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BIOMINERALIZATION, STRUCTURE AND DIAGENESIS OF THE COELENTERATE SKELETON

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Review of biomineralization and microstructure in major coelenterate groups leads to generalizations regarding the locus and method of skeletogenesis. The Hydrozoa, which include the most primitive skeleton-bearing coelenterates, generally have an aragonitic skeleton formed externally of varying combinations of spherulitic crystallites modified by organic matrix material. Living Anthozoa show two markedly differing plans of skeletogenesis. In Octocorallia, internal crystallization of calcite closely controlled by organic matrix forms spicules, while the Scleractinia have external crystallization of aragonite with microstructure likewise closely controlled by envelopes of organic matrix. Fossil corals (Rugosa) followed the same architectural plan as the Scleractinia, although building of calcite. As a result of differing biogenic mineralogy, diagenetic structures differ greatly between the two especially where vadose or fresh water diagenesis was involved. Both groups are characterized by biogenic structures of a trabecular or fibro-normal nature.

K e y w o r d s: Biomineralization, skeleton structure, skeleton diagenesis, Scleractinia, Rugosa, Hydrozoa, Octocorallia.
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INTRODUCTION

This paper presents views and data concerning the locus and means of skeleton formation in the main groups of living coelenterates; the skeletal structures known to be biogenic (or assumed to be biogenic in fossil coelenterates); and some discussion of diagenetic modification of skeletal carbonate and resultant secondary structures. Although an attempt is made to present a balanced overview of the groups of living coelenterates known to possess skeletal elements, not all fossil groups regarded as coelenterates are treated.

RESEARCH INTO SKELETOGENESIS

The primary argument during the early years of research into skeletogenesis in corals related to whether calcification was of an extracellular or an intracellular nature. Von Heider, studying *Cladocora,* noted skeleton-forming cells in the basal polypal flesh, named them calicoblasts (1881: 284) and concluded that the calicoblast cells became filled with calcareous deposits by intracellular crystallization, thus incorporated into the coral skeleton. Ogilvie found cell remnants on the skeleton of *Galaxea* and regarded them as calcified calicoblast cells (1896: 116). Most zoologists and paleontologists have followed the works of von Koch (1882) and Bourne (1899) observing that crystallization was extracellular. However, Kawaguti and Sato (1968), studying *Acropora* by electron microscopy, found what they regarded as calicoblastic cells accumulating calcareous materials within them "thus turning into a skeleton" (1968: 91). Hayes and Goreau (1977*a, b*) and Goreau and Hayes (1977) have recently presented arguments in favor of intracellular precipitation of the coral skeletal material. These authors reported granular vesicles within ectodermal cells (in *Astrangia danae* and *Porites porites*) containing "electron-lucent crystal configurations" (1977*a*: 31). They stated that "further analysis... is in progress to confirm the lattice configuration which is expected to be that of aragonite" (op.cit.: 31). They also noted that examination of adult coral specimens established the electron-lucency of aragonite crystals in ultra-thin-section. This is erroneous, as the electron density of aragonite is much greater than that of the adjacent cellular tissue and embedding medium.

Von Koch (1882: 290) was the first to hypothesize that the coral skeleton is not only the result of ectodermal activity but also that crystallization is extracellular, the result of secretion by ectodermal cells. This general approach was favored by other early authors (Bourne 1899; Fowler 1887), and has been the basis for development of more recent models. T. F. Goreau (1959: 71) noted that, "The weight of histological evidence now indicates that the mineralization process occurs outside the calicoblastic epidermis which secretes an organic matrix that may act as a template on which the final stages of skeletogenesis takes place". This "matrix" material was characterized by Goreau as an acid mucopolysaccharide-like substance; seen by Vahl (1966: 33) in transmission electron micrographs as an amorphous material filling the space between the calicoblastic ectoderm and the skeletal aragonite. Johnston (1978: 56) however, feels that the subectodermal space is filled with a fluid which does not play an important role in forming the skeleton.

This last is an important aspect of skeleton formation, as some have suggested that crystallization is not only extracellular, but also with only a tenuous connection to the calicoblastic ectoderm. Barnes, in arguing the importance of physical laws of crystallization and interferring clusters of crystals in determining skeletal structure, suggested that crystals grow into spaces created by the pulling up of ectoderm to form pockets within which crystallization occurs syntaxially on pre-existing skeletal carbonate, with the animal generating a "supersaturated solution of calcium carbonate above the skeleton" (1970: 306). Johnston (1977, 1978, 1979) lately has shown conclusively the presence of an organic matrix in *Pocillopora damicornis,* external to the calicoblastic ectoderm, below the "sub-ectodermal space", but at the upper surface of the skeletal aragonite. The matrix material is most likely secreted by Golgi bodies within calicoblastic cells. Skeletogenesis by mature ectoderm is thus extracellular and matrix-controlled, as discussed in the following section.

SCLERACTINIA, SKELETOGENESIS

Larval skeleton. Studies by Vandermeulen (1974, 1975), Vandermeulen and Watabe (1973), and Johnston (1976) have illustrated the formation of the coral basal plate, a true larval skeleton differing in structure and manner of formation from the adult coral skeleton.

The epidermis of the planula larva is composed of columnar and flagellated cells; upon settling, there is the secretion of a mucoid substance which provides for attachment and the isolation of the basal, calicoblastic epidermis. This portion of the epidermis flattens (40 μm after 6 hours, Vandermeulen 1975) and eventually forms a tissue layer one cell thick. Calcification begins approximately 6 hours after settling (Vandermeulen and Watabe, 1973; figs 3, 6) and rapidly formed spherulitic clusters are deposited, which fuse laterally to form the basal disk, "a flat two-dimensional calcareous disc on which all subsequent structures arise" (op.cit.: 48). By 48 hours, these authors found that the basal disc of *Pocillopora damicornis* was a unified calcareous mat. Post-larval skeleton begins to form by 72 hours (op.cit.: 49).

The composition of this basal plate is largely aragonite, but with some small but persistant amount of calcite and much organic debris (Vandermeulen and Watabe 1973: 54). Johnston found also that lamellae of organic material are present, oriented parallel to the basal surface of the calicoblastic ectoderm (1976: 252, fig. 2). It is not clear how this organic matter affects crystallization patterns; the presence of spherulites reported by Vandermeulen and Watabe suggests that the crystals grew in the mucoid layer without constraint by matrix materials.

