

SKELETAL MICROSTRUCTURE AND MICROARCHITECTURE IN SCLERACTINIA (COELENTERATA)

by J. E. SORAUF

ABSTRACT. Scanning electron microscopy allows new insight into the manner of construction of coral exoskeleton of aragonite needles, largely arranged in modified spherulitic clusters. The needles grow directly into the underside of a template-like material, as previously suggested by Goreau. Septa are composed of a framework of trabeculae, filled in with laterally directed spherulitic aragonite. Several types of walls are developed, all of which are composed of fibrous aragonite arising (1) from inflation of septa, (2) by thickening of parathecal dissepiments, or (3) infilling of spaces between synapticulae with spherulitic aragonite. Epithea and stereome both are formed of subhorizontal (transverse) bundles of aragonite, but apparently are quite different in their mode of formation. Dissepiments are formed of a primary layer (which grows centripetally to a central junction), and thickened by spherulitic growth on the upper side (and sometimes also on the underside, as in *Manicina*). Synapticulae are modifications of septal granulations in most genera, but are more basic to the skeleton of *Fungia*. Minor features in septal microarchitecture are apparently of considerable use in the taxonomy of the Scleractinia.

THIS report presents the results of scanning electron microscope study of nine genera of Recent scleractinian corals. Although few genera have been studied to date, this relatively new method has yielded striking new data regarding the microarchitecture and microstructure of the exoskeleton. Enough data exist now to make preliminary inferences of what is hoped will be of broad implication regarding the formation of exoskeleton in other genera of scleractinians and of other groups of coelenterates.

The genera studied belong to four of the five suborders of the Scleractinia, as listed by Wells (1956, p. F369). These are the Fungiina, Faviina, Caryophyllina, and Dendrophyllina. The genera and species investigated with their hierarchical placement are:

Suborder Fungiina
Superfamily Agariciidae
Family Siderastreae
 Siderastrea radians
Superfamily Fungiidae
Family Fungiidae
 Fungia scutarea
Superfamily Poritiidae
Family Poritidae
 Porites porites

Suborder Faviina
Superfamily Faviidae
Family Faviidae
 Cladocora caespitosa
 Manicina areolata
 Montastrea cavernosa
 Trachyphyllia amaratum
Suborder Caryophyllina
Superfamily Caryophyllicae
Family Caryophyllidae
 Lophelia prolifera
Suborder Dendrophyllina
Superfamily Dendrophylliidae
Family Dendrophyllidae
 Astroides calycularis

The distribution of genera in suborders is broad, and the cluster of genera within the Faviidae can provide some insight regarding variation of architecture and structure within a family group.

METHODS

Specimens reported on here were studied in thin section in polarized light and by scanning electron microscopy. With a few exceptions illustrations are by the latter. Sample preparation for the latter varied somewhat depending on the type of view desired. Samples to be investigated for surficial microarchitecture or for internal structure in broken section were cleaned of organic material by boiling for 20–30 minutes in a mixture of 10% KOH and Glycerine or left for the same amount of time in a 5% solution of NaOCl. The dried specimen was then mounted on the necessary sample-holder and coated with gold (thickness approximately 200 Å) in high vacuum. Specimens to be studied in etched section were first smoothed with progressively finer carborundum powder and finally polished with jeweller's rouge (CuO) until no pits were visible on the surface under a binocular microscope. The samples were then etched for 10–25 minutes with 1 Normal EDTA. Most samples to be polished and etched first need to be impregnated with a suitable epoxy resin. They are then coated as above.

The microscope used was the Stereoscan (Cambridge Instruments) at the Institute for Palaeontology at the Friedrich Wilhelm University in Bonn, Germany.

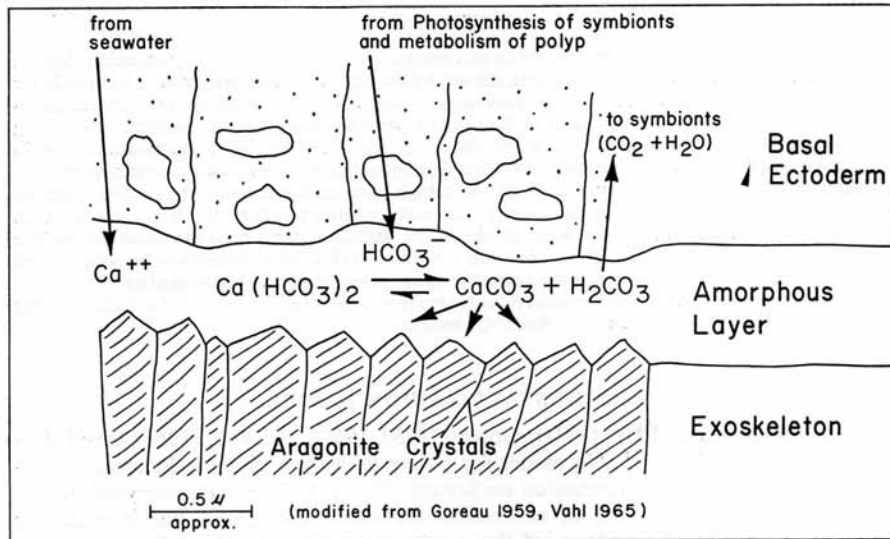
BIOCRYSTALLIZATION MODEL

Studies by Bryan and Hill (1941), Goreau (1959, 1961), and Vahl (1966) have led to the formulation of a workable model for biocrystallization of the scleractinian exoskeleton (for more lengthy discussion see Sorauf 1970, p. 4). The term biocrystallization is used here for the process of exoskeletal formation outside of, but immediately adjacent to, the basal ectoderm of the coral polyp. The term biomineralization is reserved for mineral impregnation, or crystallization within, a pre-existing cellular membrane or network, as in the Mollusca.

Bryan and Hill (1941, p. 80) recognized that much of the skeletal material of scleractinians occurs in the form of spherulitic clusters of aragonite needles, and proposed that the spherulites crystallized in a gel secreted by the basal ectoderm of the polyp. Goreau (1959, 1961) has outlined the biochemistry and physiology of the crystallization process in hermatypic corals, in which Ca^{++} and CO_3^- ions finally unite beneath a mucopolysaccharide-like matrix to form aragonite (text-fig. 1). He also suggested that the mucopolysaccharide-like layer acts as a template controlling the microarchitecture of aragonite needles (1961, p. 38). Vahl (1966, p. 34) has shown clearly in electron micrographs that the growth of aragonite is with the apex of the needle directed into this basal portion of the polyp. The *c*-axis of the aragonite crystal is the long axis of the needle with *a*- and *b*-axes apparently random in orientation (Wainwright, 1964, p. 220).

With almost no exceptions (see below) this model of crystallization fits data, noted in study of skeletal structures to present. Aragonite needles always occur in spherulitic clusters (or in trabeculae, which are themselves modified and long-continued spherulitic growths), and the axes of the spherulites are always more or less perpendicular to the margin of the skeletal elements. The sole exception to this generality is the mode of formation of the basal layer in the scleractinian dissepiment, as is discussed below.

The configuration and role of the 'mucopolysaccharide' material has been investigated to a limited extent. This layer has been isolated in *Fungia* by removing underlying skeletal material with the decalcifying agent EDTA. The underside of this template is definitely a reversed replica of the septal flank (Pl. 11, figs. 1, 2). One is tempted to conclude that the 'mucopolysaccharide' layer is truly a template in the fullest sense of the word. However, before this conclusion can be reached, further study is necessary to



TEXT-FIG. 1. Diagram based on the work of Goreau (1959) and Vahl (1965) to illustrate sources of calcium and bicarbonate ions, and their precipitation to form skeletal aragonite needles growing into a 'mucopolysaccharide-like' amorphous layer lying between the basal ectoderm of the polyp and the exoskeleton.

determine whether this is truly a durable material, preformed and performing the function of controlling growth patterns, or whether the apparent durability of the material is an artifact of the method of preparation of the specimen. Prior to decalcification, the material was oxidized for three days in 5% NaOCl, so that this is not simply remnant tissue clinging to the side of the septum. The possibility does exist that this 'mucopolysaccharide' was extruded as a gel (as suggested by Bryan and Hill 1941) and has since

EXPLANATION OF PLATE 11

Figs. 1, 2. *Fungia scutarea*, Recent, Pacific. 1, Underside of 'mucopolysaccharide-like' material liberated from septum by decalcification, showing template nature, $\times 2000$. 2, Septal flank showing clustering of microcrystals presenting aspect of original replicated by 'template', $\times 900$.

Fig. 3. *Lophelia prolifera*, Recent, Blake Plateau, Atlantic, etched transverse section of adaxial portion of septum to show remnant material (arrow) along growth lamellae unaltered by EDTA decalcifying agent, $\times 1000$.

Figs. 4, 5. *Cladocora caespitosa*, Recent, Mediterranean, transverse section etched with EDTA. 4, One simple septal trabecula showing very small crystallite size in centre, $\times 2000$. 5, Septal trabecula at left, with infilling of surrounding intertrabecular space by aragonite in spherulitic clusters terminated at growth lamellae, $\times 1000$.

Fig. 6. *Manicina areolata*, Recent, Florida Keys, polished and etched section oblique to septal denticulation to illustrate nature of growth of aragonite crystallites away from trabecular centre, $\times 1000$.

hardened as a replica of the surface. Study of living corals should yield the data necessary to resolve this question.

A problem regarding the 'template' is its presence or absence along growth surfaces within the skeleton. In almost all genera studied, no clearly recognizable remnant 'template' was noted in etched sections of the skeleton. However, in *Lophelia prolifera*, such remnant 'mucopolysaccharide' is seen in etched transverse sections (Pl. 11, fig. 3) where it is apparently confined to growth surfaces.

Thus, in this instance, withdrawal of the polyp left the somewhat chitinous material behind as a coating. The presence or absence of such layers of organic material should play a very important role during the recrystallization or inversion of aragonite to calcite and might even influence the types of secondary structures produced by diagenetic processes.

Two recent reports resulting from scanning electron microscope studies of coral skeletal material have shed important light on considerations of a biocrystallization model for this group. Wise has illustrated the clustering of aragonite needles that he termed fasciculi seen on the septal flanks (1970, p. 978). These are referred to here as clusters so as to avoid confusion with the term fascicules that Ogilvie (1897) utilized for what are now named trabeculae. Most important is that Wise found what are apparently muscle scars on septal surfaces in *Pocillopora* and in *Pectinia* (1970, pp. 978, 979). This would necessitate the penetration of polypal muscular fibres through any 'mucopolysaccharide-like' templating material in the region of the attachment scars. In the genera here studied, areas of incomplete crystallization are noted, but not with sufficient order to their distribution to warrant regarding them as attachment scars.

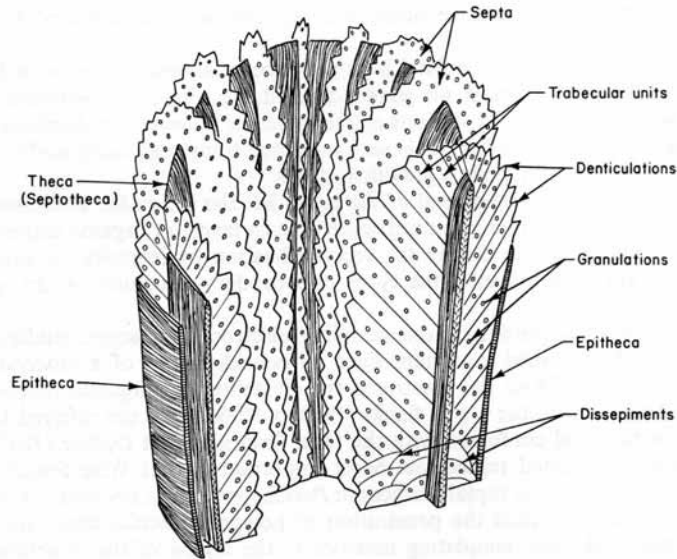
A second important contribution is that by Barnes (1970, p. 305), who has presented an excellent exposition of the development of competitive, interfering growth of three-dimensional fans of aragonite crystals (spherulites of Bryan and Hill 1941). I have continued to follow the terminology of Bryan and Hill because of the similarities of this fan-like growth to spherulites in avian and reptilian egg shells.

Important to the concept of a biocrystallization model is the finding of Barnes that the basal flesh may be lifted away from the exoskeleton in order to form a cavity into which crystallite clusters grow (1970, p. 1305). Further study is needed to confirm this possibility, as this would preclude the templating action of the mucopolysaccharide-like layer. The question would then arise as to how genetic control of crystallization patterns is transmitted from the polyp to the exoskeleton.

SKELETAL ELEMENTS

A general classification of the structural elements can be easily visualized if one regards the scleractinian corallite skeleton as a modified tube. The fleshy coral polyp sits at the upper end. This tube then has a number of longitudinal elements to it and also various transverse elements (text-fig. 2).

