

THE HELIOPORACEAN OCTOCORAL *EPIPHAXUM*,  
RECENT AND FOSSIL

A Monographic Iconography

*Frederick M. Bayer*

ABSTRACT

Recent and fossil specimens of *Epiphaxum* Lonsdale were examined and two species from the Recent fauna, one from the western Atlantic and the other from the western Indian Ocean, are described as new and compared with *E. auloporoides* Lonsdale from the Danian of Denmark and *E. micropora* (Bayer and Muzik) from the Recent of the western Atlantic. Gross morphology of all specimens is extensively illustrated by stereoscopic scanning electron micrographs. Sclerites from two colonies of the new Recent species from the western Atlantic are illustrated by scanning electron micrographs. Diversity of crystal microstructure of skeleton and sclerites of *Epiphaxum* also is illustrated by SEM and compared with other octocoral taxa. Taxonomic significance of skeletal microstructure is discussed.

The unique type colony of *Epiphaxum auloporoides* Lonsdale (1850) from the Sussex Chalk consisted only of narrow, creeping stolons attached to the test of a spatangoid echinoid. Voigt (1958) convincingly demonstrated that Nielsen's (1925) *Primnoa gracilis* from the Bryozoan Chalk of Fakse represents detached calyces of *Epiphaxum auloporoides* rather than the axes of a primnoid gorgonian. Specimens of *Primnoa gracilis* received from the Mineralogical and Geological Museum of the University of Copenhagen show that it is undoubtedly congeneric with *Epiphaxum*.

Lonsdale's (1850) original illustrations leave little doubt that *Epiphaxum auloporoides* is congeneric with *Lithotelesto micropora* Bayer and Muzik, 1977 (Bayer, 1979). Accordingly, the genus *Lithotelesto* Bayer and Muzik, 1977, was reduced to synonymy of *Epiphaxum* but, in the absence of conclusive evidence to the contrary, the species *Lithotelesto micropora* was retained as valid in the genus *Epiphaxum*. Voigt (1958: 8) redefined the genus in the following words: "Von kriechenden bandartigen Stolonen, die aus parallelen oder anastomosierenden Kalkrippen bestehen, erheben sich—wenn auch meist abgebrochen—in kettenförmiger Anordnung kalkige röhrenförmige Kelche. Diese sind langgestreckt, außen gerippt und lassen an ihrem Boden 8 rundliche Grübchen erkennen. Von ihnen gehen neue Kelche, jedoch nicht durch Gabelung der Kelchröhre, aus."

MATERIAL AND METHODS

The present study is based upon two large colonies of living *Epiphaxum* recently collected in western Atlantic waters. Although both were obtained alive, they were, unfortunately, dried after collection, thus limiting useful observations to details of the skeleton. Samples of sclerites and supporting skeleton of both colonies were prepared for examination by SEM following procedures previously outlined (Bayer and Stefani 1987: 450).

Examination and documentation of the holotypes of *Lithotelesto micropora* Bayer and Muzik, 1977 (= *Epiphaxum micropora*), *Primnoa gracilis* Nielsen (= *Epiphaxum auloporoides* Lonsdale, 1850), *Epiphaxum breve* n. sp., *Epiphaxum septifer* n. sp., and comparative material of *Heliopora*, *Paracyathus*, and various genera of octocorals were accomplished over a period of several years. Consequently, the resulting micrographs that illustrate this paper vary considerably in quality as they were made with 5 instruments: Cambridge Stereoscan Mark 2, S4-10 and 250-Mark 2, Coates and Welter Cwicscan model 106B, and Hitachi model S-570.

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# The Helioporacean Octocoral *Epiphaxum*, Recent and Fossil: A Monographic Iconography

FREDERICK M. BAYER

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This work is dedicated to the memory of Gilbert L. Voss, longtime friend and colleague, accomplished seaman, dedicated scientist, tireless defender of our threatened environment.

*Frederick M. Bayer*  
*Washington, D.C.*

## FOREWORD

In 1963, the then Institute of Marine Science, University of Miami, established a series of publications entitled *Studies in Tropical Oceanography* to accommodate research reports too large for inclusion in regular periodicals. The preceding 14 volumes of this series are in-depth references on diverse marine science research subjects such as systematics, ecology, pollution and faunal distributions, and abundances. We are now privileged to publish, as the 15th volume, Dr. Frederick M. Bayer's illustrated monograph on the octocoral genus *Epiphaxum*.

Two new species of *Epiphaxum*, one from the western Atlantic and one from the western Indian Ocean, are described, profusely illustrated with scanning micrographs, and both are also compared with a fossil form from Denmark. The symbiotic association of *Epiphaxum* with polychaete tube worms and sponge boring organisms is described in detail.

This octocoral is most remarkable in that it has been in continuous existence since the Danian without significant alteration. Dr. Bayer reasons that "By extrapolation, it (*Epiphaxum*) provides information about the morphology and some insight into the possible life style of an octocoral that lived some 65,000 years ago."

Dr. Frederick M. Bayer is a Research Zoologist in the Department of Invertebrate Zoology at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560. For many years he was Professor of Marine Biology at the Rosenstiel School of Marine and Atmospheric Science and is currently on the adjunct faculty.

The Editors

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Lonsdale's (1850) original illustrations leave little doubt that *Epiphaxum auloporoides* is congeneric with *Lithotelesto micropora* Bayer and Muzik, 1977 (Bayer, 1979). Accordingly, the genus *Lithotelesto* Bayer and Muzik, 1977, was reduced to synonymy of *Epiphaxum* but, in the absence of conclusive evidence to the contrary, the species *Lithotelesto micropora* was retained as valid in the genus *Epiphaxum*. Voigt (1958: 8) redefined the genus in the following words: "Von kriechenden bandartigen Stolonen, die aus parallelen oder anastomosierenden Kalkrippen bestehen, erheben sich—wenn auch meist abgebrochen—in kettenförmiger Anordnung kalkige röhrenförmige Kelche. Diese sind langgestreckt, außen gerippt und lassen an ihrem Boden 8 rundliche Grübchen erkennen. Von ihnen gehen neue Kelche, jedoch nicht durch Gabelung der Kelchröhre, aus."

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TAXONOMY

Order HELIOPORACEA Bock, 1938  
Family Lithotelestidae Bayer and Muzik, 1977  
Genus *Epiphaxum* Lonsdale, 1850

*Epiphaxum* Lonsdale, 1850: 261 (type species, *Epiphaxum auloporoides* Lonsdale, by monotypy).—Bayer, 1956: 184; 1981: 904 [in key only].

*Epifaxum* Nielsen, 1937: 123 [erroneous spelling, in fauna list only; incorrectly assigned to Hexacorallia].

*Primnoa*.—Nielsen, 1925: 5 (not *Primnoa* Lamouroux, 1812).

*Lithotelesto* Bayer and Muzik, 1977: 983 (type species, *Lithotelesto micropora* Bayer and Muzik, by original designation and monotypy).

**Diagnosis.**—Creeping, ribbon-like stolons giving rise at intervals to polyps that may or may not produce daughter polyps in turn. Stolons and polyps with a supporting skeleton composed of crystalline aragonite; anthosteles forming tubular calyces having 16 external alternating longitudinal grooves and ridges; calicular wall perforated by pores through which solenial canals connect the gastrovascular cavity of the polyp with the solenial system following the grooves of the calyces and stolons; pores aligned along bottom of longitudinal grooves, those of adjacent grooves arranged in pairs meeting beneath the intervening ridge and opening as a single pore, aligned in 8 rows alternating with the 8 mesenteries. Anthocodia and tentacles completely retractile within calicular aperture; pharyngeal wall, anthocodial wall and tentacles with numerous sclerites of typical octocorallian form, composed of calcite.

**Remarks.**—As Voigt (1958: 9) pointed out, there can be little doubt that Nielsen's *Primnoa gracilis* (1925: 5) is actually *Epiphaxum auloporoides* Lonsdale, 1850. Similarly, there is no doubt that *Lithotelesto micropora* Bayer and Muzik, 1977, is congeneric. Further, it is possible that *Lithotelesto micropora* as illustrated in Verrill's originally unpublished illustration as reproduced by Bayer and Muzik (1977: 977, fig. 1) is not only congeneric with *Epiphaxum* Lonsdale but also conspecific with Nielsen's *Primnoa gracilis*. It follows, then, that *Lithotelesto micropora* could be conspecific with *Epiphaxum auloporoides*. Nielsen's specimens are branched; Verrill's specimen was branched in a similar manner. The type specimen described by Bayer and Muzik (1977) shows no evidence of branching, but may not represent a fully developed colony as its growth was limited by its habitat on the spine of a cidarid echinoid.

*Epiphaxum auloporoides* (Lonsdale, 1850)  
Figures 1, 2

*Epiphaxum auloporoides* Lonsdale, 1850: 261, pl. 18, figs. 35–37.—Felix, 1914: 248.—Voigt, 1958: 9, pl. 1; pl. 2, figs. 7–12; pl. 10, fig. 3.

*Primnoa gracilis* Nielsen, 1925: 5, figs. 2, 3.

**Material Examined.**—Denmark: Upper Danian bryozoan limestone at Fakse, Sjælland. Received (as *Primnoa gracilis* Nielsen [possibly syntypic, certainly topotypic]) from the Mineralogical and Geological Museum of the University of Copenhagen. 2 calyces, 1 mounted for SEM (SEM 180).

**Diagnosis.**—*Epiphaxum* with tall primary calyces giving rise laterally to secondary calyces; septa not developed in distal parts of calyces.

**Description.**—See Voigt, 1958: 9.

**Remarks.**—Authentic specimens of *Primnoa gracilis* Nielsen are morphologically similar to Recent material from Madagascar, the Gulf of Mexico, Bahamas, and

Barbados (Figs. 1, 2). Voigt (1958: 10) observed “sehr deutlich 8 regelmäßige Nischen oder Grübchen” in a ring around the insertions of the calyces in the stolons. Clearly, these are the openings leading to the longitudinal canals of the stolons and correspond to the “eight indentations or blunt lamellæ” of the “visceral cavities” of *Epiphaxum auloporoides* mentioned by Lonsdale (1850: 261, 262, 263). They are clearly visible in the bottom of the secondary polyp of the specimen scanned (Fig. 2).

*Epiphaxum micropora* (Bayer and Muzik, 1977)  
Figures 3–6

*Lithotelesto micropora* Bayer and Muzik, 1977: 976, figs. 1–6.  
*Epiphaxum micropora*.—Bayer, 1979: 874.

**Material Examined.**—Lesser Antilles: west coast of Barbados, 50–400 m. Coll. Dr. John B. Lewis. Holotype, USNM 52523 (SEM 128).

**Diagnosis.**—*Epiphaxum* with primary calyces reaching a height of 6 mm, possibly more; production of secondary calyces assumed but not confirmed; calyces, stolons and sclerites white.

**Description.**—See Bayer and Muzik, 1977.

**Remarks.**—As mentioned in the original description and in the expanded generic diagnosis above, stolons and polyps are unusual in having a supporting skeleton of aragonite in addition to sclerites composed of calcite. The supporting skeleton of the anthostele (Fig. 3, top) is composed basically of eight vertical pillars of aragonite designated as “principal trabeculae” aligned with the mesenteries, alternating with 8 intermediate trabeculae alternating with the mesenteries (Fig. 4, top; Bayer and Muzik, 1977: 983, fig. 6). The 16 vertical trabeculae are laterally united to form the tubular calyces marked by 16 deep longitudinal grooves between the trabeculae (Fig. 3, bottom) perforated by pores 0.04–0.05 mm in diameter. The pores along the grooves of the outer wall unite in pairs to open as a single pore, aligned in longitudinal rows on the interior of the anthostelar wall (Fig. 6, top; cf. Bayer and Muzik, 1977: 976; 982, fig. 6). Therefore only 8 longitudinal rows of pores alternating with the mesenteries perforate the inner surface of the anthostelar wall. The pores are formed during upward growth of the trabeculae, which at intervals produce lateral outgrowths that unite adjacent trabeculae (Fig. 5, bottom), leaving apertures through which gastrodermal canals extend to join with the solenia following the anthostelar grooves. The stolons contain longitudinal canals that originate at the floor of the gastric cavity of the polyps as well as solenia extending from the anthostelar grooves into the superficial grooves in the skeleton of the stolons. The tops of the ridges separating adjacent grooves may widen and meet in such a way as to roof over the grooves and form skeletal canals through which solenia pass.

Vegetative increase of colonies takes place from stolons, which produce new polyps at intervals. New polyps are budded terminally on the stolons from their longitudinal canals, some of which proceed from the gastric cavity of the polyps, and others from the canals lying along the external grooves of the supporting skeleton (Fig. 5, top). No evidence of new polyps arising between older ones was observed.

Originally, no functional interpretation was ventured for the numerous impressed punctae roughly 15  $\mu$ m in diameter (Fig. 6, bottom) scattered along the bottom of the skeletal grooves. It appears likely that these represent the site of attachment of desmocytes, cells that serve to anchor the soft tissue to the skeleton.

There is no histological evidence for this interpretation, which is made solely on the basis of comparison with similar structures observed in the skeleton of Gorgonacea.

*Epiphaxum breve* new species

Figures 7–27; 32, top; 33, 34

*Material Examined.*—(1) Gulf of Mexico off Pensacola, Florida: 29°49'N, 87°11'W, 250–350 feet. Access VI-90, station B, coll. T. Hopkins, 21 Aug 1990, by trawl. USNM uncatalogued (SEM 1952–1957; 1981, 1987, 1988).

(2) Great Bahama Bank, vicinity of Riding Rocks: 25°20.9'N, 79°12.9'W, 183 m, coll. Ken Rasmussen, site 1830.02, 18 Jun 1990. USNM uncatalogued (SEM 1969–1980; 1986).

*Diagnosis.*—*Epiphaxum* with anthosteles short, not branching, colored orange or yellow; sclerites yellow or bright red.

*Description.*—Specimen no. 1 (Fig. 7, top) occupies a flat piece of worm rock about 9 × 7 cm in diameter and about 3.5 cm thick in the thickest parts. Meandering ribbon-like stolons about 1.5 mm wide with a supporting skeleton of aragonite are distributed over the irregular upper surface, chiefly concentrated along the thickest edge, where the skeleton of a solitary scleractinian coral also has been overgrown. The stolons branch, anastomose, and in some places widen to form sheet-like expansions of limited extent; they stand free and bridge any crevices and spaces in the substrate that may lie in their path. Rigid, cylindrical polyps with anthosteles supported by aragonite arise at intervals of about 3.75 mm along the narrow parts of the stolon, and in groups of a few more closely-set individuals on the widened areas. In no case does any polyp produce secondary daughter polyps by vegetative budding as illustrated by Verrill's original drawing of *Lithotelesto micropora* (Bayer and Muzik, 1977: 977, fig. 1a). Dead, overgrown stolons are recognizable among the worm tubes in some of the depressions and crevices of the mass, indicating that the association of the octocoral with the polychaetes has been a long-standing one.

The tallest intact polyp observed rises 4.3 mm above the stolon, but most individuals are shorter, commonly less than 1 mm tall. Those polyps near the ends of stolons are very short and commonly slant toward the growing tip; the youngest may be little more than a low circular rim with serrated margin, which is only slightly raised above the surface of the stolon. The octamerous symmetry of the polyps is reflected in the lumen of the anthostelar skeleton, which often has a slightly octagonal outline (Fig. 4, bottom).

Skeletal morphology is basically similar to that described for *Epiphaxum micropora* (Bayer and Muzik, 1977: 976). The most obvious difference is the distinctly orange color of the stolons and anthosteles, and the bright red color of the sclerites. Although the color of Verrill's original material is unknown, as his specimens are lost and his unpublished description is not extant, the specimen collected at Barbados much later by Dr. John B. Lewis and used as type material when the species was formally published (Bayer and Muzik, 1977) shows no sign of any coloration whatever, a fact regrettably omitted from the original description.

The cylindrical, aragonitic anthosteles are sculptured by 16 deep longitudinal grooves separating prominent ridges (Figs. 9, top; 11, bottom). The ridges are here and there interrupted by cross channels between adjacent grooves, which seem to occur at more or less regular intervals that may represent pauses in upward growth. Solenial canals penetrate the mesogloea filling the grooves, and a conspicuous horny cuticle that resists maceration in sodium hypochlorite solution covers the entire surface.

Along the bottom of each groove the anthostelar wall of fully developed calyces is perforated by a row of pores about 0.05 mm in diameter and 0.15–0.3 mm apart; the pores in grooves flanking the intermediate trabeculae unite in pairs to emerge within the calyces as single pores aligned with the intermediate trabecula, thus producing eight rows of pores alternating with the mesenteries. In young calyces that have not reached their full height and thickness, the rows of pores occur only in alternate grooves, hence are only eight in number, and the pores pass directly through the anthostelar wall (Fig. 14, top) in rows that must of necessity alternate with the eight mesenteries of the polyp.

The surface of the anthostelar skeleton is further marked by shallow, roughly circular depressions about 0.025–0.03 mm in diameter, called "punctae" by Bayer and Muzik (1977). The bottom of most punctae is flat, but in some cases that may represent developmental stages, it is occupied by a low, conical prominence (Figs. 14, bottom; 27, top). Similar but larger structures are present in the axis of gorgonaceans (Bayer and Stefani, 1987: 950, fig. 6f; Bayer, 1990: 920, figs. 10d, 13c, 14) and are interpreted as representing the sites of attachment of desmocytes that anchor the soft tissue to the skeleton.

The soft tissue, including anthocodiae as well as the mesogloea filling the channels between the ridges of both anthostele and stolons, contains bright red calcite sclerites morphologically similar to those of the type specimen of *E. micropora* from Barbados, which differ principally in being colorless. Sclerites are clearly visible, sparsely distributed in the mesogloea along the grooves of the aragonitic skeleton, and densely concentrated in the anthocodial wall below the tentacles. The summit of every anthostele is closed by soft tissue of a bright red color that results from the sclerites densely packed in the bases of the tentacles. Smaller, colorless sclerites are present in the pharyngeal wall, distributed in eight narrow tracts lying between the mesenteries. Thanks to their color, sclerites can be seen embedded in the translucent orange aragonitic skeleton of the anthosteles. Several examples of sclerites cemented to and partly embedded in the anthostelar wall were observed by SEM (Figs. 9, 10, 43, 44).

Stolons advance along the substrate by extending a thin ribbon of coenenchyme containing numerous red sclerites, which appears to be able to smother anything in its path—foraminiferan, sponge, bryozoan. New polyps develop a short distance behind the advancing tip, presumably from the solenial system permeating the mesogloea. Depending upon individual circumstances, new calyces may stand vertically (Fig. 15, bottom) or slant toward the tip of the stolon (Fig. 15, top). Bright red sclerites concentrated in the bases of the retracted tentacles form an eight-rayed figure surrounded by a circle of about 16 whitish points that are precursors of the primary and secondary vertical trabeculae and the 16 marginal teeth of the anthostelar skeleton. The skeleton of the stolons begins as a thin basal membrane bearing minute spines aligned between the longitudinal solenial canals. Upon reaching a certain height, these spines unite with adjacent spines to form longitudinal ridges, and the basement membrane attached to the substrate thickens to form the floor of the grooves separating the ridges. At the base of the polyps some of the developing ridges and grooves join the vertical trabeculae and grooves forming the anthostelar skeleton and some are diverted around the base of the anthostele, but none extends under the polyp.

The polyps of *Epiphaxum* show a well-developed capacity for repair of damage to the aragonitic anthostelar skeleton. In one example examined by SEM, a little more than 1.5 mm of the distal portion of the anthostelar skeleton had been broken off and the fragments cemented to the part remaining below (Fig. 11), which subsequently resumed upward growth and formed a new calicular margin

(Fig. 12). As the mass occupied by this colony shows no evidence of solid attachment to the substrate, such breakage can be attributed either to unstable bottom conditions, strong water movement, or the activities of other animals exploring the bottom in search of food or shelter.

Specimen no. 2 (Fig. 7, bottom) occupies an irregular, flattened calcareous mass about 10 × 11 cm in diameter and 7 cm thick along the line where it was detached from the substrate. As in specimen no. 1, colonies of *Epiphaxum* are distributed most abundantly on one surface of the substrate, presumably the lower, and are concentrated along its edge. Stolons are about 1 mm wide, meandering and occasionally anastomosing, with calyces uniserially disposed at intervals of about 3 mm; here and there the stolons widen and the calyces are more closely placed, no longer in a clearly uniserial disposition (Figs. 18, 19).

Except for color, morphologically the aragonitic skeleton of anthosteles and stolons of specimen no. 2 does not differ significantly from that of *E. auloporoides*, *E. micropora* and specimen no. 1. However, in this specimen, the anthosteles are yellowish, and in many cases the proximal portion of fully developed polyps is more or less swollen (Figs. 17, bottom; 19). Just above the stolon, the diameter is about 1.5 mm, smoothly tapering distally to a uniform diameter of about 0.75 mm in the distal 2 mm. This enlargement appears to be accomplished by peripheral thickening of the calicular wall, accompanied by a coarse infilling of the calicular lumen with trabecular aragonite (Fig. 20). Although the anthosteles of specimen no. 1 may be somewhat wider at the base (Fig. 11, top), the almost bulbous enlargement that occurs in specimen no. 2 is not present and there is only scant indication of trabecular infilling of the lumen. There is no evidence of the development of septa in the distal part of the anthocodiae (Figs. 4, bottom; 21).

The calcite sclerites of specimen no. 2 (Fig. 16, bottom: SEM 1969) are of the same general size and shape as those of specimen no. 1 (Fig. 16, top: SEM 1952) and *E. micropora* (Bayer and Muzik, 1977: 980, fig. 4), but those of specimen no. 1 are bright red, those of no. 2 are yellow, and those of *E. micropora* are colorless.

The advancing stolons produce a thin, membranous basal skeleton forming a floor from which new calyces arise. This may be cemented to the substrate as was usually the case in specimen no. 1 (Fig. 15), or stand free wherever the stolon bridges gaps in the substrate (Fig. 25); the floor of the calyces is liberally sprinkled with punctae (Fig. 26).

As the substrate of this specimen was firmly attached, there is less evidence of breakage and repair of calyces than is the case in specimen no. 1. However, one calyx was found to have repaired damage and then been occluded by a foreign organism that formed a cap completely covering its aperture (Fig. 24, bottom). It can only be assumed that the polyp was smothered by this overgrowth, while the remains of the gastric cavity continued to function as a part of the coelenteric system of the colony.

*Epiphaxum septifer* new species  
Figures 28–31

*Material Examined.*—Madagascar Plateau: Walter Shoal, 33°12.0'S, 43°58.2'E, 360–200 m, MARION DUFRESNE cruise MD 08, sta. 6, DC 3, 16 Mar 1976. Isolated calyces, some with parts of stolon, 7 prepared for examination by SEM (SEM 166, 166A–E, 179); syntypes USNM uncatalogued. Additional material in Muséum National d'Histoire Naturelle, Paris.

*Diagnosis.*—*Epiphaxum* with calyces reaching or exceeding 6 mm in height, show-

ing evidence of lateral budding from the coenenchymal canals of the anthostelar wall; principal trabeculae sometimes forming 8 distinct sclerosepta on the interior wall of calyces, largely or completely confined to the distal portion; primary calyces may produce secondary calyces arising from the solenial system situated in the grooves.

*Description.*—Morphologically, the aragonitic stolons and anthosteles are virtually identical with those of *E. auloporoides*, *E. micropora*, and *E. breve*. They exceed 6 mm in height (Fig. 28, top) and show evidence of lateral budding from the primary anthostelar wall (Fig. 28, bottom) in a manner similar to that of *Telesto*. The principal trabeculae of some, but not all, of the calyces of a specimen consisting of a stolon expansion bearing 5 calyces (Fig. 29) are developed as well-formed sclerosepta in the distal portion of the calyx (Fig. 30, top); as the septa alternate with the 8 internal rows of pores, it follows that the mesenteries must be associated with the septa, although no soft tissue is preserved to confirm this assumption. The septa of *Epiphaxum* do not appear to be analogous to the septa of Scleractinia, which arise in a regular sequence in association with the development of mesenteries in the polyp, but to the so-called septa of *Heliopora* (Fig. 32, bottom), which vary in number from 11 to 16 (Moseley, 1881: 104, 116). These are ridges extending into the calyx from the vertical trabeculae that comprise its wall. Moseley observed that their number often diminished to 8 in the deeper part of the calyces, with "a mesentery of the polyp passing to each internal projection" (Moseley, 1881: 104). A section of *Heliopora* made with skeleton and soft tissue intact examined for this study shows that mesenteries may be attached either along the septum-like ridges or between them, so it is not unreasonable to assume that the mesenteries of *Epiphaxum* could be inserted along the septa.

Owing to the absence of soft tissue in all specimens obtained, the presence, mineralogy and morphology of sclerites cannot be confirmed.

*Etymology.*—Latin *septifer*, in allusion to the development of septa in the distal part of the anthosteles. Noun in apposition.

*Comparisons.*—Owing to the extreme limitation of material, it is impossible to distinguish the present specimens from *Epiphaxum auloporoides* at the species level. However, on the basis of the development of undisputed septa along the principal trabeculae in the distal part of some calyces, a feature not reported in any fossil specimens, as well as of the geological age of *E. auloporoides*, the present Recent specimens are now treated as a distinct species.

*Epiphaxum septifer* differs from *E. micropora* (Bayer and Muzik) and *E. breve* n. sp. from the western Atlantic by its taller calyces that may produce secondary calyces, and the inconsistent occurrence of sclerosepta, a feature not present in any western Atlantic material so far examined.

SYMBIOTIC ASSOCIATIONS

*Polychaeta.*—Both colonies of *E. breve* show an association, possibly fortuitous, with polychaete annelids. The solid substrate of specimen no. 1 consists almost entirely of the tubes of serpulid worms, and the coralline limestone providing the substrate for specimen no. 2 contains numerous worm tubes. More significant, roughly circular, tubular apertures in the skeleton of stolons of both colonies appear to be the apertures of worm dwellings (Figs. 13, top; 21, bottom; 25, top; 26, top; 32, top). Whether the openings of the worm tubes were surrounded by the stolon of the coral as it grew and thus pass completely through it or the entire



tube with its worm is enclosed within the coral skeleton has not been determined. Further, no specimen of the worm has been recovered as both colonies are in dry condition.

A similar association of *Heliopora* with a polychaete worm was reported by Moseley (1876: 91; 1881: 103, 112) in specimens collected at the island of St. Cruz Major opposite the harbor of Samboangan, Mindanao, Philippine Islands, during the expedition of H.M.S. CHALLENGER. Moseley identified the worm as "a species of *Leucodora*, closely resembling *Leucodora nasuta*. . . ." These worms temporarily misled Saville-Kent (1890) into thinking that *Heliopora* was a colony of worms rather than a coelenterate, a misconception that he soon clarified (Saville-Kent, 1893: 192–194).

Several colonies of *Heliopora coerulea* from Indonesia, The Philippines, Guam, Gilbert, Caroline and Marshall Islands, the Great Barrier Reef, and Aldabra, Seychelles, in the collections of The U.S. National Museum of Natural History are conspicuously permeated by worm tubes that are larger than those observed in *Epiphaxum*. Worms extracted from a specimen collected at North Aru Island in the Moluccas have been identified as *Polydora armata* Langerhans by Dr. Kristian Fauchald and Ms. Linda Ward. In any one colony of *Heliopora*, worms may be widespread, or locally distributed, common in some places but scarce or absent elsewhere. Their appearance in a heavily infested colony is shown in Figure 32, bottom.

*Endolithic Organisms.*—When viewed at moderate magnifications with transmitted light, fragments of calicular skeleton of both colonies show fine, meandering, occasionally branching tubes of an endolithic microorganism. Although such tubes can be seen to approach the surface of the skeleton, no openings on the intact surface were found with SEM. However, longitudinal sections of tubes were clearly revealed at the fractured surface of broken fragments (Fig. 33). As these tubes are present in the skeleton of living polyps, which is enclosed within the tissues of the coral, they must be part of a symbiotic association rather than the burrows of borers that attack exposed, dead skeleton. Similar but more profuse microborings occur in living scleractinian corals (Macintyre and Towe, 1976) and were observed by SEM in the skeleton of a specimen of *Mycetophyllia* having a bright lime-green corallum when living.

One calyx of specimen no. 2 broken off and cleaned revealed the presence of sponge borings, which penetrated the circumference of the anthostele with interconnecting chambers up to 0.12 mm in diameter (Fig. 35). The surface of these chambers is pitted by conchoidal fracture marks characteristic of sponge borings (Fig. 35, bottom). As no spicules were obtained, taxonomic identity of the sponge could not be determined.

Microborings intercepted by the sponge chambers (Fig. 35, bottom) are lined by crystals different in size and shape from those of intact borings, suggesting that the causative organism may have been killed by the activity of the sponge, with subsequent alteration of the lining of the borings.

The presence of microborings in *Epiphaxum* is here reported only to call attention to their existence. Owing to the limited amount of material available and means of preservation, no further investigation of their morphology and taxonomy was attempted. As Golubic (1969: 750) maintains that taxonomically distinct boring algae produce specific boring patterns that are recognizable even without the alga itself, it would seem possible that the organism in the skeleton of *Epiphaxum* may be identifiable given sufficient material for examination.

## MICROSTRUCTURE

*Supporting Skeleton.*—The skeleton of the calyces and stolons consists of crystalline aragonite composed of microcrystals similar in form to those of the blue coral (Fig. 41), *Heliopora coerulea* (Pallas) (Bayer and Muzik, 1977: 978, fig. 5c), and scleractinian corals (Fig. 42).

In describing the fine structure of the skeleton of *Heliopora coerulea*, Moseley (1881: 105) wrote that "it is composed of doubly refracting calcareous matter, which has a half-crystalline, half-fibrous structure. On transverse section (Pl. I, fig. 4), it is seen to be made up of a series of systems of radiating fibres, i.e., areas of calcareous tissue showing a radiate fibrous structure. In each system the fibres radiate from a central axis, and diverge to fuse at the margin of the system with the margins of the contiguous systems, a suture-like line being often observable where two systems join. . . . The central axes of the systems correspond to the centres of the vertical beams already described, which are prolonged above on the surface of the coral into papilliform projections." Bourne (1895) described and illustrated the skeletal structure of *Heliopora* in even greater detail.

Vaughan and Wells (1943: 32) stated that in thin sections of Scleractinia they observed "numerous [sic] dark spots, called *centers of calcification* (Pl. 3, fig. 1; Pl. 15, fig. 6) from each of which fascicles of fibrous crystals radiate toward those of neighboring centers. The centers of calcification and their fascicles of fibers are taken for practical purposes as the primary (but not necessarily fundamental) units of the skeleton, known as *sclerodermites*." These fascicles of "fibers" are clearly revealed by SEM even at relatively low magnification (Fig. 42, top), and the flattened, blade-like prisms of aragonite of which they are composed are visible at greater magnification (Fig. 42, bottom).

The "radial fibrous structure" observed in *Heliopora* by Moseley is confirmed on examination by SEM, which reveals aragonite crystals arranged in radiating bundles (Fig. 41, top), visible even in unbroken surfaces. The ends of these crystals form at the surface of the corallum a pattern of irregular polygons composed of smaller polygons representing the terminal faces of the component crystals (Fig. 41, bottom).

Fascicles (or "bundles") of large, radiating "fibrous" aragonite crystals not unlike those of *Heliopora* and *Paracyathus* also are present in the skeleton of stolons and anthosteles of *Epiphaxum* (Fig. 38), but are not regularly organized as sclerodermites and do not represent the predominant organization of crystals in the skeleton, possibly owing to its small size. Hence, the skeleton of *Epiphaxum* appears to be composed of aragonite crystals similar to those of *Heliopora* and Scleractinia, but not organized as a regular system of sclerodermites. In *Epiphaxum*, euhedral crystals comparable in size to those of the radial bundles are also present in parallel bundles immersed in randomly organized anhedral crystals (Fig. 39).

At the unbroken surface of the skeleton of *Epiphaxum* euhedral crystals of aragonite can be seen in various orientations (Fig. 36), sometimes in bundles or fascicles projecting above surrounding anhedral structure (Figs. 44, 45), sometimes with the c-axis parallel with the surface (Figs. 37a; 46, bottom), sometimes with the c-axis normal to the surface (Fig. 36, top), as well as at angles apparently at random (Figs. 37b, d; 46, top). Sometimes when oriented with the c-axis normal to the corallum surface, the crystals have the appearance of a stack of pseudo-hexagons of decreasing size (Fig. 46, top). The tissue between the fascicles of large, euhedral crystals appears to be a sort of cement composed of randomly organized anhedral or subhedral rods of small size ( $2\ \mu\text{m} \times 0.2\ \mu\text{m}$  or less) (Fig. 45).

Sclerites composed of calcite, situated in the grooves between the trabeculae near the margin of the calyces, sometimes become trapped in the calicoblastic layer of the anthostele and embedded in the aragonite comprising the calicular wall (Figs. 9, 10, 43). In one example examined by SEM, the free end of the sclerite shows microstructure (Fig. 43, bottom) typical of the calcite comprising completely free sclerites (Fig. 49, top), while the embedded end is overgrown with crystals (Fig. 44, top) indistinguishable from the aragonite of calicular walls and stolons (Fig. 45, top).

*Sclerites.*—The sclerites of *Epiphaxum* are composed of calcite, as is the case in all orders of Octocorallia, from Protoalcyonaria (if that taxon is accepted as distinct from Stolonifera) to Pennatulacea, so far as is known.

The microcrystals of *Epiphaxum* sclerites are anhedral and have the appearance of elongated rice grains or blunt, weakly tapered rods up to about 0.4  $\mu\text{m}$  in diameter and of variable length (Fig. 49). Adjacent crystals may fuse together during growth, and may be oriented either more or less uniformly with their c-axes parallel or completely at random. The calcite rods of *Epiphaxum* most closely resemble those comprising the minute, lenticular sclerites of *Efflatounaria* sp. (Fig. 50a–c). In that case the rods must at first lie loose in the cytoplasm of the scleroblast, subsequently becoming incorporated in the substance of the sclerite (Fig. 50c), as great numbers of them can be found unassociated with any sclerite (Fig. 50b). It is probable that the calcite rods forming the sclerites of *Epiphaxum* are formed and incorporated in the sclerite in a similar manner, but oriented in a more uniform manner (Fig. 49, bottom).

