

The mineral component of the axis and holdfast of some gorgonacean octocorals (Coelenterata: Anthozoa), with special reference to the family Gorgoniidae

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Abstract.—This is the first detailed investigation of the mineral component of axes and holdfasts of Gorgonacea, including 58 species belonging to 5 families and 21 genera of Holaxonia and 4 families and 13 genera of Calcaxonia. X-ray diffraction, electron probe, and scanning electron microscope analyses indicated that aragonite or Mg-calcite occurred in most axes and holdfasts of 6 families. In marked contrast, amorphous carbonate hydroxylapatite occurred solely in the family Gorgoniidae, which in some species also had Mg-calcite or aragonite in holdfasts. These skeletal minerals appear to be taxonomically controlled. The distinctive morphology of carbonate hydroxylapatite in Gorgoniidae is illustrated by scanning electron micrographs.

Early studies of gorgonian corals provide only a smattering of information on their chemical composition, all but ignoring their mineral content (Cook 1904; Clarke & Wheeler 1915, 1917). As far as known, sclerites of all octocorals are composed of Mg-calcite (Chave 1954, Lowenstam 1964, Milliman 1974). Lowenstam (1964:379) documented the co-occurrence of calcite and aragonite in Octocorallia and discussed the possible relationship of skeletal mineralogy to temperature of the environment. More recently, Kingsley & Watabe (1982: 325, 337, 338) reported "amorphous calcium material" in the axis of *Leptogorgia virgulata* but ruled out calcium phosphate owing to insufficient amounts of phosphorous; and Lewis et al. (1992:283) described amorphous carbonate in *Leptogorgia virgulata*, *Lophogorgia cardinalis*, *Gorgonia ventalina*, and *Plexaura flexuosa*. In addition, Jeyasuria & Lewis (1987:218) reported that some gorgonians contain as much as 85.36 mole% of MgCO₃.

To obtain a broader view of the mineral content of the axial skeleton of gorgonians,

Macintyre et al. (2000) examined 51 samples of Gorgonacea belonging to 47 species in 28 genera and 6 families of the orders Holaxonia and Calcaxonia. Any mineral present in the axes and holdfasts of the holaxonian families Keroeididae, Acanthogorgiidae, Paramuriceidae and Plexauridae, and the calcaxonian families Ellisellidae, Chrysogorgiidae, Ifalukellidae, and Primnoidae was either Mg-calcite or aragonite; no phosphorous was detected by X-ray microprobe energy dispersive scans. The axes of Isididae and all families of Scleraxonia were not considered in that study as they are known to consist of Mg-calcite sclerites or crystalline calcite.

Macintyre et al. (2000) also observed mineralization in the axes and holdfasts of the genera *Eugorgia*, *Gorgonia*, *Leptogorgia*, *Pacifigorgia*, *Phycogorgia*, *Phyllogorgia*, and *Pseudopterogorgia*. In some cases it was extensive, in others weak, and was detected by X-ray diffraction only in *Leptogorgia setacea* and *L. stheno*, which yielded weak patterns consistent with dahll-

ite as the authors reported for mammoth teeth.

Analysis by electron microprobe showed that this "amorphous" mineral is carbonate hydroxylapatite $\text{Ca}_5(\text{PO}_4)_3(\text{OH})$ (Gaines et al. 1997), hereafter abbreviated CHAp; see Macintyre et al. (2000).

No CHAp was found in the axis and holdfast of the gorgoniid genera *Eunicella*, *Rumphella* and *Pterogorgia*, and a single species of *Leptogorgia* (*L. caryi*). The axis of *Olindagorgia marcgravii* and *Pseudopterogorgia bipinnata* contained CHAp, but the holdfast was strengthened with crystalline aragonite. No mineral was detected in the axis or holdfast of *Eunicella*. Although the axis of *Rumphella* and *Pterogorgia* yielded no mineral, the holdfast was strongly reinforced with crystalline CaCO_3 .