Post-larval skeleton. The crystallization of aragonite to form the skeletal features of mature Scleractinia occurs within matrix material, as shown for *Pocillopora damicornis* by Johnston (1977, 1979). What follows is a summary of his findings (1979: 423). Small vesicles (diameter 50—75 μm) accumulate in intercellular spaces within the calicoblastic ectoderm adjacent to the mesogloea and also along the cell boundary (diastasis) closer to the base of the cellular layer (1979: fig. 15). These rounded vesicles are released into the subectodermal space and join with pre-existing matrix material to enlarge the matrix network, simultaneously discharging their contents into matrix sheaths which are 0.15 to 0.25 μm in width and up to 3 μm in length. These sheaths or crystal envelopes are the locus of crystallization for aragonite needles of the same size and orientation (1977: figs 15, 16). The matrix material is 1) short lived, and 2) visible by electron microscopy only after fixation with a technique which employs tannic acid. The matrix partially breaks down within hours and only larger crystal bundle sheaths remain, apparently modified in composition. They might be composed of fibrils of chitin, as proposed by Wainwright (1963). Johnston concludes that matrix breaks down due to an aging process, so that in older portions of the skeleton the matrix is more disorganized and consists of the "chitin" fibrils only. Perhaps too, early recrystallization of crystals to form crystal fibers may have a destructive effect on the delicate matrix.

The route of the Ca^{++} and CO_3^{--} is thus perhaps much as proposed by T. F. Goreau (1959) with Ca^{++} removed from sea water and passing through the gastroderm

(endoderm) to the site of crystallization, and with metabolic CO_2 forming H_2CO_3 with water and following a similar route. The mechanism for part of this transfer at least could be the matrix precursor vesicles noted by Johnston, who suggests that the fluid within these vesicles might be highly charged with calcium and/or carbonate ions which are then discharged into the matrix sheath and crystallize epitaxially on the existing crystal contained in the sheath. Some ions may well make their way through the ectoderm itself from the endoderm or mesogloea and unite at the matrix sheaths. Preliminary study by Johnston (1978) utilizing sodium fluoride to precipitate CaF_2, indicates that a large amount of ionic calcium is present in both endoderm and calicoblastic ectoderm in the lateral intercellular spaces but not in the subectodermal space, suggesting transport by vesicles as the final pathway to growing crystals.

We owe to Johnston the identification of matrix material and illustration of not only the matrix sheaths but also matrix precursor vesicles in the intercellular spaces and in the medium filling the subectodermal space linking with existant matrix material. He has presented a truly plausible hypothesis for the migration and/or delivery of necessary ions to the site of crystallization within the matrix.

OCTOCORALLIA, SKELETOGENESIS

Few up-to-date studies have concentrated on skeletal elements and histology of associated octocoral tissues, thus much of what can be said about octocorallian skeletogenesis comes from structural analogy.

Kawaguti (1964: 23) reported that electron microscopic study of the gorgonian *Euplexaura* revealed that skeleton-forming cells (the scleroblasts) are found in both ectoderm and endoderm when immature, but later migrate to form a spicule-forming cell cluster in the mesogloea. He also noted that electron dense calcareous material was precipitated in the scleroblasts within vacuoles. Most octocorals probably utilize a scheme of spicule formation similar to that shown for the pennatulacean genus *Renilla* by Dunkelberger and Watabe (1974: fig. 1). Crystallization in *Renilla* is intracellular and takes place in large vacuoles within scleroblasts. Subparallel or parallel orientation of elongate crystals of calcite is achieved by organic matrix which surrounds each needle, with matrix also responsible for the configuration of each spicule. Dunkelberger and Watabe (1974: 583) also noted that within the scleroblast, nearby Golgi bodies surround the vacuole containing the spicule and secrete precursor vesicles which provide the organic matrix material to the spicule-bearing vacuole.

The mesogloeal spicules characteristic of most octocorals are calcitic, and composed of elongate parallel crystals, as in gorgonaceans (pl. 13: 1, 2). The pipe organ coral, *Tubipora musica*, is also calcitic and composed in large part of solid tubules that are mesogloeal in origin, with a network of spicular elements forming tabulae (pl. 13: 3—5 and Spiro 1971: 280). Unique among the octocorals is the genus *Heliopora*, composed of aragonite, with a structure and microarchitecture (pl. 14: 1—3) which

warrant assuming that at least some crystallization results from scleroblasts moving freely in the mesogloea, as in other octocorals (fig. 1).

A rather different type of biocrystallization is seen in the central skeletal rod of the pennatulacean *Veretillum* (Ledger and Franc 1978), where bundling of fibrils of collagen forms the pennatulid central stalk which is uncalcified and flexible at its lower tip. Further up the stalk, the rod is calcified, with clusters of elongate calcite crystals in nodules surrounding but *not* impregnating the collagen fibrils (as in

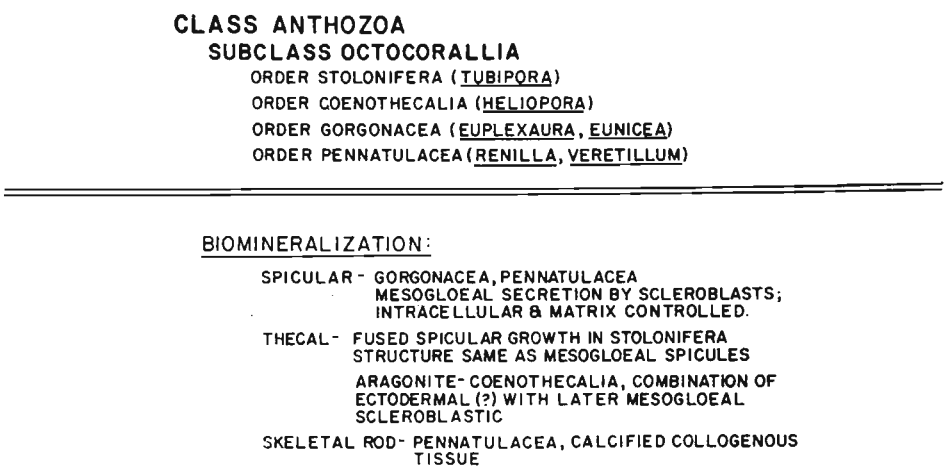

Fig. 1. Classification of major groups within the Subclass Octocorallia that are discussed in this paper, along with a summary of biomineralization for skeletal elements within the group.

vertebrate bone). Where best developed and thickest, the rod consists of irregular columns of calcite radiating out from a nodular core, underlying an epithelial coating and with fibrils of collagen extending through the columns (op.cit.: figs. 13, 15). The columns of calcite are composed of slightly radiating crystals which interfere with crystals of neighboring clusters (much the same way as aragonite in scleractinians) to produce the columns. In contrast to the formation of octocoral spicules, the axial rod in *Veretillum* is apparently extracellular, an intimate association of calcite and collagen fibrils (Ledger and Franc 1978: 265).

HYDROZOA

Within the Class Hydrozoa, aragonitic exoskeletons are present in all orders, rare in the Hydroidea, but abundant in the Milleporina and Stylasterina. These are perhaps the most primitive of the skeleton-forming coelenterates.

Modern studies of the histology and processes of biomineralization in the hydrozoans are lacking, and modern electron microscopic studies of their skeletons are few; an excellent study of microstructure by Fenninger and Flajs (1974) and a general study by Sorauf (1974). This paper summarizes the structures noted within the class and hypothesizes methods of biomineralization.