Crystals at the surface of the sclerite may lie with their c-axis parallel with the surface, normal to the surface, or virtually any angle in between. Macro-ornamentation of the sclerites is produced by appropriate orientation and stacking of microcrystals of various sizes.

*Taxonomic Significance.*—Utilizing microcrystals of calcite, octocorals produce sclerites of extremely diverse forms, ranging from minute discoidal, lenticular or spherical bodies only 20 to 30  $\mu\text{m}$  in diameter (Xeniidae) to large, elaborately sculptured plates that form a closely fitting protective armor (Primnoidae). The component crystals range in size from minute anhedral rods 1  $\mu\text{m}$  or less in length (Fig. 50b, c) to euhedral, trigonal prisms nearly 1  $\mu\text{m}$  in width and several  $\mu\text{m}$  long (Fig. 51, bottom). Among the various higher taxa of Octocorallia—i.e., family and above—the structural units, microcrystals of calcite, display a bewildering diversity of size and shape.

The simplest of all octocoral sclerites, the minute, corpuscle-like platelets, spheroids and rodlets of the family Xeniidae (order Alcyonacea) are in some cases composed of anhedral calcite rods in shape not unlike rice grains (Fig. 50a–c), in others of irregular, branching, dendritic rodlets (Fig. 50d), or of minute (2  $\mu\text{m}$ ) calcite rhombs (Fig. 62, top), aggregated to form sclerites of shape and size characteristic of the various taxa.

Elsewhere in the Alcyonacea and in the other orders of Octocorallia, crystals comprising the sclerites range in size from small, sharply pointed dentate forms about 0.1  $\mu\text{m}$  in diameter (Figs. 51, top; 52, top; 53, top) to euhedral, trigonal prisms about 0.75  $\mu\text{m}$  in diameter (Fig. 51, bottom). Sometimes they are flattened laths (Fig. 54, top) that can become foliate (Fig. 54, bottom) as in *Xenogorgia* (Holaxonia, Chrysogorgiidae), and sometimes they are 3-flanged and blade-like as in other Chrysogorgiidae (Fig. 60, bottom). Not uncommonly the prisms are subhedral or even anhedral and therefore more rod-like (Fig. 53, bottom), sometimes fused into compound crystals as much as 1.5  $\mu\text{m}$  in diameter (Fig. 52,

bottom). In areas presumed to be regions of active mineral deposition, the distal, growing ends of the crystals (c-axis) are distinctly separated by space originally occupied by the organic matrix within which they were formed (Fig. 62, bottom). In genera such as *Muricea* (Holaxonia, Gorgonacea), the sclerites of which are extremely variable in minor details within a given basic form, areas of active crystal formation appear to move from place to place during the development of the sclerite, resulting in some regions of extremely compact, tightly crowded crystals of “mature” growth, and others with widely separated crystals that appear to have been undergoing rapid growth (Fig. 51, bottom). Such a distinction between regions of tightly crowded, scarcely projecting crystals (Fig. 49, top) and distinctly separated and strongly projecting crystals (Fig. 48) is recognizable in sclerites of *Epiphaxum*, presumably representing areas of little or no calcite deposition and areas of active mineral deposition in one and the same sclerite (Fig. 47). Similarly, near the ends of sclerites that have not yet reached full size, the euhedral prisms of calcite generally are oriented with their c-axis directed toward the ends of the sclerite (e.g., Fig. 55, top), but toward the middle, where the sclerite is increasing in diameter, the c-axis of the crystals is directed increasingly toward the surface of the sclerite (Fig. 55, bottom).

At the family level, the size and shape of the component crystals are consistent only within very broad limits, and within sclerites of a given gross form. It can be seen, for example, that the crystals forming the plate-like sclerites of Primnoidae are always of a similar form and distinctly different not only from those comprising different sclerite forms such as the slender, needle-like sclerites of *Lepidisis* and other Keratoisidinae, but also from those of other taxa having flattened or plate-like sclerites. Therefore, the microstructure of sclerites may provide supplementary evidence about the relationships of taxa having ambiguous or equivocal gross morphology.

The case of *Paragorgia* and *Corallium* may be cited as an example. Both genera are dimorphic, both are similar in colonial form, both have sclerites of similar size and form, but currently they are classified in different families, and have even been placed in different orders of Octocorallia. Verseveldt (1940: 137) placed *Paragorgia* and the Paragorgiidae in the order Alcyonacea (along with *Briareum* and the Briareidae) rather than in the suborder Scleraxonia of the Gorgonacea, to which both *Paragorgia* and *Corallium* are traditionally assigned. However, the 8-radiate sclerites of *Corallium* are composed of sharply dentate calcite formed by anhedral crystals of small size (Fig. 51, top) virtually indistinguishable from the microstructure of *Paragorgia* sclerites (Figs. 52, top; 53, top).

This similarity suggests that *Paragorgia* is more closely related to *Corallium* than to any genera of Alcyonacea. It also might suggest no more than that sclerites of similar size and shape are formed by crystals of the same size and shape, but sclerites of similar size and shape in indisputably different taxa often have distinctly different microstructure possibly reflecting differences in the mechanism of calcite deposition that could have phylogenetic significance. However, much more extensive investigation of skeletal microstructure is required before any justifiable taxonomic conclusions can be drawn. It is not within the scope of this paper to revise the taxonomic position of *Paragorgia* and *Corallium* beyond retaining the two genera in the Scleraxonia which, itself, may eventually prove to be of doubtful validity.

In any evaluation of the taxonomic significance of spicular microstructure, the entire range of variation must be taken into account, considering the location on the sclerite, the presumed degree of depositional activity, and the relationship to gross sculptural features. The illustrations of sclerite structure presented here must

not be considered a comprehensive overview of microstructure of octocoral sclerites, but merely selected examples for comparison with *Epiphaxum* and intended to call attention to the wide spectrum of crystal forms that the calcite comprising the sclerites can assume, in the hope of stimulating interest in a neglected facet of octocoral morphology.

*Remarks.*—Although the aragonite crystals of *Epiphaxum* shown on Figure 36 do not exactly duplicate the crystal forms of that mineral recorded by Goldschmidt (1913), they resemble his Aragonit figure 11, and some of those on Figure 37 resemble his Aragonit figures 195 and 196, but they tend to form aggregates in a highly irregular manner, with each component differing in detail from every other. Minute, randomly oriented subhedral or anhedral rods 2–3  $\mu\text{m}$  in length, which dominate the skeletal tissue in many places, are perhaps crystallographically similar to Goldschmidt's Aragonit figures 88 and 89, but with crystal faces indistinct. They are not very different in size and shape from the rods of calcite comprising the sclerites of *Epiphaxum*, which, in turn, are suggestive of Goldschmidt's Calcit figure 2187.

The calcite crystals comprising the sclerites of octocorals in general assume a seemingly infinite variety of forms, although flattened, lath-like shapes (Fig. 54, top), prisms (Figs. 51, bottom; 55, top; 62, bottom), and rods (Fig. 53, bottom) are very common components, often united in shingle-like aggregations that produce an imbricated surface (Fig. 52, bottom). Cross-lamellar structure is not uncommon (Figs. 54, bottom; 57, top; 59, bottom), the ends of lath-like forms may be lobed or foliate (Figs. 54, bottom; 60, bottom), and the angles of elongate prisms may be developed as thin, foliate expansions (Figs. 58, bottom; 60, bottom).

As is the case with aragonite, none of the biological forms of calcite crystals exactly duplicates any of the 2,544 calcite forms illustrated by Goldschmidt (1913). However, the rhombs comprising the minute sclerites of *Cespitularia caerulea* (Fig. 62, top) are aggregates of rhombs similar to Goldschmidt's Calcit figure 1373 and could almost have been the model for his Calcit figure 1426.

As the crystal forms of aragonite and calcite comprising the skeletal structures of octocorals are produced in a biological environment, it is not surprising that they do not exactly duplicate the forms of those minerals produced in a geological milieu as depicted by Goldschmidt (1913). It is to be expected that not only are the circumstances of crystal growth different, but also that even on a single octocoral sclerite the depositional environment may differ from one micro-location to another, depending upon the skeletal morphology to be achieved. This, in turn, can be related to the position of any given sclerite within the colony and relative to the external environment, as sclerites at the surface of the corallum may be strongly asymmetrical, whereas those deeply immersed in coenenchyme may be nearly or quite symmetrical.

#### CONCLUSIONS

Although octocorals are known in the fossil record, they usually represent forms considered distinct from Recent taxa (e.g., Bengtson, 1981; Giammona and Stanton, 1980; Hickson, 1938; Lindström, 1978; Nielsen, 1913). Although there are exceptions, identification of Recent genera reported as fossils, e.g., *Gorgonella*, *Isis* and *Primnoa* (Nielsen, 1913), for the most part must be considered speculative because the morphological features necessary for determination were not preserved.

The Danian octocoral *Epiphaxum* is perhaps the most remarkable member of

its subclass. It, along with *Heliopora* and *Tubipora*, is generically recognizable because of its consolidated calcareous skeleton. Although the skeleton of *Tubipora* consists of inseparably fused coenenchymal sclerites composed of calcite, that of *Heliopora* and *Epiphaxum* consists of dense, non-spicular aragonite. In addition to its aragonitic supporting skeleton, *Epiphaxum* is unique in having calcite sclerites embedded in the mesogloea of the polyps and of the longitudinal grooves in the supporting skeleton.

While *Epiphaxum micropora* is similar to *Primnoa gracilis* in all respects, it cannot be proved conclusively that they are conspecific, but there can be no doubt that the Recent specimens herein described are congeneric with *Primnoa gracilis* Nielsen = *Epiphaxum auloporoides* Lonsdale. Consequently, we are dealing with a genus that has been in existence continuously since at least the Danian without significant alteration. By extrapolation it provides information about the morphology and some insight into the possible lifestyle of an octocoral that lived some 65,000,000 years ago.

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ADDRESS: Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

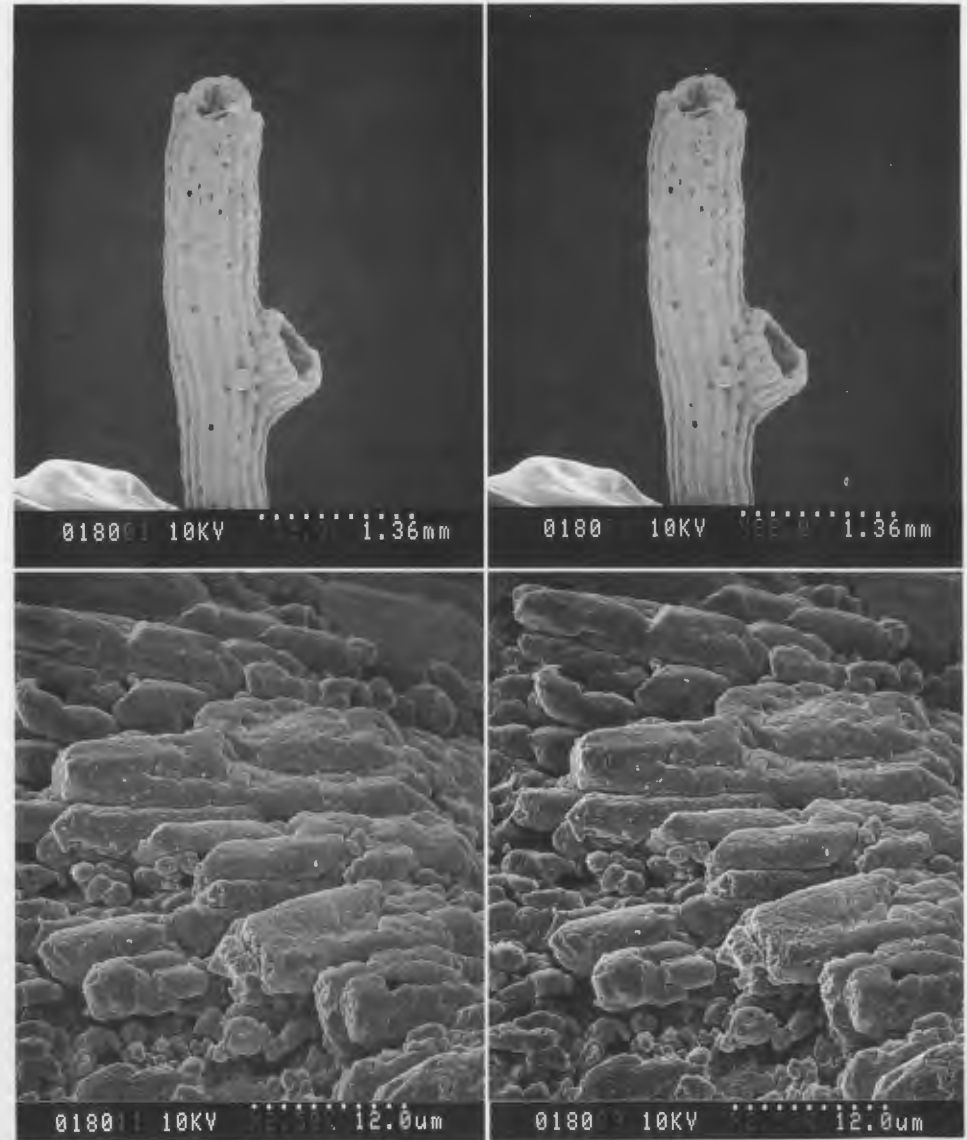


Figure 1. *Primnoa gracilis* Nielsen, 1925. Topotype (possibly syntype) from Fakse, Sjælland, =*Epi-phaxum auloporoides* Lonsdale, 1850. Top, Primary calyx with base of secondary calyx. Bottom, Microcrystals of same. Stereoscopic pairs.

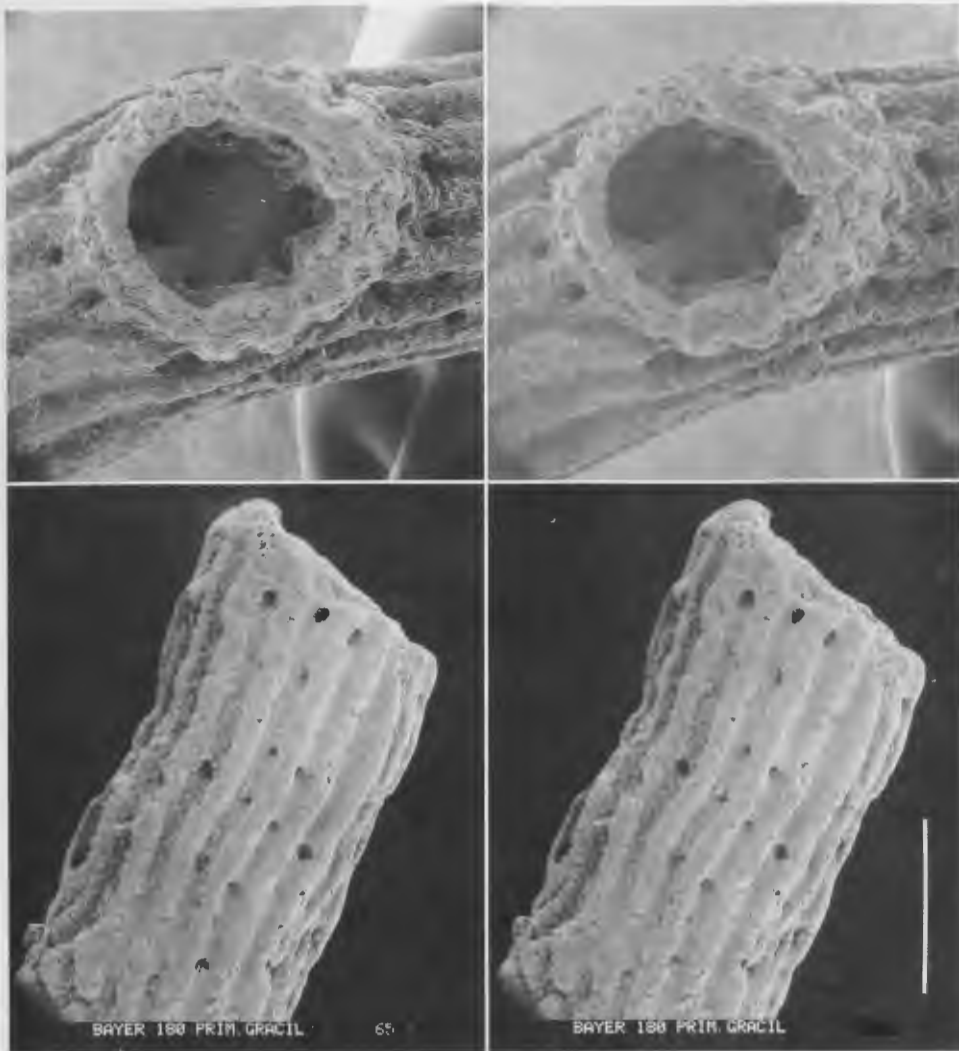


Figure 2. *Primnoa gracilis* Nielsen, 1925. Topotype (possibly syntype) from Fakse, Sjælland, =*Epiphaxum auloporoides* Lonsdale, 1850. Top, Base of secondary calyx. Bottom, Distal part of primary calyx. Scale = 0.5 mm. Stereoscopic pairs.

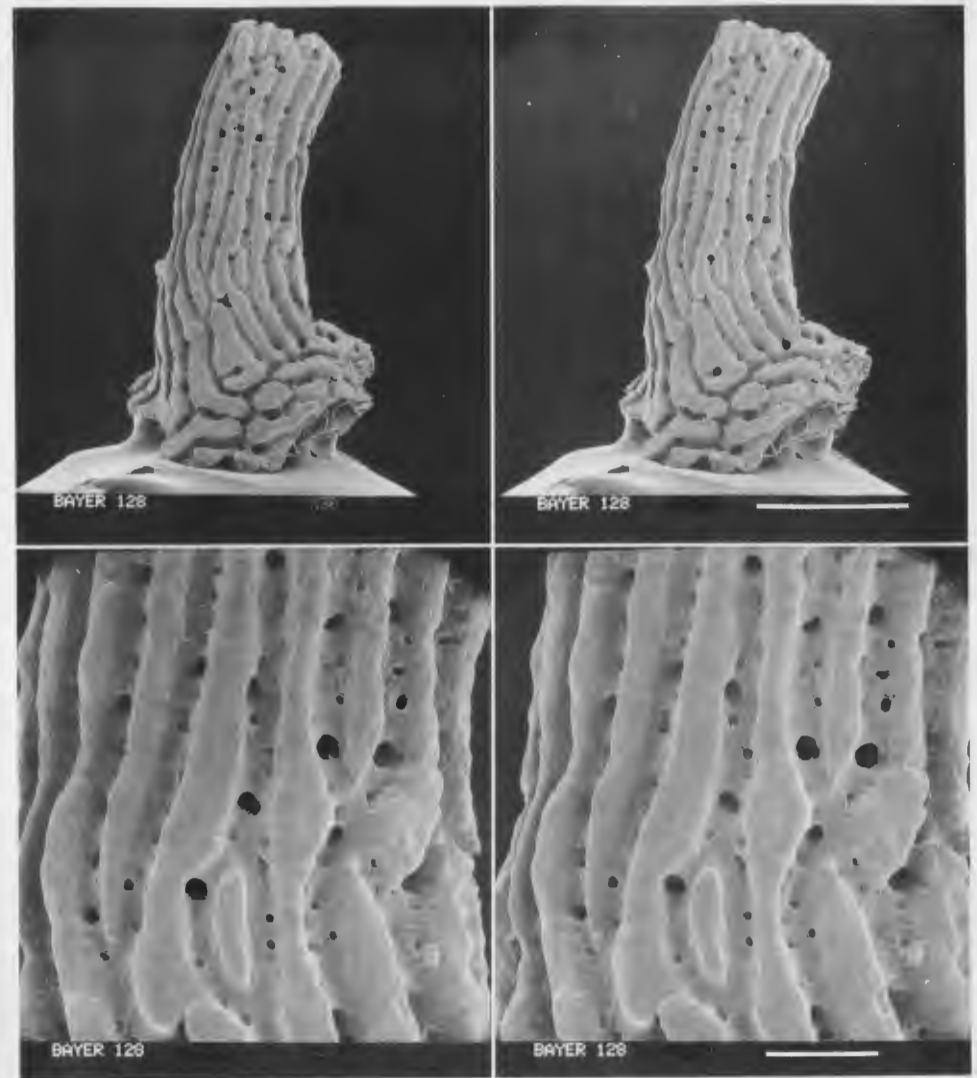


Figure 3. *Epiphaxum micropora* (Bayer and Muzik, 1977); holotype, USNM 52523. Top, Isolated calyx; scale = 1 mm. Bottom, Surface detail of same; scale = 0.2 mm. Stereoscopic pairs.

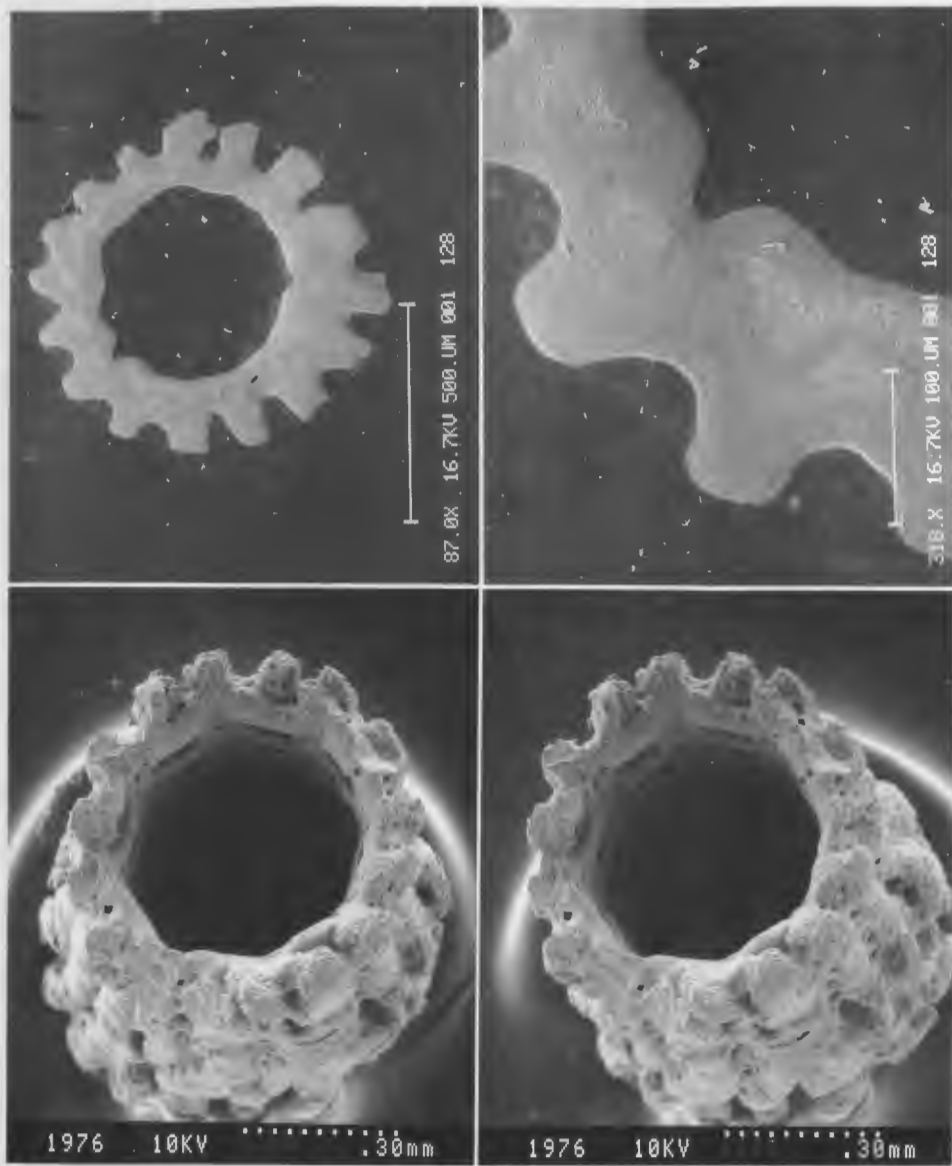


Figure 4. Top, *Epiphaxum micropora* (Bayer and Muzik, 1977); holotype, USNM 52523: cross section of calyx (left, scale = 500  $\mu$ m) and part of calyx wall (right, scale = 100  $\mu$ m). Bottom, *Epiphaxum breve* n. sp. (specimen no. 2): Apertural view of calyx. Stereoscopic pair, scale as indicated.

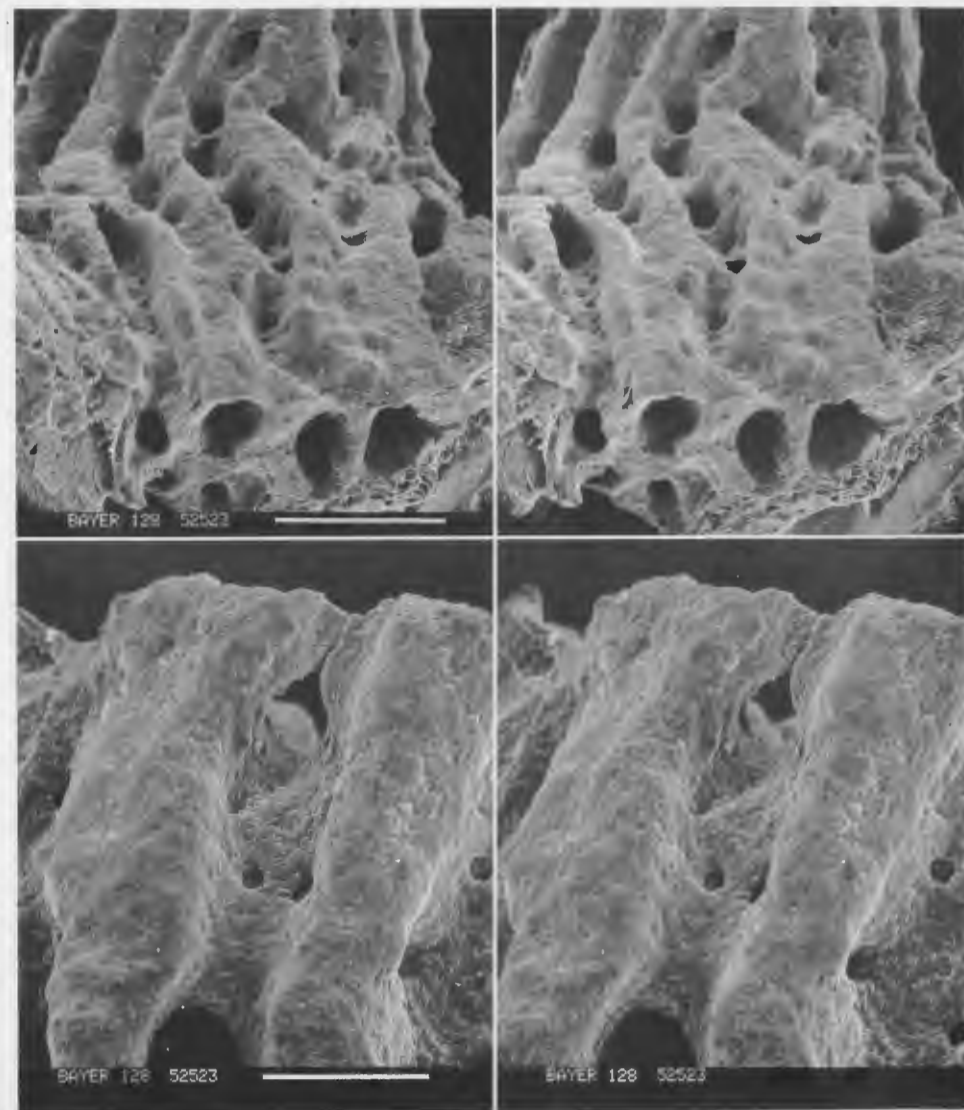


Figure 5. *Epiphaxum micropora* (Bayer and Muzik, 1977); holotype, USNM 52523. Top, Broken section of stolon; scale = 0.5 mm. Bottom, Margin of calyx showing formation of pore; scale = 0.1 mm. Stereoscopic pairs.

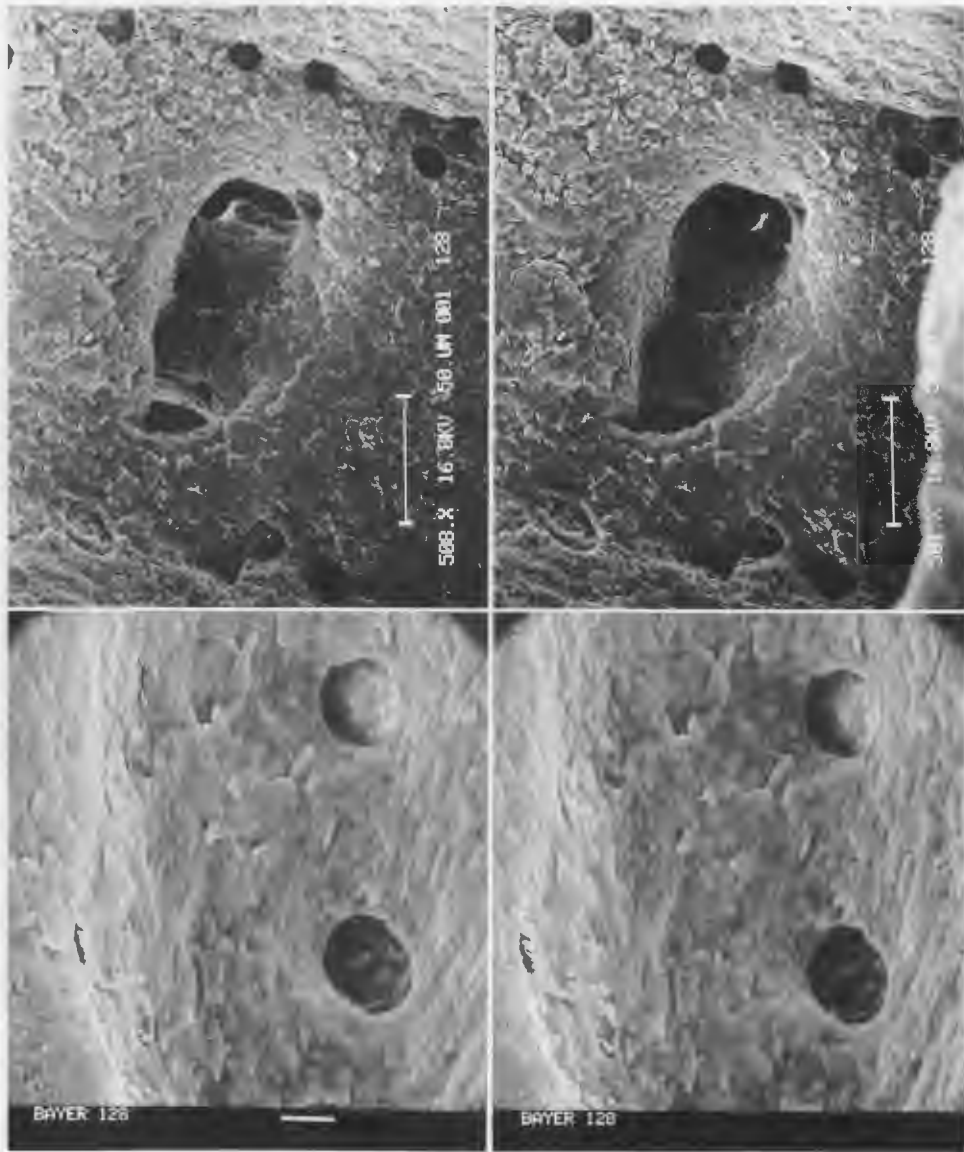


Figure 6. *Epiphaxum micropora* (Bayer and Muzik, 1977); holotype, USNM 52523. Top, Common opening of pore pair on inner wall of calyx; scale = 50  $\mu\text{m}$ . Bottom, Two punctae; scale = 10  $\mu\text{m}$ . Stereoscopic pairs.

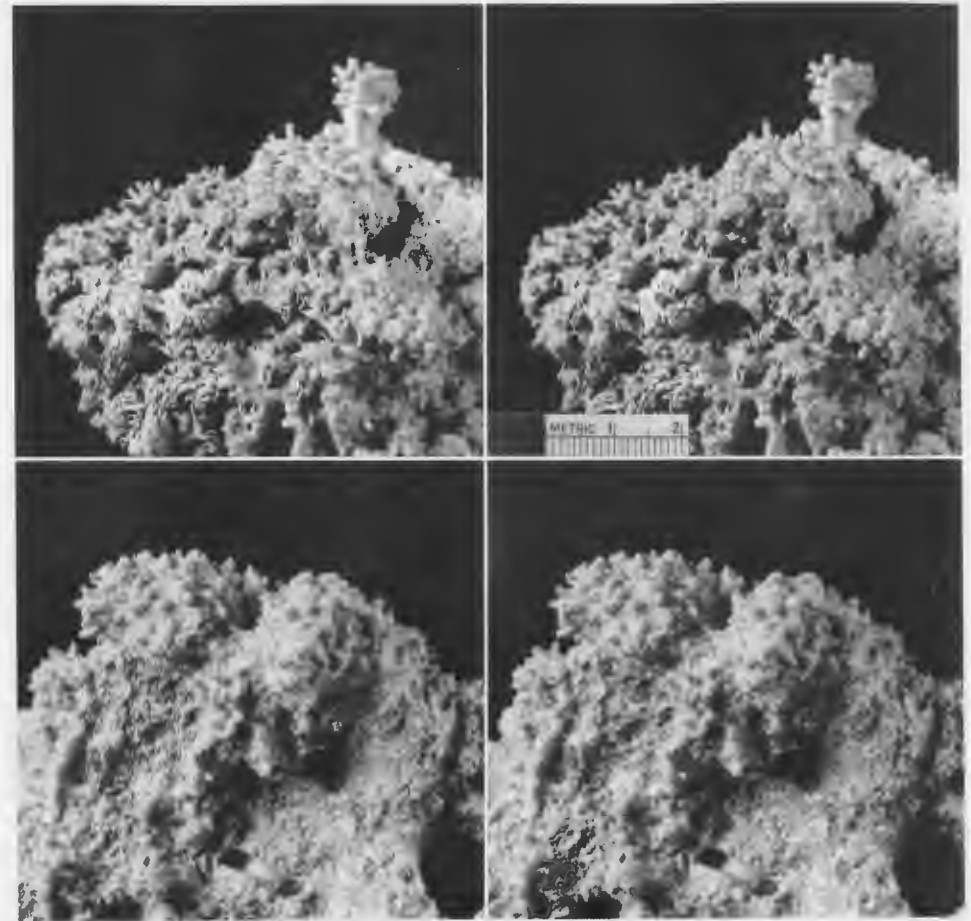


Figure 7. *Epiphaxum breve* n. sp. Top, Colony from Gulf of Mexico off Pensacola, Florida (specimen no. 1). Bottom, Colony from Great Bahama Bank off Riding Rocks (specimen no. 2).