This paper presents scanning electron micrographs of axis and holdfast morphology in representative species of Gorgoniidae to demonstrate the consistency of mineralization by CHAp in this widespread family of Gorgonacea.

Materials and Methods

All specimens examined during this investigation (Table 1) are preserved in the permanent research collections of the U.S. National Museum of Natural History, Smithsonian Institution. Some of the specimens were originally dried upon collection and have been maintained in that condition; others were preserved in alcohol and are stored in 70% ethanol.

Portions from terminal branches of the upright axis were stripped of all coenenchyme. Some pieces were split to expose the axial core, others subjected to prolonged (12–48 hours) maceration in 5.25% sodium hypochlorite solution (common household bleach). Any inorganic skeleton was thoroughly washed, affixed to 10-mm glass coverslips and mounted on aluminum stubs for examination by SEM.

Small samples were clipped from the edge of holdfasts or were peeled from the

substrate to eliminate contamination. After maceration in sodium hypochlorite solution, the inorganic residue was repeatedly washed in distilled water to remove salt. A simple pipette was used to drop suspensions of residue either on clean 10-mm glass coverslips for attachment to standard SEM stubs, or on small Hitachi stubs covered with the adhesive film of "sticky tabs." Samples were then air dried.

Mineralogical analysis of samples was carried out by standard X-ray diffraction techniques (Goldsmith & Graf 1958, Milliman 1974) using a Scintag X-Ray Diffractometer with CuK_α radiation, a Peltier detector, and zero-background quartz mounting plates.

For electron probe analyses, samples were treated for removal of organic material, embedded in resin, sectioned, and carbon coated. The analyses of the amorphous carbonate hydroxylapatite, which generally was not recorded in X-ray diffractograms, were conducted with a 8900 JEOL electron microprobe (Macintyre et al. 2000).

In cases of heavily calcified holdfast that remained intact after prolonged maceration in sodium hypochlorite, some fragments were pulverized and subjected to analysis by X-ray diffraction as described above, while others were affixed with white glue to 10-mm glass coverslips for mounting on aluminum stubs for examination of fracture surfaces by SEM.

Preparations to be examined by SEM were pre-coated with carbon and sputter-coated with gold-palladium. Examination was done with a Hitachi Model S-570 scanning electron microscope at magnifications from 100× to 30,000× at 10kv accelerating voltage. Scatter preparations on glass coverslips were examined at working distances of 1–3 mm. Preparations on Hitachi stubs were viewed within the final lens of the microscope at working distances of –2 to –4 mm. Whole mounts of crystalline holdfast tissue were examined at working distances of about 15 mm. All images were recorded on Polaroid Type 52 positive film, in some