The longitudinal elements of the scleractinian exoskeleton are the septa (and modifications of same) and the theca (in its various forms). The septa, and modifications such as pali, paliform lobes, and columella, are formed within up-pocketed folds of the basal ectoderm of the polyp, and are thus bilateral in their internal structure. The theca (with varying form; and also the epitheca, a thin dense outer covering) are formed from the



TEXT-FIG. 2. Schematic diagram to illustrate the principal parts of the corallite exoskeleton and the geometric relationships between them. The blade-like units commonly formed by each trabecula (either simple or compound) are shown on the faces of the front septa only, in order to show the common divergence of these units away from the septotheca.

vertical or longitudinal extension of the basal ectoderm of the polyp. However, in some cases, the wall is formed within a pocket formed by the internal basal ectoderm and an outer edge zone, which extends part way down the outer surface of the theca. Thus, the resultant internal structure often is bilateral also. Of the longitudinal elements, only the epitheca is universally unilateral in construction, apparently formed by the upwarping of the basal plate of the polyp, according to Wells (1956, p. F344).

Transverse elements are, generally speaking, built more or less perpendicular to the longitudinal elements. These include various types of dissepiments and synapticalae which provide supporting platforms or bars for the polyp within its calyx. In addition,

EXPLANATION OF PLATE 12

Fig. 1. *Siderastrea radians*, Recent, Florida Keys, transverse polished and etched section of simple septal trabecula, $\times 1000$.

Fig. 2. *Montastrea annularis*, Recent, Florida Keys, enlarged view of a septal granulation of knobby or pustulose aspect, $\times 500$.

Fig. 3. *Porites porites*, Recent, Florida Keys, transverse polished and etched section of septum illustrating small size and somewhat irregular nature of septal trabeculae in this species, $\times 500$.

Figs. 4, 5. *Montastrea annularis*, Recent, Florida Keys, microarchitecture on septal flanks and denticulations. 4, Septal edge showing denticulations, $\times 200$. 5, Enlargement of central portion of preceding to illustrate alignment of crystallites in junction area between denticulations, $\times 1000$.

here are included, rather arbitrarily, the extracorallite deposits coenosteum and stereome. Although these portions of the exoskeleton are often most closely related to the theca in mode of origin, they are here regarded as transverse since they provide more or less horizontal support for colonial tissue between discrete corallite polyps within the colonial skeleton.

The foregoing system of classification is used for convenience only, and is not a formal method of categorizing skeletal elements. The various elements vary in their mutual relationships from genus to genus and thus often defy simple classification.

1. *Septa*

(a) *Microstructure of septa.* A simple type of scleractinian septal structure is that shown by *Cladocora caespitosa*, in which septal trabeculae are large, simple, and widely spaced in a simple fan configuration (Pl. 11, figs. 4, 5). As shown in these transverse etched sections the trabecular centres are composed of vertical crystallites of small diameters, and progressively larger diameter crystallites are noted as one moves to the peripheral portion of the trabecula (Pl. 11, fig. 4). Filling the space between the rod-like trabeculae are spherulitic clusters of crystallites with prominent growth laminae visible (Pl. 11, fig. 5). It is thought probable (at the present stage of research) that all scleractinian septa are some variation of this rather simple response to the biocrystallization model of Hill, Goreau, Wahl, and others.

Such a septal trabecula is also seen in oblique cross-section in a septal denticle of *Manicina areolata* (Pl. 11, fig. 6). It is apparent here that the septal trabecula may vary in diameter, but not in essential nature from that described above. The same is shown in *Siderastrea radians* (Pl. 12, fig. 1).

In *Porites porites*, there is apparently less regularity to the alignment of the trabeculae making up the septal framework (Pl. 12, fig. 3). The trabeculae shown here are also considerably smaller than those of *Cladocora*.

The trabeculae in the septa of *Fungia* are compound, as noted by Ogilvie (1897, p. 173). This feature is not particularly easy to see in transverse, etched section, but is apparent in the microarchitecture of the septal flanks. It is discussed in the following sections.

(b) *Microarchitecture of septal flanks.* Preliminary investigation indicates that the microarchitecture of crystallite arrangement and configuration on the lateral flanks of septa may be of considerable taxonomic importance. In addition, differences can be observed in the types, shapes, and distribution patterns of granulations on the septal flanks. The following discussion is based on observations of all but *Porites*.

The faviids show marked denticulations (Pl. 12, figs. 4, 5), as well as clearly marked ridges positioned over the septal trabeculae. They likewise show septal granulations, although those of *Montastrea* (Pl. 12, fig. 2) are knobby and pustulose, as contrasted with those in *Cladocora* and *Trachyphyllia*, which have sharp, spine-like granulations or acantho-granulations (Pl. 13, figs. 1, 2).

There are some similarities within the faviidae, primarily a lack of order in the crystallites as displayed on septal flanks. There does seem to be some rather general alignment of crystallites into rows of varying perfection, especially adjacent to the denticulate distal margins of the septa. This is perhaps shown best in the denticulate region of *Montastrea* (Pl. 12, fig. 5), but is also apparent in *Cladocora* (Pl. 13, fig. 4). *Manicina*

shows much less sign of any sort of apparent regular configuration. A weak shingling is also apparent on the flanks of exothecate denticulations in *Cladocora* (Pl. 13, fig. 5), just as in *Montastrea*. It should be noted that both of these genera are placed in the same subfamily, the Montastreinae, by Wells (1956, p. F403). One is tempted to infer that this is a taxonomic character of subfamily level, but obviously, sufficient data is lacking.

In *Astroides calycularis* (Dendrophyllidae) the septal flank microarchitecture shows an evident lack of crystallite pattern (Pl. 14, fig. 1). Some weak ridging is shown (Pl. 14, fig. 2) and indicates the configuration of the simple septal trabeculae. The appearance of the granulations in *Astroides* justifies the name (Pl. 14, fig. 3).

In *Fungia* (Fungiidae) the compound nature of the septal trabeculae is disclosed by diverging ridges (Pl. 14, fig. 4) within a flat, blade-like 'pseudo-denticulation' formed by each individual trabecula. These blade-like trabeculae do project somewhat, as shown in this figure, approaching the configuration of a denticulation, somewhat rounded at its distal terminus. The lines of junction between trabeculae are clearly shown (Pl. 14, fig. 5). The microarchitecture of crystallites is one of 'shingles', clusters of aragonite needles, rather elongate in outline, tipped in the distal direction, and somewhat resembling overlapping fish scales in appearance (Pl. 14, fig. 5). Granulations in *Fungia* are most frequent in the proximal region, near the theca and as shown in Pl. 14, fig. 6, consist of a single spherulitic outgrowth, resembling a volcanic cone somewhat in its symmetry and attitude. These granulations apparently develop over the lateral branches of the compound trabeculae, or else have a subrandom distribution.

The septa of *Siderastrea* are characterized by prominent synapticulae, doubled spinose granulations, and spherulitic organization of fine aragonite crystallites. Here synapticulae and granulations (Pl. 15, fig. 1) are seen occurring in rather regular rows sloping upward from the septotheca. This reflects the orientation of the simple septal trabeculae. It must be concluded that each granulation is basically one spherulitic cluster of crystallites, just as is each synapticular growth (Pl. 15, fig. 1), originating under one centre of calcification. Do the synapticulae with a doubled or tripled tip then represent those in which division of cells has taken place in the centre of calcification?

The groundmass of the septal flank is apparently in greatest part composed by closely packed, subparallel aragonite needles. Pl. 15, fig. 2, illustrates the tips of these needles and the surface they form. The depressions illustrated may represent less well-calcified spherulite centres, analogous to those illustrated below in dissepimental spherulites. That crystallization is not always uniform or complete is attested to by the fact that crystallite clusters noted in some parts of some septa are very incomplete and apparently less well ordered (Pl. 15, fig. 3).

EXPLANATION OF PLATE 13

Figs. 1-5. *Cladocora caespitosa*, Recent, Adriatic. 1, Overview of septal flank showing granulations in lower part of micrograph and trabecular ridges (see fig. 4, this plate) leading to marginal denticulations above, $\times 200$. 2, Sharp, spinose granulations in the portion of the septum adjacent to and external to the septotheca, $\times 200$. 3, Enlarged portion of lower left central part of fig. 1 illustrating crystallite configuration in weakly crystallized area between granulations, $\times 2000$. 4, Enlarged portion of upper part of fig. 1 illustrating weak alignment of crystallites and position of granulations on trabecular ridge, $\times 500$. 5, Exothecate granulations and weakly shingled crystallites on septal flank external to theca, $\times 570$.

Lophelia prolifera (Caryophyllidae) is a deep-water dweller, which differs in several respects from scleractinians growing in shallow water; notably in that it lacks symbiotic algae (zooxanthellae). *Lophelia* has septa which are coated by a sheath that is continuous with the dissepimental platforms, and which is of a uniform carpet of aragonite spherulites, with a surface marked only by very slight depressions associated with the surface configuration of the spherulites (Pl. 15, fig. 4).

More research is necessary on deep-water caryophyllids in order to understand the septal structure and septal flank microarchitecture.

2. Pali

The general category of pali and paliform lobes have not been thoroughly investigated since only *Porites* of the genera examined has either of these structures.

In spite of some confusion on the part of Alloiteau (1957, p. 24), a palus can be regarded as the vertical, spine-like axial portion of any septum. Thus, the septum and palus together, are one unit, with a deep notch separating the two. As shown in *Porites porites*, the palus is composed in cross-section of trabecular skeletal material (Pl. 16, fig. 1). In this micrograph can be seen four trabecular centres clustered symmetrically around the axis of the palus, with growth parallel to the long axis of the corallite. Fig. 2 of Pl. 16 shows a slight variation from this in that there is an area of oblique growth of crystallites, and only three trabeculae within the upper part of the micrograph. It is judged that the oblique portion of this palus is more closely related to the orientation of septal trabeculae than that of the palial trabeculae.

From the above, it can be supposed that pali of *Porites porites* are formed by certain trabeculae becoming somewhat more parallel to the corallite axis as basal flesh (and calicoblasts) withdraws directly parallel to the axis of the corallite. The fully developed palus is independent of the rest of septal structure and composed of vertical trabeculae.

3. Columella

The well-developed columella in *Astroides calycularis* was the only one studied in detail. This is of the type described by Wells (1956, p. F436) as large and 'spongy', characteristic of the Dendrophyllinae. Those forms of columella referred to by Wells (1956, p. F343) as styliform and as lamellar have not yet been studied by electron micrography. The following remarks only supplement those of Wells.

As shown in Pl. 14, figs. 1, 2, the columella of *Astroides* is similar in appearance and structure (fig. 1) to the coenosteal skeletal material common to neighbouring corallites so well developed in the genus. The columella is apparently trabecular, definitely composed of spherulitic aragonite (Pl. 14, fig. 2) and is fascicular in that it has the appearance of a group of 'twisted vertical ribbons' (Wells 1956, p. F343).

More study of varied columellar types is necessary prior to further generalization regarding biocrystallization mechanisms. The complex arrangement of 'ribbons' in this fasciculate type of columella would certainly indicate that the contortions of basal flesh of the coral polyp must have likewise been extremely complex during formation of the element.

4. Theca

Following the usage of Wells, Moore, and Hill (1956), there are three types of wall (theca) in the Scleractinia: septotheca, synapiculotheca, and paratheca. All three types

can be found among the genera of Scleractinia examined in the course of this study. Some genera clearly have one type of theca; however, others have a wall which escapes simple definition. An example is the genus *Fungia* which is synapcticulothecate in youthful stages, but which has a wall more nearly septothecate when adult (as noted by Wells in his discussion of the family Fungiidae, 1956, p. F388).

(a) *Septotheca*. Apparently the most elementary type of wall developed in the Scleractinia is something similar to that seen in *Cladocora caespitosa*, a phaceloid colonial species in which every corallite is distinct and physically separated from every other. Here the wall is septothecate, formed by the lateral expansion of adjacent septa to join the two together and form a solid wall separating the calyx (and at times enclosed polyp) from the outside environment. This expansion and wall formation (Pl. 16, fig. 3) takes place along the axis of divergence of the simple trabeculae in the single fan system forming the septum. Fig. 4 in Pl. 16 illustrates the arrangement of spherulitic clusters of aragonite needles growing out from the adjacent septa to join midway between the septa (the crack in the micrograph, Pl. 16, fig. 4 is physical, due to sample treatment, not an original feature of the wall). Still to be explained is the mechanism of polypal withdrawal during continued crystallization of carbonate causing the aragonite to grow together and join to form a massive wall. Such instances decrease the credibility of the biocrystallization model which has earlier been elaborated upon and accepted in principle. In addition, one would expect spherulites to be directed upwards towards basal flesh draped over the wall, but as seen in this transverse etched section, just the opposite is noted (Pl. 16, fig. 4). The matter needs further investigation. Also remaining to be investigated is the relationship between mother and daughter corallites while the corallites are still joined laterally. A line of junction can be noted between the adjacent portions of the two thecae, but there is no apparent relationship of aragonite spherulite clusters.