Figure 8. *Epiphaxum breve* n. sp., colony no. 1. Top, Two calyces in profile. Bottom, Left calyx of above in apertural view. Stereoscopic pairs.

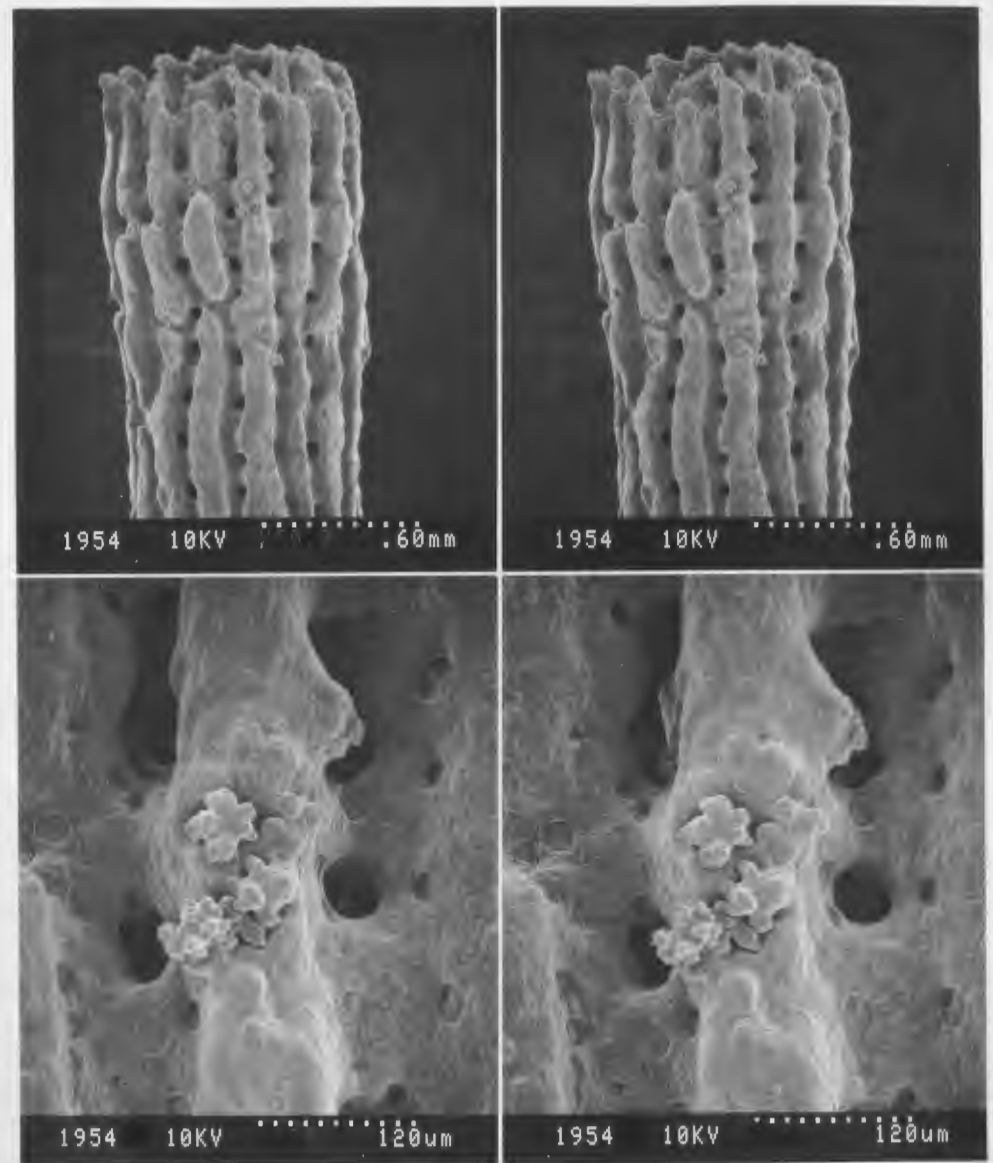


Figure 9. *Epiphaxum breve* n. sp., colony no. 1. Top, Distal part of isolated calyx. Bottom, Detail of same showing sclerites partly embedded in supporting skeleton. Stereoscopic pairs.



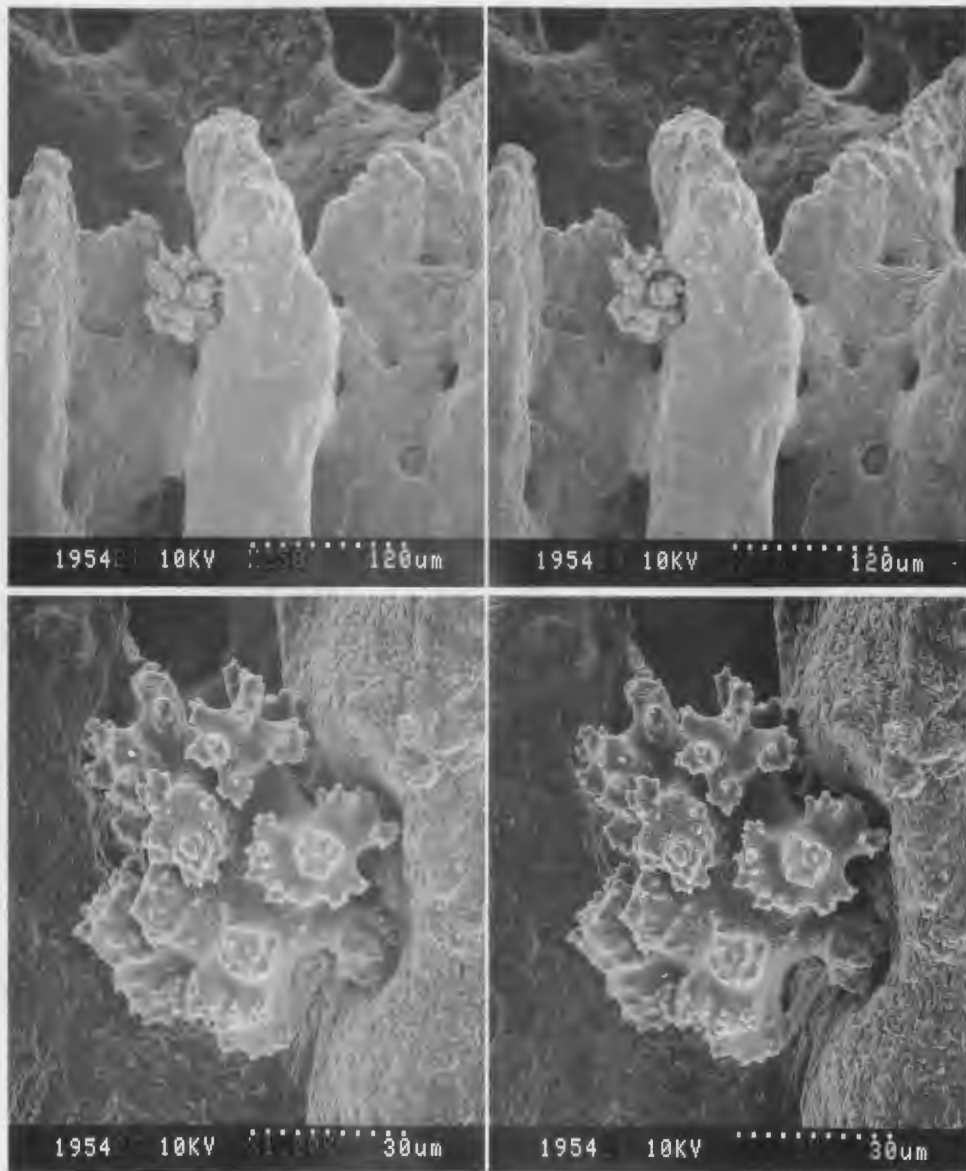


Figure 10. *Epiphaxum breve* n. sp., colony no. 1. Top, Margin of calyx with sclerite in early stage of incorporation into supporting skeleton. Bottom, Detail of same. Stereoscopic pairs.

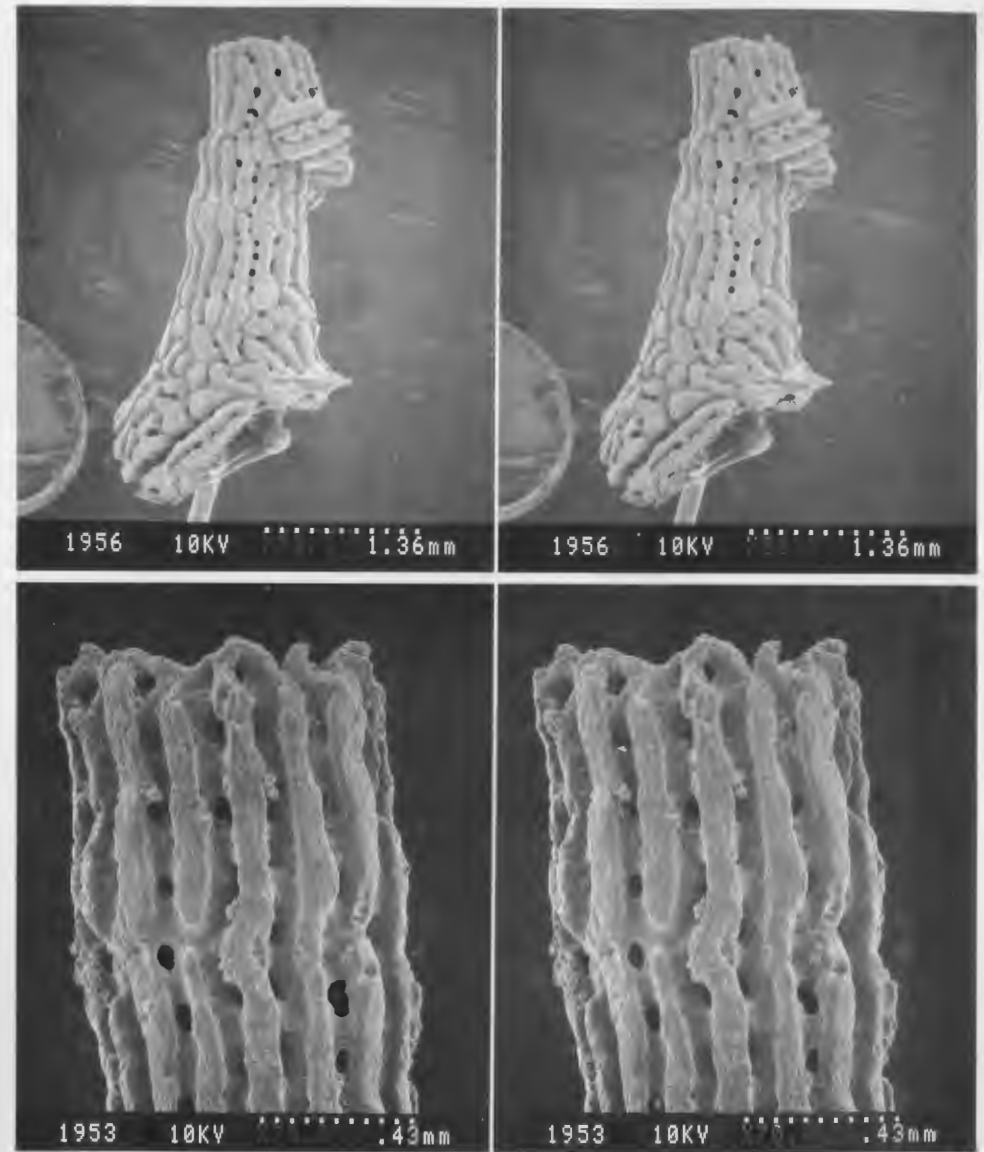


Figure 11. *Epiphaxum breve* n. sp., colony no. 1. Top, Calyx with distal part showing repaired damage. Bottom, Distal part of isolated calyx showing location of pause in upward growth. Stereoscopic pairs.

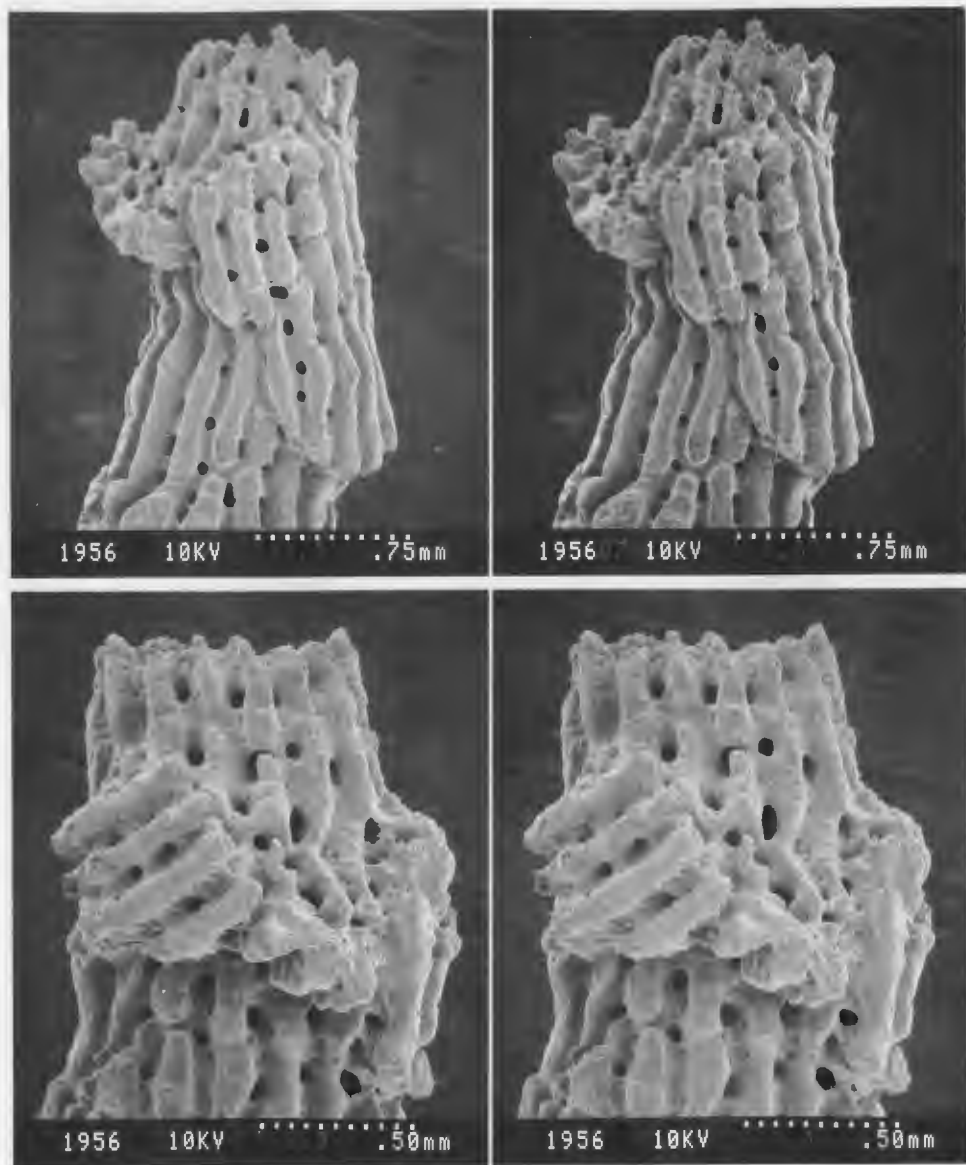


Figure 12. *Epiphaxum breve* n. sp., colony no. 1. Top, Calyx with repaired damage. Bottom, Detail of same. Stereoscopic pairs.

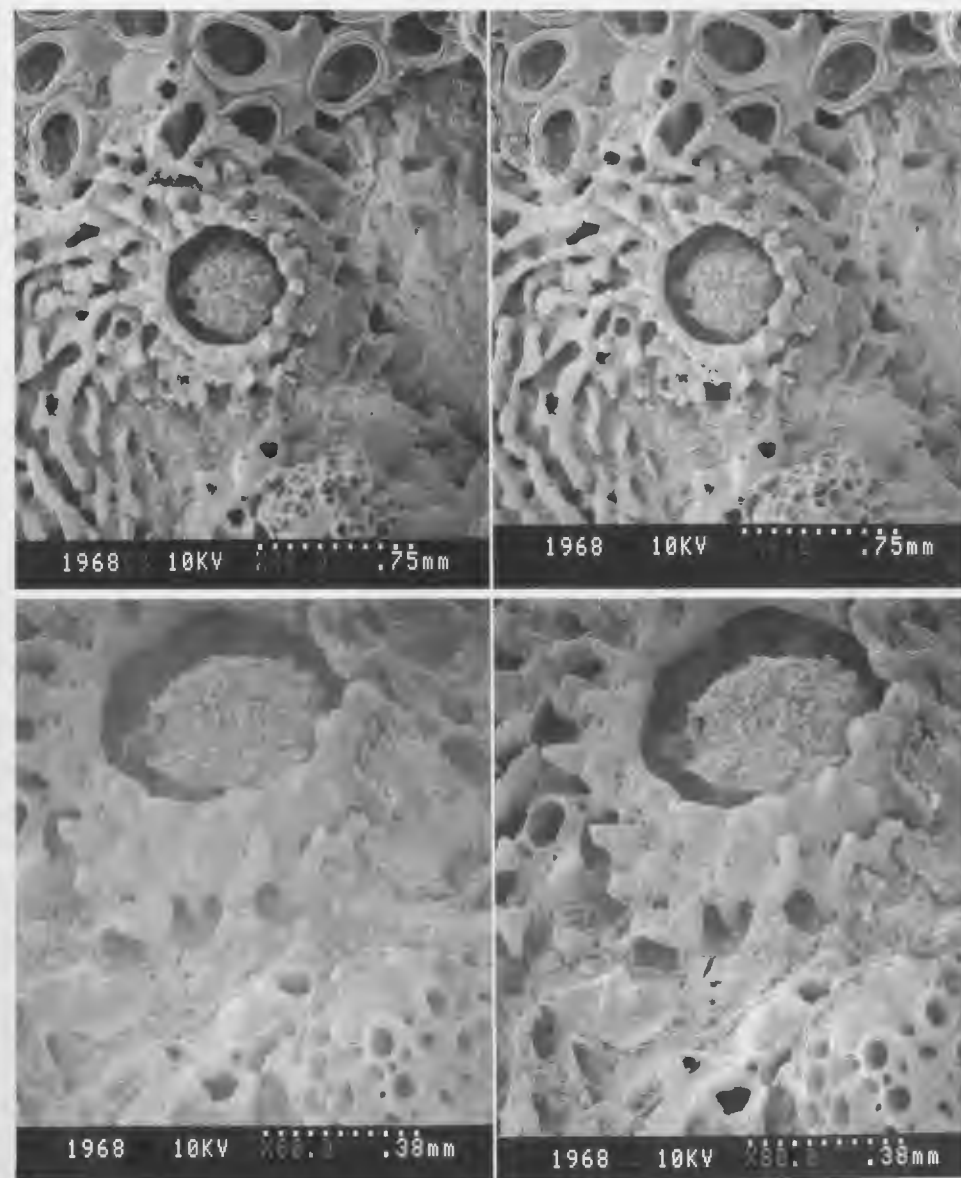


Figure 13. *Epiphaxum breve* n. sp., colony no. 1. Top, Vertically directed terminal calyx at apex of advancing stolon. Bottom, Detail of same. Stereoscopic pairs.

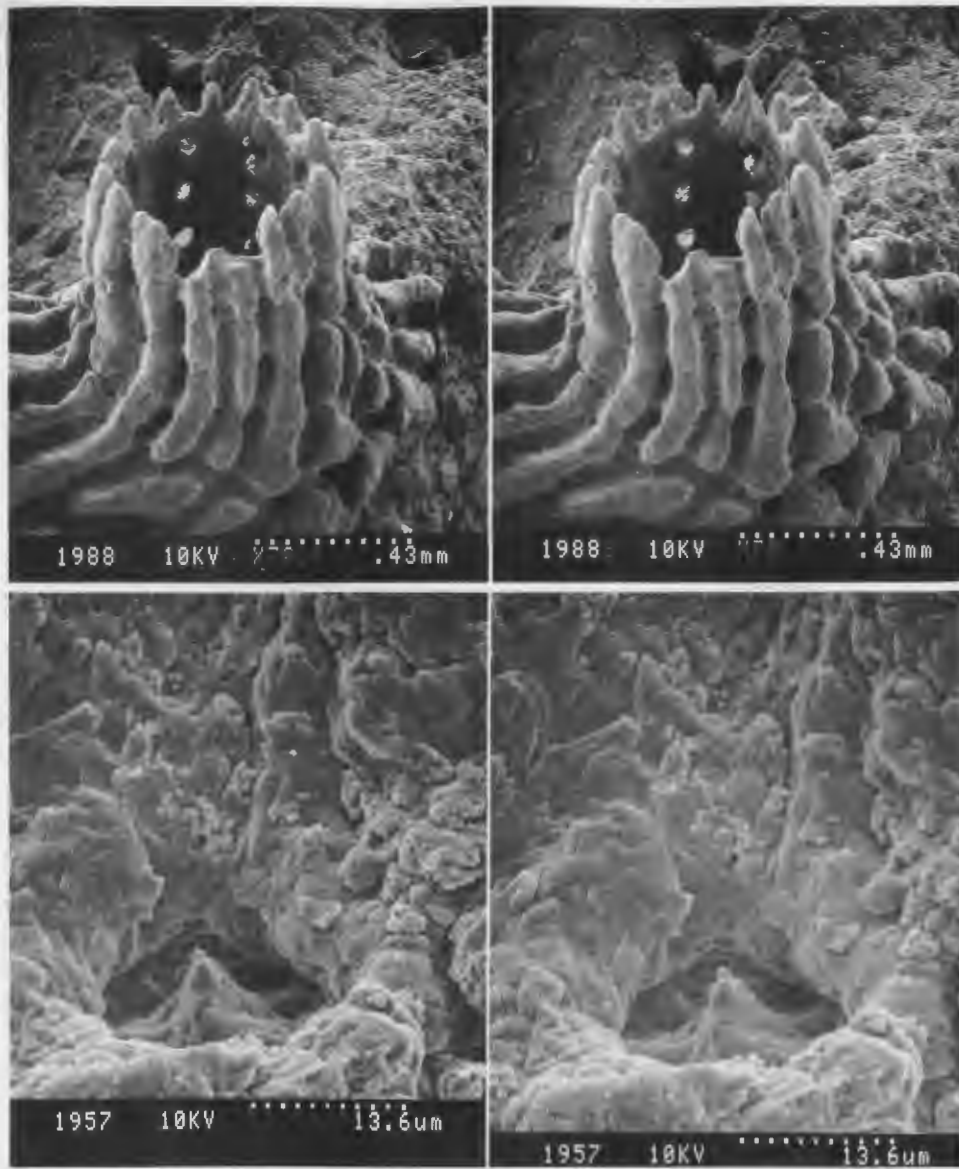


Figure 14. *Epiphaxum breve* n. sp., colony no. 1. Top, Young calyx in stage with only eight series of pores penetrating calyx wall. Bottom, Single puncta showing pointed, convex bottom. Stereoscopic pairs, scales as indicated.

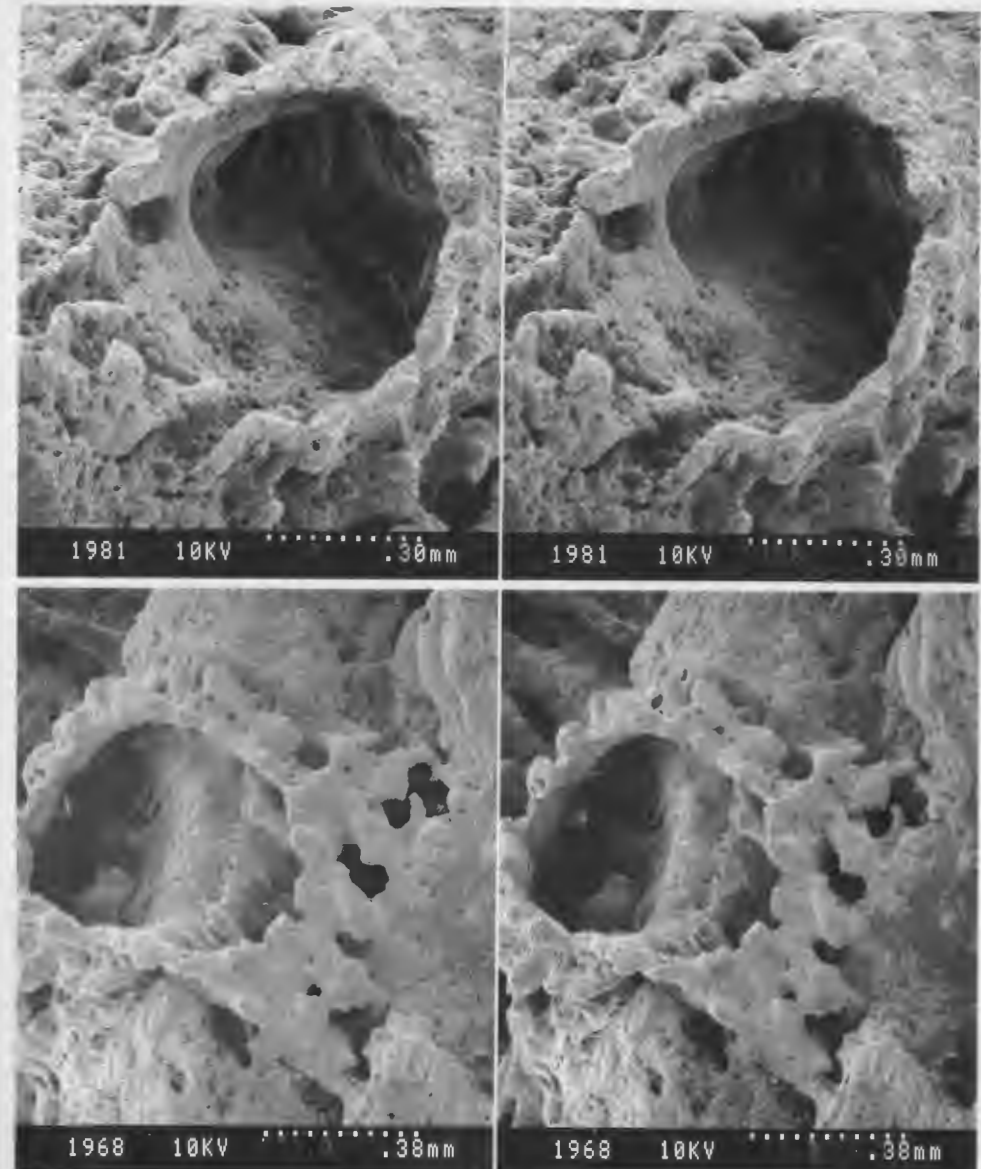


Figure 15. *Epiphaxum breve* n. sp., colony no. 1. Top, Obliquely directed terminal calyx at tip of stolon. Bottom, Vertically directed calyx at tip of stolon. Stereoscopic pairs.

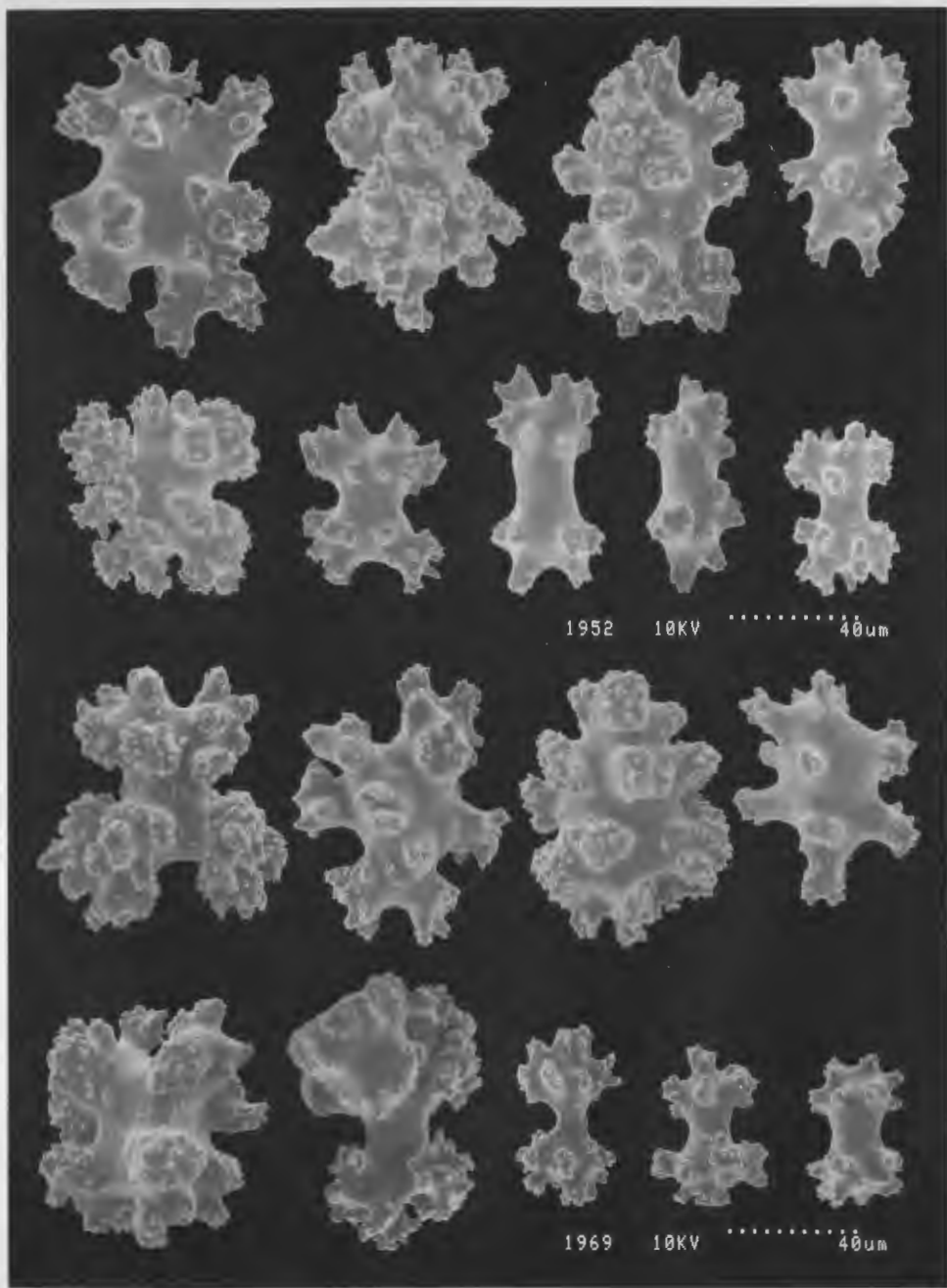


Figure 16. *Epiphaxum breve* n. sp. 1952, Sclerites of colony no. 1. 1969, Sclerites of colony no. 2.

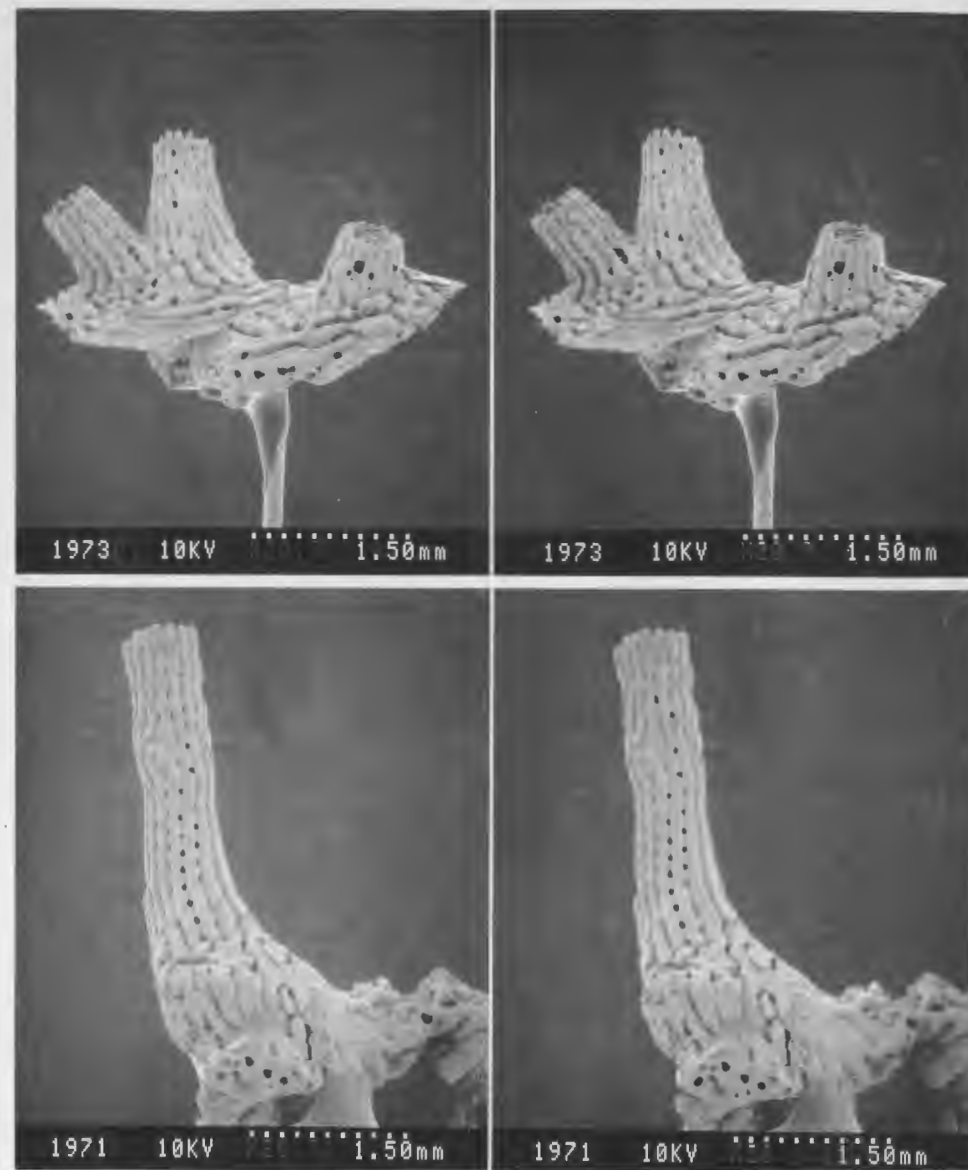


Figure 17. *Epiphaxum breve* n. sp., colony no. 2. Top, Part of stolon with three calyces. Bottom, Fully developed calyx showing broken end of stolon. Stereoscopic pairs.