In the Order Hydroidea, only one living genus forms an exoskeleton, *Hydractinia* (Hill and Wells 1956: F84). Fenninger and Flajs have shown that in this genus the basic structure is one of spherulitic growth of aragonite controlled by organic substrates to form pillars in which the spherulites are in part compartmentalized by the presence of this abundant organic secretion (1974: 72). The organic material appears to form irregular matrix compartments but does not form sheaths for individual crystal growth. The structure forms by growth of interfering clusters controlled by the irregular enclosures (op.cit.: 1, figs. 2, 4).

The Stylasterina are generally characterized by the presence of numerous fused aragonite spherulites forming the major part of the skeleton (pl. 14: 5, 6) as noted by Moseley (1879: 430), Sorauf (1974: 40), and Fenninger and Flajs (1974: 74). The latter authors have noted in addition that a lamellar fibro-normal thickening is present in at least one genus (*Allopora,* op.cit.: 75). Elongate, continued spherulitic growth of crystallite bundles is present in several genera, oriented parallel to the long axis in the central part of the stem of *Stylaster* but oriented normal to the outer surface in *Distichopora* (op.cit.: 75). Thus, the simple structure composed of aggregated roundish aragonitic spherulites illustrated by Sorauf (1974: 49) is locally modified in certain genera to form a more "typically coelenterate" structure of interfering crystal clusters resulting in elongate, bundled crystallites.

The Milleporina likewise exhibit a spherulitic to modified spherulitic structure (pl. 15: 1). On growth surface of *Millepora,* roundish spherulitic growths are noted (Sorauf 1974: 46; Fenninger and Flajs, 1974: 92) but in the mature skeleton, these spherulites are seen forming bundles of crystallites due to the interference of neighboring spherulitic clusters. In older parts of the skeleton, the structure is fibrous, with orientation of crystallites normal to the skeletal surface. Rod-like elongate spherulitic structures resembling the trabeculae of anthozoans are noted in the vertical elements of the skeleton of *Millepora* (Fenninger and Flajs 1974: fig. 4). The fibrous structure is also seen in dissepiments, where the unilateral fibro-normal structure occurs, as in other coelenterates (pl. 15: 2, 3).

CLASS HYDROZOA

ORDER HYDROIDEA (HYDRACTINIA)
ORDER STYLASTERINA (ALLOPORA, DISTICHOPORA, ERRINA, STYLASTER)
ORDER MILLEPORINA (MILLEPORA)

SKELETOGENESIS:

SPHERULITIC - (with organic lamellae)
HYDROIDEA
FULLY SPHERULITIC
STYLASTERINA
MODIFIED SPHERULITIC TO TRABECULAR
STYLASTERINA (Directed)
MILLEPORINA

Fig. 2. Classification of the orders within the Class Hydrozoa that are discussed in this paper, and a summary of hypothetical general modes of biocrystallization within each order.

In summary, in the Hydroidea one sees spherulitic growth of aragonitic skeletal crystallites controlled by large amounts of organic material, not forming fine matrix envelopes but rather forming pockets which control spherulite growth rather than individual crystallites (fig. 2). In the stylasterines and milleporines, one notes first the occurrence of round spherulites fused to form a skeleton, and then modified spherulitic growth with interference between spherulitic clusters to form a palisaded structure similar (fibro-normal) to that in the Scleractinia. Biocrystallization thus is assumed to be ectodermal in the Hydrozoa, controlled in primitive hydrozoans (in Hydroidea and to a certain extent in Stylasterina) by an exuded basal organic matter operating as matrix by controlling the spacing of nucleation sites and limiting size or shape of spherulites. In more advanced hydrozoans, the milleporines, and more mature portions of stylasterines there seems to be less "free growth" of spherulites and a greater development of the fibro-normal crystal orientation in all skeletal parts, as well as some trabeculae-like structures in *Millepora*. This suggests that the organisms developed a progressive capability to secrete matrix material similar to that in the Scleractinia, with matrix envelopes finally controlling individual crystal growth.

ANTHOZOAN MICROSTRUCTURE

Scleractinia. The model for biomineralization accepted here requires that all mineralization by the mature polyp is in the form of aragonite with crystallite growth usually perpendicular to the basal ectoderm. Wise (1972: 164) showed that fascicules, or bundles of aragonite crystals may lie at various angles to the flanks of septa. Crystal growth provides a structure palisaded normal to the outer surface of most skeletal elements (pl. 15: 4, 5) in which crystallization of aragonite follows patterns of spherulitic growth even though greatly influenced by matrix. Where there is a clustering of calicoblastic cells in the ectoderm (and/or an up-pocketing of the basal ectoderm) the elongate fibrous trabeculae of the septa result (pl. 15: 6). In septa, unilateral thickening of the septum occurs with additions of laminae of fiber clusters oriented normal to the outer surface of the septum.

Septa are thus always trabecular in the Scleractinia (as shown in Sorauf 1972; Jell 1974) although trabeculae may be of such small diameter that they form what has been called the "central dark line" within septa viewed optically in transverse thin section (pl. 16: 1—3). The thickening of septa is by unilateral crystallization in laminae, controlled by matrix but partially influenced by laws of spherulitic growth. Crystallites within these laminae are generally oriented more or less perpendicular to the flank of the septum (pl. 15: 5). If stereome is added to the flank, further reducing the interseptal space, crystallization continues to be of the same fibro-normal type. In certain scleractinians (especially some ahermatypic scleractinians) the extremely fine trabeculae mean that the major part of the septum is composed of palisaded crystals, with a continuity of crystallites through growth lamellae. In other ahermatypic corals (such as *Lophelia* and *Balanophyllia*) the blankets of palisaded crystallites have a rather notable discontinuity between lamellae (pl. 16: 4),

making them especially prominent and influencing the diagenetic structures created during fossilization. In this case, the lamellar structure will be emphasized.

Horizontal elements always have an upper palisaded structural layer (as in Sorauf 1970: 7) and commonly have a lower layer (primary layer) of horizontal crystals formed by centripetal growth of crystals from neighboring walls or septa to a central junction line. The lower primary layer clearly shows diurnal growth; the upper (spherulitic) layer shows crystallite growth upward into the basal flesh of the polyp, again presumably controlled by matrix configuration but partially by laws of spherulitic growth.

The theca, whether septotheca, paratheca or synapticulotheca, likewise is comprised of crystals growing normal to the basal ectoderm, and may be unilateral or bilateral (pl. 16: 1, 2) depending on whether the polyp has an edge zone and drapes over the theca. Where the theca is thickened by stereome, continuing crystallite growth is syntaxial and normal to basal ectoderm.

Thus, all the structural elements of the Scleractinia show the same microstructure, trabeculate in septa (or in rod-like extensions of septa, such as pali or synapticulae) and palisaded in other skeletal aragonite with crystallite orientations normal to basal ectoderm. As a result, the greatest part of the skeleton is a rather direct reflection of the configuration of the basal calicoblastic ectoderm.