In *Trachyphyllia amarantum* (Pl. 16, fig. 5) septotheca is formed as a solid vertical wall and is positioned at the line of divergence of septal trabeculae, as in *Cladocora*. In the septotheca of *Trachyphyllia* and in *Cladocora*, the axes of aragonite needle spherulites are perpendicular to the external surface. Thus, at the uppermost tip (distal) the aragonite needles are perpendicular to the top of the theca. Although the theca in *Trachyphyllia* is in the main septothecal, it does have some support and thickening as a result of the merging of dissepiments with it; thus the wall is partially parathecal if the definitions be strictly applied.

EXPLANATION OF PLATE 14

Figs. 1, 2, 3. *Astroides calycularis*, Recent, Mediterranean. 1, Overview of (left to right) columella, septal flank, and coenosteum, $\times 20$. 2, Enlargement of septal flank and portion of columella to show weak ridges developed over trabeculae, granulations positioned on these ridges, and manner of outgrowth of septa into columella, $\times 50$. 3, One granulation enlarged to show configuration of crystallites and granulo appearance, $\times 2000$.

Figs. 4, 5, 6. *Fungia scutarea*, Recent, Pacific. 4, View of blade-like septal unit made by one compound trabecular unit with ridges showing branching nature of components of trabecula, and scale-like appearance of crystallite clusters, $\times 165$. 5, Enlarged junction between two trabecular systems illustrating convergent growth of crystallite clusters and crystallite composition of 'scales', $\times 800$. 6, Enlarged portion of septal flank to illustrate nature of granulation, somewhat 'volcano-like' in appearance, $\times 750$.

The theca in *Trachyphyllia*, as that in some other species, shows evidence of recrystallization or at least the breakdown of the acicular nature of the skeletal aragonite (Pl. 17, fig. 1). Also noteworthy is evidence (Pl. 17, fig. 2) that fusing (or perhaps partial recrystallization) of aragonite needles takes place at the surface of the recently abandoned skeleton. This figure shows that on a broken surface, aragonite needles appear to be in the form of larger crystal masses. Etched sections show that these are definitely not true crystals, thus they were referred to as 'pseudocrystals' by Sorauf (1970, p. 9).

The junction of dissepiments and theca of the type seen in *Trachyphyllia* is seen to be complex (Pl. 17, fig. 3). It is judged that the intergrown nature is in large part due to the fact that the dissepiment is contiguous with that portion of the theca above it. Below can be noted a surface of discontinuity leading into the underside of the dissepiment.

(b) *Synapticulotheca*. Genera with synapticulae (discussed below) range from types such as *Porites* in which corallites are separated by several rings of unconnected synapticulae (which substitute for, but do not actually form a theca) to types such as *Siderastrea* which form a solid wall similar in some aspects to septotheca.

Ogilvie (1897, p. 180) showed a wall formed in *Siderastrea* along the axis of divergence of trabeculae belonging to neighbouring corallites. The wall (referred to by her as 'pseudotheca') was illustrated as porous, formed by a vertical row of elongate but unconnected synapticulae. As can be seen in Pl. 15, fig. 1, this is not the case in specimens of *Siderastrea radians* from the Florida Keys.

Siderastrea is noted by Wells (1956, p. F384) as having well-developed synapticulothecate walls, which are formed by several synapticular rings. *Siderastrea radians*, however, has a solid vertical wall separating adjacent corallites, with septal trabeculae diverging from it toward the axes of the two corallites (Pl. 15, fig. 1). On these trabeculae are seen aligned synapticulae (same figure) which supplement the theca. When seen in transverse section they appear as several rings of synapticulae. The solid wall is thus little different from septotheca when seen in broken longitudinal section. Although the theca is presumably formed by merging of a vertical row of synapticulae, no evidence is noted in this view to support the hypothesis. In transverse etched section it can be seen that the wall here is not formed as typical septotheca.

At low magnification the wall in *Siderastrea* is seen to be irregular in path, with the position of the wall between neighbouring corallites neither straight nor regular in a predictable way. Rather it appears (Pl. 17, fig. 4) to be the result of somewhat random lateral outgrowths of septal trabeculae. The wall segments are not aligned as in most truly cerioid species. At places it appears as though more than one wall is present. This most likely is the theca and one synapticula randomly encountered. In etched section (Pl. 17, fig. 5) electron micrographs illustrate that growth is not septothecate, as adjacent synapticular granulae sometimes encounter one another, with a clear line of junction, but continue growing past and lateral to the point of first junction.

The genus *Fungia* also is synapticulate, and according to Ogilvie (1897, p. 168) has a porous wall which she regarded as of 'small moment', as she regarded them as simply being interseptal spaces not sufficiently filled up by the basal deposits of the coral polyp. The synapticulae of *Fungia* do form a porous wall in youthful specimens, but as adults the genus is marked by a solid wall (Wells 1956, p. F388). The wall is formed of large, compound synapticulae (discussed below) with infilling between synapticulae formed identically to septotheca. The tip of the theca in *Fungia* is illustrated in Pl. 18, fig. 1, and

shows that this portion of the wall is formed prior to development of the intervening synapticulae in adult members of the species. Further enlarged, this part of the wall is seen to be bilateral, with a medial line of divergence of spherulite clusters, just as in septotheca.

(c) *Paratheca*. Wells noted that: 'In some corals having well-developed dissepiments, these may push upwards so as to reinforce the septotheca, or even replace it as the wall. In the latter instance the wall is termed paratheca' (1956, p. F346). If this definition is strictly followed, then no corals in this study have a paratheca. However, Vaughan and Wells (1943, p. 164) in a key to genera within the Faviinae, noted that *Manicina* has 'walls mostly parathecal'. It is here assumed that the implied meaning was that *Manicina* as a genus has walls that are in part septothecal, but that are so well buttressed by steeply inclined dissepiments (and spherulitic aragonite on them) that the wall can be considered as 'mostly parathecal'.

As shown in micrographs, the wall in *Manicina* is in fact composed of a thin interior wall which is truly septotheca, formed within an up-pocketing of the basal flesh. At its tip, this septotheca is characterized by vertical spherulites with individual needles difficult to discern. Below this purely septothecal tip is the more complex thickened wall. As each dissepiment is added to the calyx by the polyp, a correspondingly thick amount of spherulitic aragonite is deposited over the dissepiment and the rest of the wall (Pl. 18, fig. 2). In upper parts of the theca, the structure owes perhaps two-thirds to three-quarters of its thickness to the presence of these steeply inclined dissepiments. Note (Pl. 18, fig. 3) that the wall is thus characterized by the presence of rather large cavities occurring between the thick dissepiments and earlier formed septotheca.

EXPLANATION OF PLATE 15

Figs. 1, 2, 3. *Siderastrea radians*, Recent, Florida Keys. 1, View of portion of septal flank and broken theca (T. at right) with synapticulae (arrow upper left) and septal granulations radiating from theca and groundmass architecture, $\times 200$. 2, Enlarged view of groundmass of crystallites making up greatest part of septal flank, showing tight, compact spherulitic clusters of very small diameter crystallites, $\times 2000$. 3, Enlarged portion of septal flank to show region of much less complete crystallization as compared to that shown in Fig. 2, $\times 500$.

Fig. 4. *Lophelia prolifera*, Recent, Blake Plateau, Atlantic, showing broken portion of septal flank to illustrate inner portion of well-developed spherulitic clusters of crystallites, and thinner sheath of aragonite needles (arrow). Sheath is co-extensive with sheathing over dissepiments, $\times 810$.

EXPLANATION OF PLATE 16

Figs. 1, 2. *Porites porites*, Recent, Florida Keys, transverse polished and etched sections. 1, Palus showing approximately symmetrical grouping of four trabeculae (one is pointed out by arrow at left), $\times 1000$. 2, A second palus in the same colony with asymmetrical positioning of trabecular centres at upper right of micrograph, $\times 500$.

Figs. 3, 4. *Cladocora caespitosa*, Recent, Adriatic. 3, Overview of septum with denticulations, granulations, and vertical septotheca in lower part of micrograph, $\times 50$. 4, Transverse polished and etched section in septotheca showing junction of crystallite clusters having grown out from neighbouring septa, $\times 500$.

Fig. 5. *Trachyphyllia amarantum*, Recent, Borneo, overview of septum illustrating arrangement of septotheca and septal granulations, $\times 20$.

5. *Coenosteum*

Of the genera studied, only *Astroides* is characterized by the presence of coenosteum forming a loose porous mass of connective skeletal material between corallites, as shown in Pl. 14, fig. 1. The coenosteum is here seen to be a group of subvertical ribbons with holes in them connected by 'synapticula-like' processes. Individual elements of the coenosteum (Pl. 18, fig. 4) are seen at slightly higher magnification to have a midline with aragonite needles diverging from it. They are thus 'bilateral' in the sense of Kato (1963, p. 581); and can be regarded as forming in up-pocketed basal flesh, here apparently colonial basal flesh shared by neighbouring polyps. Spherulitic clusters of aragonite needles are seen in coenosteal elements, just as in other skeletal elements of the Scleractinia.

6. *Stereome*

Vaughan and Wells (1943, p. 31) stated that, '... thecal structures are frequently thickened by a deposit of stereome, similar to epitheca'. *Lophelia* is noted by Wells (1956, p. F427) as having a calyx covered by stereome. This stereome is a mass of spherulitic clusters of aragonite needles having the following characteristics:

1. The carbonate mass is massive and dense, but commonly more porous toward the inside of the theca (Pl. 19, figs. 2, 3).
2. In the inner portion of the theca, there is easily visible retention of septal and interseptal structures (as in photomicrograph, Pl. 19, fig. 4). The inner part of the theca then is apparently septothecal, with lamellar addition and thickening at the calycinal surface.

3. In thin or etched section it can be noted that the other part of the thecate stereome is composed of aragonite needles arranged in bundles, with the long axis of the bundle perpendicular to the outer surface of the carbonate wall. There the bundles are perpendicular to the outer surface of the epitheca. In scanning micrographs this bundling is very obvious, and the obliquely-cut boundary between two such bundles is shown in Pl. 19, figs. 2, 3. Apparently the differing orientation of crystallites shown here is the result of different positions within a bundle and differing orientations between bundles.

In the portion of the theca adjacent to the calyx, the internal structure of the wall displays the relict structure of grown-over and thickened septal ends and more lamellar additions of aragonite spherulites growing perpendicular to the calyx. Pl. 9, fig. 4 illustrates the 'root' of such a septum within the corallite wall, with a dark axis and divergence of crystallites. The axis is coextensive with the axial plane of the septum.

4. Stereome, at least in deep water species, such as *Lophelia prolifera* studied here, may have solution cavities within the thick wall. These lie within stereome and at their borders illustrate abrupt termination of crystallites. There is no coincidence between primary configuration of crystallites, such as tips of spherulitic crystallite clusters, and the margin of the cavities. Thus they are considered secondary.

Stereome (at least in *Lophelia*) should not be thought of as similar in nature to epitheca. The bundling of fibres shown here is not analogous to the stacked configuration of crystallites in epitheca (see below for description). There may also be a difference in the growth direction of crystallites. Here, in the outer, bundled portion of the stereome, growth is apparently towards the exterior of the wall. As will be discussed below, some evidence exists to suggest that epitheca grows from the outside in.

7. *Epitheca*

The epitheca of the coral skeleton is not always present. In solitary corals, and in corals without edge zone, it is commonly present, but in colonial forms is frequently lacking.

The epitheca in colonial corals, when present, forms a common sheath, around all corallites of the colony (see text-fig. 2). It consists of a generally whitish crust, showing the now well-known growth wrinkling or ridging.

In the present group of genera studied, the only species possessing epitheca is *Manicina areolata*, discussed in the chronological study of Wells (1963). At present no broadly valid generalizations can be made, as I have been unable to study this external wall in more than one species. However, the structure has been studied on both internal and external surfaces and both in broken and in polished and etched cross sections. Thus, its structure is known in detail and some inferences can be made regarding its formation.

Looking at the external surface of epitheca in *M. areolata* one is struck by two observations; first, that boring by blue-green algae causes much destruction of this outer aragonitic sheath, and second, that no obvious structures are to be noted except for the growth ridges themselves (Pl. 20, fig. 1). Seen at high magnification, these growth ridges are only slightly less featureless (Pl. 20, fig. 2). In this high magnification, one notes a certain expression of the crystallinity of the epithecal material, but the crystallite ends are apparently fused.

The internal surface of the epitheca, where it is free from contact with the septa or dissepiments, is more instructive. Pl. 20, fig. 4 illustrates the broken surface (here upper

EXPLANATION OF PLATE 17

Figs. 1, 2, 3. *Trachyphyllia amarantum*, Recent, Borneo. 1, Broken section through septotheca showing apparent recrystallization (or at least lack of apparent crystallites) in central, or left-hand part of micrograph, and acicular crystallites at margin, at right, $\times 160$. 2, Enlarged portion of Figure 1 to illustrate fibrous nature of aragonite, but also incipient recrystallization here to form larger 'pseudocrystals', $\times 800$. 3, Junction of septotheca at left and dissepiment (pointed out by arrow at right), with some continuity apparent between aragonite crystal growth in the two skeletal elements, $\times 380$.