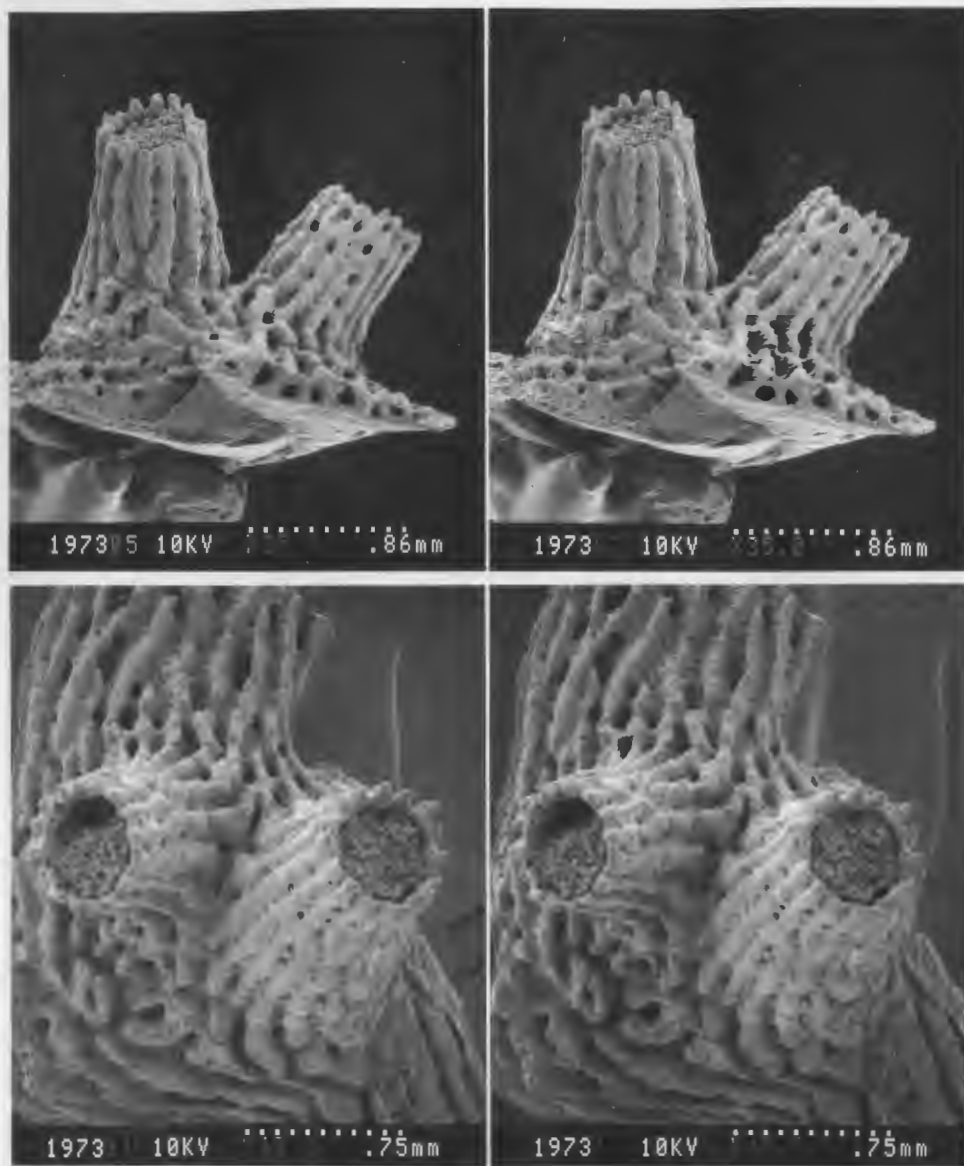


Figure 18. *Epiphaxum breve* n. sp., colony no. 2. Part of stolon with two contiguous calyces. Top, Profile view. Bottom, Apertural view. Stereoscopic pairs.

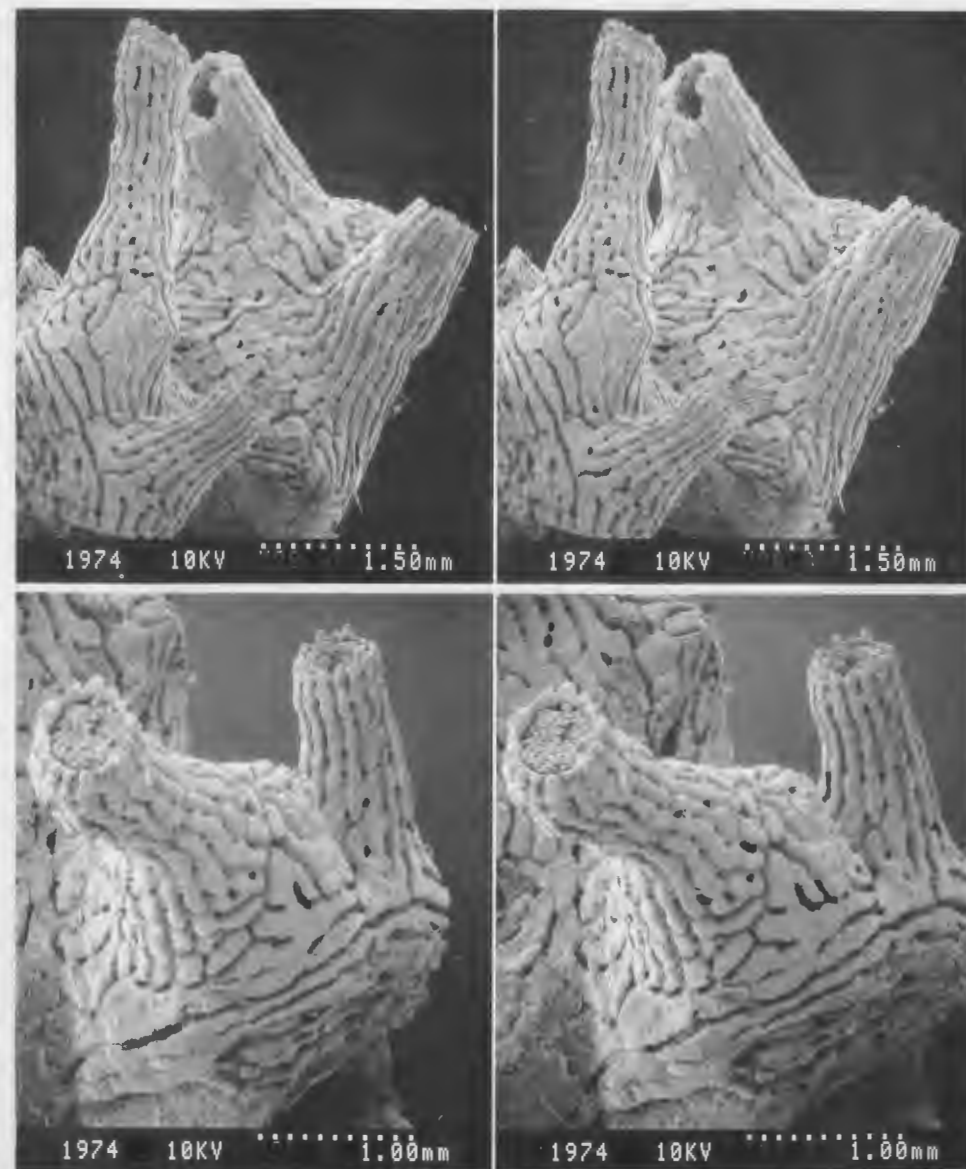


Figure 19. *Epiphaxum breve* n. sp., colony no. 2. Top, Widened part of stolon with several calyces. Bottom, Oblique view of two calyces. Stereoscopic pairs.

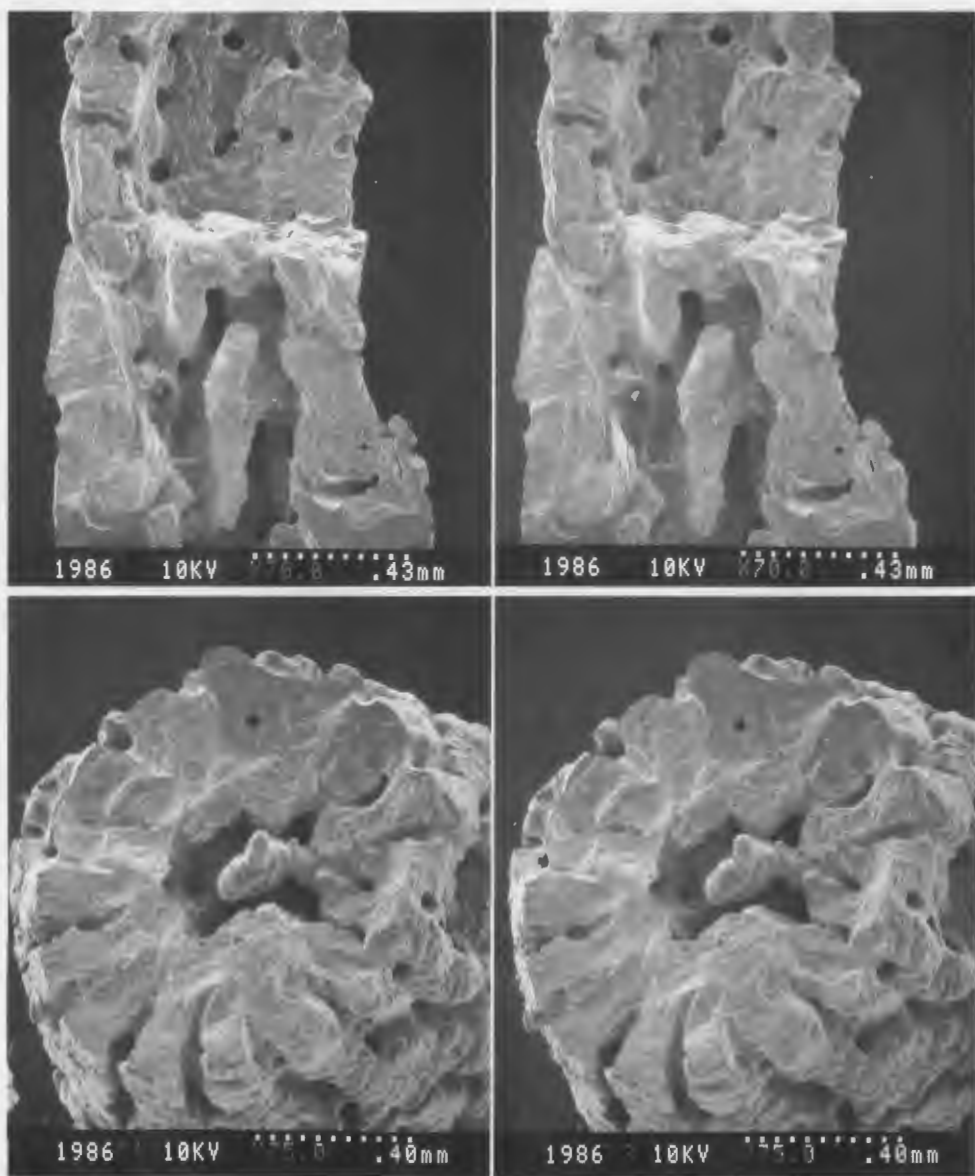


Figure 20. *Epiphaxum breve* (specimen no. 2). Top, Fractured sections of anthocodiae to show trabecular in-filling of lumen of calyces near base. Stereoscopic pairs, scales as indicated.

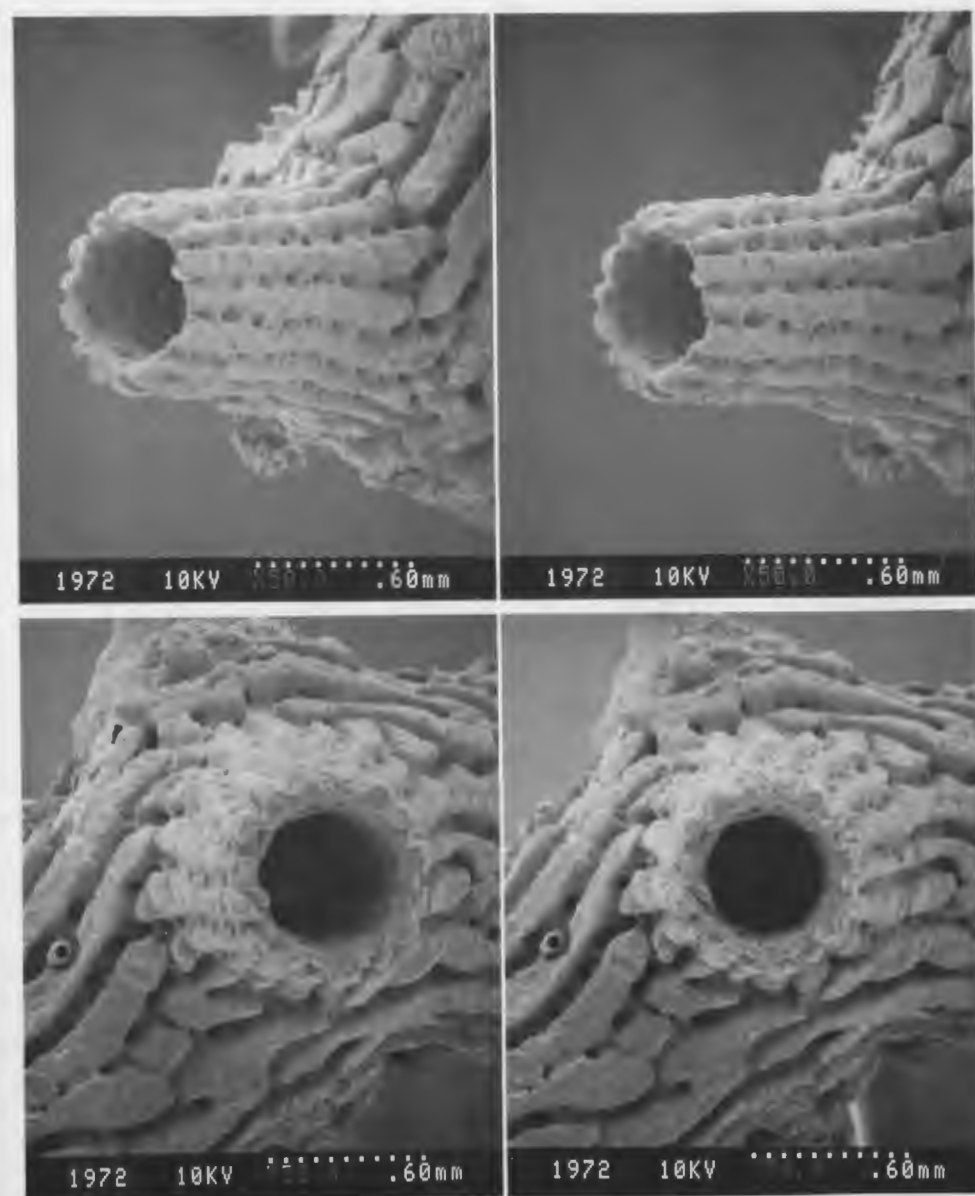


Figure 21. *Epiphaxum breve* n. sp., colony no. 2. Oblique and apertural views of calyx showing absence of septa. Stereoscopic pairs.

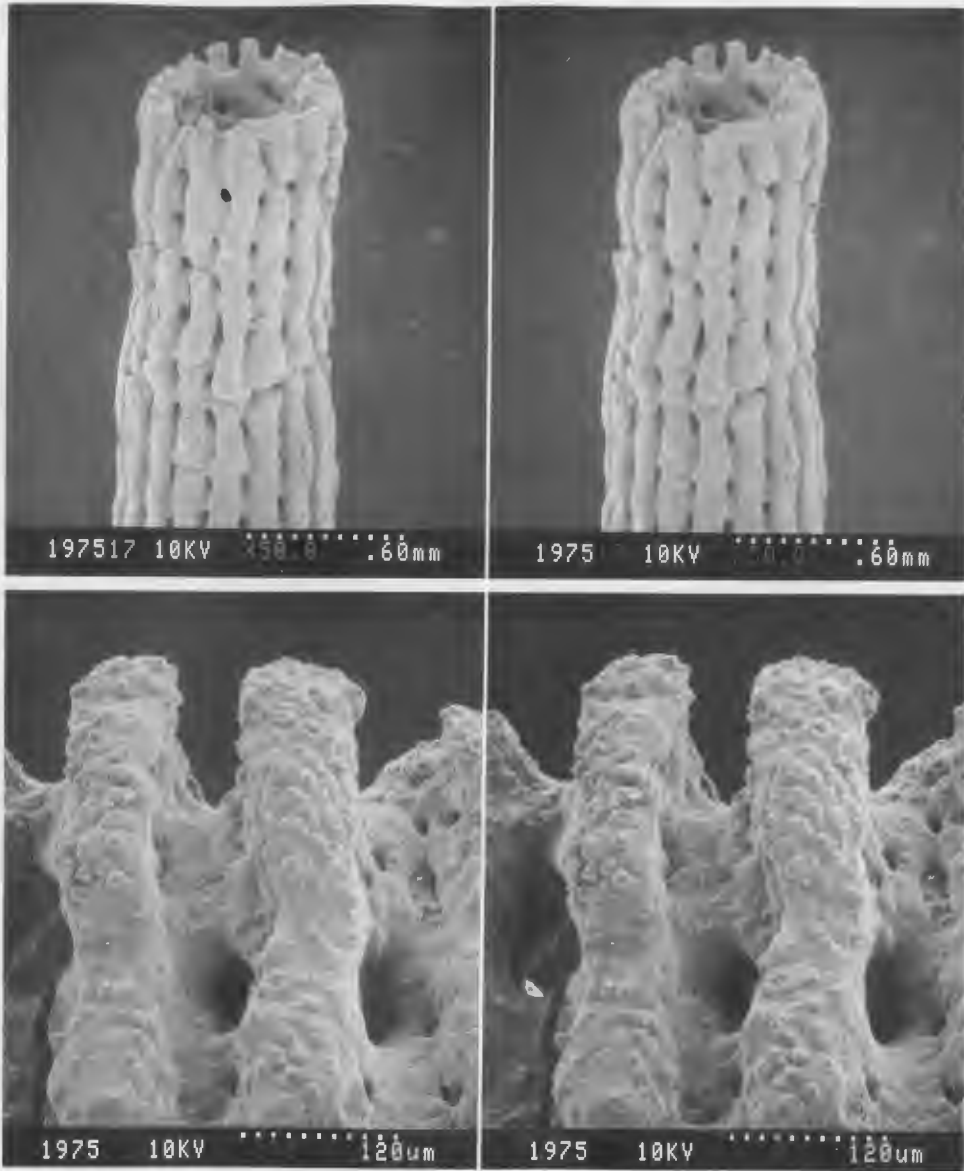


Figure 22. *Epiphaxum breve* n. sp., colony no. 2. Top, Distal part of isolated calyx. Bottom, Marginal teeth of same. Stereoscopic pairs.

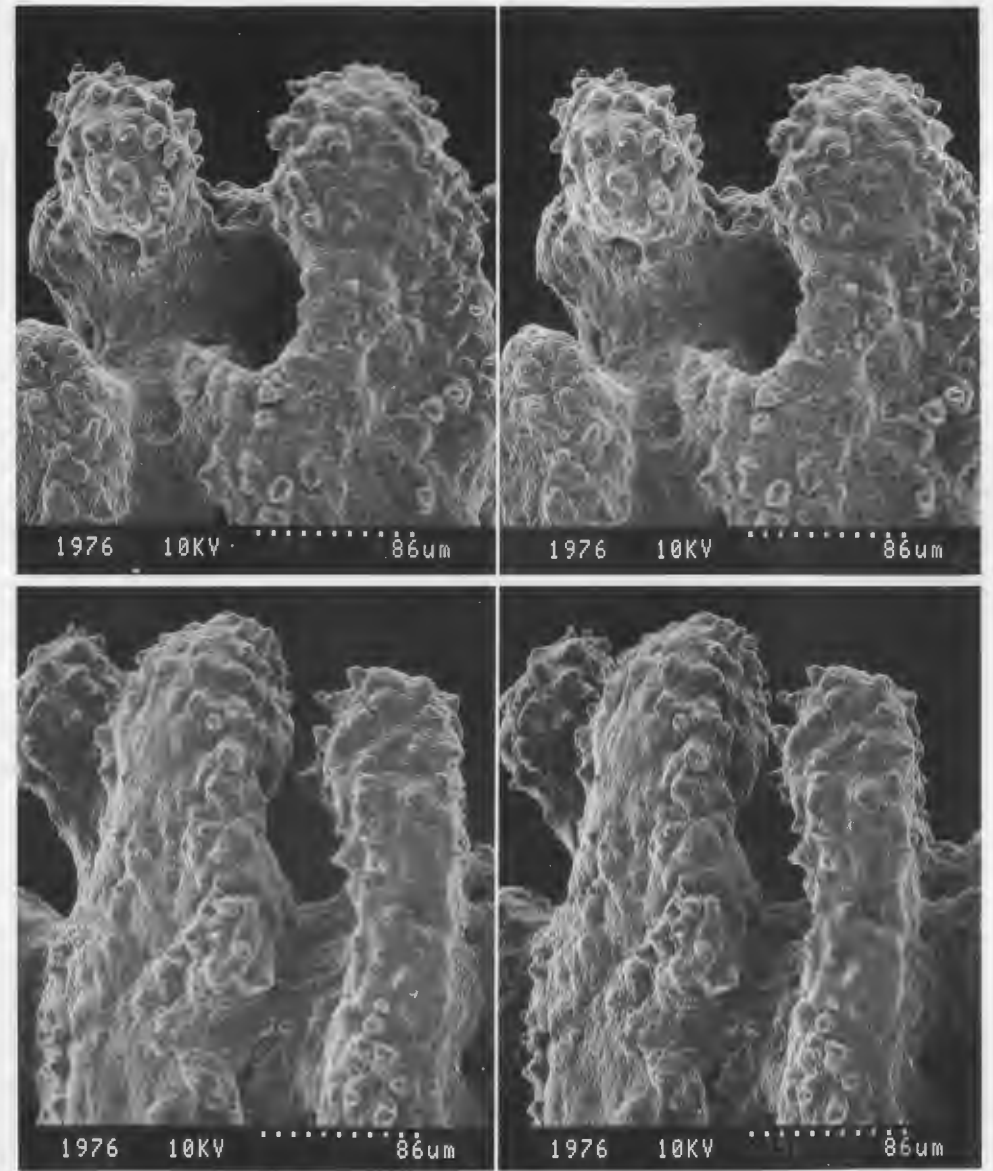


Figure 23. *Epiphaxum breve* n. sp., colony no. 2. Marginal teeth of calyx showing formation of pores. Stereoscopic pairs.

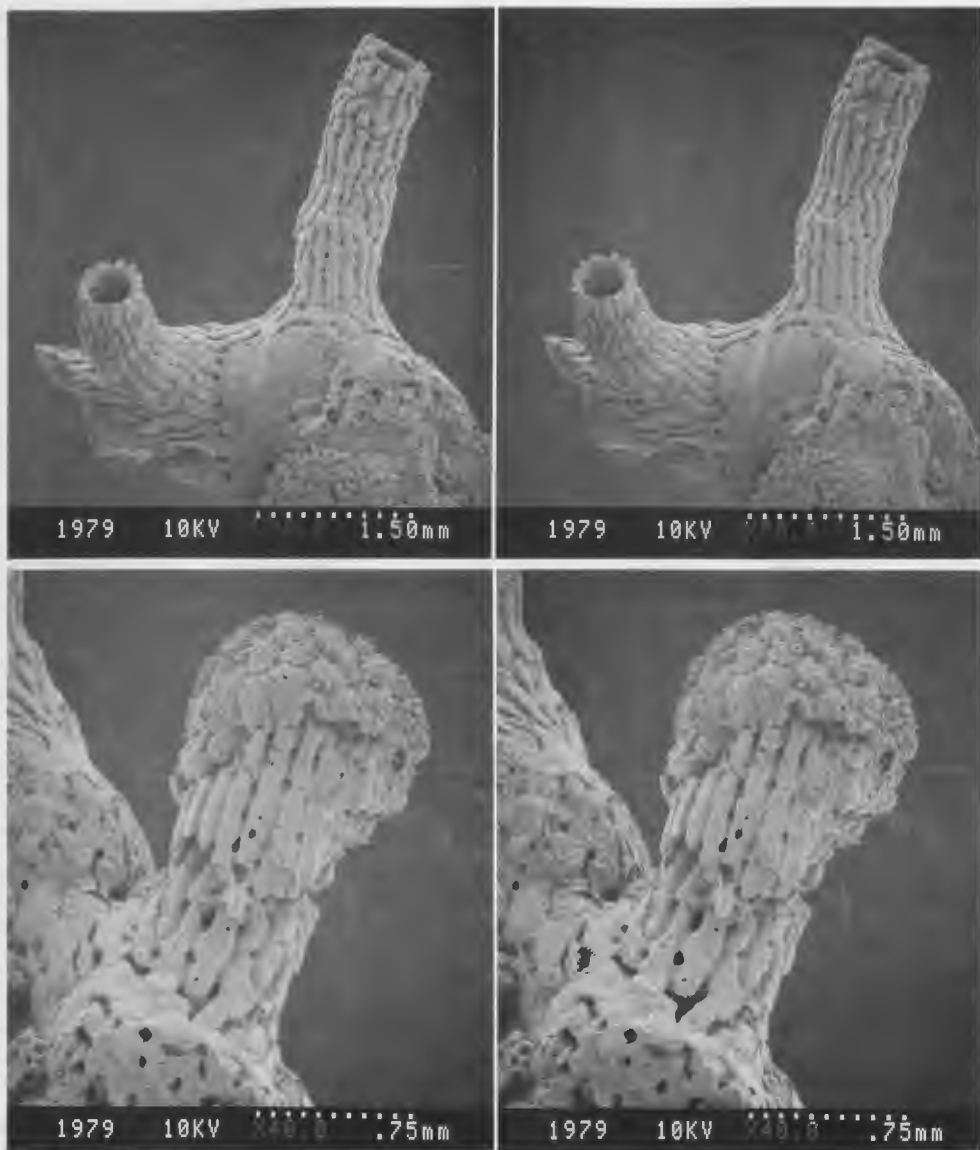


Figure 24. *Epiphaxum breve* n. sp., colony no. 2. Top, Part of stolon with 3 calyces, one not visible. Bottom, Third calyx of above, showing repair of damage and overgrowth by foraminiferan. Stereoscopic pairs.

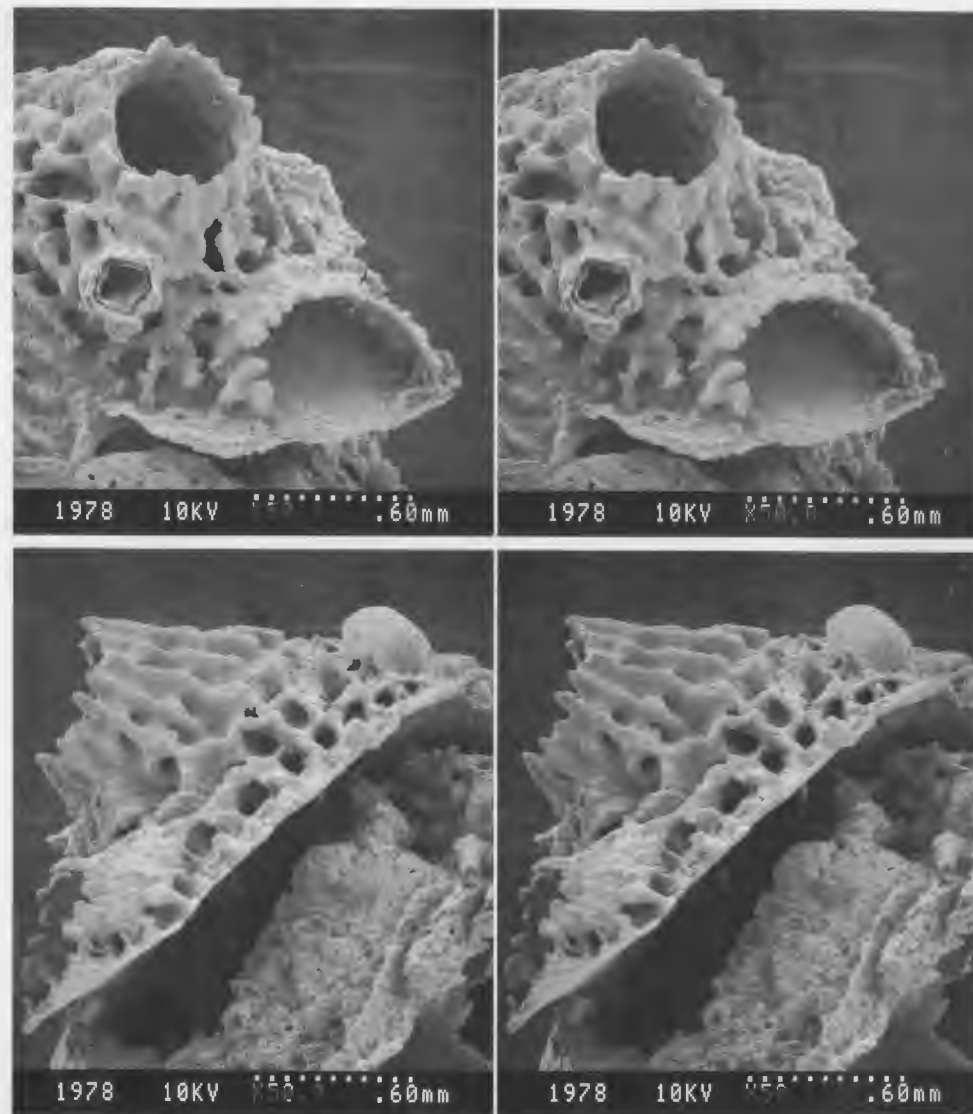


Figure 25. *Epiphaxum breve* n. sp., colony no. 2. Free-standing apex of advancing stolon, with incompletely formed terminal calyx and penultimate calyx. Top, Oblique view. Bottom, Side view. Stereoscopic pairs.



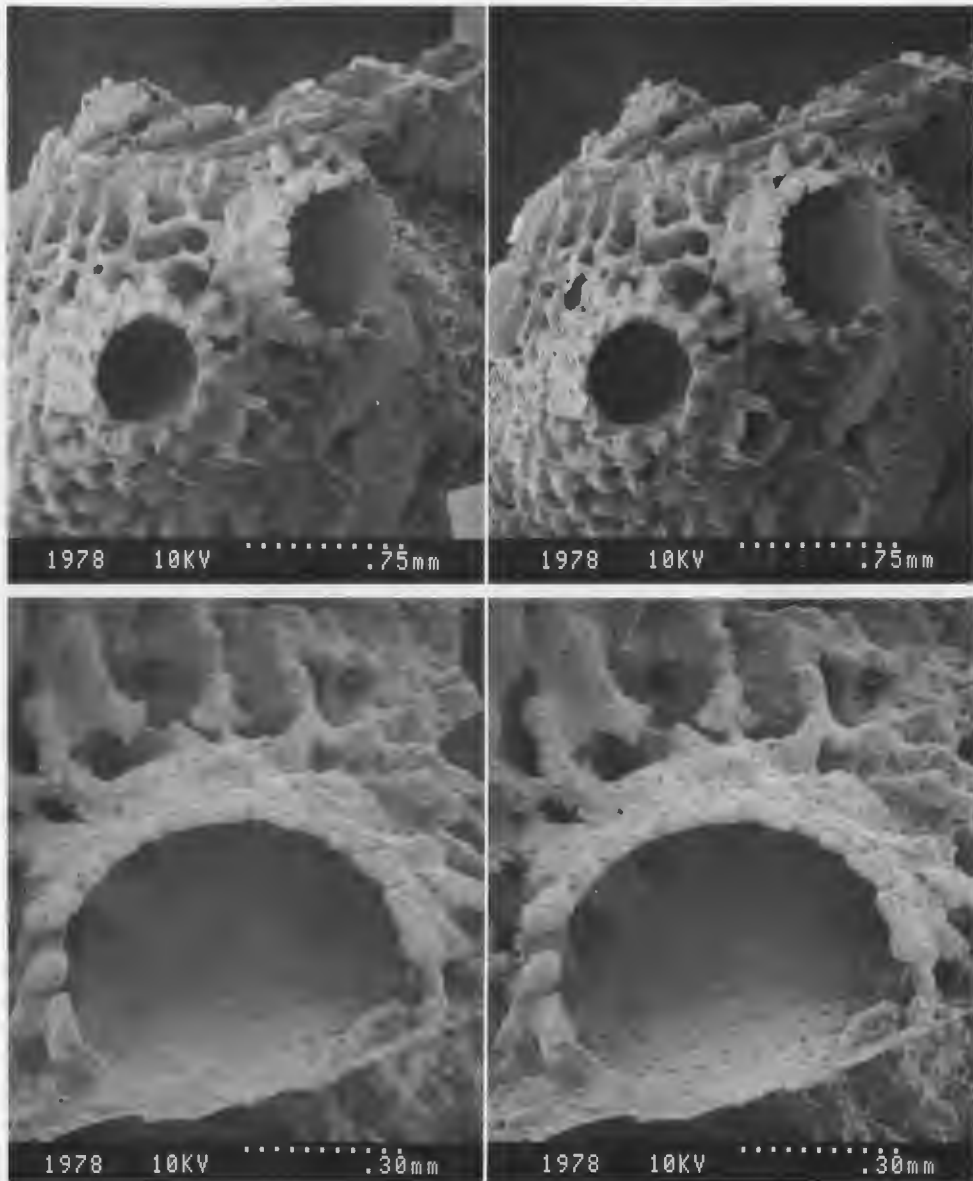


Figure 26. *Epiphaxum breve* n. sp., colony no. 2. Apex of advancing stolon with two calyces. Top, View from above. Bottom, Apical view of partly formed terminal calyx. Stereoscopic views.