There are two exceptions to this rule, the epitheca and the basal disc (or larval skeleton). The epitheca has been shown by Barnes (1972) to be composed of subhorizontal bundles of aragonite crystals growing inward within the lappet of the polyp (a fleshy fold at the margin of the calicoblastic ectoderm). This is apparently due to biocrystallization at the junction of the free body wall and the calicoblastic body wall and the interplay of cells at this junction during diurnal expansion and contraction (Barnes 1972: 336).

The larval skeleton has been shown by Vandermeulen and Watabe (1975) to form from spherulites coalescing to produce the basal disc. Johnston (1976) observed some laminae of matrix present within the larval skeleton forming the basal disc. Growth of crystals is upward from the disc as aragonite forms trabecular pillars initiating growth of the vertical elements. The basal disc itself is apparently a mixture of aragonite and calcite (Vandermeulen and Watabe 1975: 54), the only occurrence of the mixture within the scleractinians.

Rugosa. In this summary of microstructures in the rugosans, several assumptions are made regarding the model of biocrystallization and resultant biogenic structures as opposed to diagenetic ones in rugosans.

The assumption is made that rugosan biomineralization was very much the same as that in present day scleractinians. The rugosan skeleton was thus 1) extracellular, and 2) composed of crystallites that are formed within matrix envelopes and have had their long dimension approximately perpendicular to the basal flesh of the polyp. The assumption is also made that the original mineralogy of the rugosans was calcite, with elongate needle-like or fiber-like shape determined by the matrix-envelopes.

Kato's 1963 publication regarding the structure of the Rugosa is an important

one. In this paper, he suggested that there are only two basic types of biogenic septal structure, fibro-normal and trabecular. Trabecular septa are analogous to those in the Scleractinia, while fibro-normal septal structure was defined as having a median dark line and crystallites perpendicular to the outer surface of the septum (1963: 582). Fibro-normal septa are here regarded as slightly altered trabecular as seen in such scleractinians as *Desmophyllum* (see Sorauf and Jell 1977: 6). Kato likewise suggested that this could be the case (1963: 583).

Like Kato, I recognize lamellar and zigzag septal and thecal structures as diagenetic in origin (Kato 1963: 593). Lamellar structures may at times have taxonomic value due to the uniformity of occurrence in some genera (as in the Devonian genus *Tabulophyllum*). It is thought that this is a reflection of prominent growth lamellae, characteristic of genera and modified diagenetically into a uniformly lamellar structure. Zigzag structure has little or no taxonomic value and is wholly diagenetic.

Thus, as Kato did, I conclude that the Rugosa have a basic plan of biomineralization which results in crystal orientations perpendicular to the calicoblastic ectoderm. With matrix control of crystal size, shape and orientation, as in Scleractinia, rugosan biogenic structures closely resemble those of the scleractinians. I consider all septa to be trabecular in nature, with apparent fibro-normal septa resulting from modification of very small trabeculae, as observed in many modern ahermatypic genera.

Theca and stereome have formed by unilateral (or bilateral) crystallization, with crystallites perpendicular to the outer surface (fibro-normal), and exhibit the same biogenic structure as in the Scleractinia, except that there is no paratheca or synapticulotheca in the Rugosa, and in addition, there is apparently a more intimate joining of theca and epitheca in the rugosan skeleton. Tabulae and dissepiments are formed the same way, with identical structures in rugosans and scleractinians (as suggested indirectly by Wedekind 1937, and Wells 1969).

DIAGENESIS

Diagenetic change in corals which have been fossilized is obviously of importance to the paleontologist who interprets structure for function or taxonomic usefulness. It is important to understand the original carbonate mineralogy of the biogenic material and characteristic changes in different diagenetic environments in order to determine the identity and origin of secondary structures in fossil corals.

Scleractinia. The carbonate mineralogy of all living representatives of the Scleractinia is aragonite. Bøggild (1930: 241) later followed by Sandberg (1975: 600) proposed that some Cretaceous species were originally calcitic. This should not be accepted until modern x-ray and electron microscopic studies have been carried out on the material. Of the five genera with "calcitic" species mentioned by Bøggild, four are represented by living ahermatypic, aragonitic species. In my judgment, it is best to regard all fossil scleractinians as having originally had aragonitic skeletons until further proof to the contrary is available.

The diagenesis of scleractinians (fig. 3) today apparently begins just below the growth surface of the skeleton as composite crystals of aragonite form through the

fusion of pre-existing crystals during the breakdown of organic matrix. The first major diagenetic change is the infilling of pore spaces by aragonite needles (pl. 16: 5) or marine lime mud (Pingatore 1976: 988), with aragonite needles growing syntaxially over existing biogenic aragonite prior to burial (Hubbard, 1975: 79) and even in dead portions of live colonies (Pitman 1974: 1815). Later submarine diagenesis can apparently lead to recrystallization of fibrous aragonite in skeletal elements to micritic high magnesium calcite by inorganic processes (Sherer 1974: 499) or to lime mud by boring algae and other microorganisms (Bathurst 1975: 383).

In fresh water phreatic (below water table) or vadose (above water table) environments recrystallization is to spar calcite, either through solution and reprecipitation along a very narrow (10—15 μm) zone or through dissolution of aragonite to a porous, chalky state and subsequent infilling of voids by precipitation of calcite (James 1974, Pingatore 1976). The best known sequence for corals is in the vadose zone, studied in Barbados by James (1974). He has noted that diagenesis here, whether dissolution or solution-reprecipitation on a microscale, begins within the coral skeleton, first affecting the very fine crystallites at trabecular centers and subsequently moving outward to affect the remainder of the trabecula (pl. 17: 1, 2). During dissolution, the contacts between aragonite crystals are etched, resulting in a "chalky" appearance (pl. 17: 3). If dissolution continues, entire trabeculae are dissolved and void spaces remain and are filled by calcite spar (pl. 17: 4). During replacement, dissolution and concomitant reprecipitation follow the same pathway as outlined above, but the resulting structure is a mosaic of equant calcite crystals with remnant structure present only as faint ghosts. These ghosts have also been

DIAGENESIS
(SCLERACTINIA)

ENVIRONMENT	SUBMARINE (MARINE PHREATIC)	FRESH WATER PHREATIC	VADOSE (ABOVE WATER TABLE)
PROCESS	1. PRECIPITATION OF ARAGONITE IN PORES.	1. BROAD CHALK ZONE CHALKIFICATION.	1. NARROW ZONE CHALKIFICATION.
	2. MICRITIZATION DUE TO RECRYSTALLIZATION.	2. SOLUTION & PRECIPITATION OF COARSE SPARRY CALCITE (CROSS-CUTTING).	2. CREATION OF VOID SPACES.
	3. BORING & MICRITIZATION.	3. CALCITIZATION OF ALL ARAGONITE WITH LOSS OF MICROSTRUCTURE.	3. PRECIPITATION OF SPARRY CALCITE (FABRIC SELECTIVE).