Figs. 4, 5. *Siderastrea radians*, Recent, Florida Keys. 4, Transverse thin section through colony to illustrate large simple trabeculae making framework of septa, and lateral outgrowths from septa to form synapticulae, crossed nicols, $\times 37.5$. 5, Transverse polished and etched section of synapticula with growth of trabeculae to join each other along line indicated by arrow, $\times 200$.

EXPLANATION OF PLATE 18

Fig. 3 is photomicrograph.

Fig. 1. *Fungia scutarea*, Recent, Pacific, overview of septal flank to show tip of theca, here formed prior to massive compound synapticulae, and similar in appearance to septotheca, $\times 160$.

Figs. 2, 3. *Manicina areolata*, Recent, Florida Keys. 2, Transverse polished and etched section of dissepiment and adjacent theca (T. above). Note three-layered nature of dissepiment and interfering spherulitic growth of upper layer and thickening of theca, $\times 460$. 3, Photomicrograph of septum and theca to show 'mostly parathecal' wall with void space between later formed dissepiment (arrow) and earlier formed wall, crossed nicols, $\times 15$.

Fig. 4. *Astroides calycularis*, Recent, Mediterranean, illustrating complex geometry of coenosteum and bilateral nature of coenosteal elements, $\times 50$.

right) and the inner surface of the wall material. It is obvious that we are here looking at subhorizontal aragonite crystallites with their terminal pyramids present on the inner surface. A rough horizontal layering is to be noted in Pl. 20, fig. 5, with prominent growth hiatus lines periodically present, as here. It is worth repeating, however, that this inner surface is apparently the surface of free growth of crystallites, a highly significant fact in the interpretation of mode of formation (Pl. 20, fig. 5).

The most typical aspect of the epitheca, viewed in broken section, is illustrated in Pl. 20, fig. 3. Here are noted the elongate, perhaps partially fused aragonite needles arranged in subhorizontal fashion. However, when the broken epitheca is seen from a somewhat different vantage point, the presence of inter-leafed radiating (or chevron-like) clusters is readily apparent (Pl. 20, fig. 6). Although seen in this view, the geometric relationships of crystallites can be more exactly studied in etched cross-section.

In etched section is clearly noted a chevron-like stacking of crystallite groups. Also, particularly clear is the fact that the epitheca is attacked and thoroughly bored by blue-green algae filaments, here seen (Pl. 21, fig. 1) on the left side of the figure, filled with impregnating plastic and etched into prominence. Also evident is what may be a spherulitic configuration so common in the scleractinian exoskeleton. An interesting, but not yet solved problem is the relationship between the growth lines on the outer surface of the epitheca and the clusters of crystallites. If each growth ridge is the end of one cluster then each layer is a diurnal one. If the clusters are spherulites then one spherulitic layer would be diurnal; rather unlikely.

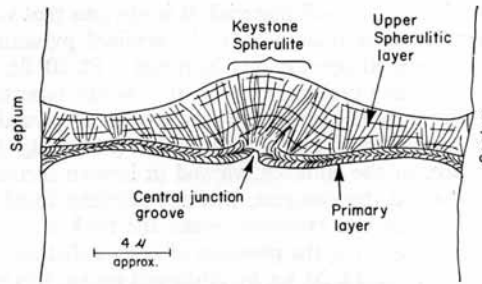
In order to understand the mode of crystallization of the epitheca it is necessary to take the following into account:

1. Crystallite tips are seen on the inner surface of the epitheca and apparently represent the growth surface of the aragonite crystal needle (Pl. 20, figs. 4, 5).
2. The outside surface shows little evidence of individual aragonite crystals (Pl. 20, fig. 2).
3. In transverse section, subhorizontal crystallites are seen and are arranged in clusters. These clusters resemble, but are not demonstrably spherulites. In etched sections, vertical growth lamellae are evident. The crystallites comprising the epitheca do apparently grow from the outside towards the centre of the corallite rather than outwards towards the overlapping flesh of the edge zone. The sum effect of crystallite growth adds height to the epithelial sheath and the epitheca is extended upwards.

8. Dissepiments

The dissepiments of the scleractinians have been discussed at some length in an earlier paper (Sorauf 1970); thus the following discussion will only be a summary of findings regarding the structure and formation of dissepiments.

This study focused on the dissepiments in the genera *Trachyphyllia*, *Cladocora*, *Manicina*, and *Lophelia*. Of these four, the former three genera are all characterized by the presence of zooxanthellae (single-celled algae) as symbionts living in the polypal mesogloea. *Lophelia* is a deep-water dweller, having been found at up to 475 fathoms on the Blake Plateau (Stetson *et al.* 1962, p. 10), and has no symbiotic algae. The dissepiments of *Manicina* are subvertical and are involved in the building of a parathecal wall, those of *Cladocora* are completely isolated one from another, and are horizontal, whilst those of *Trachyphyllia* are intermediate between the two others in manner of occurrence.



TEXT-FIG. 3. Simplified and generalized cross-section of a dissepiment in *Cladocora*. This is the most basic structural type of dissepiment noted among the Scleractinia to date.

The dissepiments in *Lophelia* are flat and co-extensive, all joining together in the axial area of the corallite to form a flat floor to the calyx. These are the type labelled tabular by Wells (1956, p. F344).

All dissepiments in the species studied have certain characteristics in common. The underside of all dissepiments have a central junction line and evidence that the basal, first-formed part of the structure grew centripetally from septa and theca. All dissepiments are characterized by an upper layer (extending to the upper surface) that is composed of an interferring mass of upward growing spherulites of aragonite needles. The schematic drawing (text-fig. 3) illustrates terminology used with respect to the cross-sectional structure of dissepiments, the primary layer, usually basal, and the upper spherulitic layer. In *Manicina* (Pl. 18, fig. 2) dissepiments that are 'parathecal' also have what has been termed the lower spherulitic layer in the upper portion of the dissepiment where it abuts against the theca. *Lophelia* does not have a primary layer thick

EXPLANATION OF PLATE 19

Fig. 4 is photomicrograph.

Figs. 1-4. *Lophelia prolifera*, Recent, Blake Plateau, Atlantic. 1, Transverse polished and etched section (same as Pl. 11, Fig. 3) with septum at right side of composite micrograph, showing remnant organic material along growth lines, $\times 500$. 2, Overview, polished and etched, of theca with stereome, composed of clusters of crystallites, and slightly more porous in the inner portion (extreme top of figure), $\times 50$. 3, Portion of fig. 2, enlarged to show differing orientation of crystallites in darker area (above) and lighter area below, $\times 1000$. 4, Photomicrograph (crossed nicols) of stereome (lower arrow), and septa (upper arrow) to illustrate retention of septal structure in secondarily thickened skeleton, $\times 25$.

EXPLANATION OF PLATE 20

Figs. 1-6. *Manicina areolata*, Recent, Florida Keys. 1, External view of epitheca showing growth ridges, $\times 420$. 2, Portion of fig. 1 with greater magnification to show weak expression of crystallites on growth ridges, $\times 8200$. 3, Broken cross-section of epitheca showing algal borings and chevron-like arrangement of crystal clusters, $\times 1000$. 4, View of interior surface of epitheca with subhorizontal growth lines, and also broken edge at upper right, $\times 1000$. 5, Enlarged portion of fig. 4, to show crystallite terminations on interior face of epithecal sheath, $\times 5000$. 6, Broken cross-section of same specimen showing angularity between crystallite clusters 1, at base of micrograph, 2, in centre and 3, at top, $\times 2000$.

enough to show in etched cross sections, and may not have any at all. Nevertheless, as shown by the central junction groove (Pl. 21, fig. 2) and faint growth lines, the method of formation in this genus is apparently the same as in the other genera examined.

In genera such as *Manicina* (Pl. 21, fig. 3) and *Cladocora* (Pl. 21, figs. 4, 5), the underside of the dissepiments show distinct cording of microcrystals, especially adjacent to irregularities or granulations on the septal flanks. *Cladocora* (Pl. 22, fig. 1) shows very well-developed growth lines, with each growth increment considered to be a diurnal one. This would be the result of rapid growth of microcrystals in daylight under the dual influence of zooxanthellae and enzymes, with slower growth in darkness when only enzymal action would aid in the biocrystallization process (as noted by Goreau 1959, p. 72).

The upper spherulitic layer is seen in *Cladocora* (Pl. 22, fig. 2) to be composed of rather random, upward oriented spherulites of aragonite, except for a single row of large, very well-developed spherulites situated directly over the central junction groove. This row, called the keystone spherulites after their resemblance to the keystone of an arch (Sorauf 1970, p. 7), can be somewhat exaggerated in their growth and actually form a central ridge on the upper surface of the dissepiment (as in *Trachyphyllia*, Pl. 22, figs. 3, 4). Generally, the upper surface of the dissepiments of shallow water corals are a series of spherulite clusters of aragonite needles which may or may not show a depressed centre to the cluster (see *Manicina*; Pl. 22, fig. 5).

The lower spherulitic layer noted in *Manicina* dissepiments (Pl. 18, fig. 2) is regarded as the result of the manner of withdrawal of the polypal flesh from this parathecal area (see Sorauf 1970, p. 6). This lower layer decreases in thickness away from the theca, so that the central and lower portion of this steeply tilted dissepiment has the primary layer as its basal (or innermost) part of the plate.

The external microarchitecture and internal structure of dissepiments in *Lophelia* differ from that in shallow water corals, in that growth lines are almost lacking; there is no cording of microcrystals; no visible primary layer can be noted; and the upper surface of the dissepiments are apparently contiguous with a spherulitic sheath covering the septa (Pl. 23, fig. 2). The specimen is a deep-water dweller, lacking zooxanthellae. Whether depth of water, absence of symbionts, or genetic differences are most accountable for the marked difference in structure is not yet known.

9. *Synapticulae*

Synapticulae are defined as bars positioned in the interseptal spaces connecting the septa. Their function is varied; they provide a strengthening of the septal blades, they provide a false wall between corallites, and they provide support for the base of the polyp. This last function is perhaps most marked in genera such as *Fungia*, where synapticulae are large and grow continuously upward as the polyp grows larger.

The structure of synapticulae is either compound or simple. *Fungia* has compound synapticulae, composed of a number of trabeculae; it is thought likely that the compound nature of the synapticulae is related to the compound nature of septal trabeculae in this genus. A lateral outgrowth of a compound trabecular bundle would logically be compound itself. The microphotograph (Pl. 23, fig. 1) shows more than ten trabecular centres in each synapticula. The ability of the basal flesh of the polyp to form compound centres of calcification has previously been discussed, and is here reflected in

the synapticalae. However, each of these trabecular centres is identical in nature (although smaller in size) with the general model of trabecular crystallization centres.

Simple synapticalae are well shown in *Siderastrea* (Pl. 15, fig. 1). Rows of the bars are aligned along a single septal trabecula. They apparently result from the enlargement and lateral growth of a trabecula (perhaps due to branching) and are not much different from septal granulations when small. However, they do grow out and join protrusions from the neighbouring septum. Since they are the result of the outgrowth of a single large, simple trabecula, they are simple synapticalae. From time to time, such a completed bar does show the secondary development of an extra trabecular centre. This led Ogilvie (1897, p. 180) to name those bars without any true development of separate trabeculae as pseudosynapticalae, reserving the term synapticala for the form possessing new trabecular centres. This is unnecessary, and I refer to all connecting bars as synapticalae, although recognizing a basic difference between those of the sort seen in *Fungia* (compound, with a much greater role in skeletal formation and polypal support) and those in *Siderastrea* and *Porites* (simple, with or without great significance in polypal support).

The formation of synapticalae in *Siderastrea* is well illustrated by the two sets of micrographs here presented. A majority of the bars are formed by the simple junction of laterally adjacent septal granulations (Pl. 15, fig. 1). The other micrograph here presented (Pl. 23, fig. 4) shows a rather extraordinary growth of spherulitic clusters below the synaptical bar. Note also that along the top of the bar there is upward growth of spherulitic aragonite. No reason is apparent for the rather wild, disoriented growth of

EXPLANATION OF PLATE 21

Fig. 1. *Manicina areolata*, Recent, Florida Keys, polished and etched section through epitheca to illustrate chevron-like arrangement of crystallite clusters. At left (outside of epitheca) are seen algal borings, filled by impregnating plastic and left in relief by etching, $\times 1000$.

Fig. 2. *Lophelia prolifera*, Recent, Blake Plateau, Atlantic, with tabular dissepiments, here seen from the underside, illustrating junction line in middle of each, and manner of merging to form a flat floor to the calyx, $\times 50$.