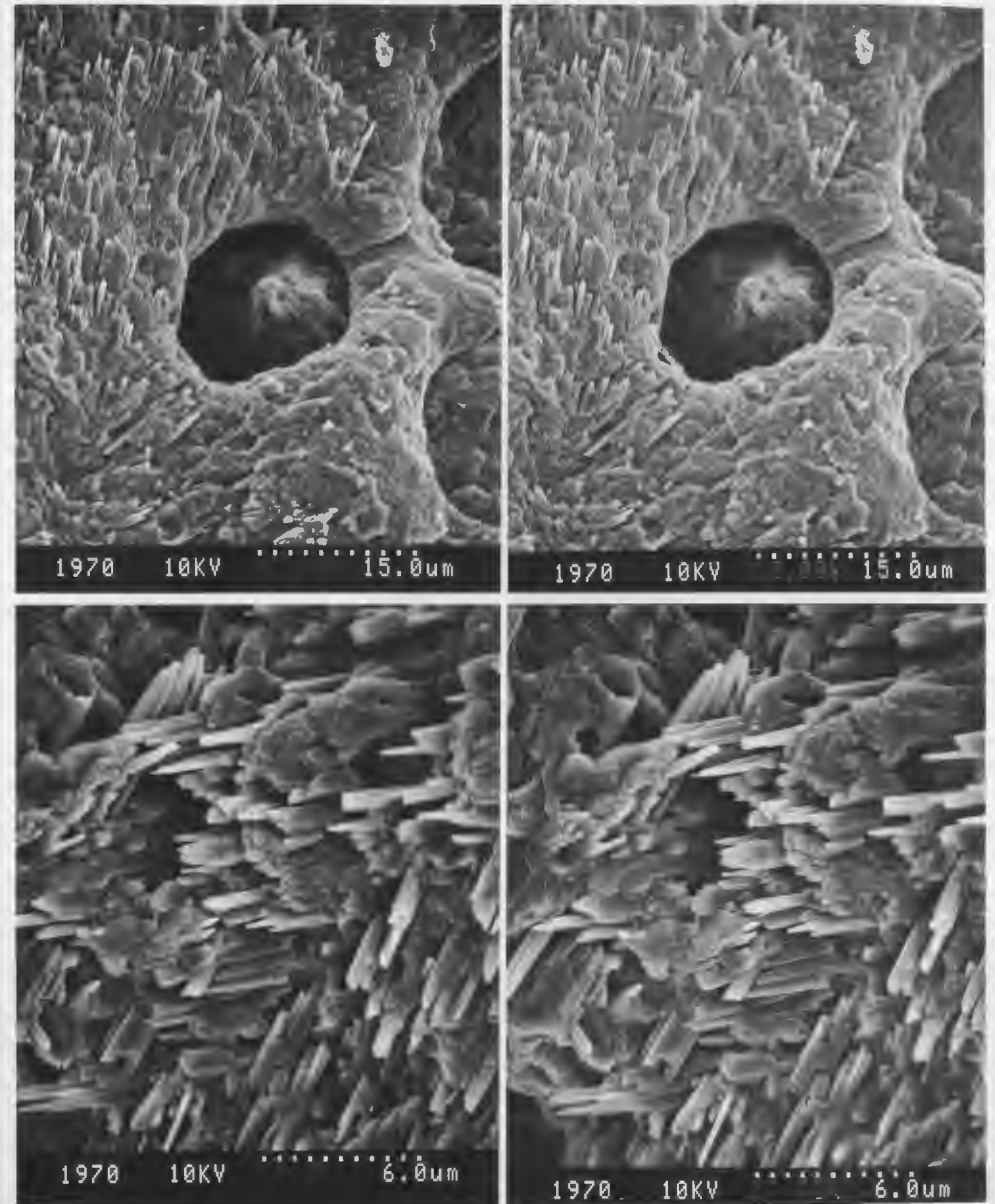


Figure 27. *Epiphaxum breve* n. sp., colony no. 2. Top, Single puncta showing pointed, convex bottom. Bottom, Microcrystals at surface of supporting skeleton showing diverse orientation. Stereoscopic pairs.

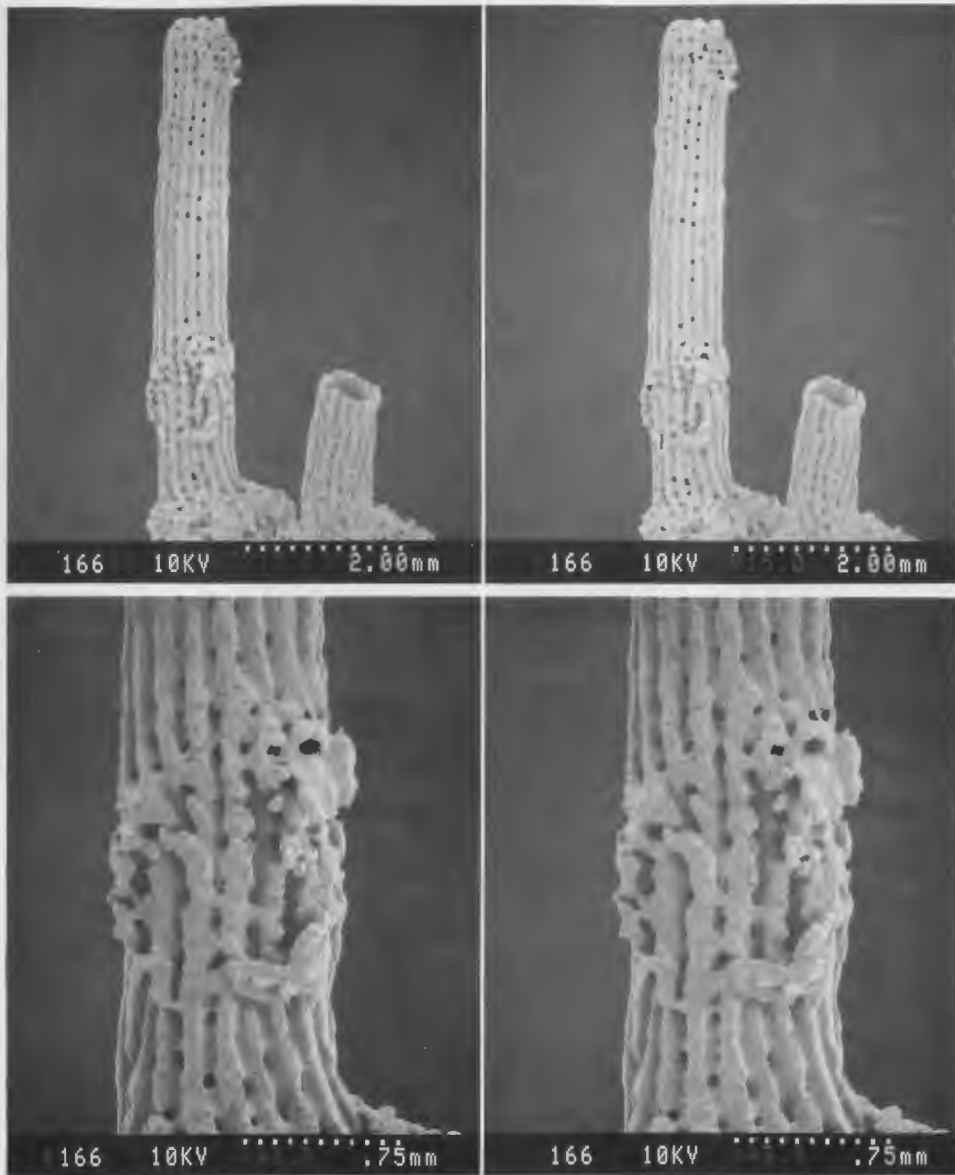


Figure 28. *Epiphaxum septifer* n. sp. Top, 2 calyces, one fully developed and showing bases of two secondary calyces. Bottom, Origin of secondary calyx. Stereoscopic pairs.

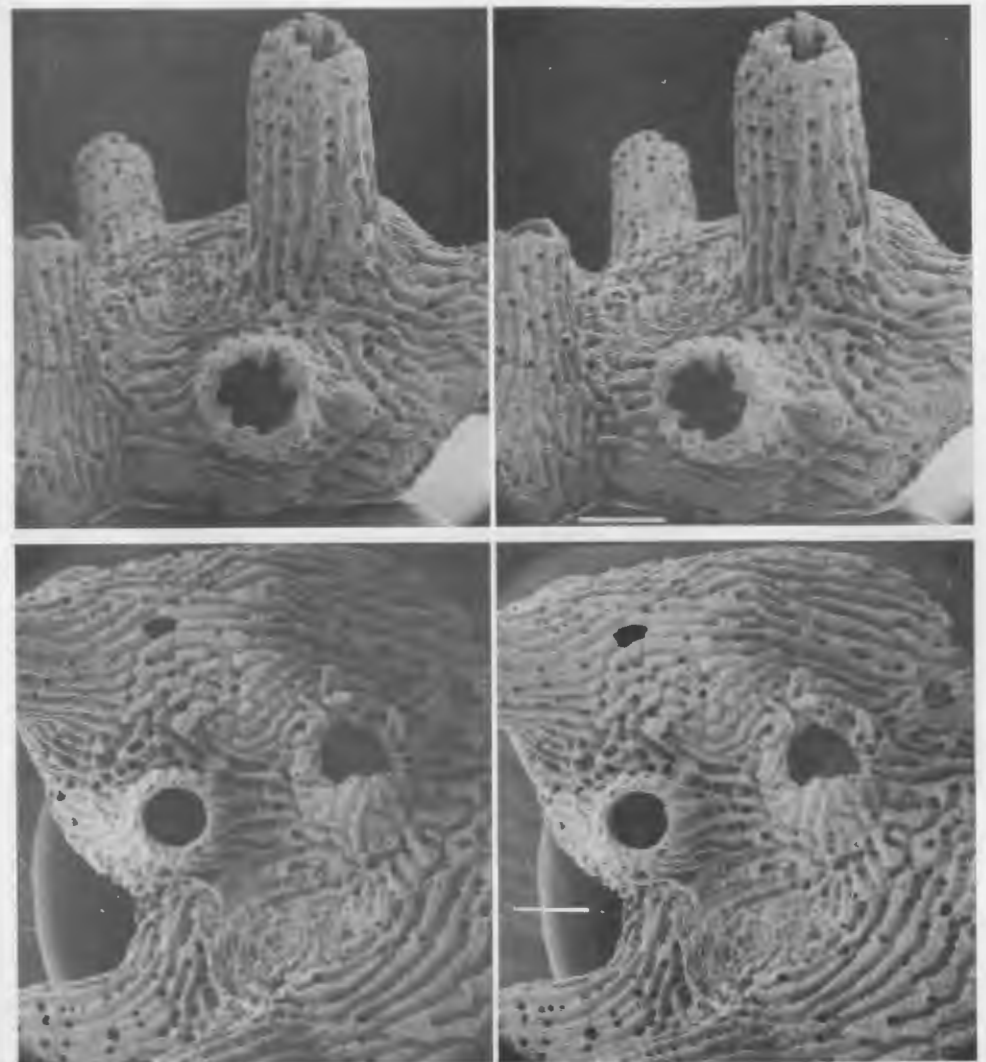


Figure 29. *Epiphaxum septifer* n. sp. Wide portion of stolon with 6 calyces. Top, Profile view. Bottom, Oblique view. Scale bars = 1 mm. Stereoscopic pairs.

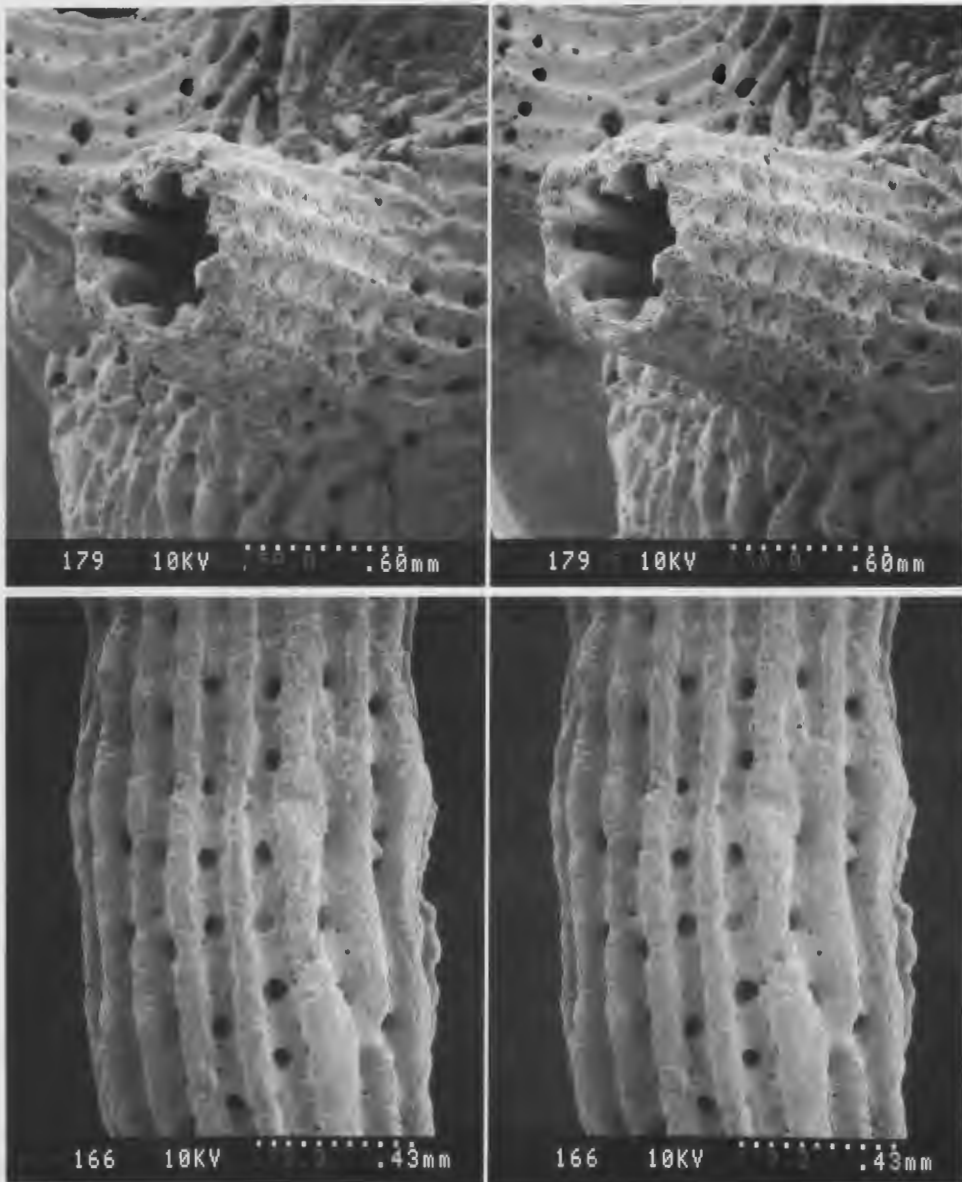


Figure 30. *Epiphaxum septifer* n. sp. Top, Oblique view of calyx showing septa. Bottom, Detail of calyx wall. Stereoscopic views.

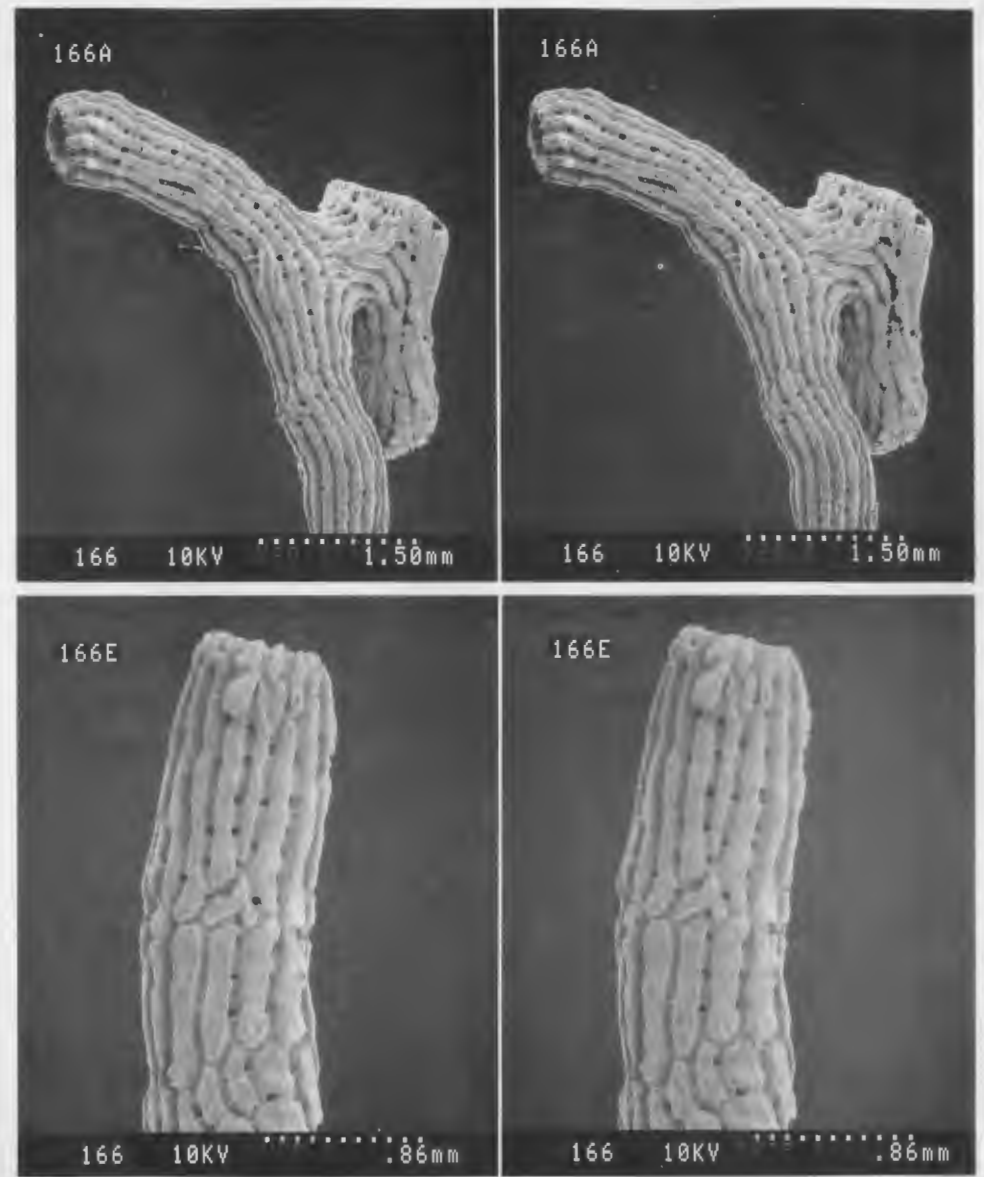


Figure 31. *Epiphaxum septifer* n. sp. Top, Partly recumbent calyx with lateral connection with stolon. Bottom, Distal part of isolated calyx. Stereoscopic pairs.

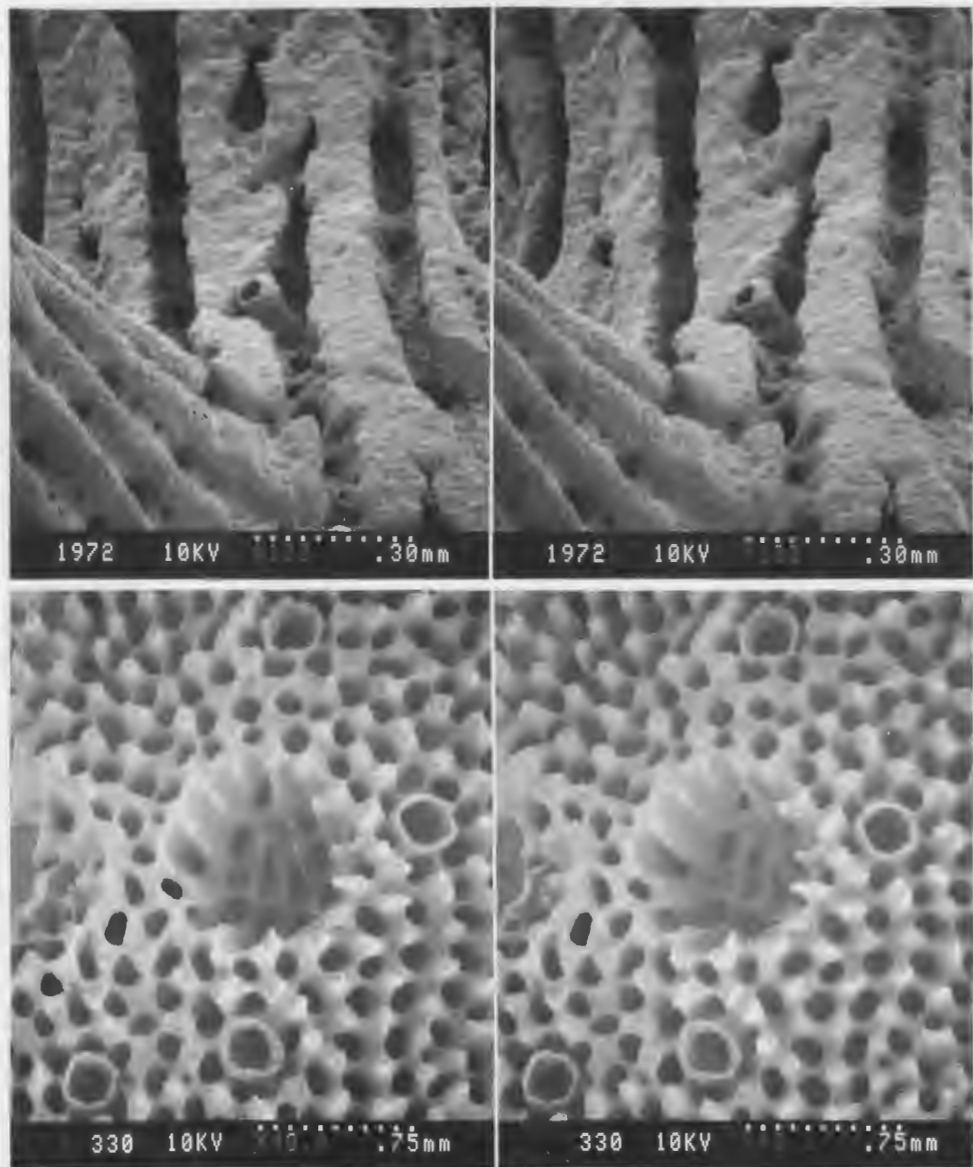


Figure 32. Symbiotic associations. Top, Aperture of presumed worm tube in skeleton of *Epiphaxum breve* (specimen no. 2). Bottom, Apertures of tubes of *Polydora armata* Langerhans adjacent to calyx of *Heliopora coerulea*.

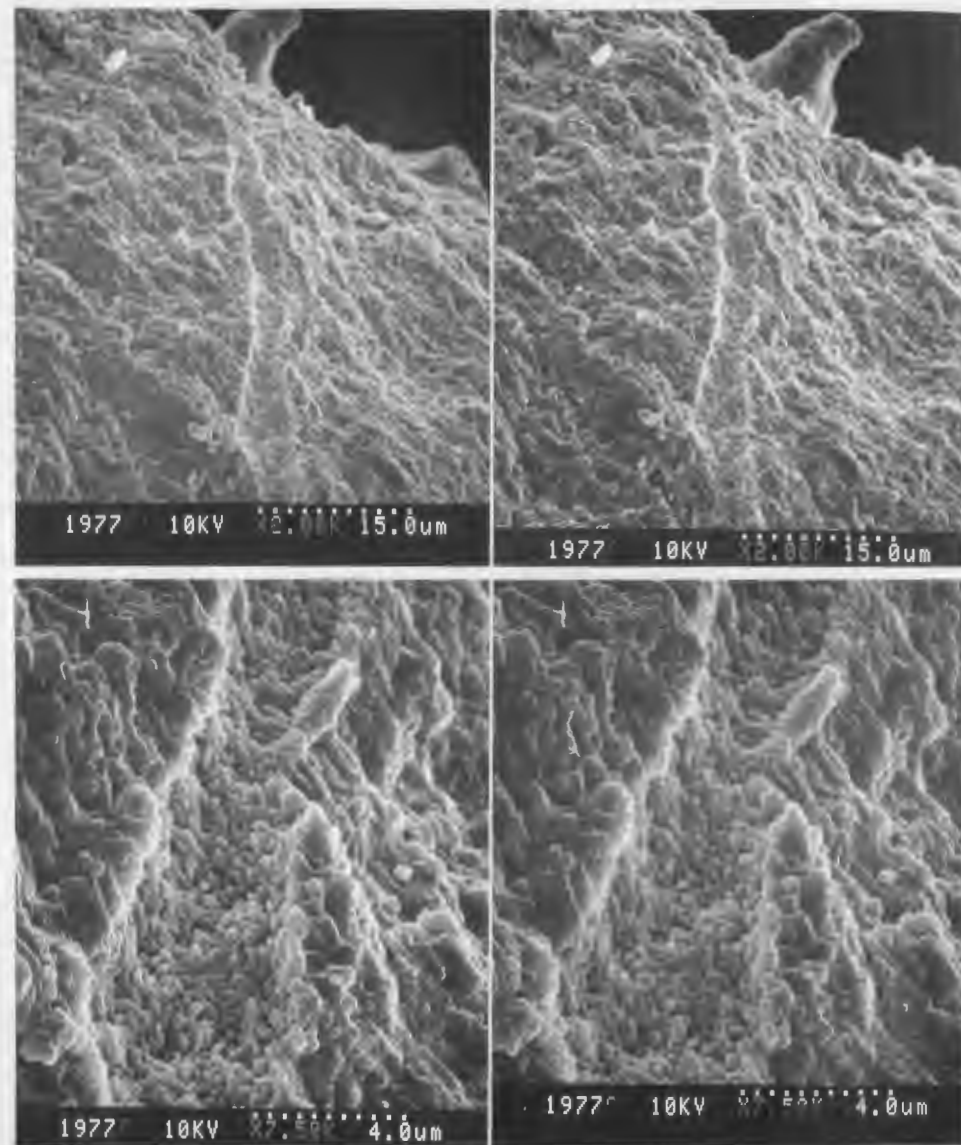


Figure 33. Symbiotic associations. Microboring produced by endolithic microorganism in calicular skeleton of *Epiphaxum breve* (specimen no. 2). Stereoscopic pairs, scales as indicated.

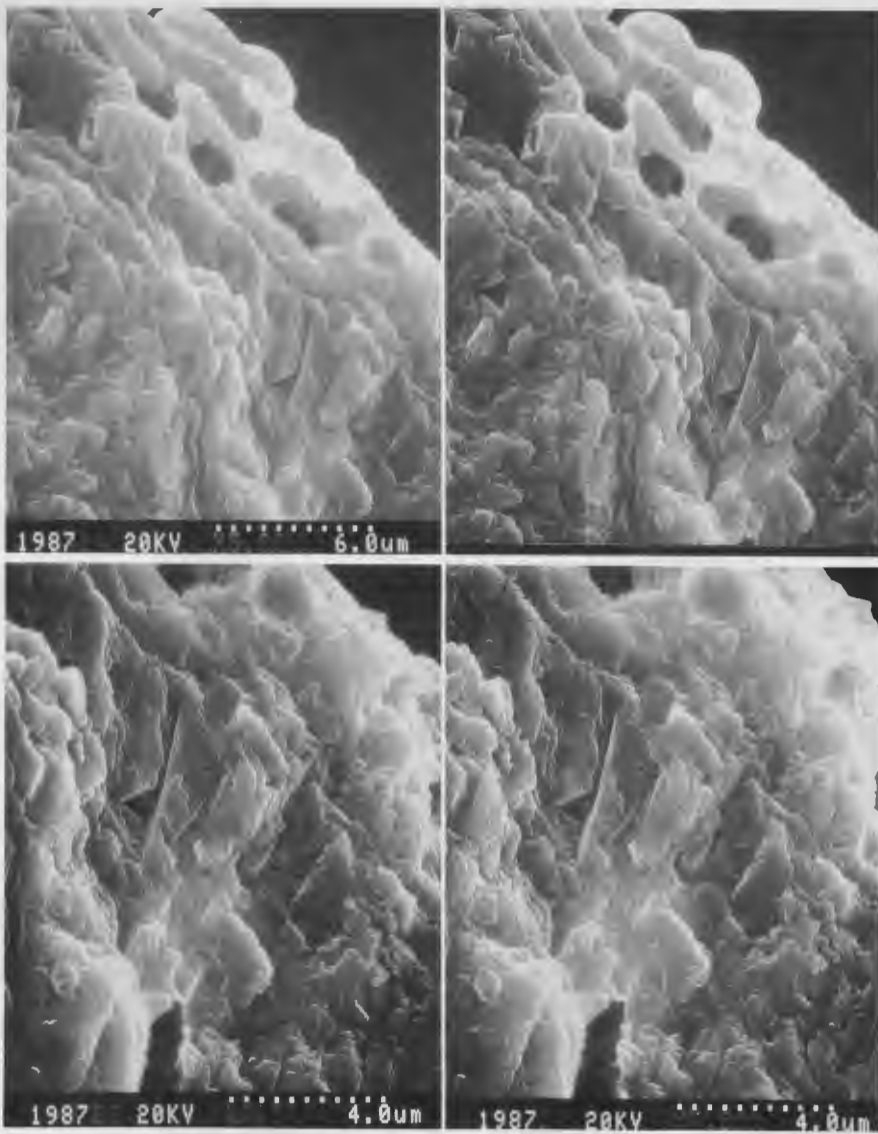


Figure 34. Symbiotic associations. Top, Galleries excavated beneath surface of calyx wall of *Epiphaxum breve* (specimen no. 1) by unknown microborer. Bottom, Aragonite crystals at broken surface in vicinity of microborer galleries. Stereoscopic pairs, scales as indicated.

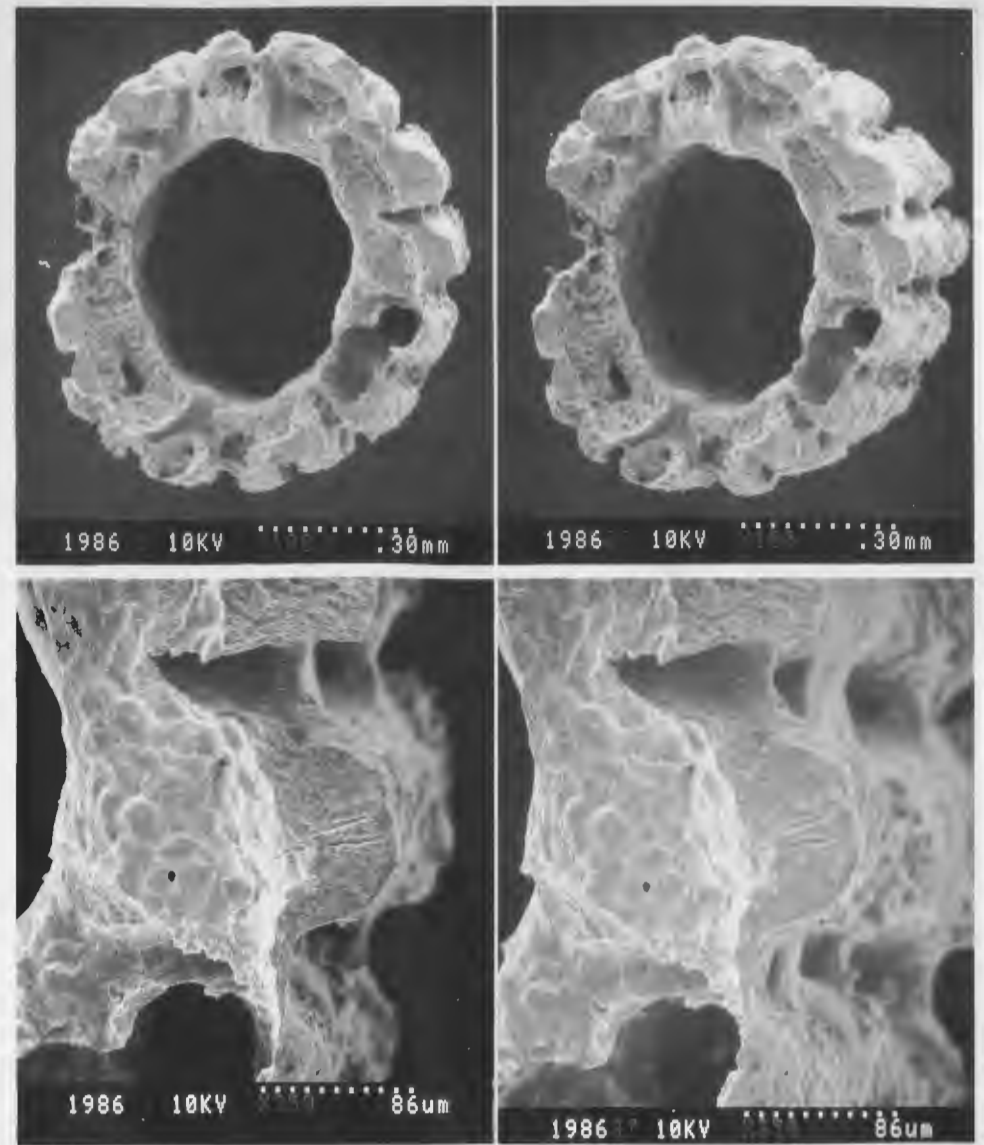


Figure 35. Symbiotic associations. Cavities excavated by sponge in calyx wall of *Epiphaxum breve* (specimen no. 2) while polyp was still living. Borings visible in trabecula probably were not produced by the sponge but by some unknown microorganism. Stereoscopic pairs, scales as indicated.