Fig. 3. Summary of the environments of diagenesis of Scleractinian corals and structures resulting from various processes.

observed in Pleistocene corals from Florida (pl. 17: 5, 6). Pingatore also noted that calcite mosaics produced in the vadose zone tend to be almost exclusively fabric-selective, that is, conforming to boundaries of pre-existing skeletal elements, while those in the phreatic zone are commonly cross-cutting boundaries of pre-existing structures (1976: 992).

How explain the numerous scleractinians that are well-preserved, occasionally even as aragonite? The remarkably preserved Triassic corals reported on by Montanaro-Gallitelli (1973, 1974), Montanaro-Gallitelli *et al.* (1973), Cuif (1975, 1977), Scherer (1977), and Sorauf (1978) are sufficient evidence that such is possible. Apparently the pre-requisites for such preservation are 1) infilling of coral void spaces in a marine diagenetic environment of normal salinity, and 2) early isolation from dissolving solutions, such as percolating rainwater in the vadose zone. It is commonly noted that excellent preservation of scleractinians occurs where the corals are in relatively impermeable shales, and worst preservation or total loss occurs in porous rocks, whether carbonates or non-carbonates.

Diagenetic structures present in scleractinian corals are generally related to calcitization of aragonite and are dependent in large part on diagenetic environment. Granular microstructure (Alloiteau 1957: 21) must be diagenetic, the result of either organic or inorganic micritization. Likewise the development of lamellar structure, whether total or partial (as in the case of Jurassic *Montlivaltia* described by Gill 1970: 2), is a diagenetic modification of prominent growth lamellae during recrystallization or during calcitization of a prominently laminar fibro-normal septal stereome. Fenninger and Flajs (1974: 83) present a pictorial summary of results of diagenetic changes in the Hydroza that may also be regarded as valid for scleractinian skeletal material.

Rugosa. It has been remarked earlier in this paper that rugose corals are regarded as being analogous in their structure to scleractinian corals although differing in original mineralogy. Assumption of a similar biomineralization model leads to agreement with Kato (1963: 582) that the only two types of structures possible are trabecular and fibro-normal types. Fibro-normal septa are apparently septa with very small trabeculae forming the dark line visible in the center of the septum, as has been illustrated for both scleractinian and rugose corals (Sorauf 1977, 1978). Theca, dissepiments, tabulae and other structural elements are in a sense fibro-normal in structure (either unilateral or bilateral in nature, as in Kato, 1963: 578).

Sandberg presented arguments for rejecting an original aragonitic mineralogy for rugosans while concluding that they had a calcitic skeleton of "a variety of structures, including lamellar, fibro-normal, trabecular, zigzag, and others" (1975: 603). Sorauf (1977) showed that in *Lophophyllidium*, both zigzag and lamellar structures are diagenetic, with septa showing a sequence from trabecular structure through intermediate stages to zigzag structure, and showing zigzag laminae grading into laminae of irregularly lamellar areas. In the Permian coral *Polycoelia*, broken sections show wall structure which is zigzag in cross section, but with crystals greatly enlarged in the direction normal to the zigzag direction by recrystallization (Sorauf 1978). These structures are peculiar to the Rugosa and may be characteristic of

diagenetic alteration of rugosan calcitic skeletal material. Oekentorp likewise (1972, 1974*a*, 1974*b*) has presented numerous arguments for regarding zigzag structures as secondary. As noted above, some taxa of the Rugosa seem to show a constant lamellar structure, as *Tabulophyllum*; this is presently regarded as a diagenetic overprint on corals with strong lamellation of fibro-normal structure, but more work is necessary to clarify this.

In summary, recognition of biomineralization models provides the best rationale for interpreting biogenic structures in corals and differentiating between them and diagenetic fabrics. If we assume that the general scleractinian model is valid for rugosans, fibro-normal or trabecular structures are then the only ones that can be formed under the constraints of the biomineralization system.

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EXPLANATION OF THE PLATES 13—17

Plates 13 to 17: all figures are scanning electron micrographs with the exception of pl. 15: 1, pl. 16: 1, 2 and pl. 17: 1.

Plate 13

Eunicea palmeri, Recent, Florida Keys

1. Overview of central portion of octocoral spicule to illustrate the axis and frills upon it, ×550.
2. An enlargement of a portion of 1, to illustrate the arrangement of individual crystals in the frill and on the axial surface to parallel the long axis of the rod-like spicule, ×5000.

Tubipora musica, Recent, Pacific

3. Overview of *Tubipora*, illustrating the tube-like vertical wall, tabula, and proximal portion of stolon-bearing platform, to show the porous nature of each, ×44.
4. Tube wall (broken) and platform, showing spacing of perforations. The next micrograph (5) is an higher magnification view of broken tube wall in exact center of this illustration, ×100.
5. Enlargement of portion of tube wall with pore shown as tunnel in lower center of micrograph, to show the fibrous nature of constituent calcite crystallites, ×2000.

Plate 14

Heliopora coerula, Recent, Maldive Islands

1. Illustration of colony autopore, with prominent, upward projecting skeletal processes and prominent rounded scars on their surfaces, ×100.
2. Longitudinal view of autopore with tabula and broken wall with large crystal fibers of aragonite and smaller crystallites lining surface of pore, ×550.
3. Broken autopore wall illustrating large oriented-upward aragonite crystals somewhat oblique to wall, while smaller crystallites lining autopore walls are parallel to the long axis of the pore, ×1050.

Stylaster elegans, Recent, Bikini Atoll

4. Overview of colony flank showing autopore with surrounding dactylopores sharing opening; grainy-appearing spherulitic surface is covered with canal pores, ×100.
5. Illustrating section broken parallel to axis of pores showing structure of packed roundish spherulites, ×200.
6. Closeup of spherulites to show emergent crystal growth edges, ×2,300.

Plate 15

Millepora alcicornis, Recent, Bermuda

1. Growth surface of bars and pillars forming skeleton illustrating the rounded spherulitic nature of the first-formed part of the skeleton, ×550.
3. View of autopore with tabulae showing the growth of component crystallites oriented perpendicular to the growth surface, ×200.
3. Closeup of tabula illustrating palisaded structure (fibro-normal) with crystals growing towards lower left, ×2,300.

Caryophyllia communis, Recent, off east coast USA

4. Polished and etched section of septum with trabeculae and continued crystal growth forming lamellae of fibro-normal crystals, ×1,000.

Desmophyllum cristagalli, Recent, North Atlantic

5. Septal cross-section, polished and etched to show syntaxial growth of aragonite crystals thickening first formed portion of septum with small diameter trabeculae, ×1,000.

Balanophyllia malouinensis, Recent, Scotia Sea

6. Thin section longitudinal to septum illustrating arrangement of large diameter trabeculae forming framework, ×15.

Plate 16

Flabellum curvatum, Recent, Patagonian Shelf

1. Transverse thin section through theca composed of unilaterally added, inward-directed crystallite growth commencing at outer dark line (epitheca) and continuing towards center of calyx. Note also that septum has central dark line of very small sized trabeculae, ×63.