Fig. 3. *Manicina areolata*, Recent, Florida Keys, to show cording of microcrystals in the primary layer on underside of dissepiment, $\times 200$.

Figs. 4, 5. *Cladocora caespitosa*, Recent, Adriatic. 4, View of underside of dissepiment illustrating central junction and growth lines on the undersurface of the primary layer, $\times 85$. 5, An enlarged view of the underside of a dissepiment to show the central junction and crystallites growing towards it, $\times 1000$.

EXPLANATION OF PLATE 22

Figs. 1, 2. *Cladocora caespitosa*, Recent, Adriatic. 1, Underside, flank of dissepiment with luxuriant crystallite growth occurring with definite periodicity, most likely diurnal, $\times 4000$. 2, Polished and etched transverse section of dissepiment (placed vertically to save space) illustrating primary layer and formation of central keystone spherulites and upper layer of dissepiment (see text-figure), $\times 400$.

Figs. 3, 4. *Trachyphyllia amarantum*, Recent, Borneo. 3, Upper surface of dissepiment illustrating rather smooth mat of crystallite tips and central spherulite ridge, $\times 50$. 4, Enlarged portion of fig. 3 showing clustered crystallites of upper surface slightly tipped towards central ridge apparently composed of a single line of spherulites, $\times 1000$.

Fig. 5. *Manicina areolata*, Recent, Florida Keys, illustrating rather incompletely crystallized spherulitic clusters, with central depression, that occur on the upper surface of some dissepiments, $\times 5500$.

spherulites beneath the synaptacula; and perhaps it simply represents formation of the structure during a period of extremely rapid growth. Such rapid crystallization could result in excess aragonite clustering in the void space beneath the synaptacula.

In transverse view (Pl. 23, fig. 3), *Porites* has very simple, symmetrical synaptaculae. These bars apparently function to form a porous, weak theca separating the neighbouring corallites. Their occurrence appears random.

CONCLUSIONS

1. A workable model of biocrystallization has resulted from the studies of Goreau (1959, 1961), Bryan and Hill (1941), and Vahl (1965). Aragonite needles comprising the skeleton grow directly into neighbouring mucopolysaccharide-like material, most often in spherulitic clusters. The mucopolysaccharide may act as a template controlling the microarchitecture of the exoskeleton. Several problems exist in the blanket application of this model, particularly the presence of what are thought to be muscle scars on septa (Wise, 1970), and spatial problems that result wherever spherulites grow together to form a tight junction, as in septotheca.

2. The basic unit of septal construction is the trabecula, a modified spherulite, formed within an up-pocketing of the basal ectoderm of the coral polyp. Around the framework of trabeculae are formed clusters of spherulitic aragonite. Trabeculae generally are arranged in some modification of a fan shape. Trabeculae are either simple or compound and form, together with additional spherulitic aragonite, the larger 'blades' seen in several genera.

3. The microarchitecture of the septal flanks is apparently of considerable taxonomic use in the Recent Scleractinia. In *Fungia* clusters of aragonite microcrystals are arranged in an overlapping scale-like fashion, while most Faviids (*Manicina*, *Trachyphyllia*) generally show clusters of microcrystals (fasciculae, Wise 1970) but no easily recognized pattern to these clumps. In the Dendrophyllid *Astroides caiycularis*, no pattern was apparent. The Caryophyllid *Lophelia prolifera* is characterized by sheaths of spherulites coating the blade-like septal centre.

4. Pali and ribbon-like columellae can be regarded as extensions of the trabecula-forming processes into the axial part of the corallite. The former are composed of easily recognized trabeculae while the latter are ribbons of spherulitic aragonite in *Astroides*.

5. The theca (wall of the corallite) forms in the ways characterized by previous work (Wells 1956, p. F346). Septotheca is formed by spherulitic outgrowths from neighbouring septa and are thickened within a pocket formed by the internal and external basal flesh of the polyp. Synapticulotheca is porous when formed of rings of synaptaculae, but where these elements are coalesced, as in *Siderastrea*, the resulting structure is indistinguishable from septotheca. Paratheca in *Manicina* is formed of a septothecate portion and accessory dissepiments which are subvertical and contain an extra, internal spherulitic layer when compared to subhorizontal dissepiments.

6. Coenosteum, as noted in *Astroides* is remarkably similar in configuration and structure to the ribbon-like columella in this genus.

7. Stereome, as seen in *Lophelia* is composed of transverse bundles of aragonite needles varying in orientation one bundle from another. The formation of this is

apparently due to action of the peripheral edge zone of the polyp, but is not well understood.

8. Epithea, present only in *Manicina* among the species studied, is composed of sub-horizontal crystallites which have a chevron-like appearance in transverse section. The crystallites have grown from the outside in, although the apparent growth of the epithea itself is upward.

9. Dissepiments are constructed of a first-formed primary layer with an overlying upper spherulitic layer. The primary layer grew centripetally from septa to a central junction line. The upper spherulitic layer is composed of vertically oriented aragonite spherulite clusters, with a keystone row of spherulites aligned over the central junction of the dissepiment. Growth lines are readily apparent on the undersurface of shallow water corals studied. Tabular dissepiments in *Lophelia*, a deep water coral, are markedly different from others in that no growth lines or primary layer can be observed, and the spherulitic layer is continuous with a spherulitic sheath coating the septa. *Manicina*, in its parathecal dissepiments, has a lower spherulitic layer below (inside of) the subvertical primary layer. This lower spherulitic layer is only present in the area near the theca and indicates a somewhat different mode of origin from that in other genera.

10. In their simplest form, synapticalae are the junction of gradulations on opposing septal flanks, as in *Siderastrea*. In *Fungia*, synapticalae are formed of a multiplicity of trabeculae and play a much more important role in polyp support and wall construction.

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EXPLANATION OF PLATE 23

Fig. 1 is photomicrograph.

Fig. 1. *Fungia scutarea*, Recent, Pacific, photomicrograph (crossed nicols) illustrates compound nature of synapticalae (arrows), with upwards of 10 trabecular centres evident in each, $\times 25$.

Fig. 2. *Lophelia prolifera*, Recent, Blake Plateau, Atlantic, polished and etched section to show sheath of crystallites (at right) coating septum (far right) and contiguous with dissepiment at left, $\times 500$.

Fig. 3. *Porites porites*, Recent, Florida Keys, polished and etched section of very simple, symmetrical synapticalae formed by junction of septal trabeculae outgrowths, $\times 850$.

Fig. 4. *Siderastrea radians*, Recent, Florida Keys, polished and etched section to illustrate continued and disoriented growth of spherulites under synapticala, $\times 450$.

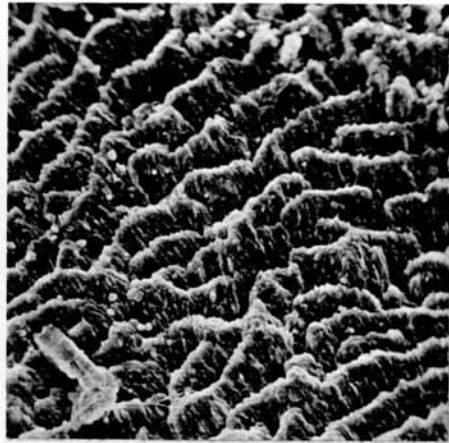
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J. E. SORAUF
Department of Geology
State University of New York
Binghamton
New York, 13901
U.S.A.

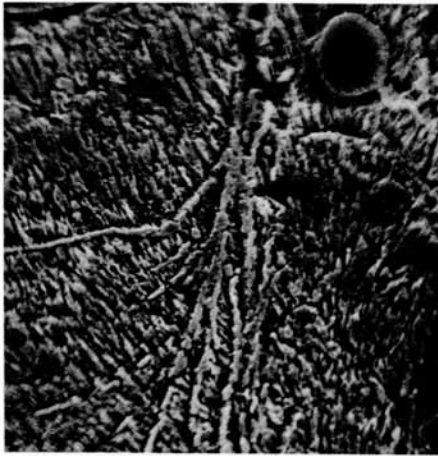
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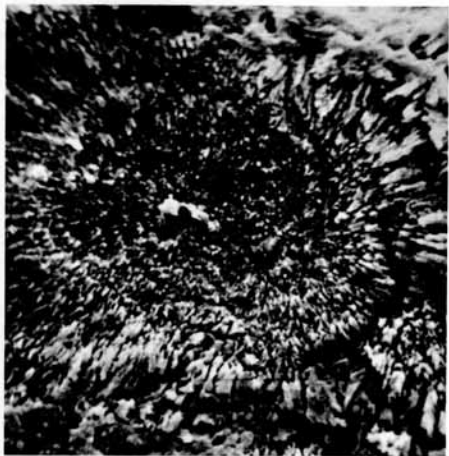
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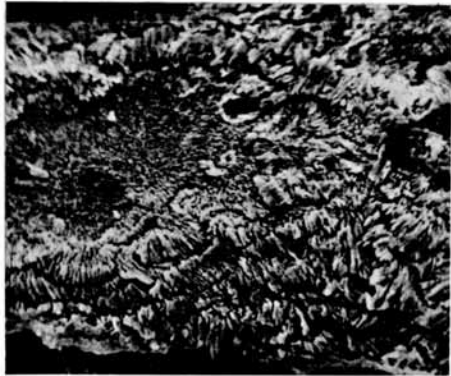
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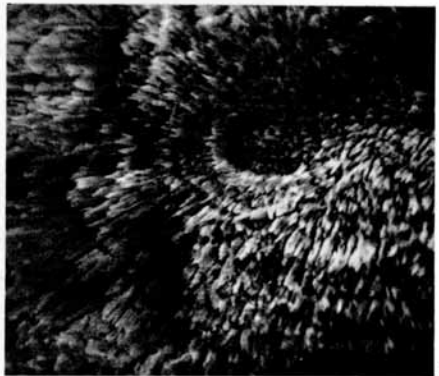
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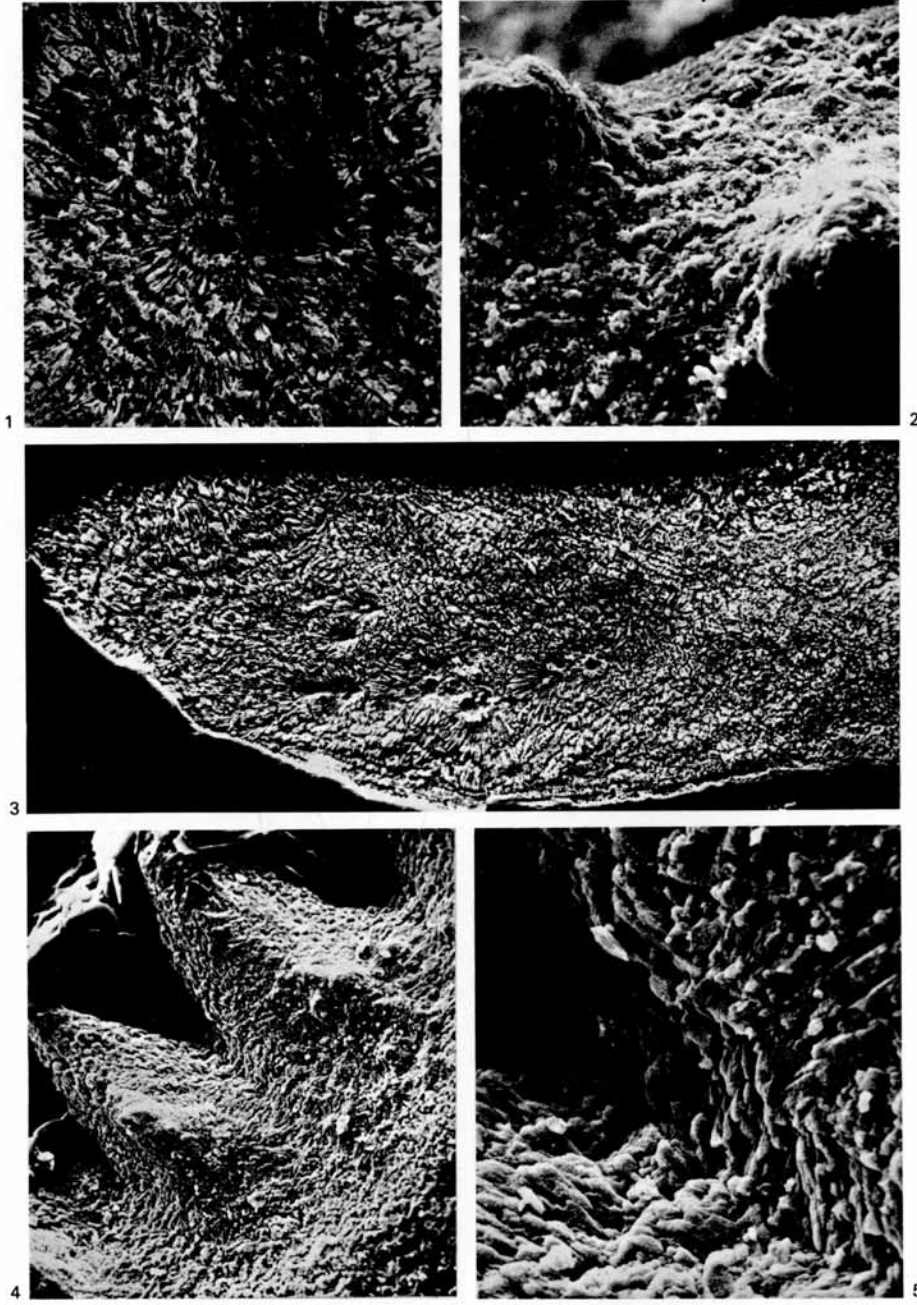