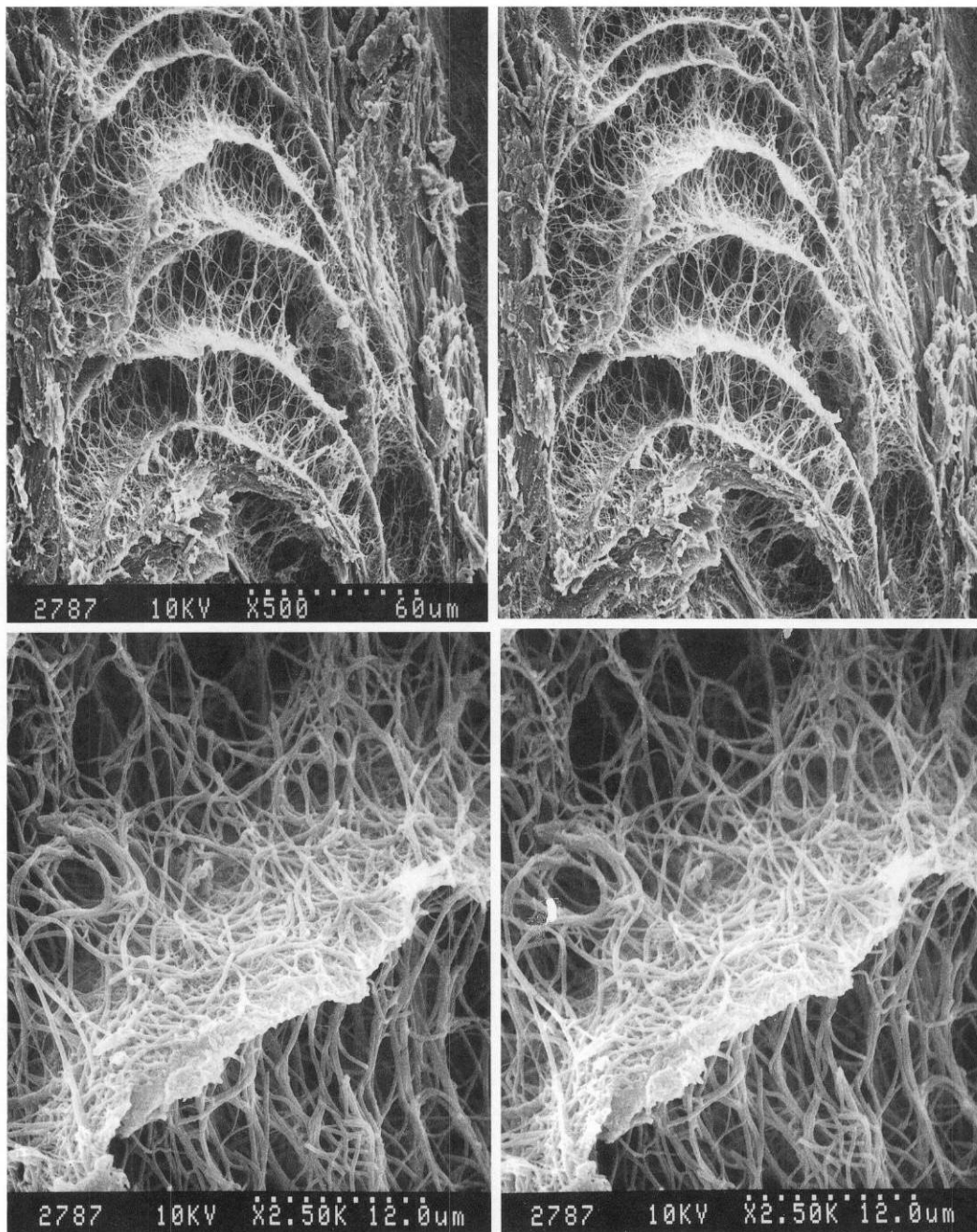


Fig. 1. Structure of non-mineralized gorgoniid axis. Top, longitudinal section of axial core of *Leptogorgia caryi* showing chambers; bottom, partition between chambers of core showing filamentous structure (SEM 2787—stereo pairs).