Caryophyllia communis, Recent, off east coast USA

2. Septa and walls (in thin section) showing bilateral growth of wall, with a dark line of crystal divergence connecting septa, ×25.
3. Septal trabeculae of very small diameter in specimen illustrated in *2,* where trabeculae form central dark line in septa, ×500.

Balanophyllia malouiensis, Recent, Patagonian Shelf

4. Broken section through the flank of a septal rod illustrating strongly developed laminae with crystals oriented perpendicular to septal surface, but with lamellation of a solid nature, ×2,000.

Siderastrea radians, Pleistocene, Bermuda

5. Broken synapticula formed by one trabecula with syntaxial overgrowth of aragonite needles, ×200.

Plate 17

Siderastrea radians, Pleistocene

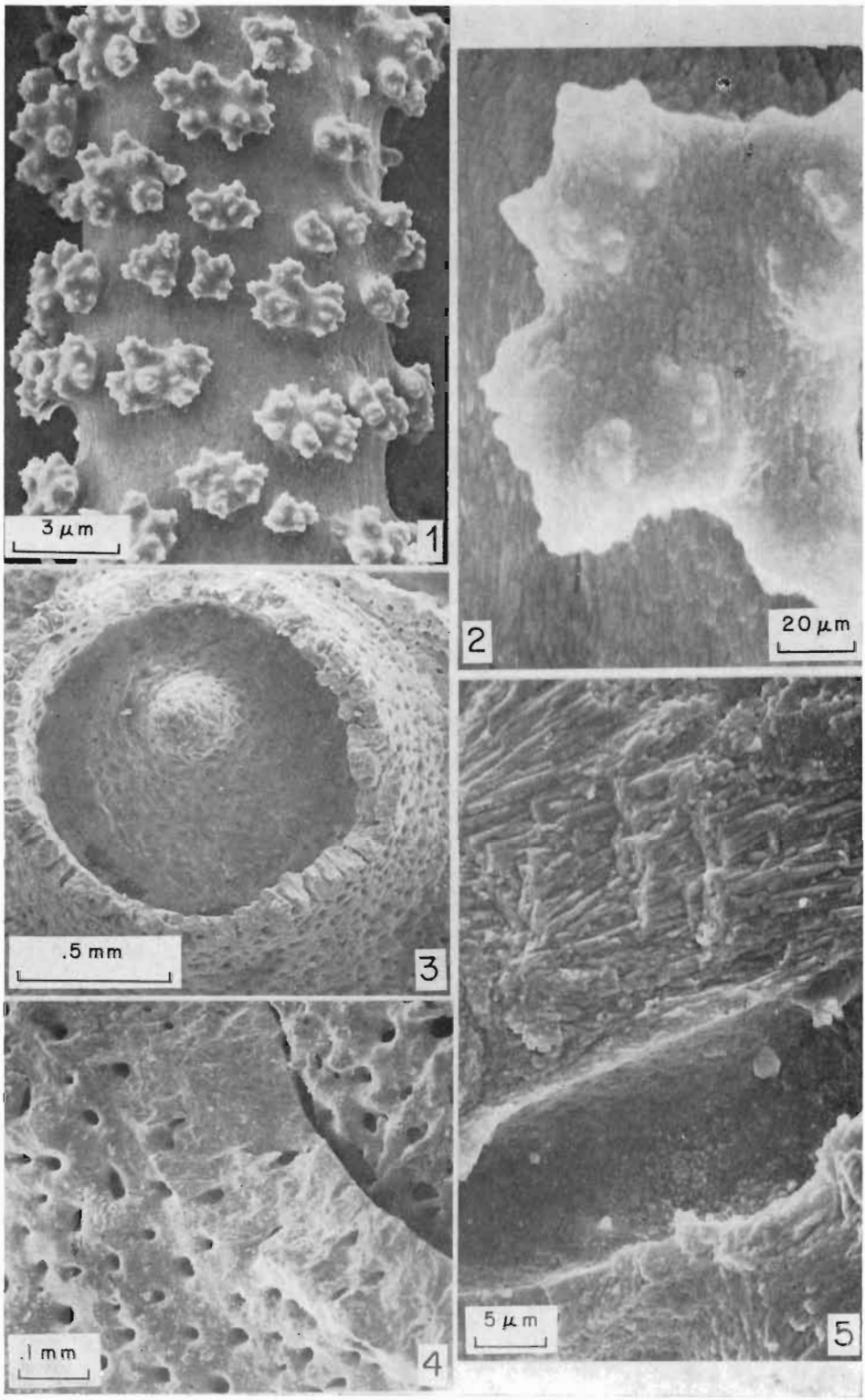
1. Broken synapticula showing dissolution at center of trabecula and precipitation of calcite spar to infill space between dissepiment and synapticula, Bermuda, ×400.
2. Longitudinal view of septal trabecula broken open to show dissolution concentrated at center of trabecula, Windley Key, Florida, ×200.
3. Broken synapticula showing results of chalkification of major part of trabecula from center outward, Bermuda, ×200.