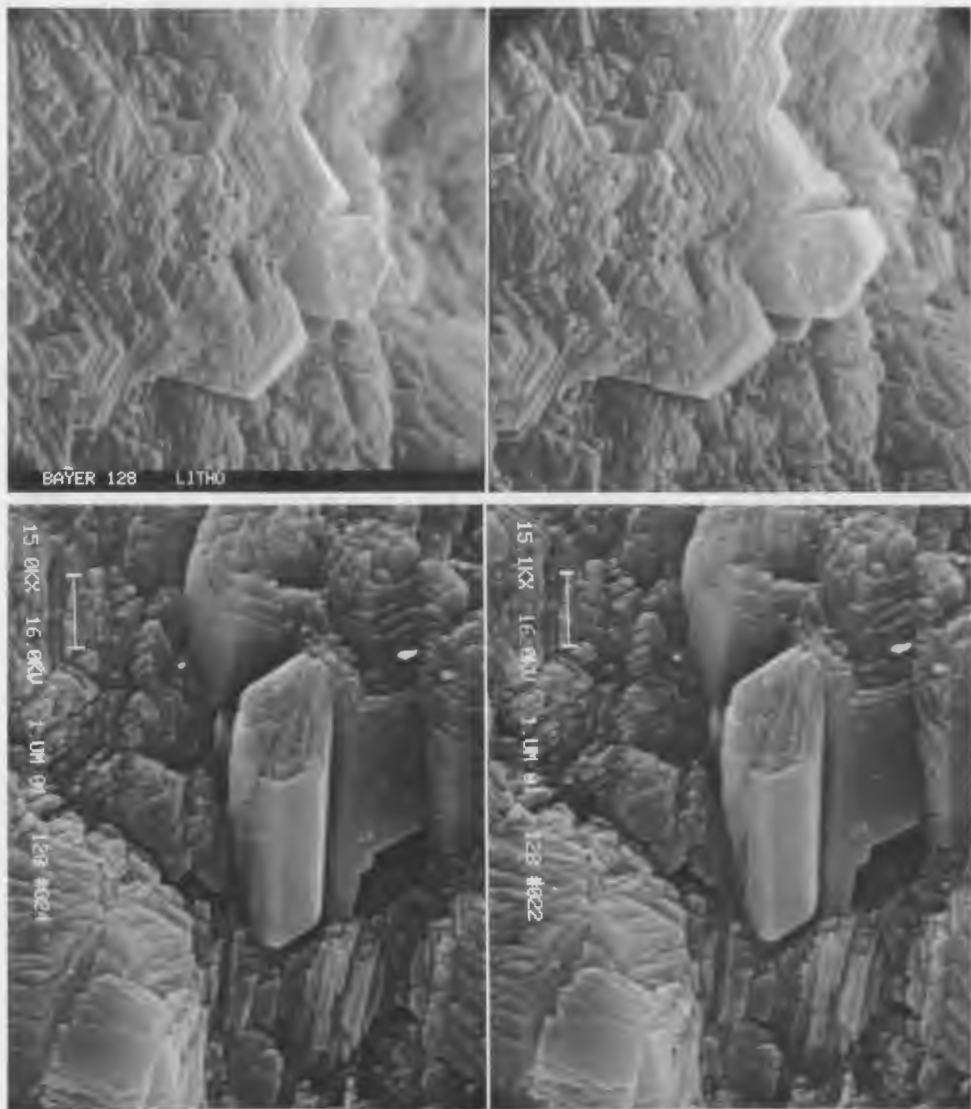


Figure 36. *Epiphaxum micropora* (Bayer and Muzik, 1977); holotype, USNM 52523. Euhedral aragonite crystals of external calyx wall.

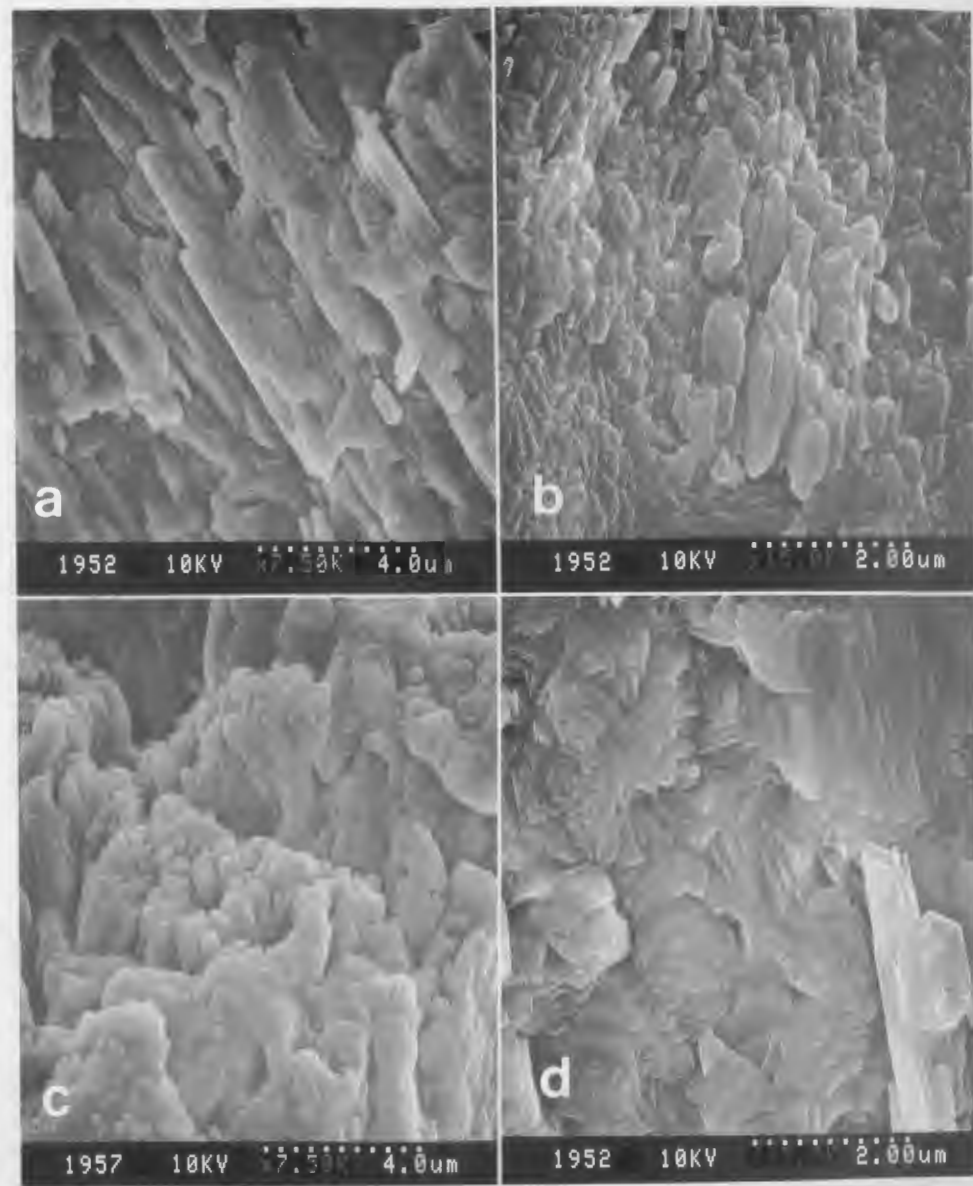


Figure 37. *Epiphaxum breve* n. sp. (specimen no. 1). Geometrical aggregates of lath-like forms of aragonite often approximating pseudo-hexagonal euhedral prisms; from natural surface of calyx wall.

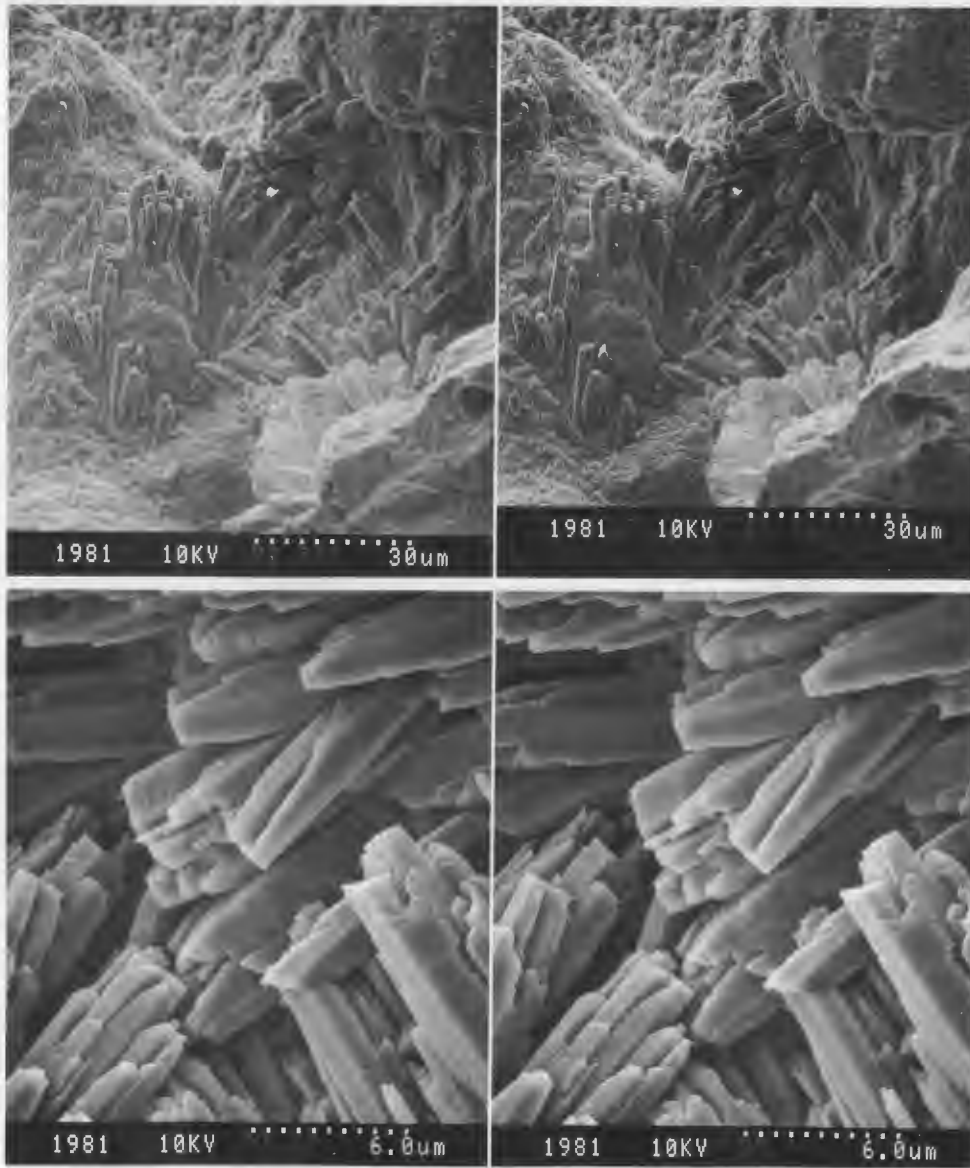


Figure 38. *Epiphaxum breve* n. sp. (specimen no. 1). Stubby pseudo-hexagonal euhedral prisms of aragonite; from natural surface of calyx wall.

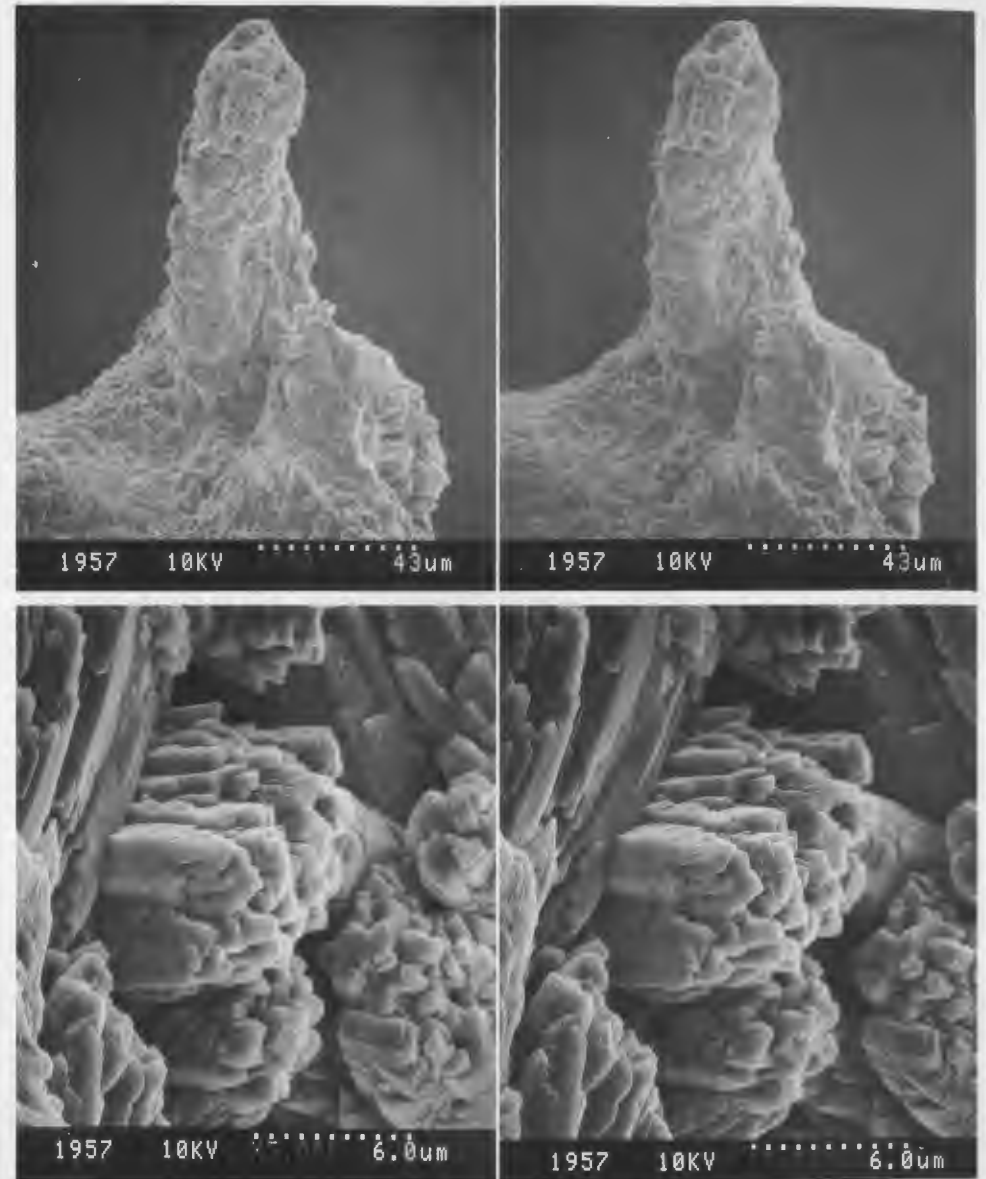


Figure 39. *Epiphaxum breve* n. sp. (specimen no. 2). Top, New trabecula from advancing tip of stolon; scale = 43  $\mu\text{m}$ . Bottom, Broken surface at base of same showing bundle of stubby pseudo-hexagonal euhedral aragonite crystals; scale = 6  $\mu\text{m}$ . Stereoscopic pairs.

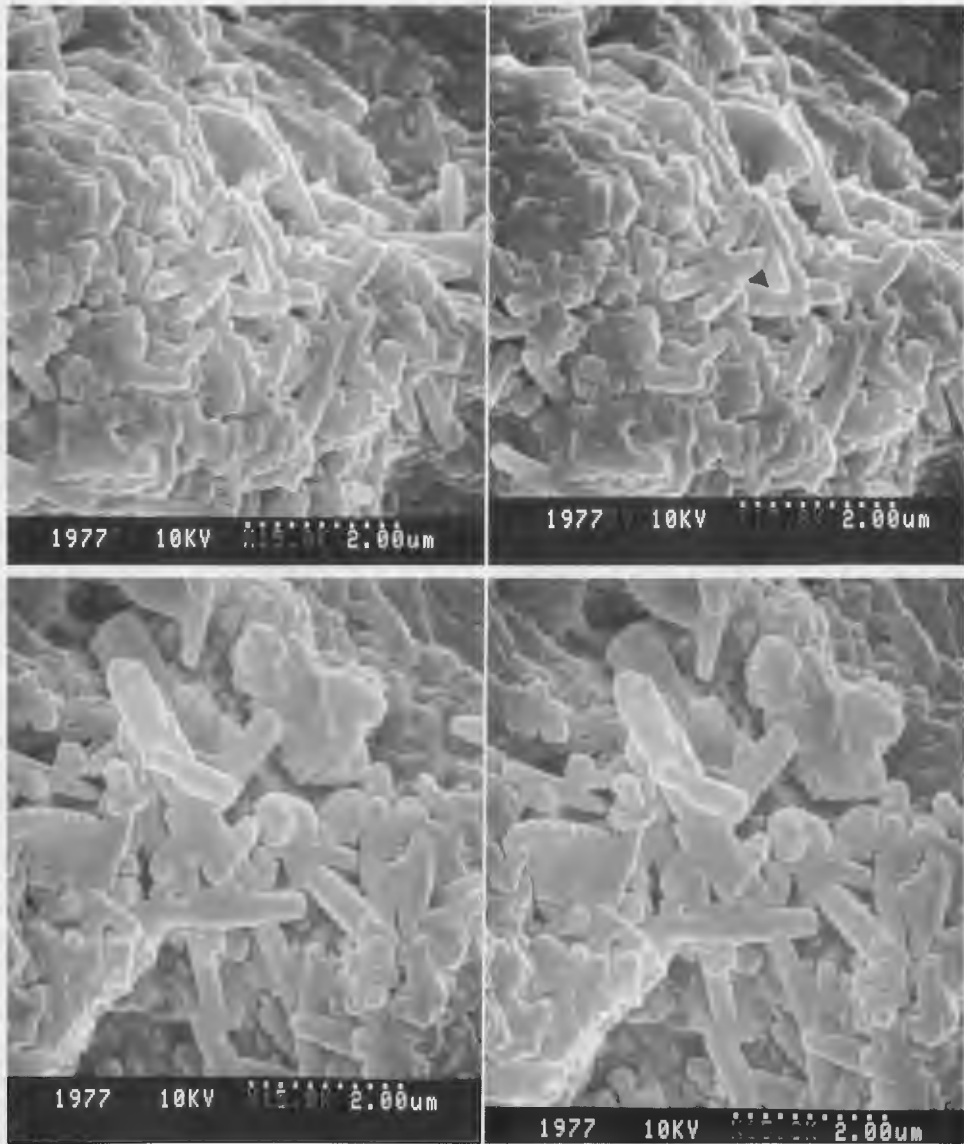


Figure 40. *Epiphaxum breve* n. sp. (specimen no. 2). Subhedral aragonite rods from natural surface of calyx wall.

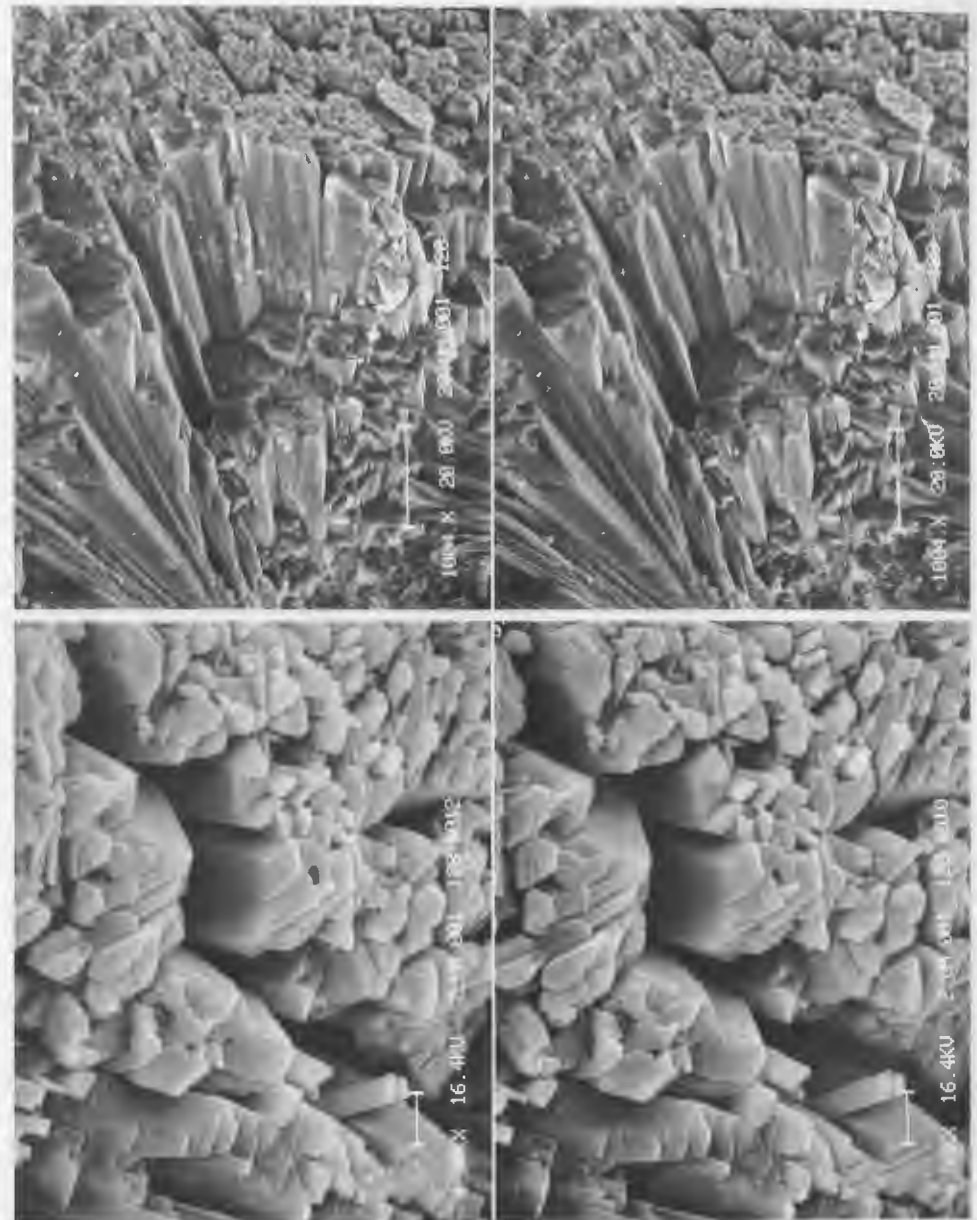


Figure 41. *Heliopora coerulea* (Pallas). Fascicles of euhedral aragonite prisms; surface of corallum. Top scale = 20 μm; bottom scale = 2 μm. Stereoscopic pairs.



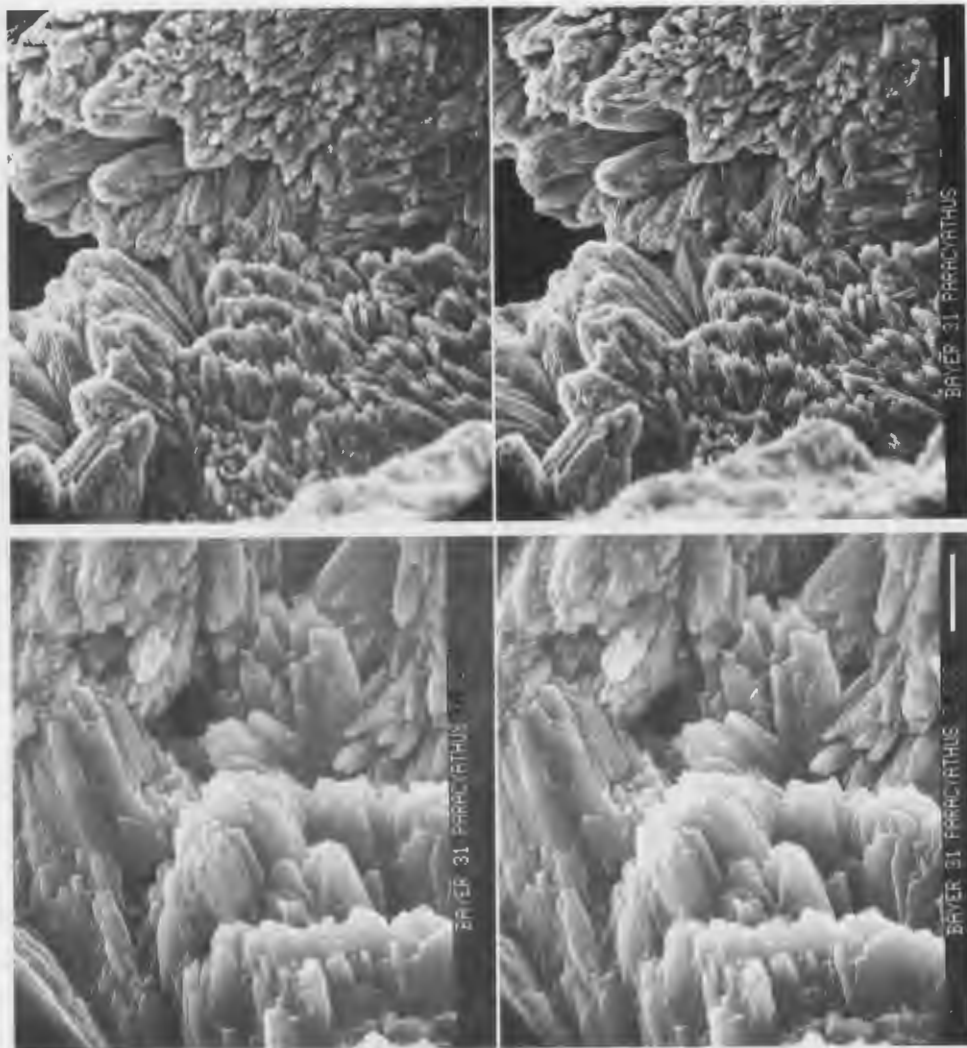


Figure 42. *Paracyathus* sp. Top, Sclerodermites consisting of aggregates of flattened, blade-like prisms of aragonite; at margin of calice; scale bar = 10  $\mu$ m. Bottom, View at higher magnification showing ends of sclerodermites; scale bar = 5  $\mu$ m. Stereoscopic pairs.

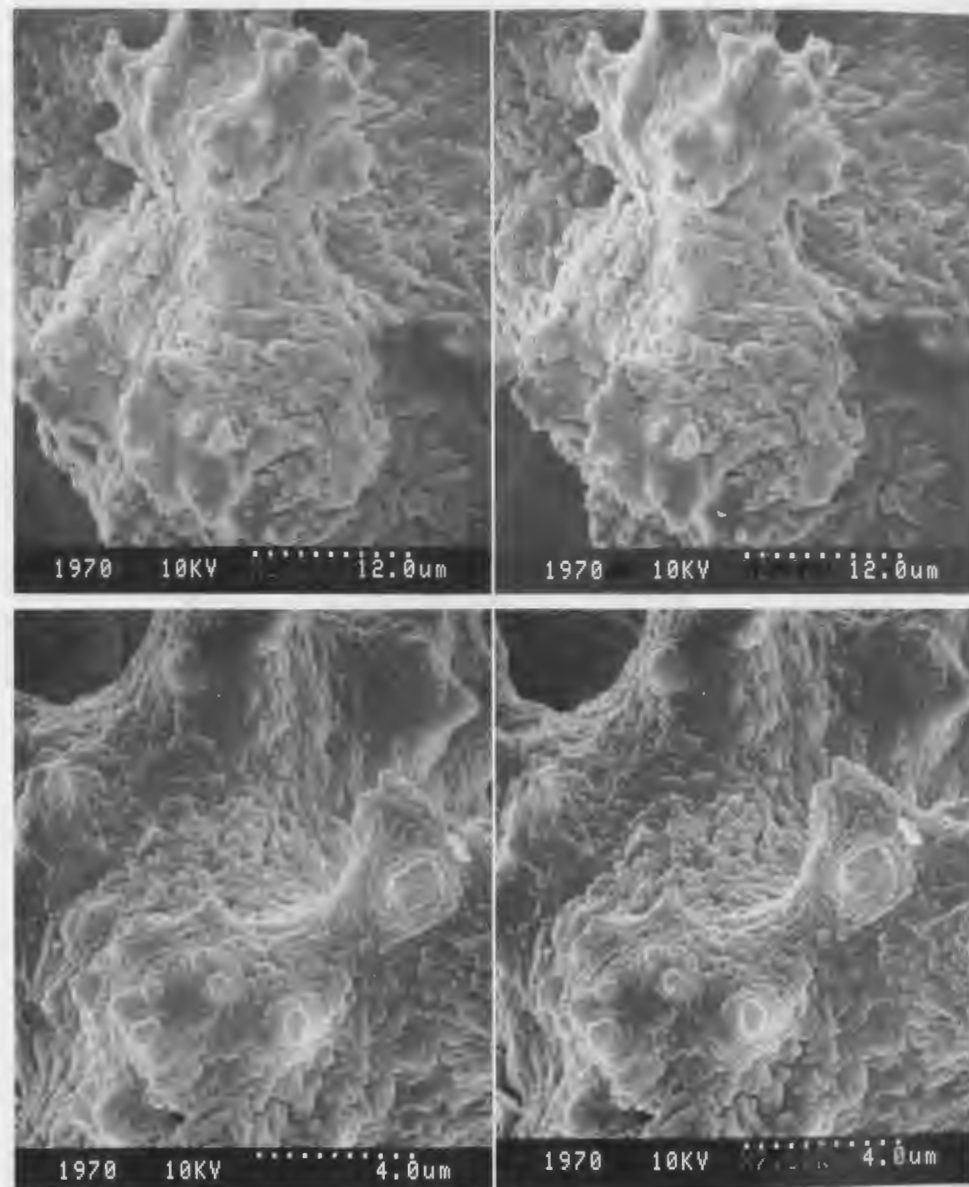


Figure 43. *Epiphaxum breve* n. sp., colony no. 2. Top, Calcite sclerite partly embedded in supporting aragonitic skeleton. Bottom, Closer view of bluntly dentate calcite surface. Stereoscopic pairs.

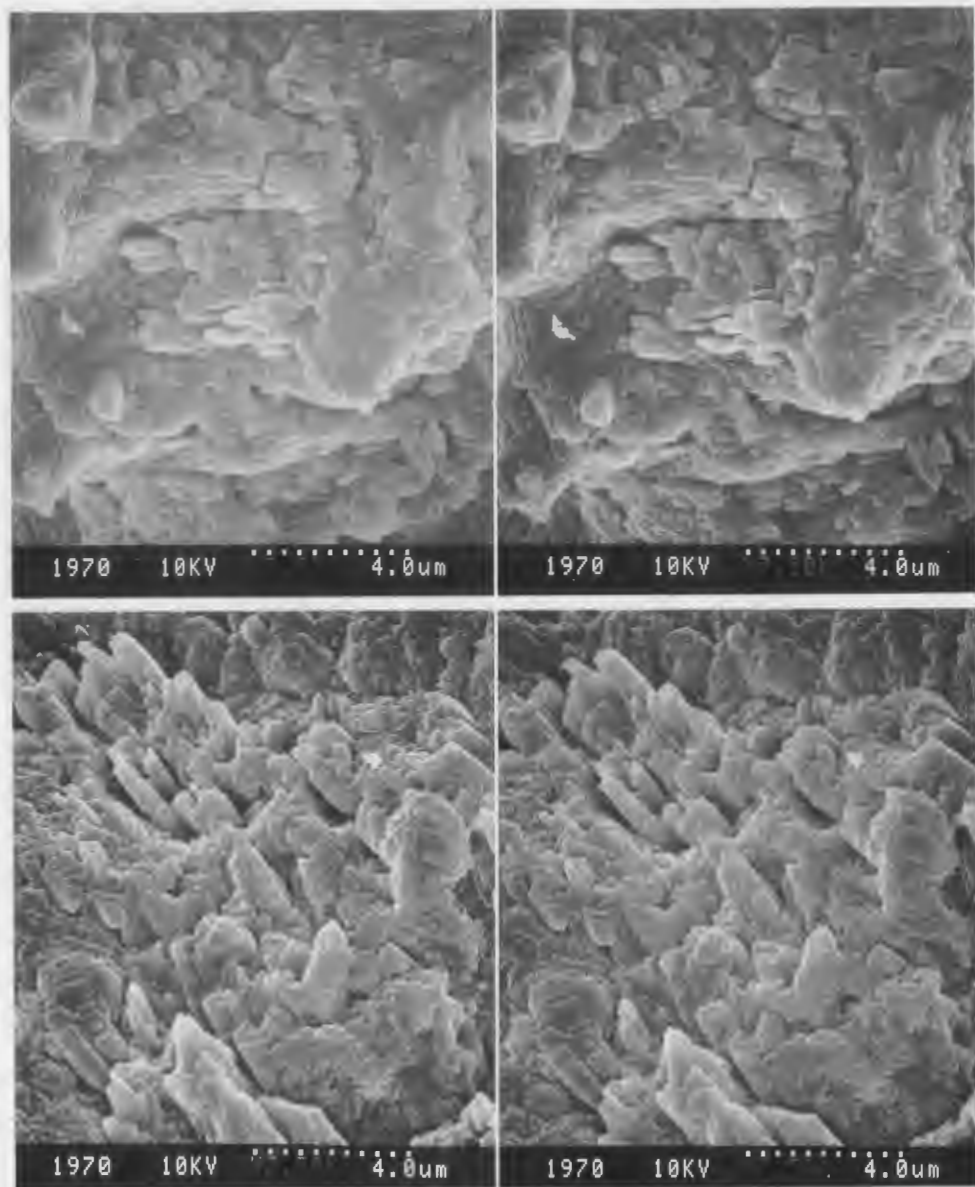


Figure 44. *Epiphaxum breve* n. sp., colony no. 2. Top, Aragonite crystals overlying calcitic sclerite. Bottom, Fascicles of aragonite crystals projecting from subhedral micrite "cement," on outer surface of calyx near sclerite. Scale bars = 4  $\mu$ m. Stereoscopic pairs.