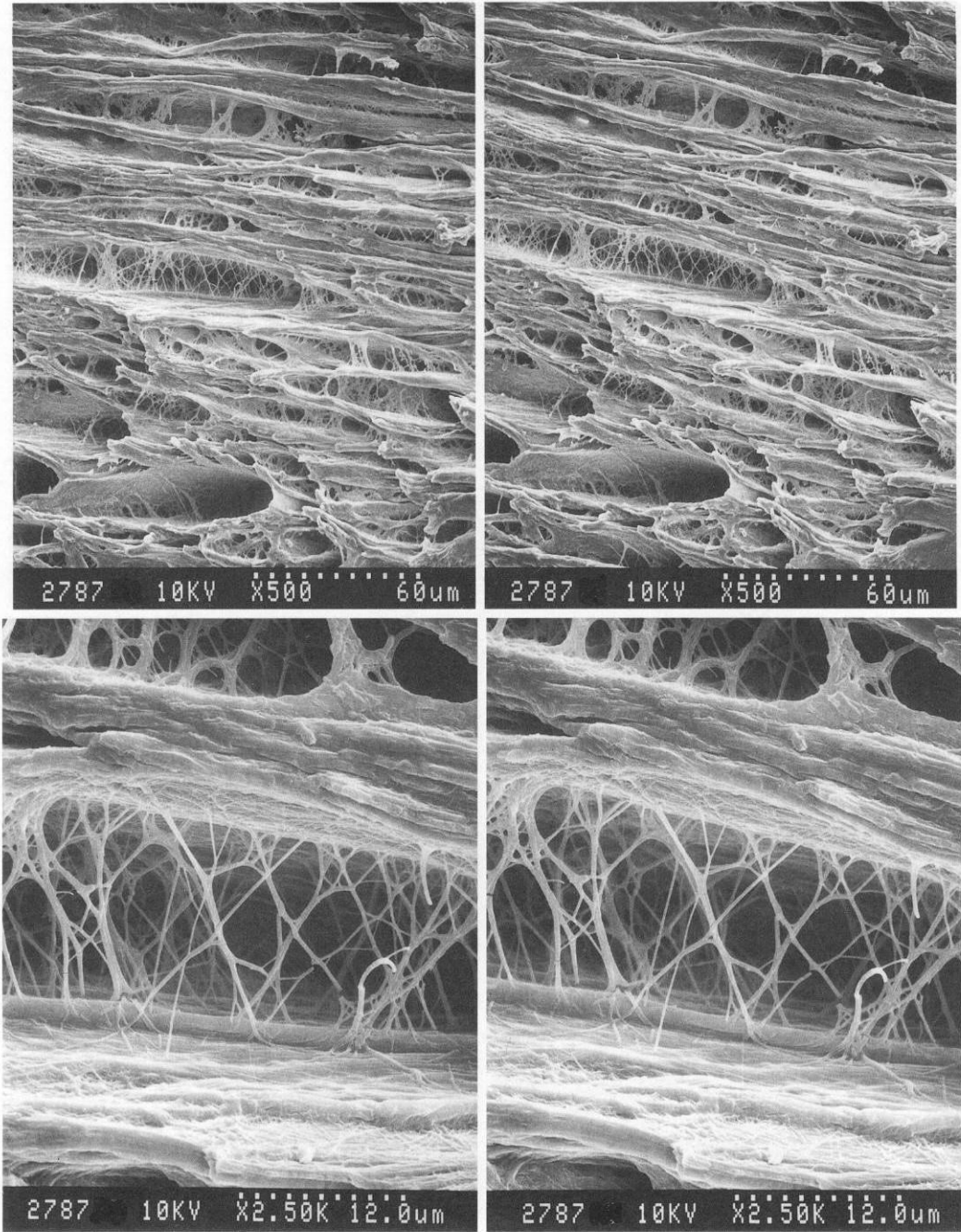


Fig. 2. Structure of non-mineralized gorgoniid holdfast: Top, section of holdfast of *Leptogorgia caryi* showing loculi between lamellae of gorgonin; bottom, part of holdfast locus and gorgonin filaments in lumen (SEM 2787—stereo pairs).