Montastrea annularis, Pleistocene, Windley Key, Florida

4. Broken columellar spine showing spar calcite replacement of greatest part of trabecula from center outward, ×400.

Porites porites, Pleistocene, Rockland Key, Florida

5. Thin section of central part of *Porites* branch with near total replacement of coral by spar calcite, with remnant ghosts, representing skeletal elements in large equigranular mosaic, ×25.
6. Polished and etched section of ghost formed of remnant aragonite needles in spar calcite, ×400.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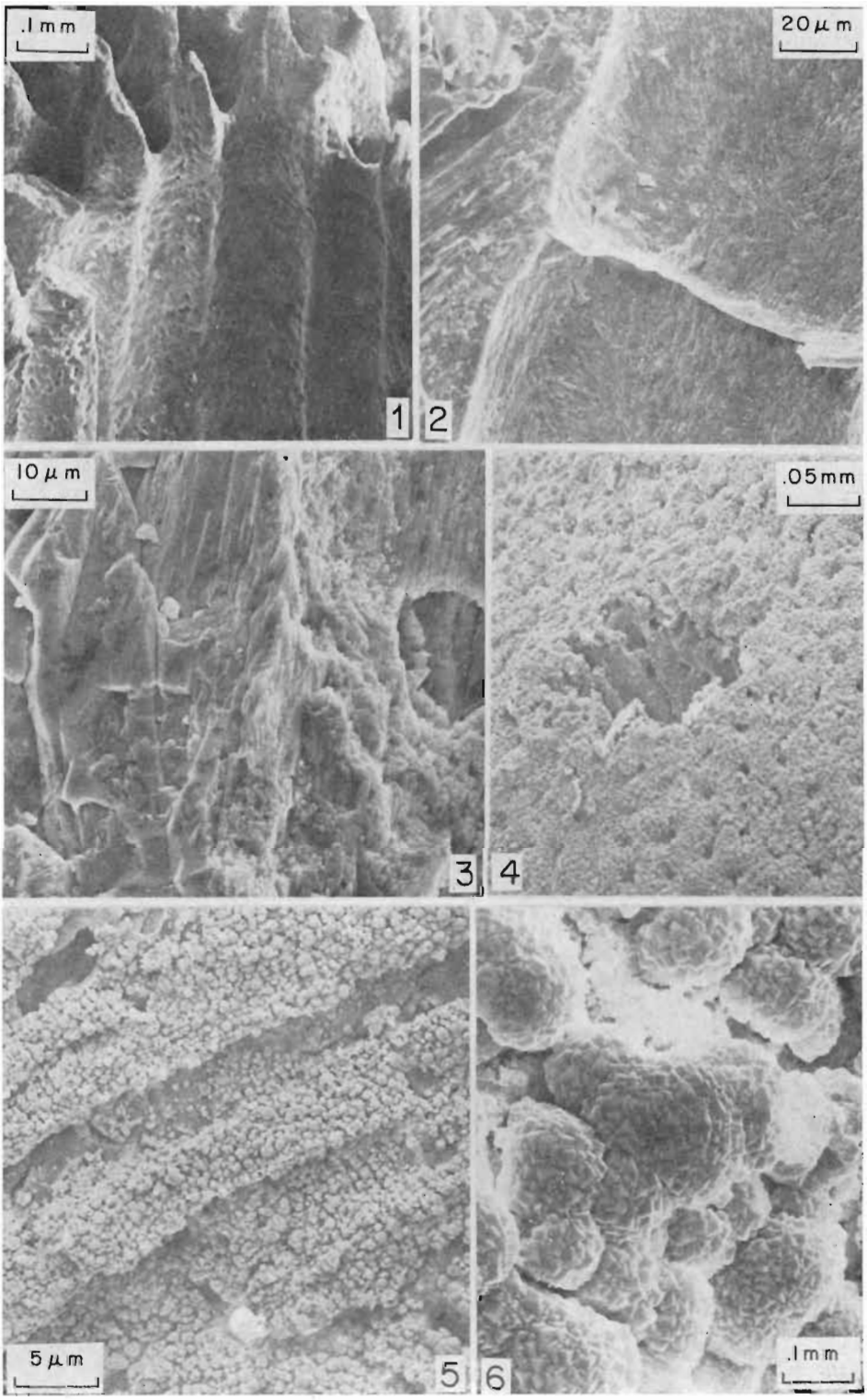
