse conditions of low carbonate concentrations, low tempera-tures, and high water pressures without the aid of algal symbionts, must have a remarkable ability for enzyme production to aid in the calcification process.

Wells (1970, p. 7) has discussed the growth periodicity in ahermatypic corals as well as in hermatypic forms. He has assumed that periodic growth in both groups has the same underlying control or set of controls. Possible causes were listed as follows: 1, daily fluctuations in nutrient supply; 2, daily tidal flux; 3, daily tempera-ture variations; 4, diurnal variations in terrestrial magnetism; and 5, biological clock control.

Of these, only the latter two are considered as potential controls in the case of the *Desmophyllum* specimens discussed here. The effect of variations in terrestrial

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EXPLANATION OF PLATE 8

Figs. 1–6. Scanning electron micrographs, *Desmophyllum cristagalli* (BMNH 1975.10.20.3), Recent, Atlantic Ocean. 1, exterior of theca near calicinal termination illustrating septal costa and interseptal area with crystal faces developed. Note also boring in this portion of specimen, ×1000. 2, enlargement of crystal faces in interseptal area, ×5000. 3, overview of upper (or distal) side of dissepiments which completely fill area between septa, here broken away to expose featureless upper surface of dissepiment, ×22. 4, enlarged view of crystal carpet forming upper surface of dissepiment, ×2200. 5, overview of underside (proximal side) of dissepiment illustrating the central junction groove and weak growth lines on this surface, ×50. 6, enlargement of undersurface illustrated in fig. 5, showing weakly bundled nature of crystallites growing from septum in lower-right corner of micrograph to junction groove at top left of micrograph. Note too the weak development of growth ridges, ×240.

PLATE 8
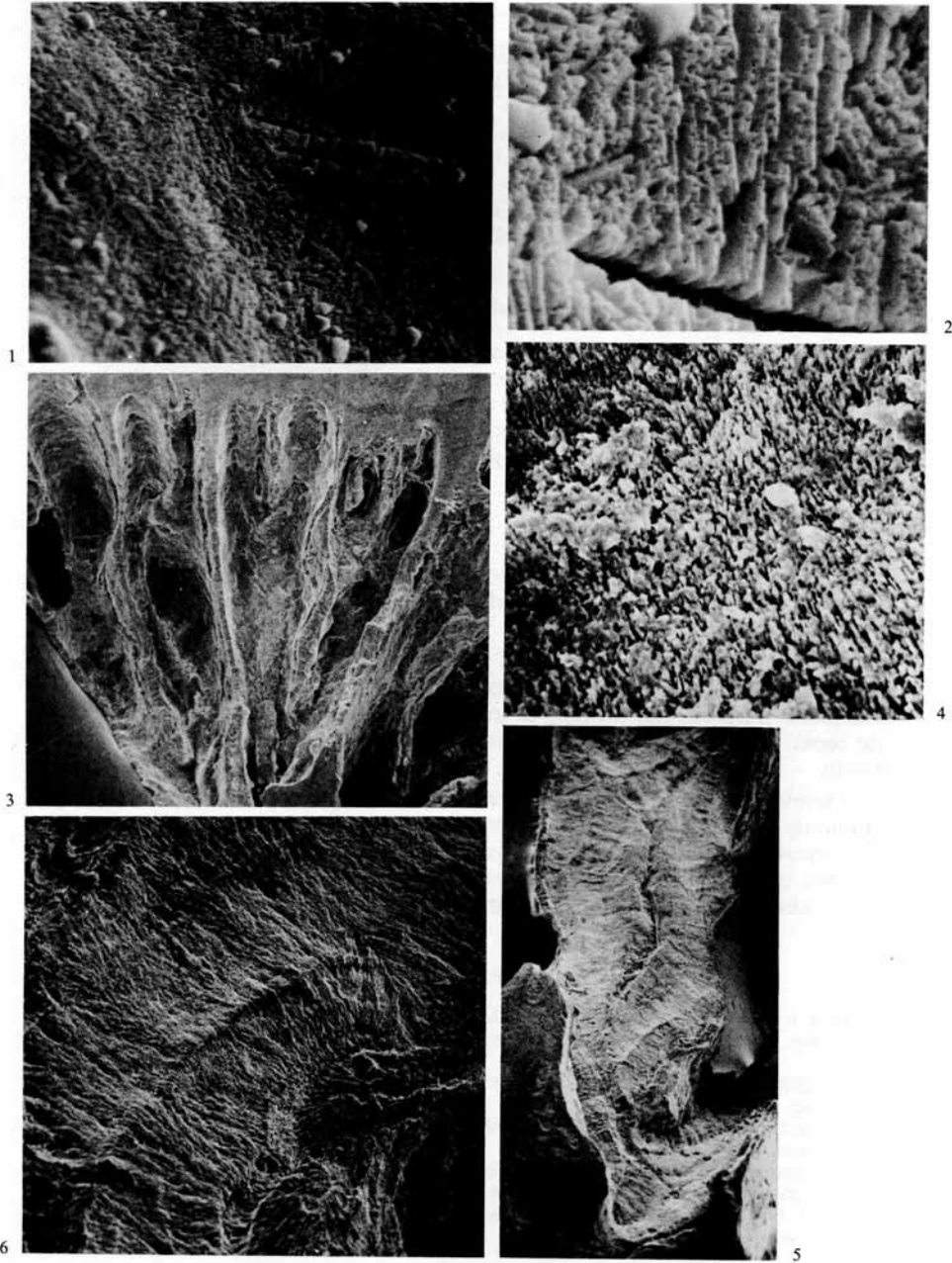
SORAUF and JELL, *Desmophyllum*

magnetism cannot at present be evaluated. The last, a biological clock control, seems possible, and may be connected with enzyme production tied to a feeding cycle based on energy requirements of the coral polyps. These requirements would by necessity be inherited, thus the feeding cycle would also be inherited in a sense, although perhaps with considerable modification. The growth increments noted here within *Desmophyllum* are in the proper size range to be diurnal, but as yet there is no real proof that they are in fact diurnal, whether in the sense of a 24-hour day or in the sense of an 'inherited' day of other than 24 hours.

CONCLUSIONS

D. cristagalli as represented by the material available to us has a certain number of skeletal characteristics which may prove helpful both in recognizing allied genera in the fossil state, and also in interpreting structures seen in other groups of fossil corals. Eventually it is hoped that knowledge of structure may help define extinct groups of ahermatypic corals and aid in the environmental interpretations of coral-bearing strata.

D. cristagalli has the following:

1. Septal structure which is similar to that recognized as fibro-normal in fossil corals. It is supposed that the very fine septal trabeculae in genera such as *Desmophyllum* would be easily obliterated during diagenesis, resulting in a truly fibro-normal structure.

2. Wrinkling along the septal axial planes caused by the divergence of rows of fine trabeculae out of the axial orientation and into an orientation normal to the axial plane. Such extreme bending of trabeculae is abnormal for corals with trabeculate septa. This wrinkling is apparently periodic and a reflection of incremental growth.

3. Development of a covering of stereome thickening both the theca and the septa, commonly resulting in the complete infilling of the basal portion of the corallite. The formation of this secondary biogenic blanketing of all skeletal features creates a definite unity of skeletal structure, more than typical for scleractinian corals. This unity is also noted in some other ahermatypic corals.

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