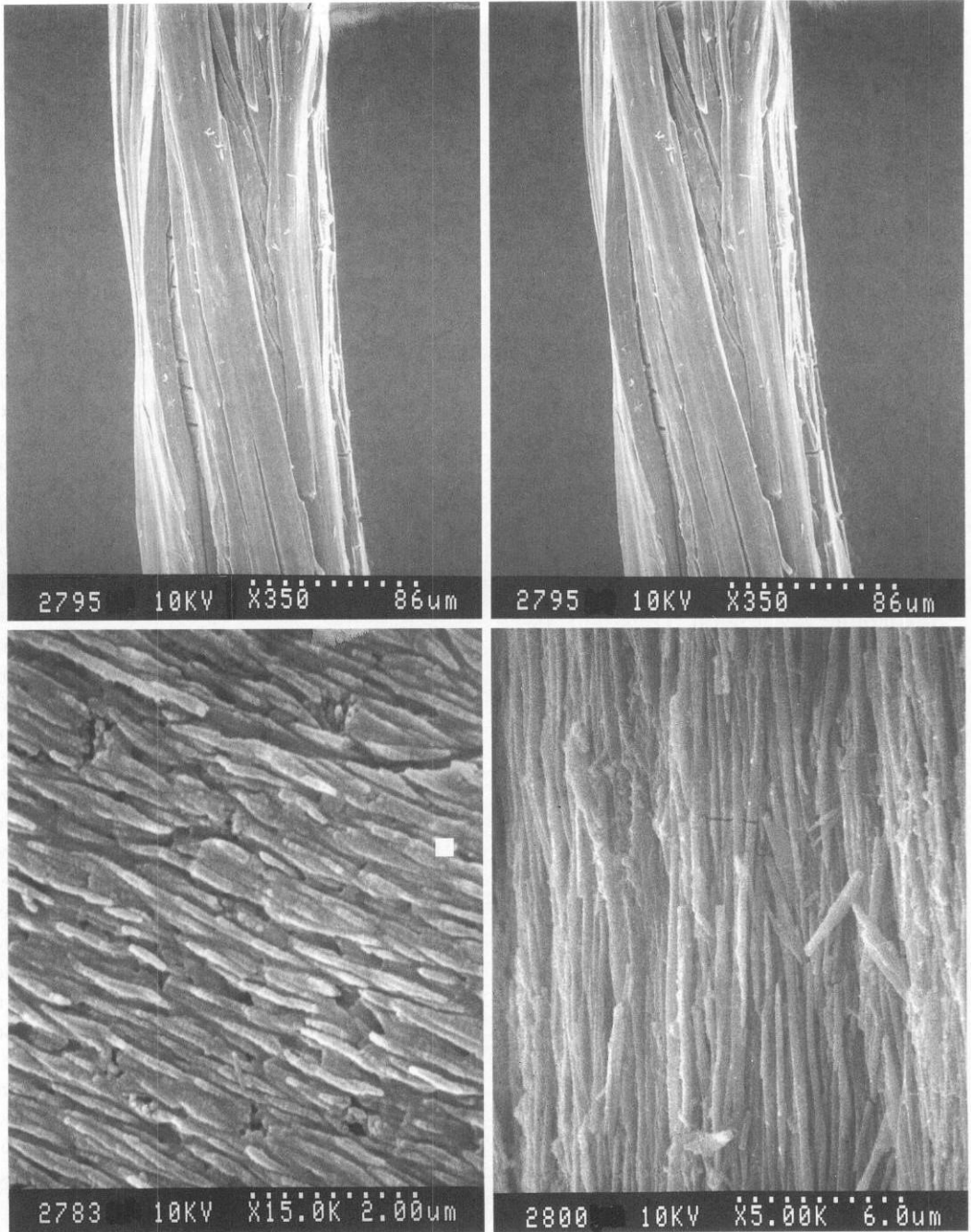


Fig. 3. Mineral component of gorgoniid axes. Top, axis of terminal branchlet of *Leptogorgia cardinalis* after removal of gorgonin by maceration in sodium hypochlorite, showing longitudinal strands of CHAp (SEM 2795—stereo pair); Bottom left, Surface of axis of *L. cardinalis* showing longitudinal fibers of CHAp (SEM 2783); Bottom right, Longitudinal break through axial cortex of *Leptogorgia stheno* showing longitudinal fibers of CHAp (SEM 2800).

cases accompanied by corresponding negatives on Kodak Tri X: film.

Axes and holdfasts of the following species in the family Gorgoniidae were examined in the present study:

Eugorgia ampla Verrill. USNM 8967 (SEM 2694, 2695, 2710, 2711, 2725, 2741, 2814). Taxonomic description: See Verrill 1869:407.

Eugorgia aurantiaca Verrill. Accession 166789 (SEM 2691, 2692); USNM 52317 (SEM 2696, 2697). Taxonomic description: See Verrill 1869:410.