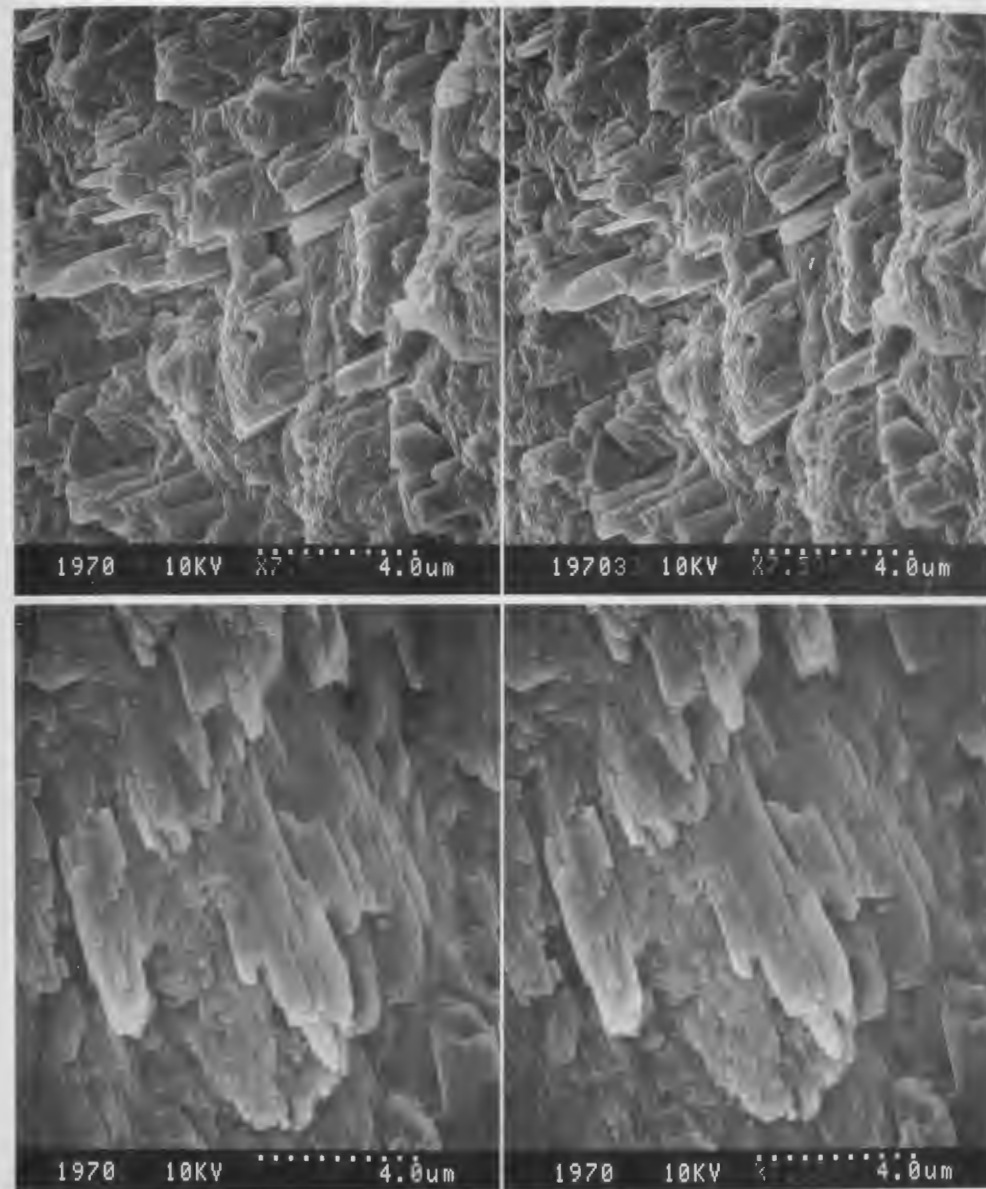


Figure 45. *Epiphaxum breve* n. sp. (specimen no. 2). Fascicles of lath-like aragonite crystals projecting from "cement" comprised of smaller subhedral units; calicular surface. Stereoscopic pairs.

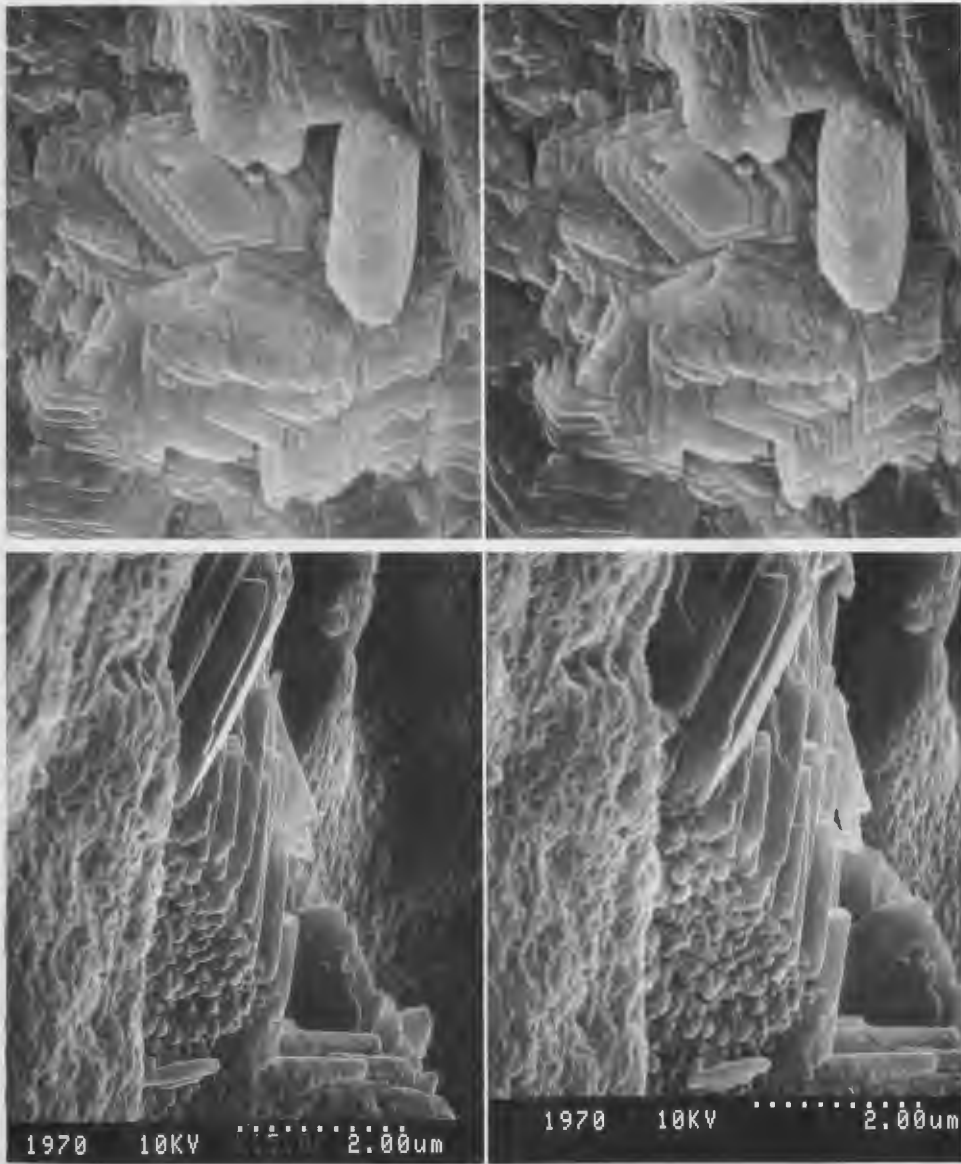


Figure 46. *Epiphaxum breve* n. sp., colony no. 2. Top, Pseudo-hexagonal euhedral crystals of aragonite exposed at unbroken surface of stolon near tip. Bottom, Euhedral prisms of aragonite at surface of stolon near tip. Scale bars = 2  $\mu$ m. Stereoscopic pairs.

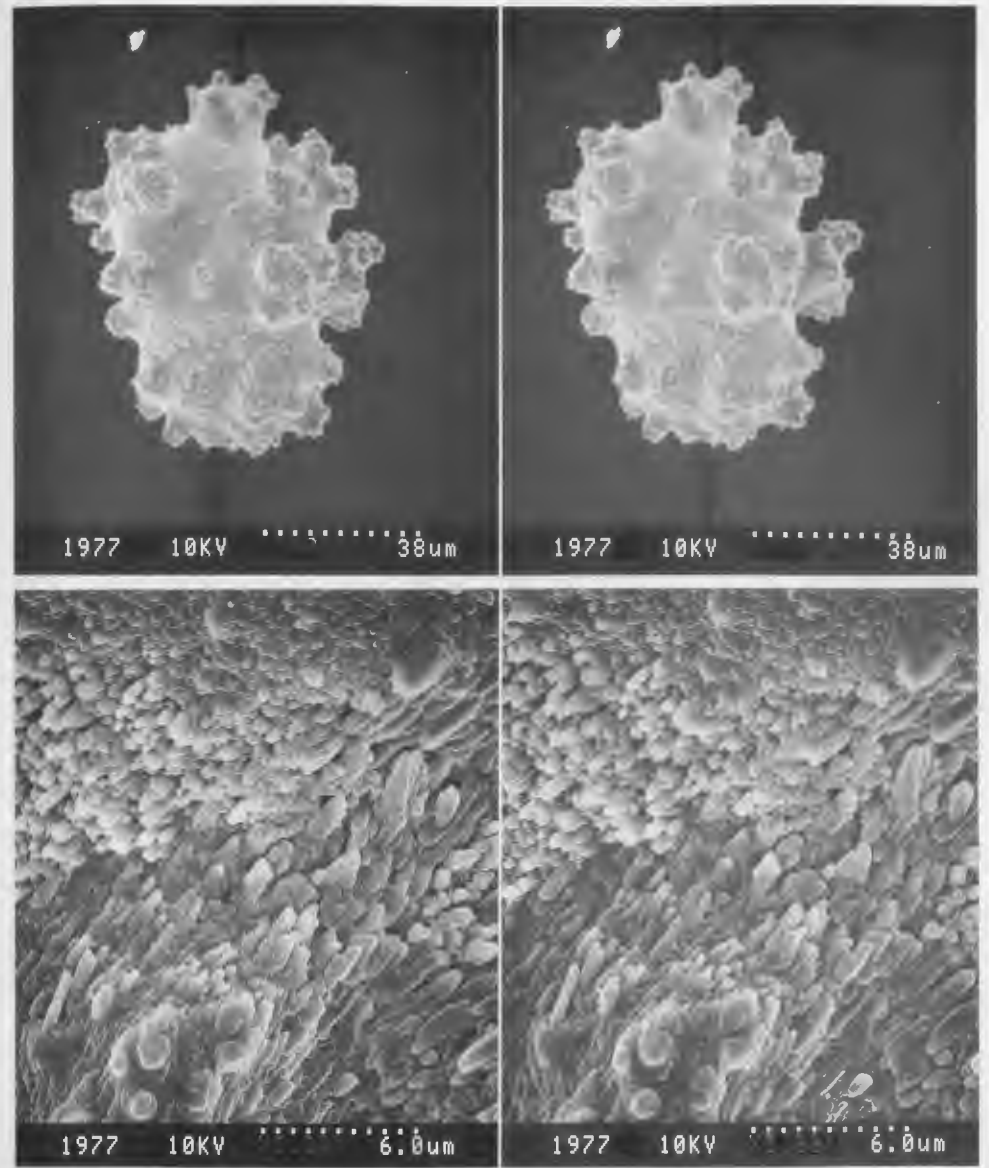


Figure 47. *Epiphaxum breve* n. sp. (specimen no. 2). Top, isolated sclerite; scale = 38  $\mu$ m. Bottom, Anhedral calcite crystals of same; scale = 6  $\mu$ m. Stereoscopic pairs.

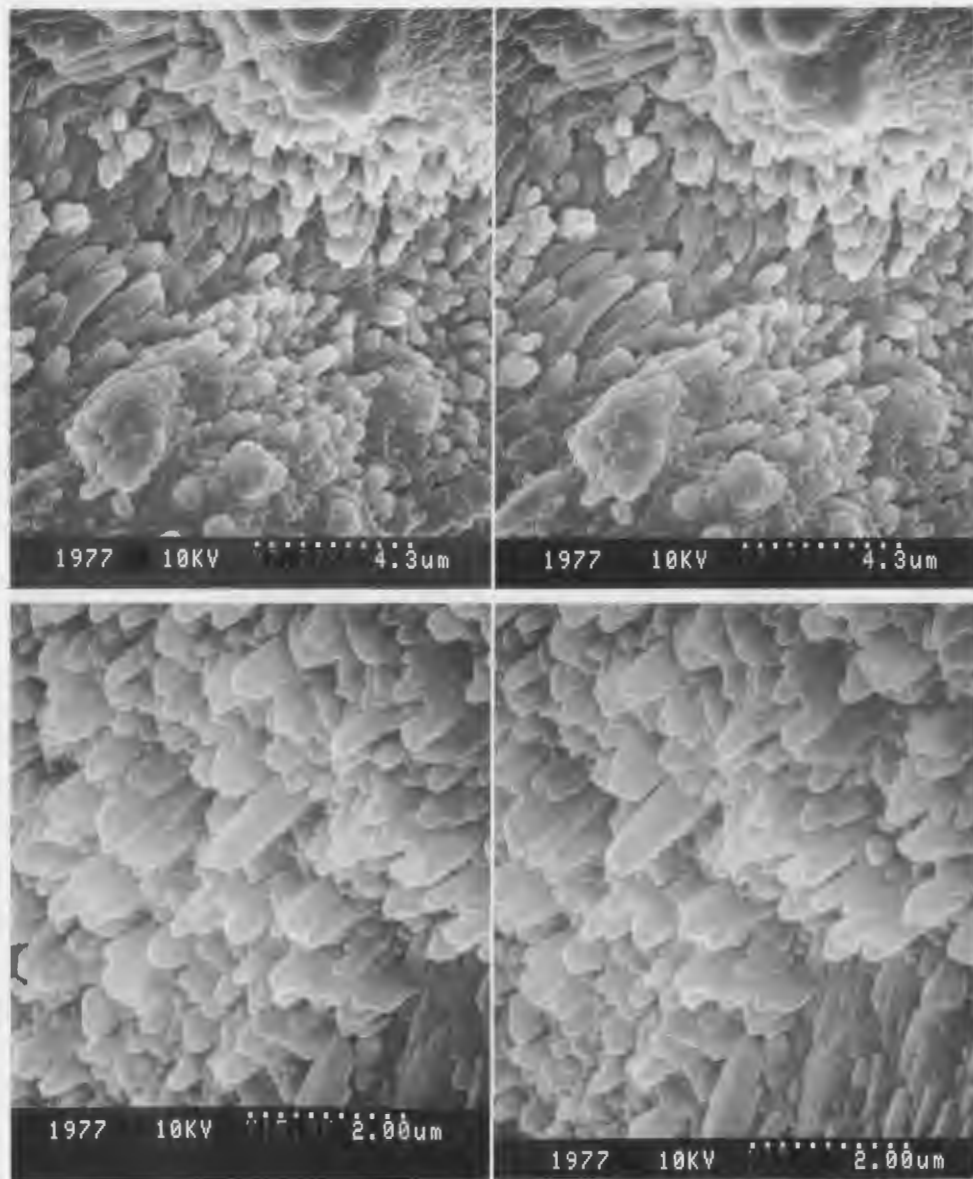


Figure 48. Sclerite of *Epiphaxum breve* n. sp. (specimen no. 2). Anhedronal calcite crystals.

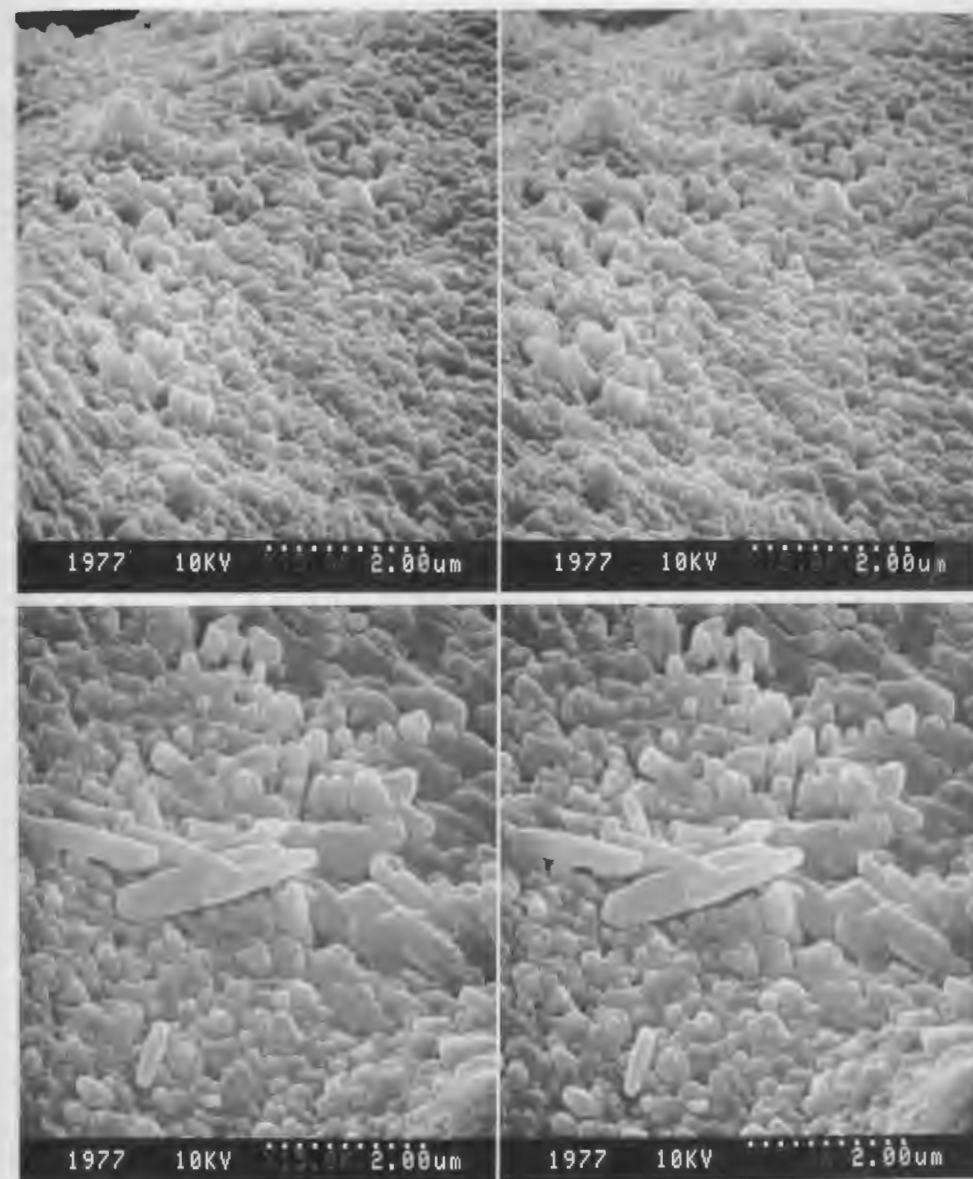


Figure 49. Sclerite of *Epiphaxum breve* n. sp. (specimen no. 2). Top, c-axes of anhedronal calcite crystals projecting at surface. Bottom, Anhedronal rods of calcite partially incorporated in sclerite mass. Scales = 2 μm.

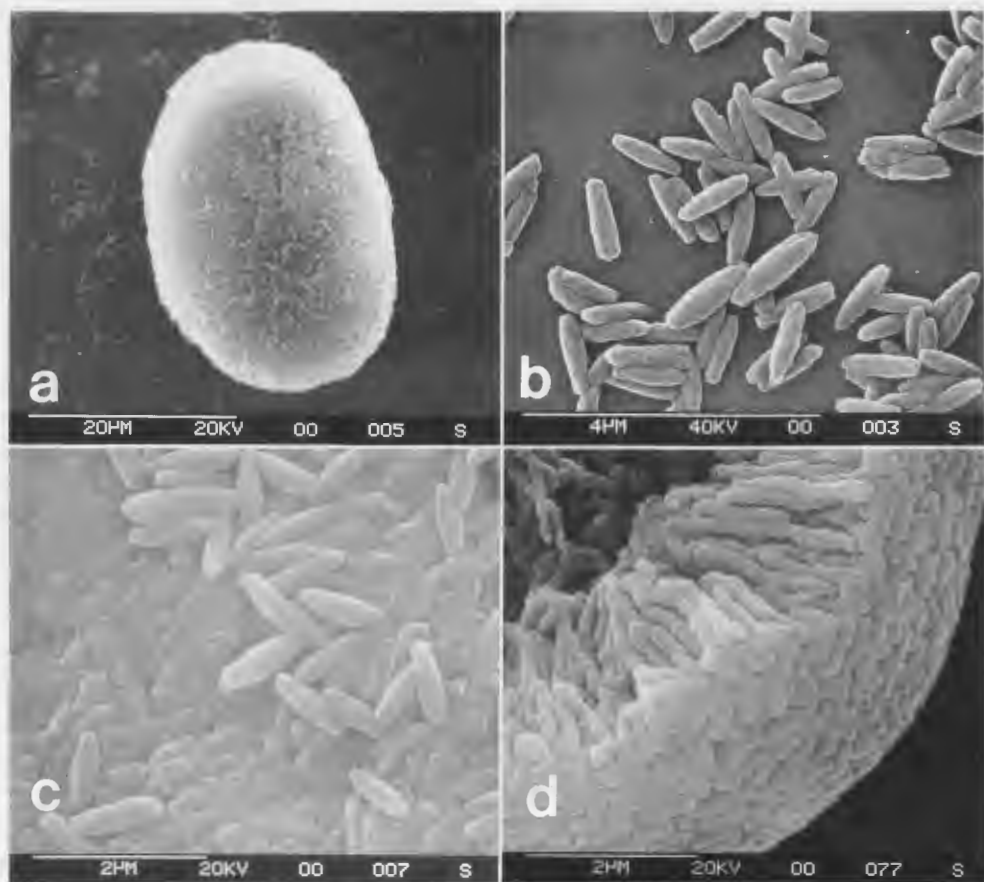


Figure 50. Comparative microstructure of sclerites. *Eflatounaria* sp. (Alcyonacea, Xeniidae): a, Isolated sclerite; scale bar = 20  $\mu\text{m}$ . b, Anhedral calcite rods before incorporation in sclerite mass; scale bar = 4  $\mu\text{m}$ . c, Surface of sclerite with calcite rods in various stages of incorporation; scale bar = 2  $\mu\text{m}$ . d, *Xenia* sp. (Alcyonacea, Xeniidae): Broken sclerite showing dendritic rods of calcite; scale bar = 2  $\mu\text{m}$ .

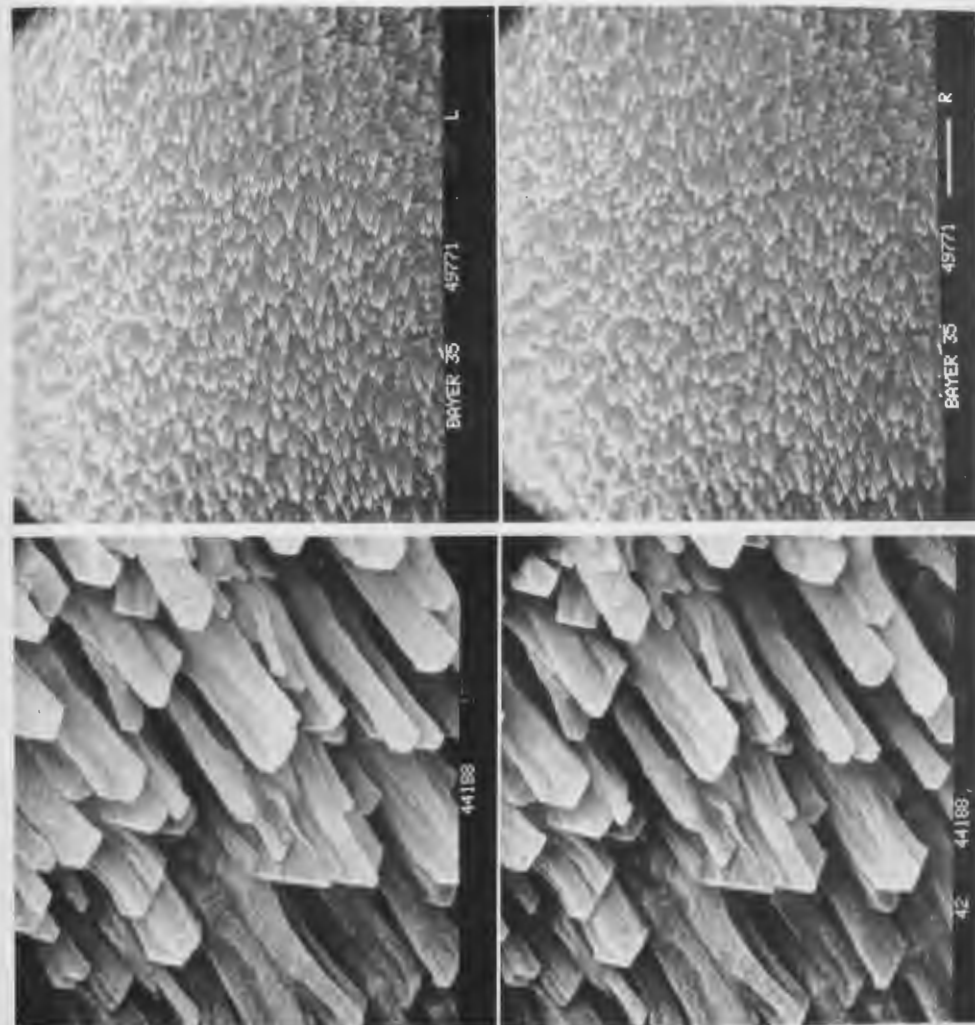


Figure 51. Comparative microstructure of sclerites. Top, *Corallium rubrum* (Scleraxonia, Coralliidae): dentate calcite. Bottom, *Muricea muricata* (Holaxonia, Plexauridae): trigonal prisms of calcite. 1  $\mu\text{m}$  scale bar applies to both figures. Stereoscopic pairs.

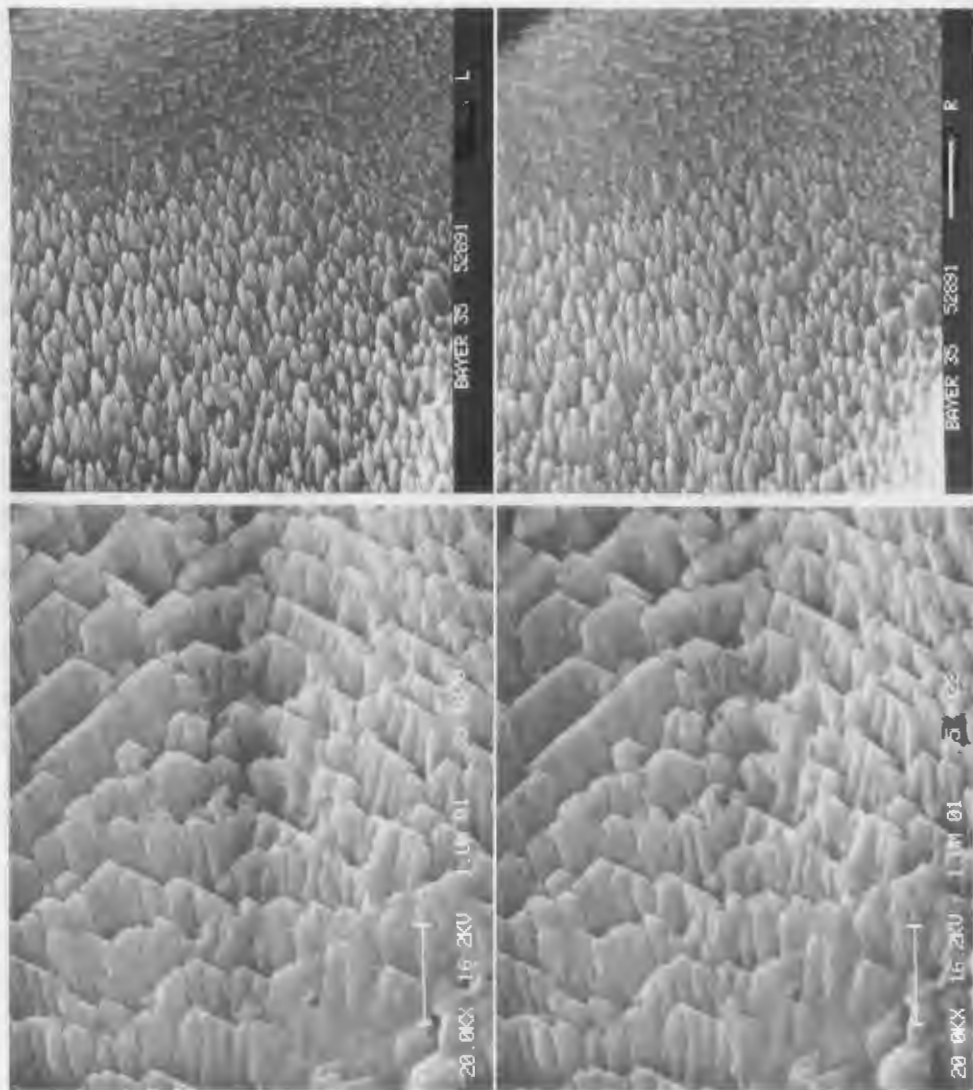


Figure 52. Comparative microstructure of sclerites. Top, *Paragorgia johnsoni* Gray (Scleraxonia, Paragorgiidae): dentate calcite. Bottom, *Mopsella aurantia* (Esper) (Scleraxonia, Melithaeidae): geometrically organized calcite rods forming imbricating plates. Scale bars = 1  $\mu$ m. Stereoscopic pairs.

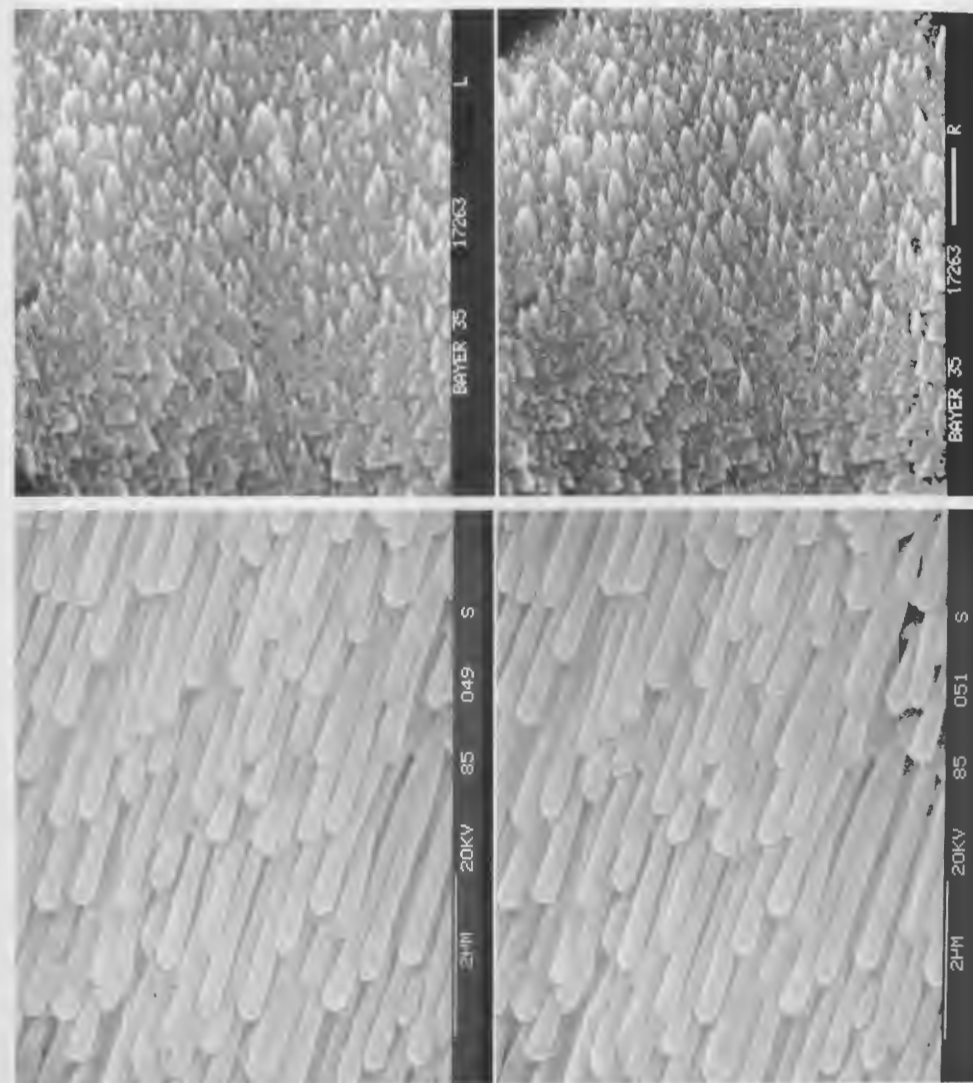


Figure 53. Comparative microstructure of sclerites. Top, *Paragorgia arborea* (Linnaeus) (Scleraxonia, Paragorgiidae): dentate calcite; scale bar = 1  $\mu$ m. Bottom, *Xenogorgia sciurus* Bayer and Muzik (Holaxonia, Chrysogorgiidae): subhedral calcite rods; scale bar = 2  $\mu$ m. Stereoscopic pairs.