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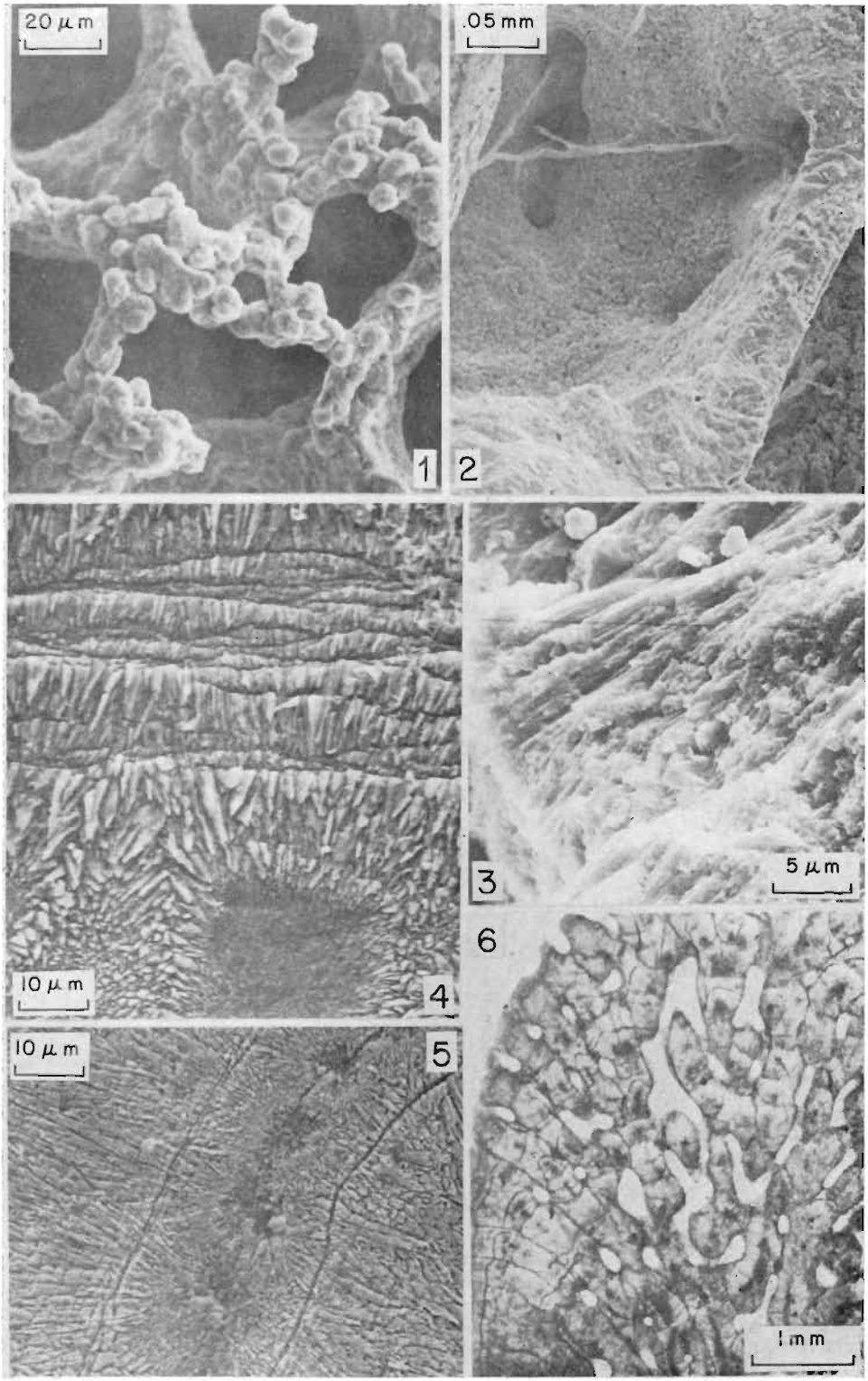
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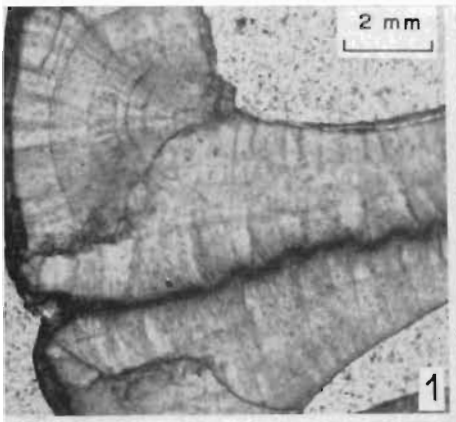
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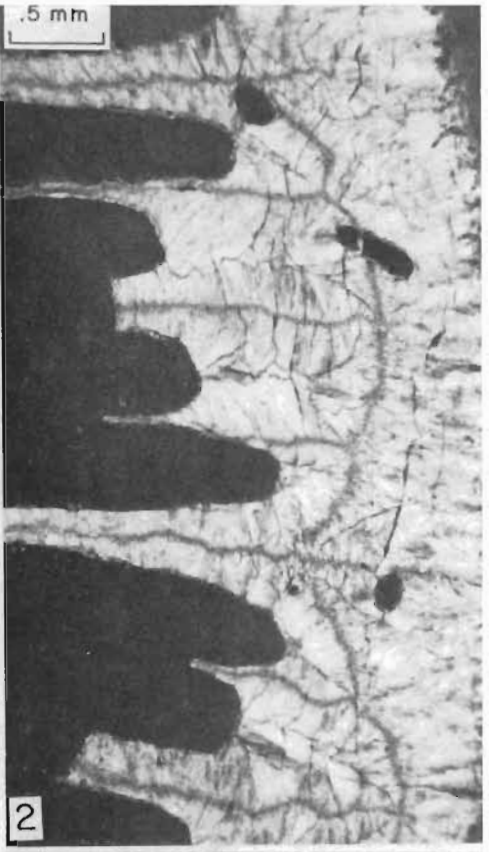
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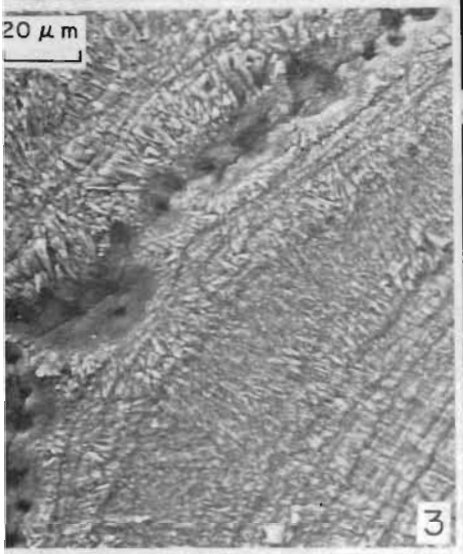
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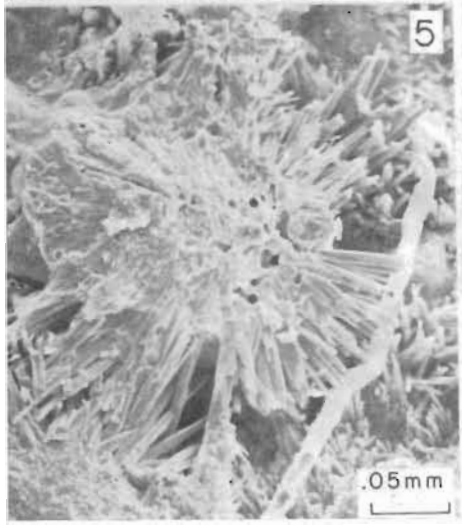
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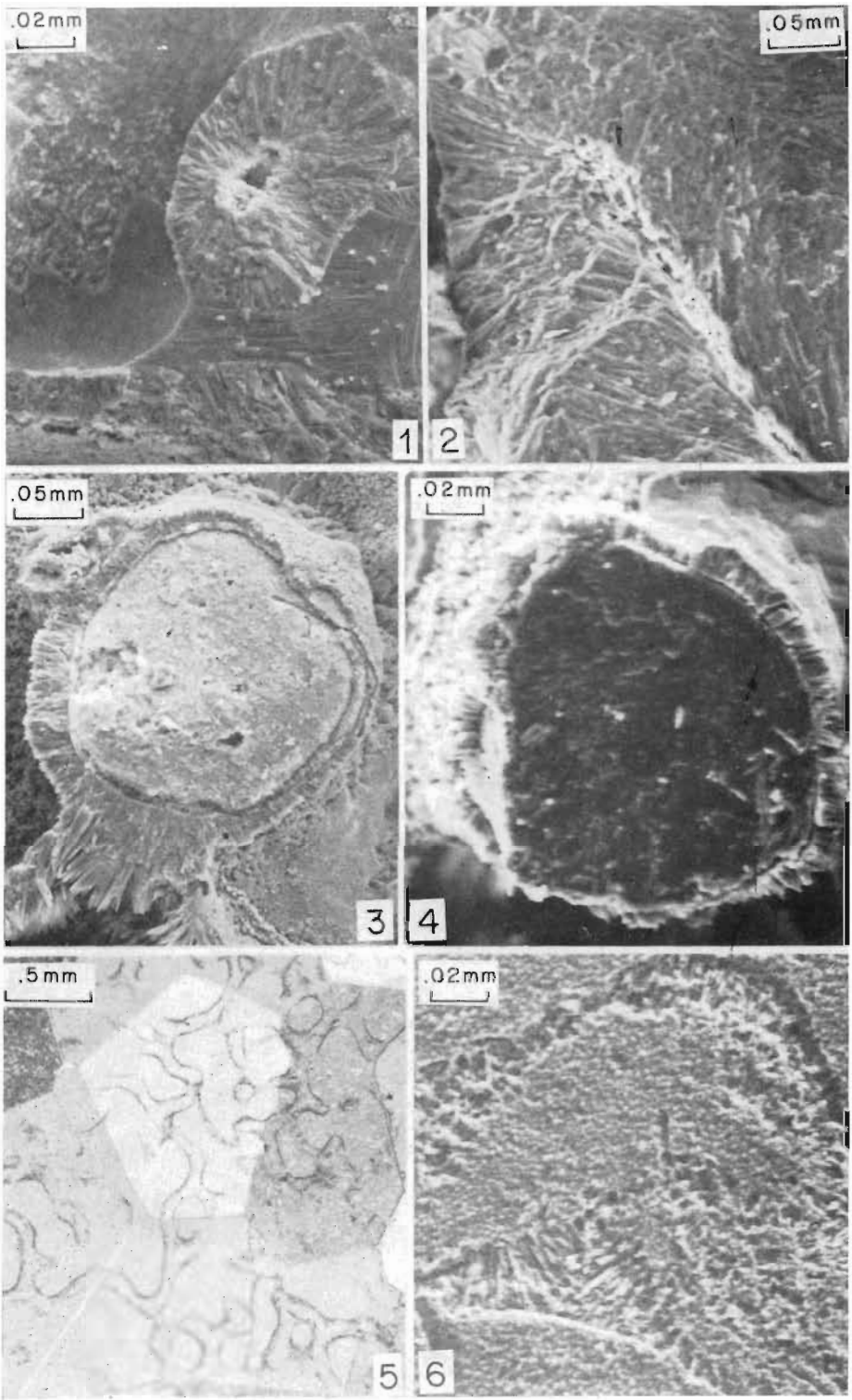
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