Eugorgia rubens Verrill. USNM 50032 (SEM 2742–2747). Taxonomic description: See Verrill 1869:411.

Eunicella cavolini Koch. USNM 89285. Taxonomic description: Grasshoff 1992: 16. Axis not mineralized.

Eunicella filiformis Studer. USNM 82909. Taxonomic description: Grasshoff 1992: 43. Axis not mineralized; no holdfast, colonies recumbent, unattached.

Gorgonia flabellum Linnaeus. USNM 51766 (SEM 2843–2846, 2884). Taxonomic description: See Bayer 1961:259.

Gorgonia mariae Bayer. USNM 93965 (SEM 2698, 2699, 2748, 2749). Taxonomic description: See Bayer 1961:266.

Gorgonia ventalina Linnaeus. USNM 55027 (SEM 2828). See Bayer 1961:262. In establishing the two species of Caribbean sea fans, Linnaeus distinguished *G. ventalina* from *G. flabellum* because its branches are "a lateribus exterioribus compressis" rather than "versus ramulos compressis." Such distinctions can be seen among specimens of *Gorgonia*, but whether they are biological realities or merely the extremes of a morphological continuum remains to be determined.

Leptogorgia africana (Kükenthal). USNM 82884 (SEM 2840). Taxonomic description: See Grasshoff 1988:117.

Leptogorgia alba (Duchassaing & Michelotti), typical flabellate colony. USNM 49363 (SEM 2839, 2857, 2858). Taxonomic description: See Duchassaing &

Michelotti 1864:19, pl. 4, fig. 2; Hickson 1928:400.

Leptogorgia cardinalis (Bayer). USNM 50052 (SEM 2781); USNM 49711 (SEM 2782–2784). Taxonomic description: See Bayer 1961:201.

Leptogorgia caryi Verrill. USNM 57157 (2787, 2790). Taxonomic description: See Kükenthal 1913:266. Verrill (1869: 404) established the species *Leptogorgia caryi* for specimens that he previously (Verrill 1864:35) had identified as *Plexaura fucosa* (Valenciennes). Material consistent with Verrill's description was described as *Psammogorgia spauldingi* by Nutting (1909:721). Two other new species assigned to *Psammogorgia* by Nutting (1909:720, 721), *P. simplex* and *P. torreyi*, are referable to *Swiftia*, but *P. spauldingi* has more the appearance of *Leptogorgia* than of *Swiftia*. Kükenthal (1913:266) further contributed to this complex history by describing specimens undoubtedly of this species as *Euplexaura marki*, although it has very little in common with *Euplexaura*. Morphologically, it resembles other species of *Leptogorgia* and many other gorgoniids in the form of its sclerites and the structure of its axis and holdfast. Unlike other species of *Leptogorgia*, the axis of *L. caryi* is not mineralized. The chambers of the axis core and the locular spaces in the lamellae of the holdfast are filled with a meshwork of fine filaments, but these lack the spherulitic mineral deposits present in other genera and species of Gorgoniidae. The gorgonin of both axis and holdfast are completely dissolved by sodium hypochlorite, leaving no mineral residue.

Leptogorgia gilchristi (Hickson). USNM 59824 (SEM 2830, 2831). Taxonomic description: See Williams & Lindo 1997: 507.

Leptogorgia lemasti (Hickson). USNM 52730 (SEM 2819). Taxonomic description: See Hickson 1928:349; Stiasny 1941:266.