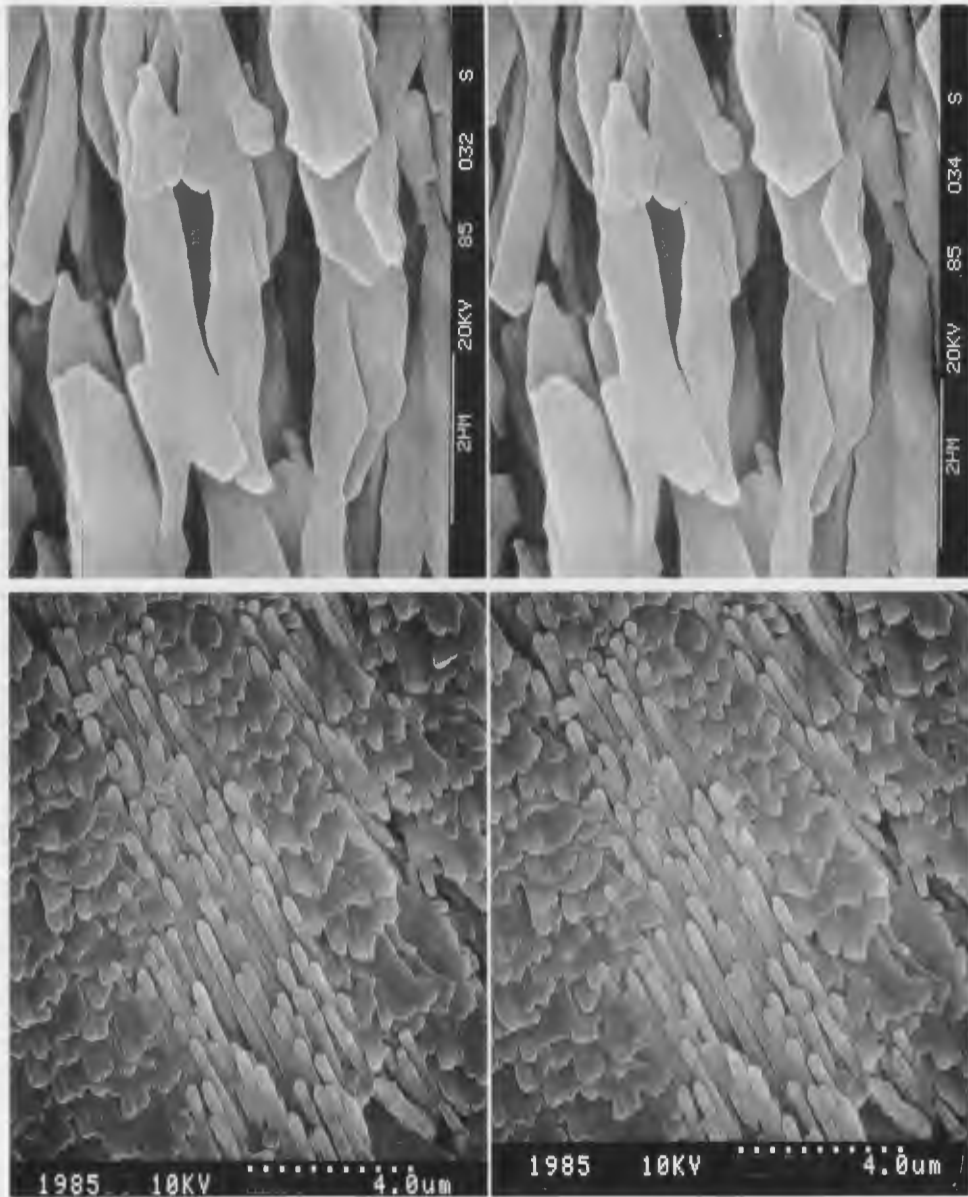


Figure 54. Comparative microstructure of sclerites. *Xenogorgia sciurus* Bayer and Muzik, USNM 54424 (Holaxonia, Chrysogorgiidae). Top, Euhedral calcite laths; scale bar = 2  $\mu\text{m}$ . Bottom, Subhedral rods and foliate laths growing in opposite directions. Stereoscopic pairs, scale bars = 4  $\mu\text{m}$ .

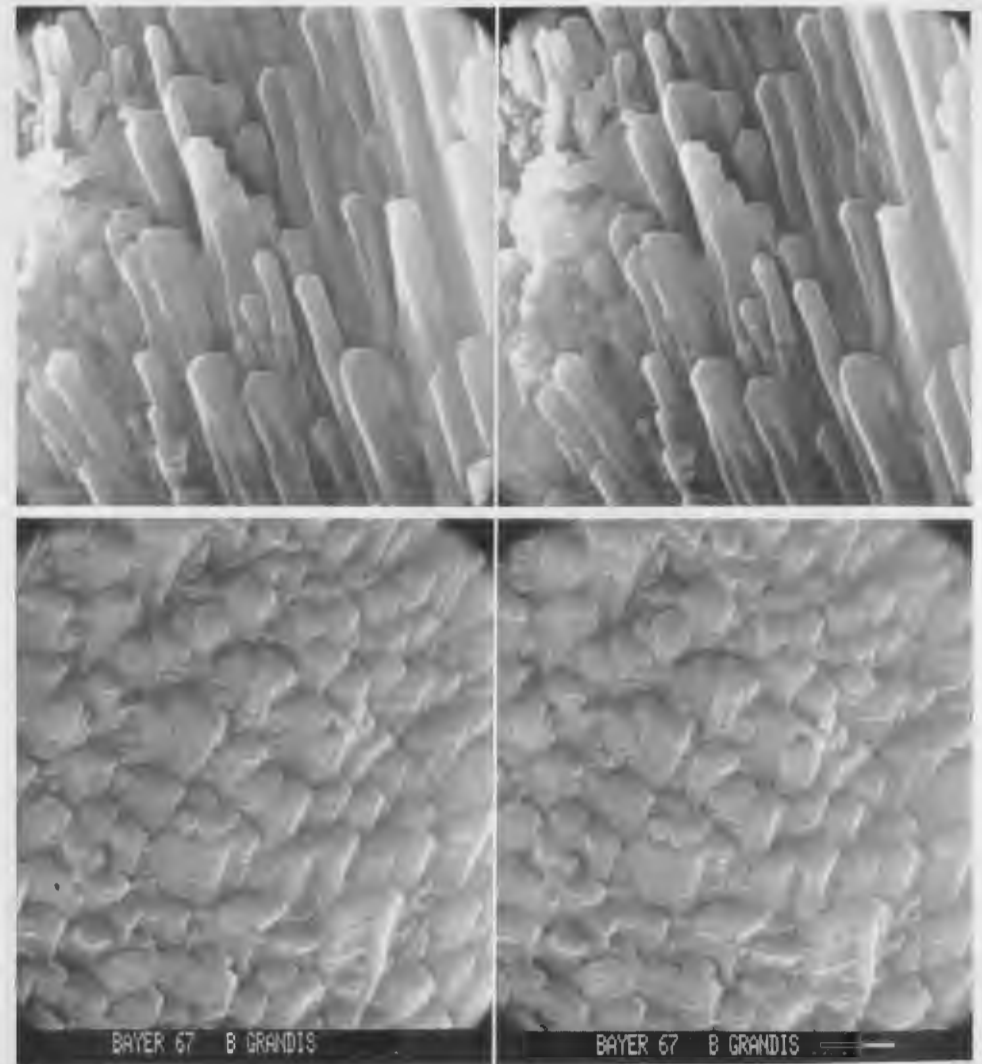


Figure 55. Comparative microstructure of sclerites. *Bebruce grandis* Deichmann (Holaxonia, Paramuriceidae): rosette sclerite from outermost cortex. Top, Subhedral calcite rods with c-axis nearly parallel with surface, from distal end of sclerite. Bottom, Calcite rods with c-axis almost normal to surface, from proximal end of sclerite. Scale bar = 1  $\mu\text{m}$ . Stereoscopic pairs.

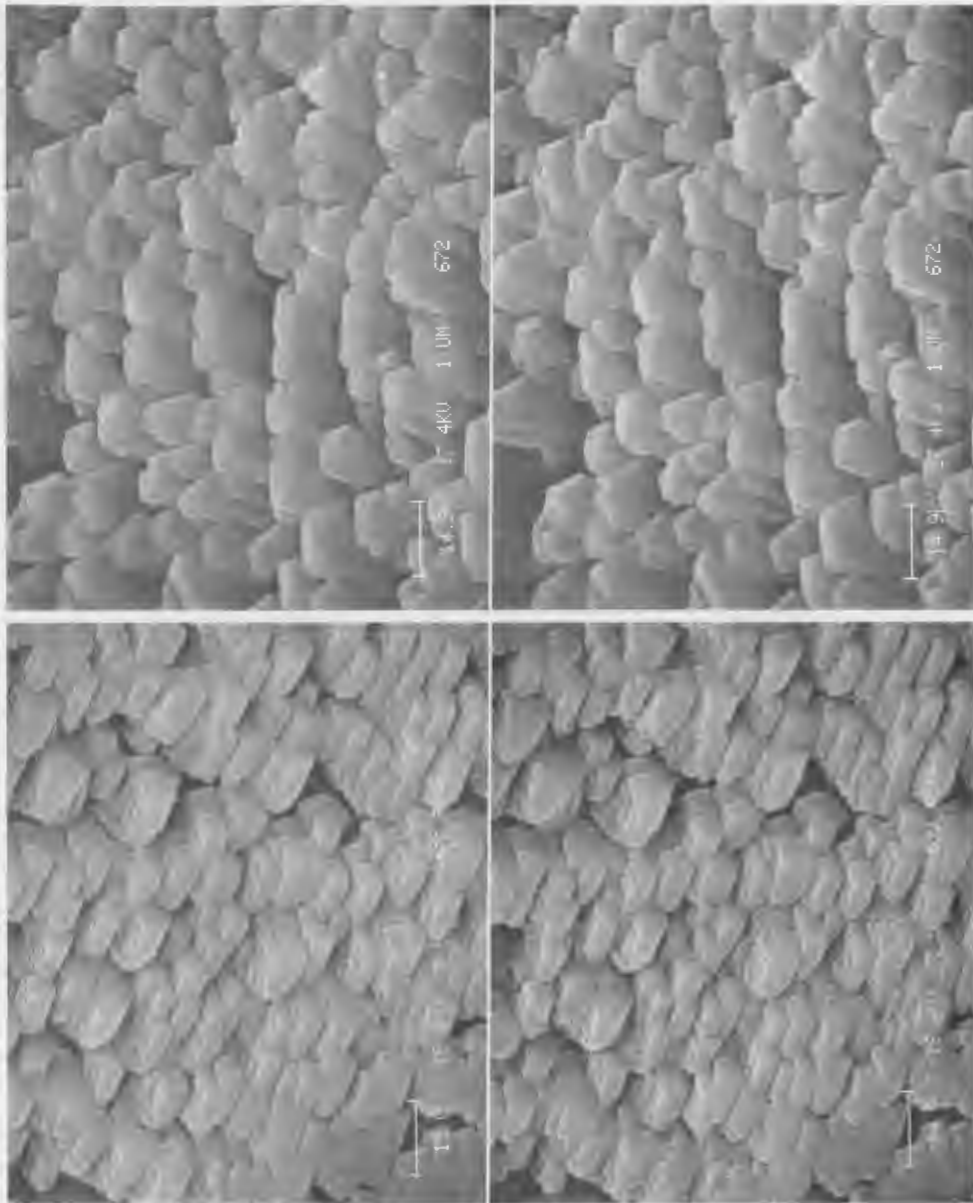


Figure 56. Comparative microstructure of sclerites. Top, *Acabaria* sp. (Scleraxonia, Melithaeidae). Bottom, *Parisis fruticosa* Verrill (Scleraxonia, Parisididae). Scale bars = 1  $\mu$ m. Stereoscopic pairs.

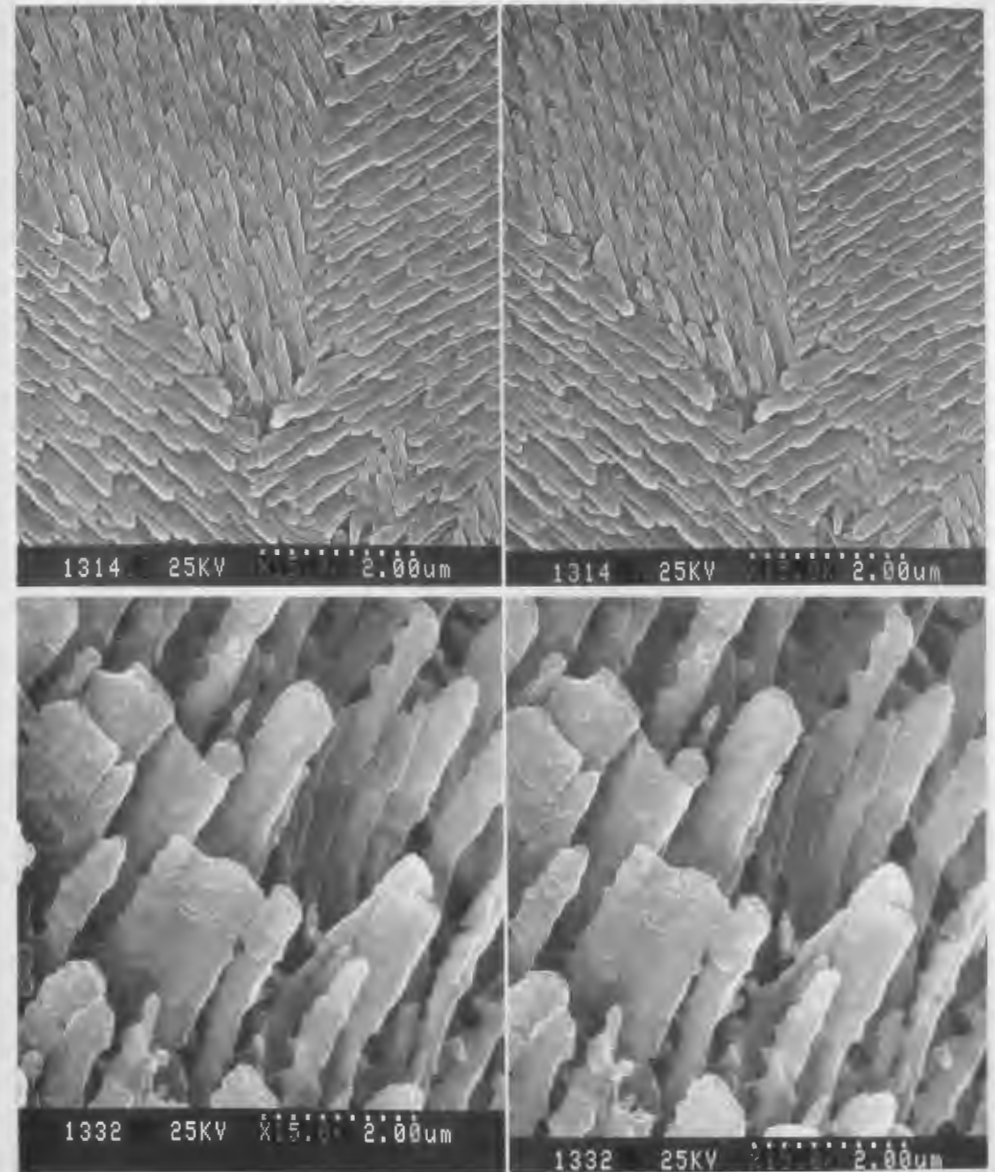


Figure 57. Comparative microstructure of sclerites. Top, *Clavularia modesta* Verrill (Stolonifera, Clavulariidae): cross-lamellar calcite laths and rods. Bottom, *Paralcyonium elegans* (Milne-Edwards) (Alcyonacea, Maasellidae): irregular calcite rods. Scales = 2  $\mu$ m. Stereoscopic pairs.



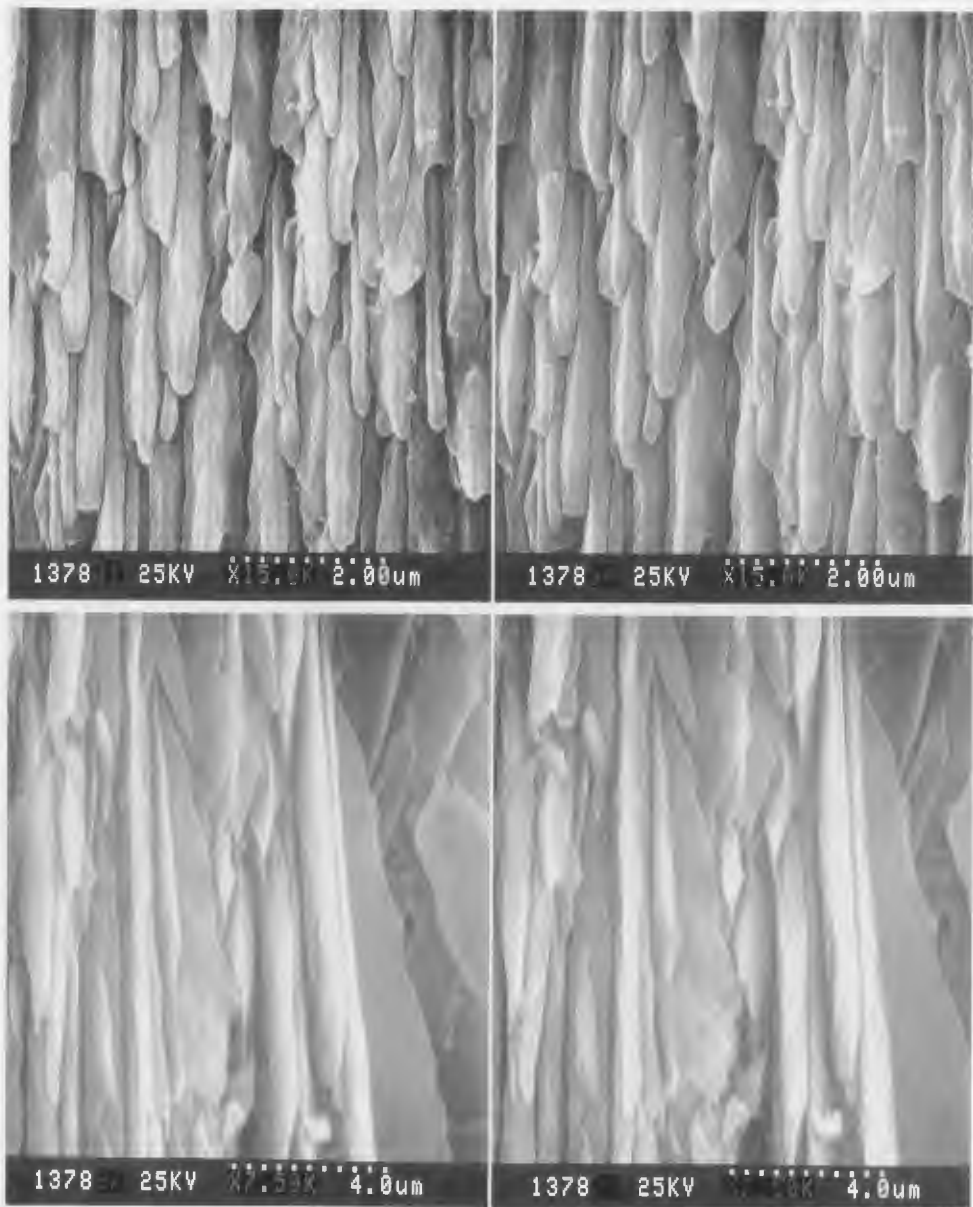


Figure 58. Comparative microstructure of sclerites. *Isidella trichotoma* Bayer (Holaxonia, Isidiidae). Top, Trigonal prismatic calcite rods; scale bar = 2  $\mu$ m. Bottom, Foliate calcite rods; scale bar = 4  $\mu$ m. Stereoscopic pairs.

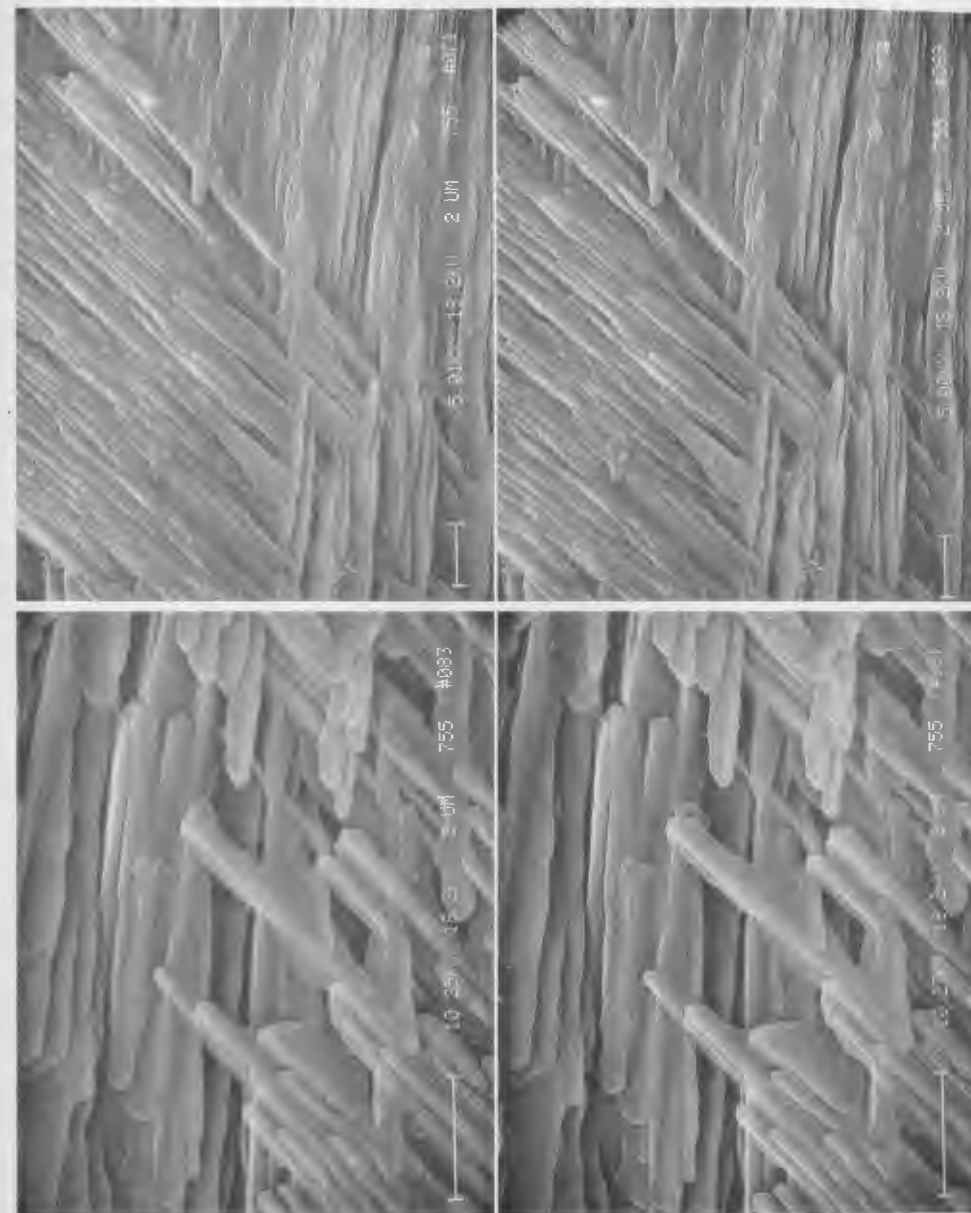


Figure 59. Comparative microstructure of sclerites. *Lepidisis evelinae* Bayer (Holaxonia, Isidiidae). Trigonal calcite prisms crossing at 60°. Scale bars = 2  $\mu$ m. Stereoscopic pairs.

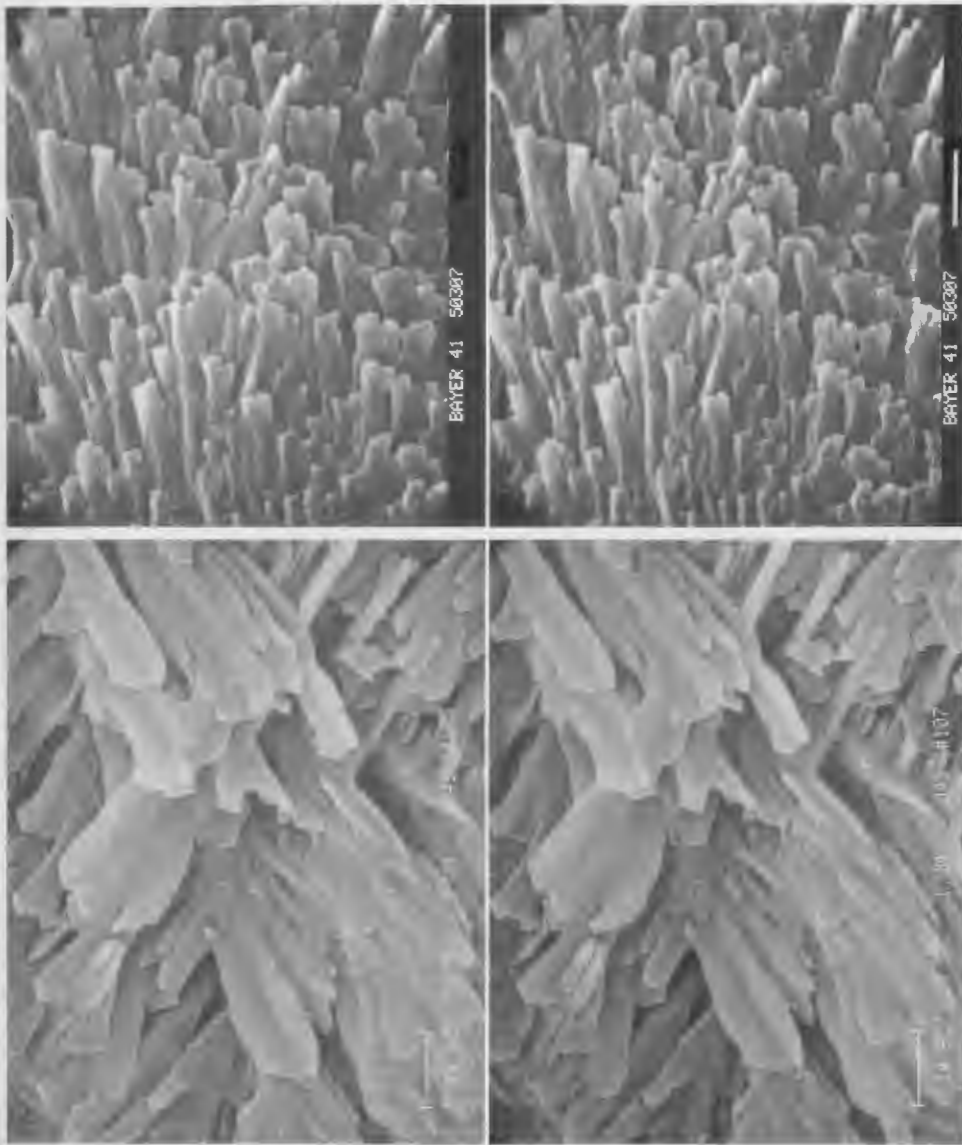


Figure 60. Comparative microstructure of sclerites. Top, *Plexaura homomalla* (Esper) (Holaxonia, Plexauridae): foliate calcite laths. Bottom, *Chrysogorgia flavescens* Nutting (Holaxonia, Chrysogorgiidae): trigonal blade-like laths. Scale bars = 1  $\mu$ m. Stereoscopic pairs.

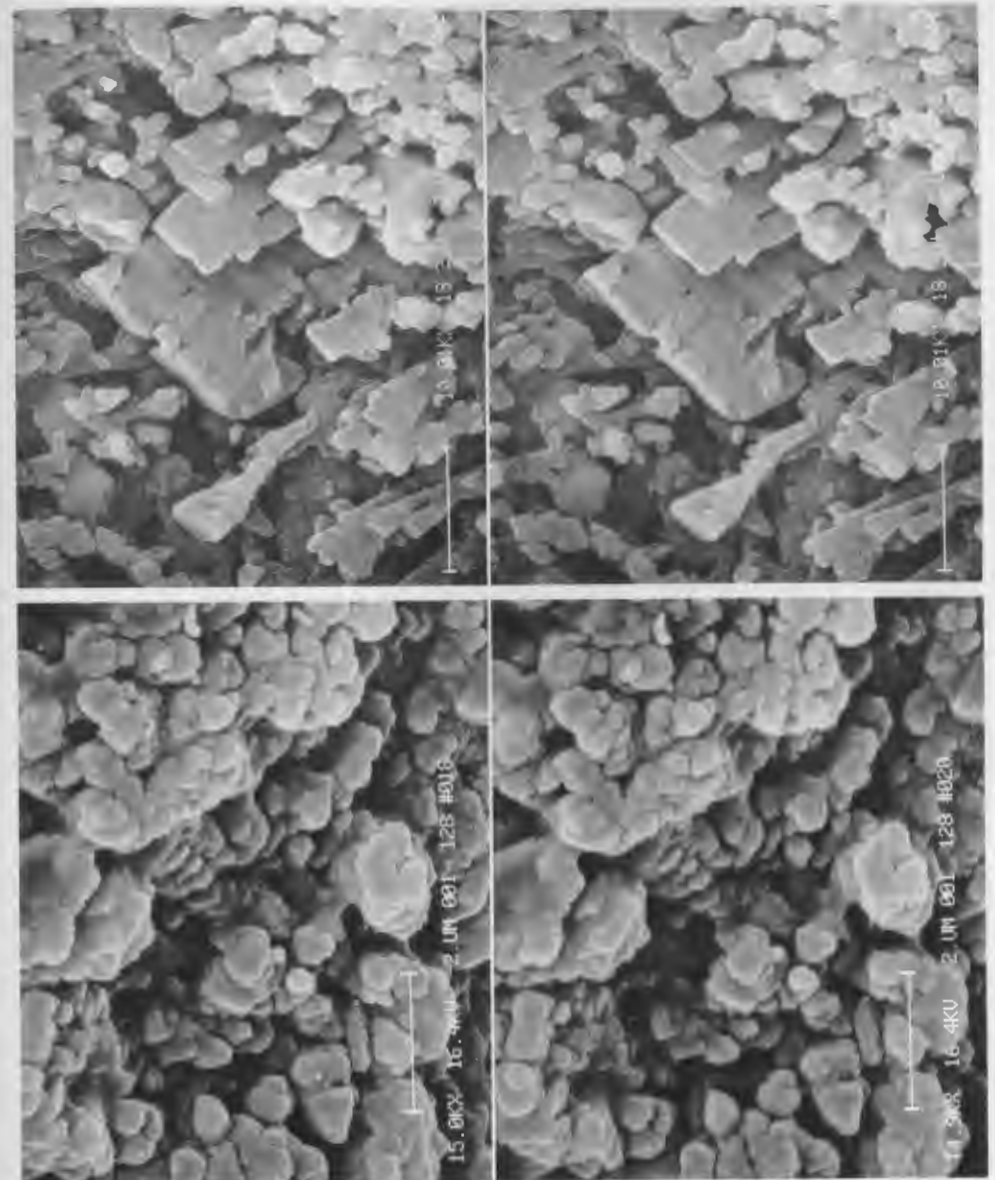


Figure 61. Comparative microstructure of sclerites. Top, *Plumigorgia hydroides* Nutting (Holaxonia, Ifalukellidae). Bottom, *Scleranthelia rugosa* Studer (Stolonifera, Clavulariidae). Scale bars = 2  $\mu$ m. Stereoscopic pairs.

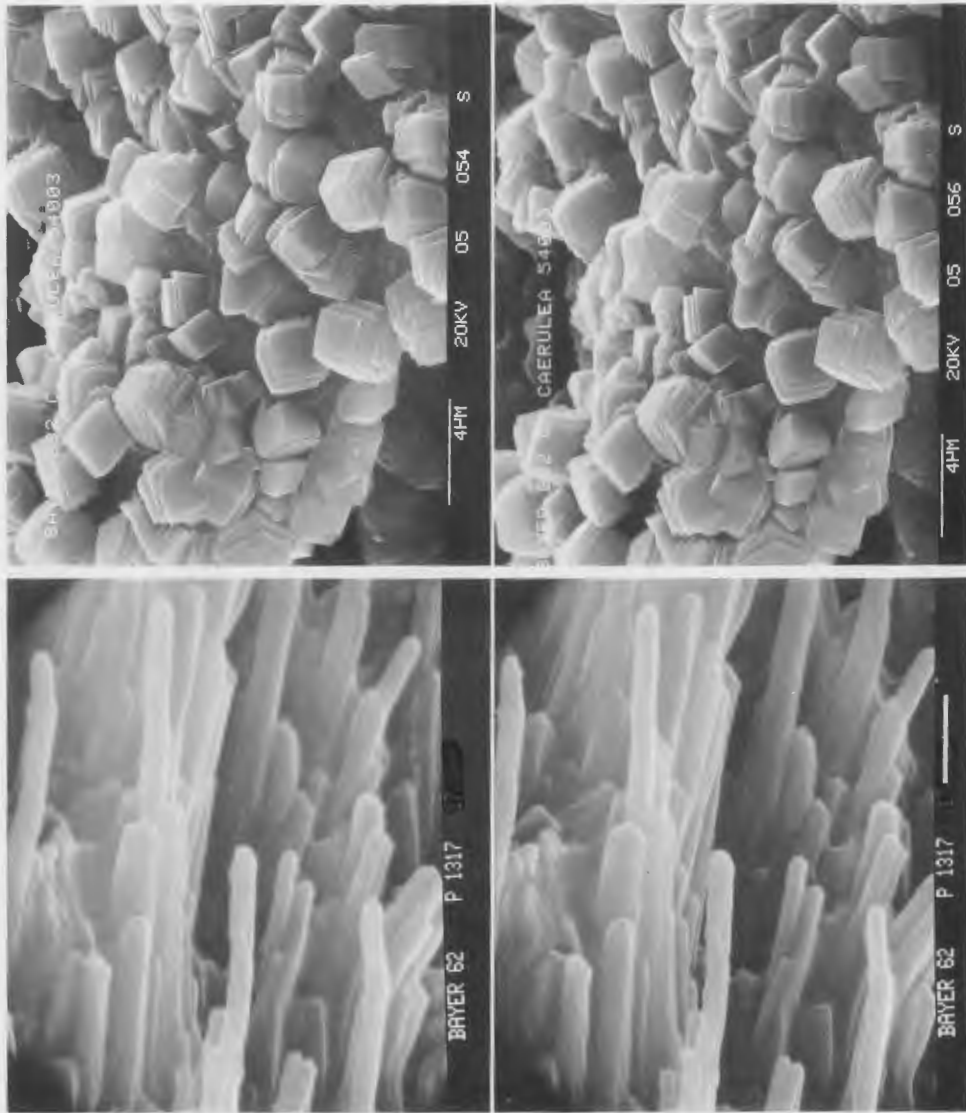


Figure 62. Comparative microstructure of sclerites. Top, Rhomboidal calcite of *Cespitularia caerulea* (Ehrenberg) (Alcyonacea, Xeniidae); scale bar = 4 µm. Bottom, Subhedral rods of *Lytrea plana* (Deichmann) (Holaxonia, Paramuriceidae); scale bar = 1 µm. Stereoscopic pairs.