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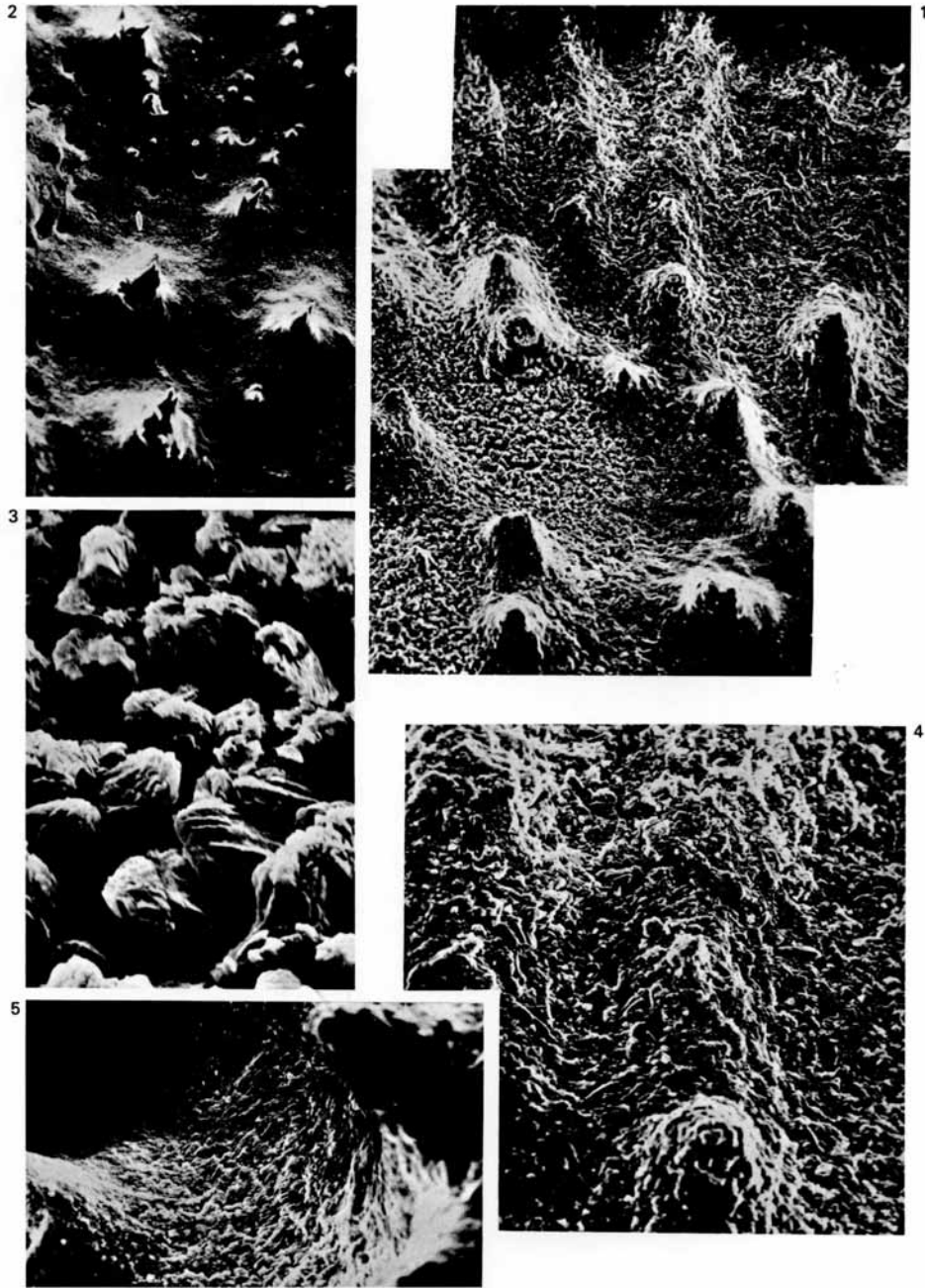