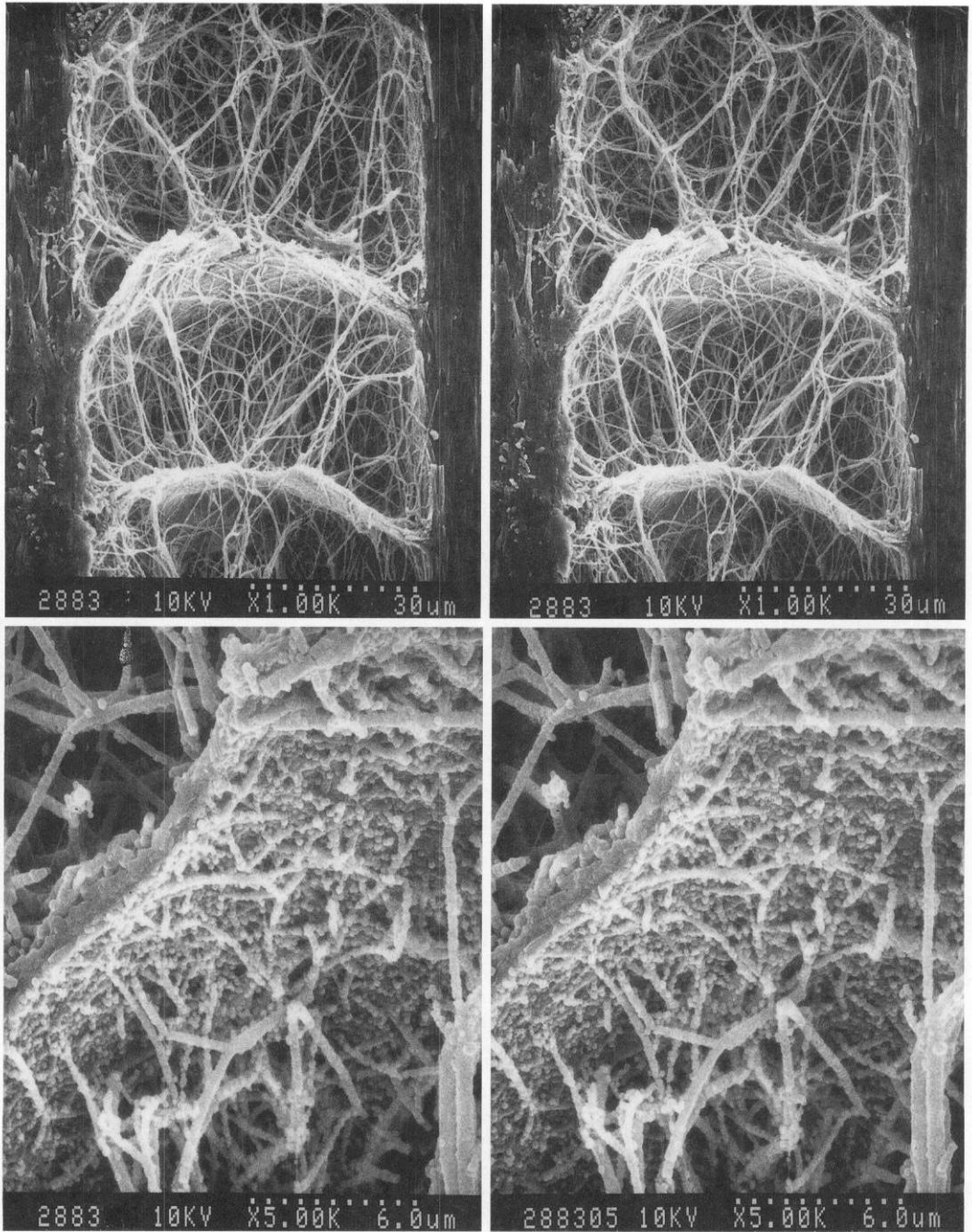


Fig. 4. Mineral component of gorgoniid axis. Longitudinal section of mineralized axis of *Leptogorgia viminalis* after removal of gorgonin showing chambers and filaments of core. Top, Chambers containing filaments mineralized with CHAp (SEM 2883, stereo pair); Bottom, Partition between chambers showing filaments mineralized with microspheres of CHAp and coalesced microspheres on chamber wall (SEM 2883, stereo pair).