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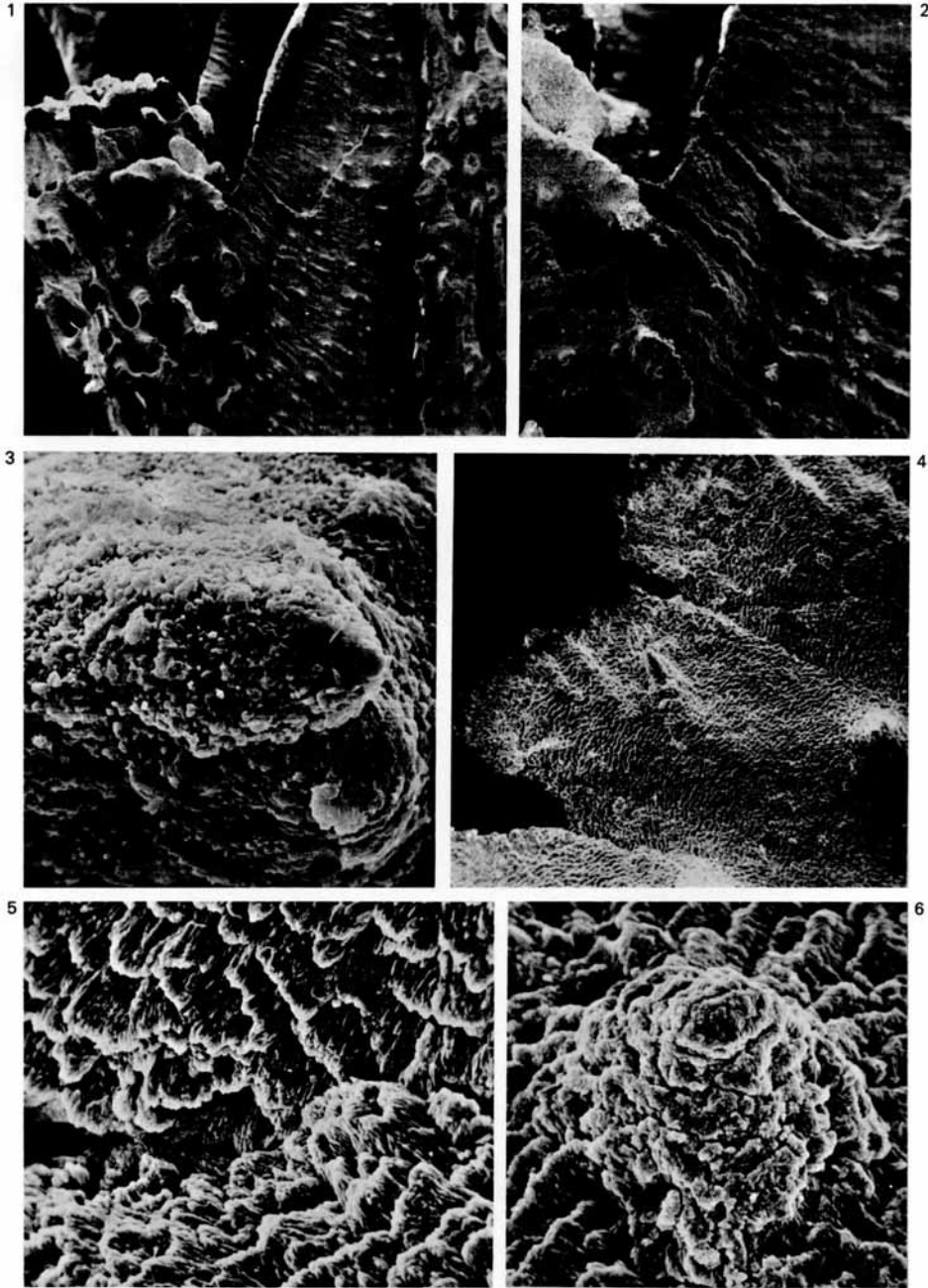
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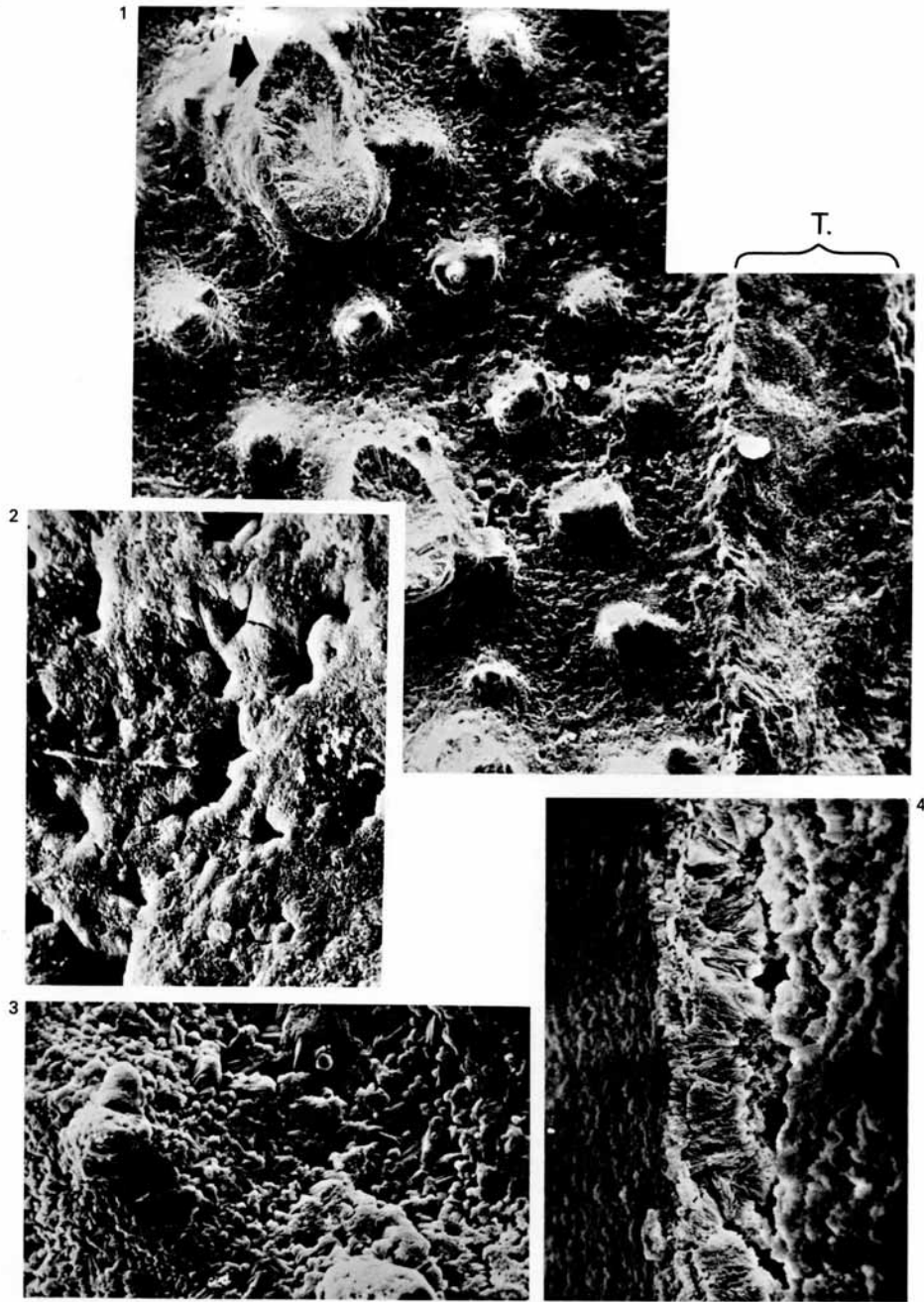
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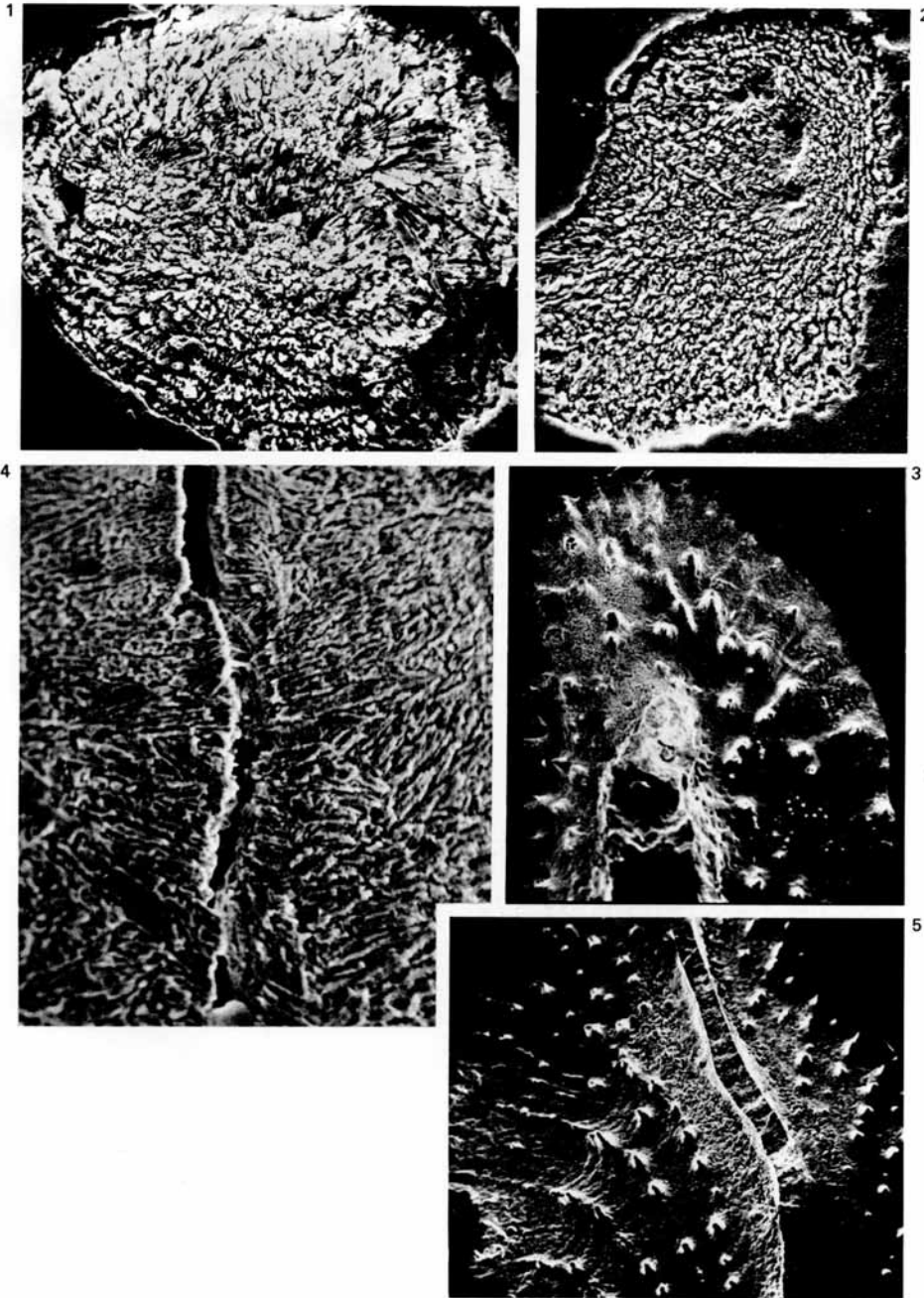
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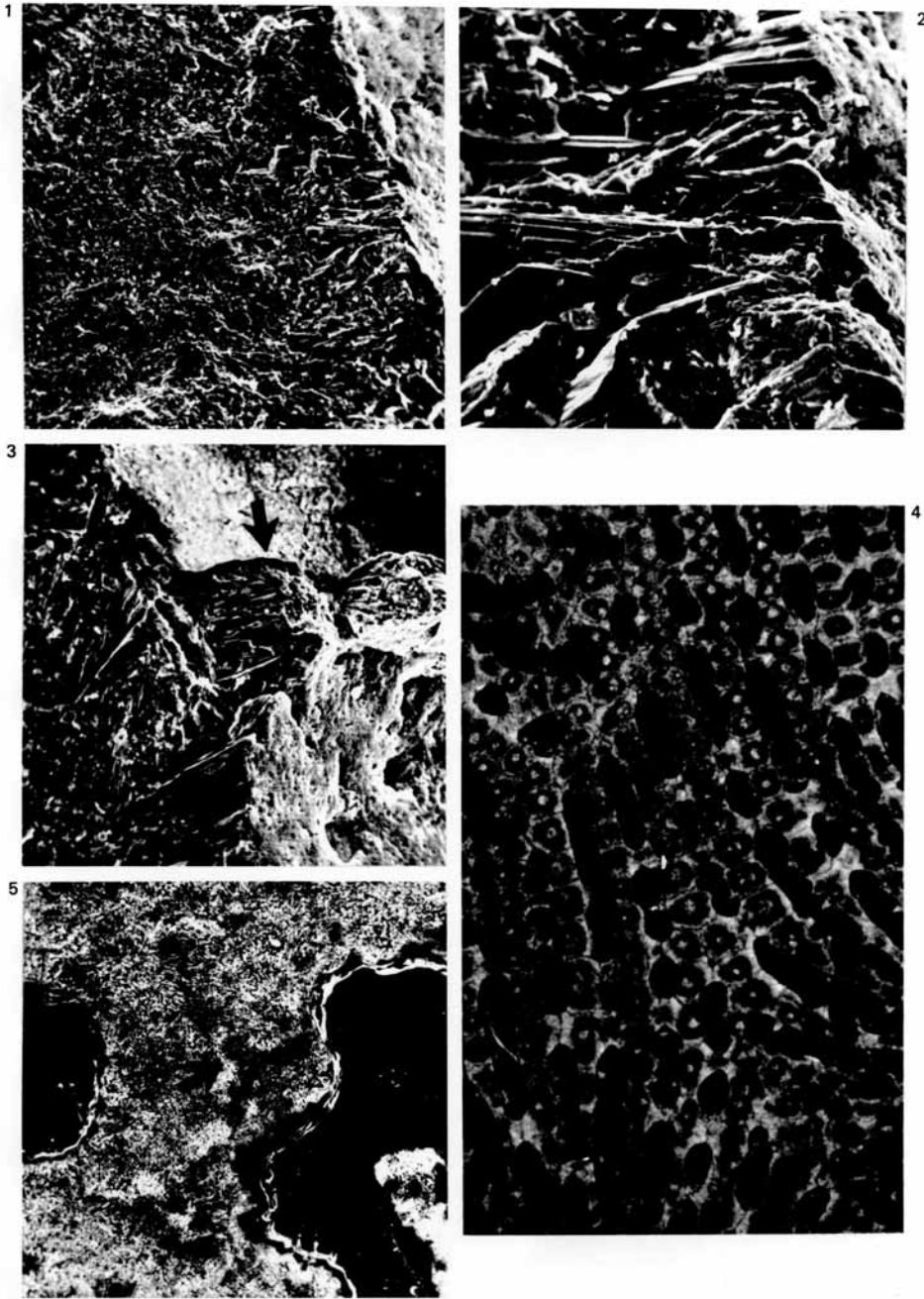
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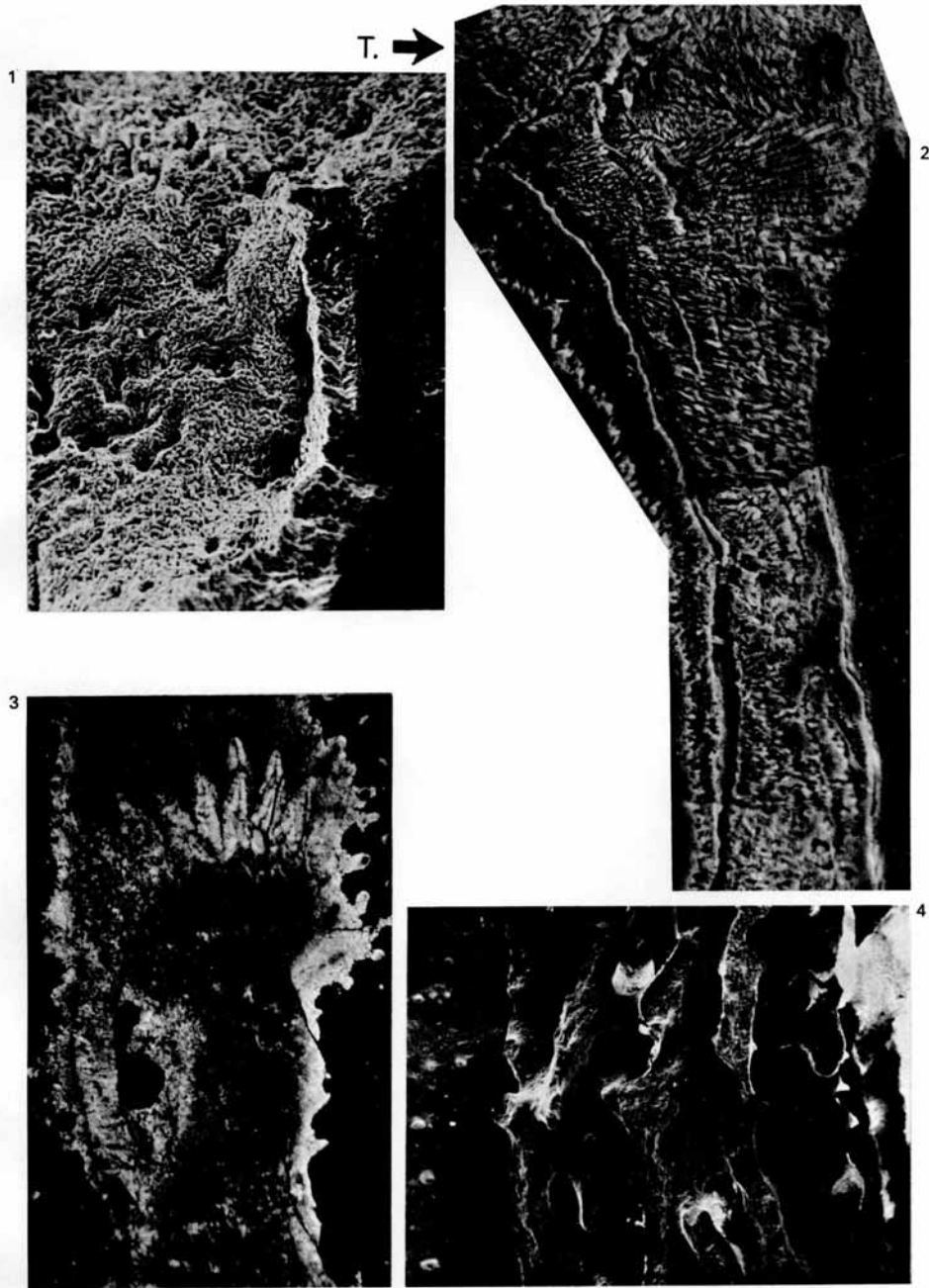
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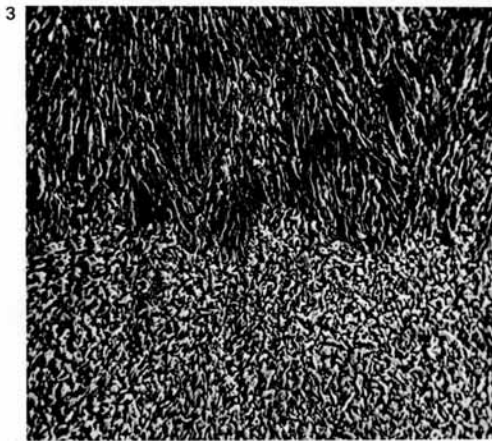
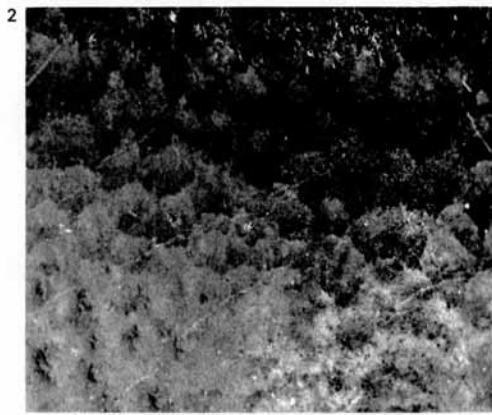
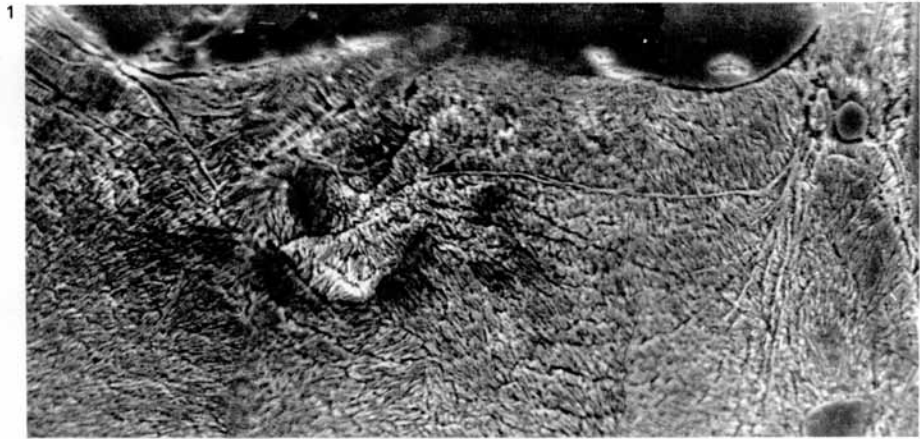
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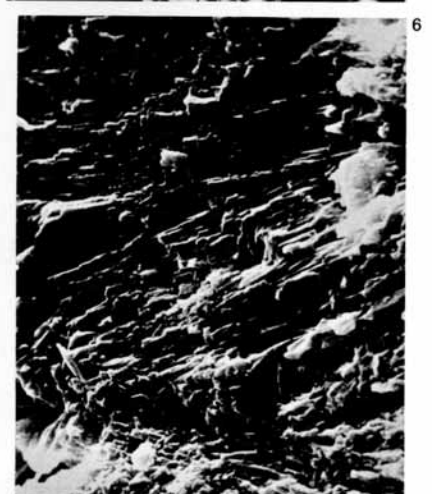
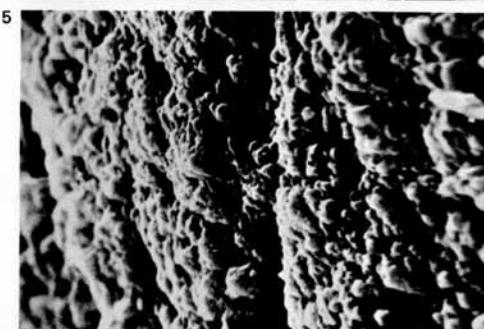
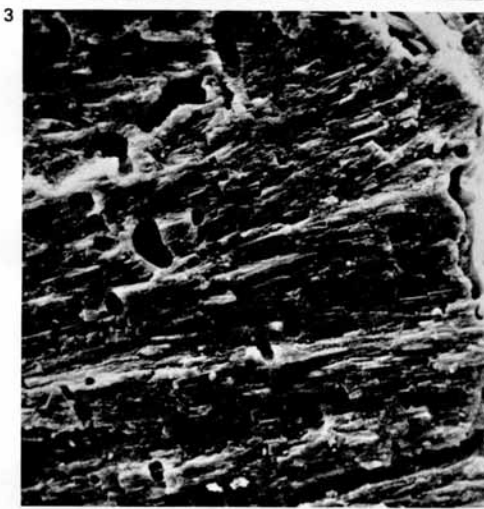
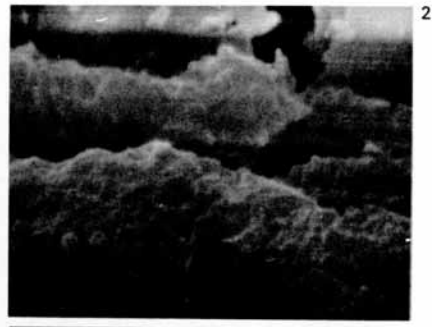
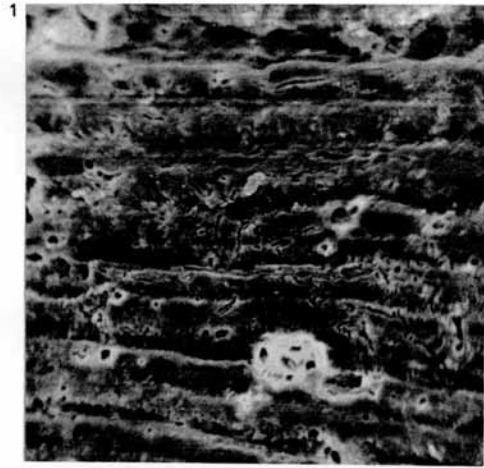
SORAU, *Trachyphyllia* and *Siderastrea*



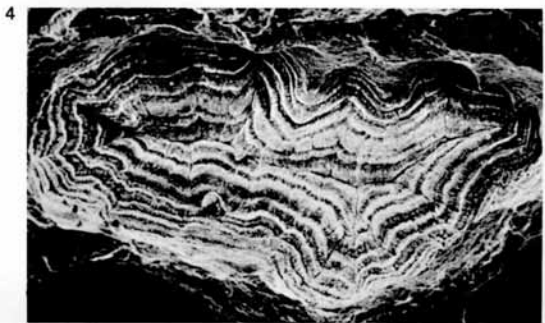
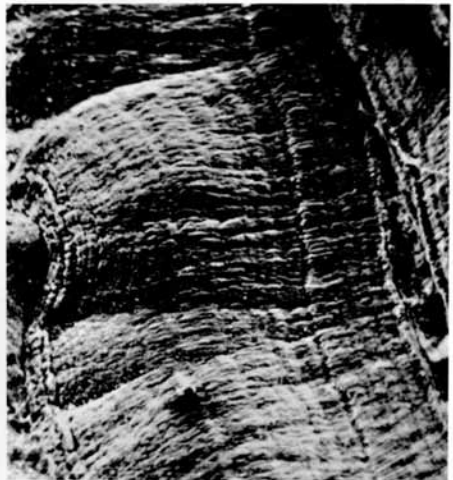
SORAU, Scleractinia



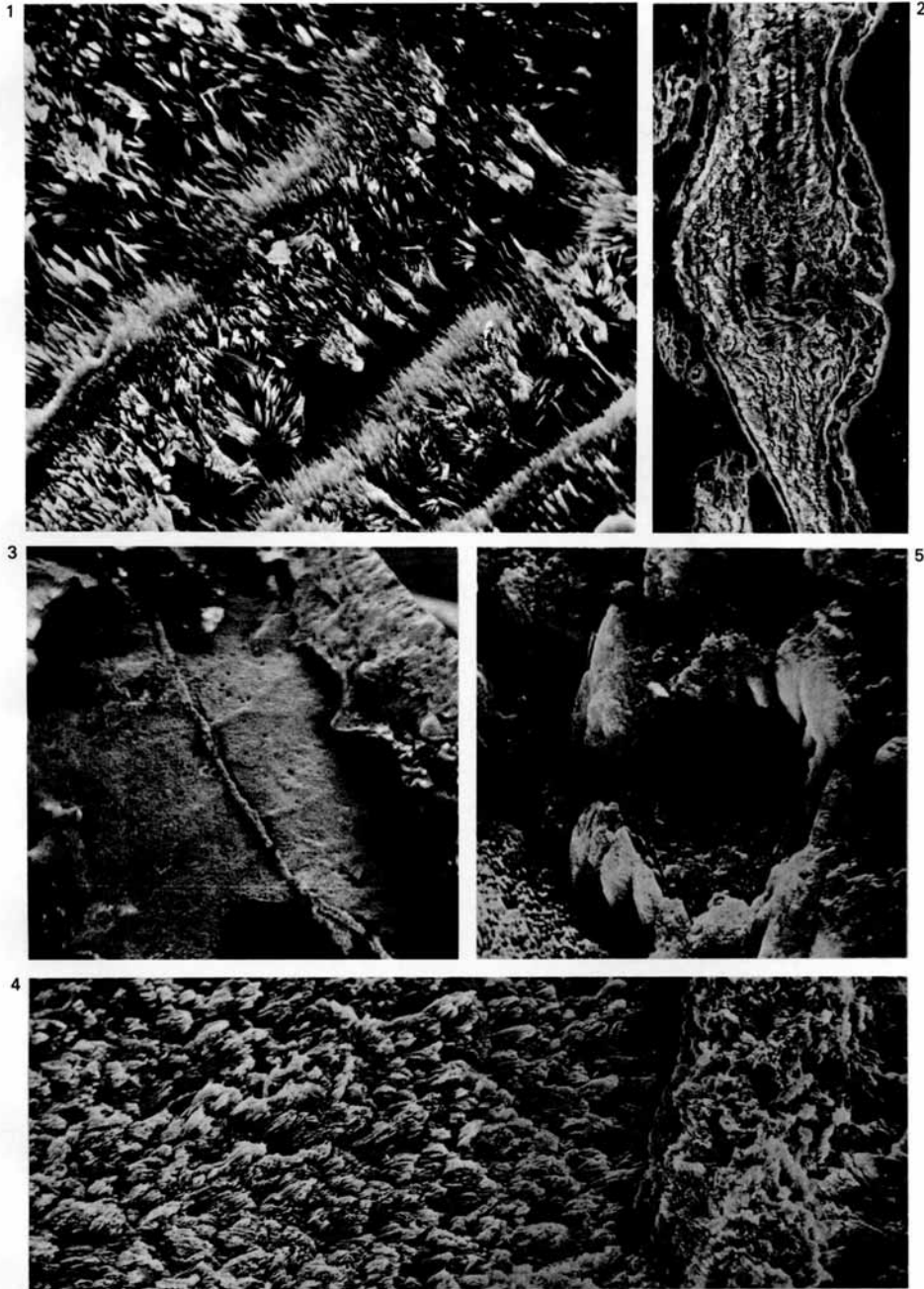
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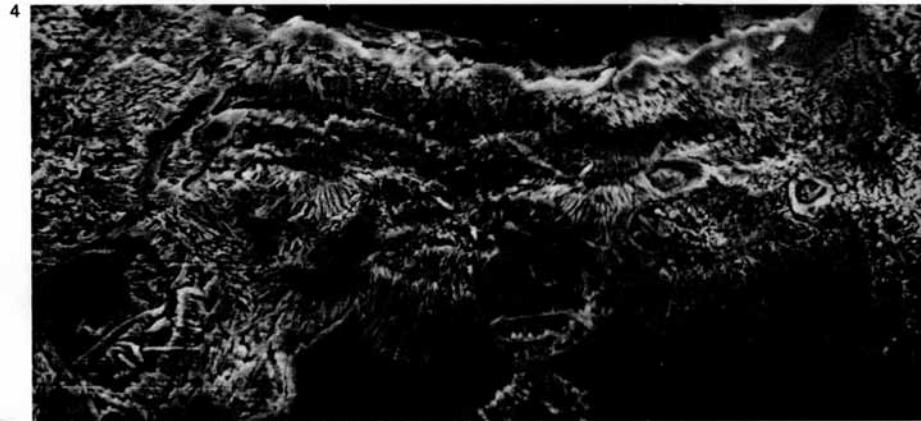
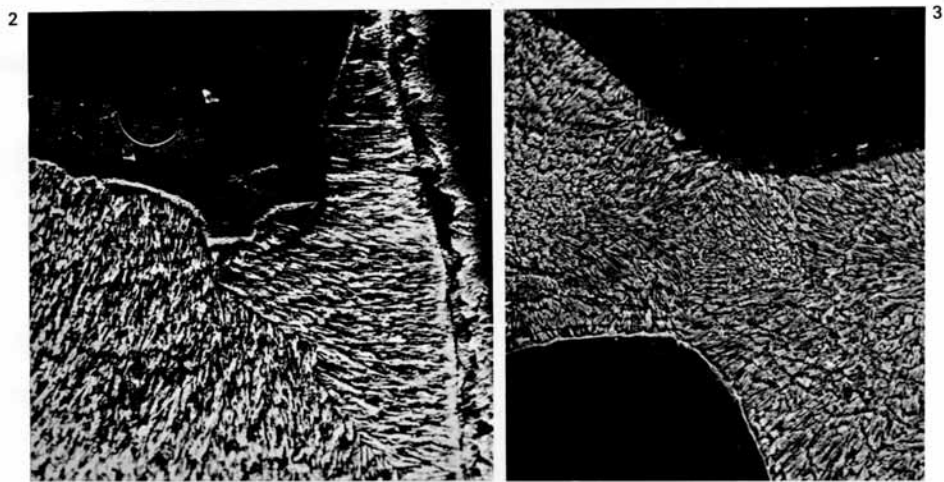
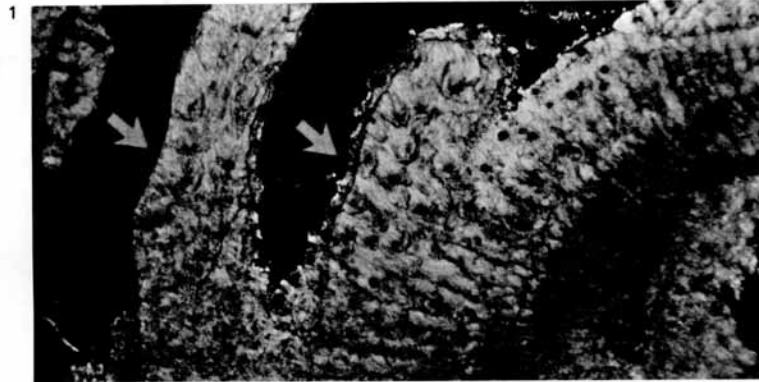
SORAU, *Manicina*



SORAU, Scleractinia



SORAU, Scleractinia



SORAU, Scleractinia