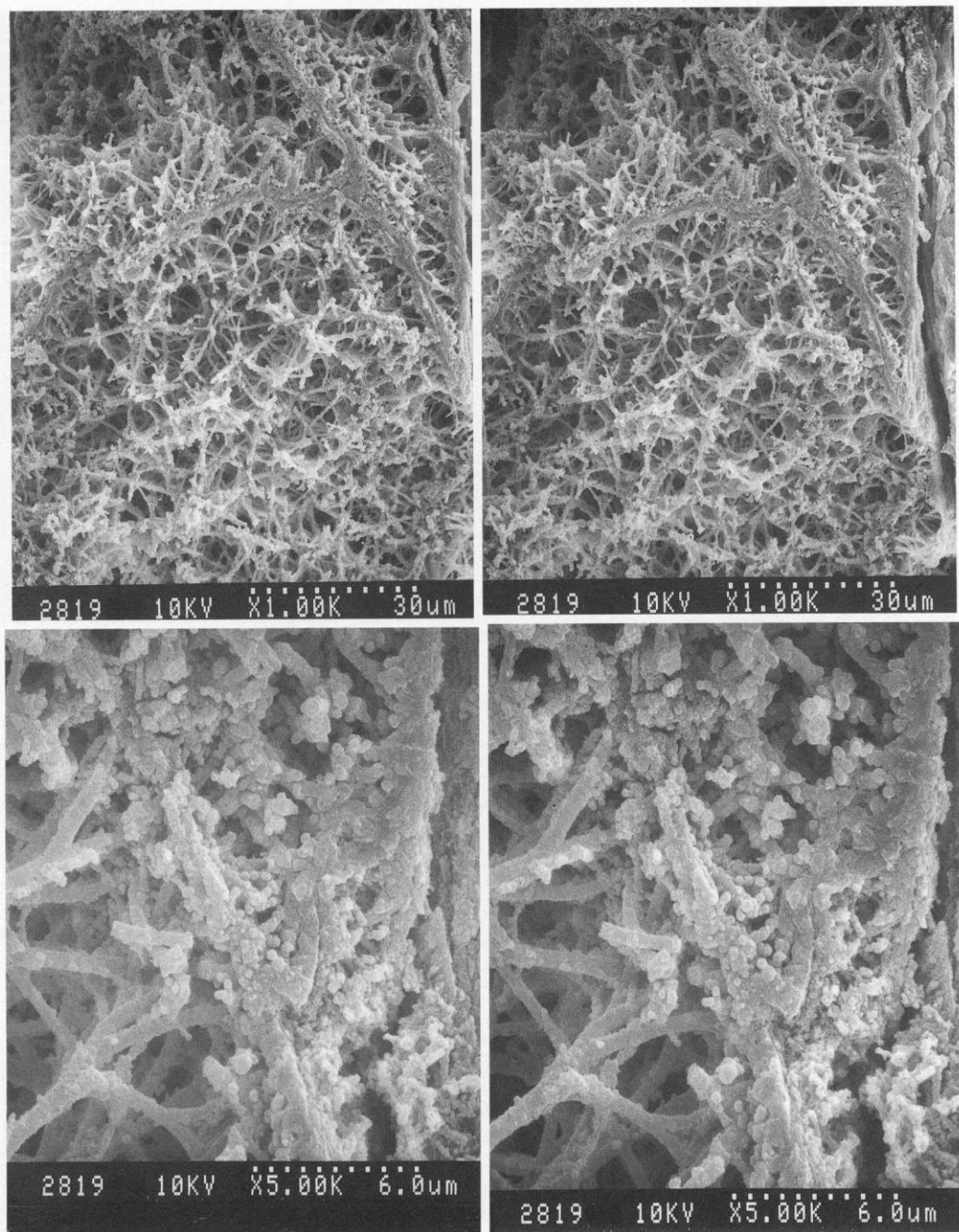


Fig. 5. Mineral component of gorgoniid axis. Longitudinal section of mineralized axis of *Leptogorgia lemasti* after removal of gorgonin. Top, Chambers of core containing filaments mineralized with CHAp (SEM 2819, stereo pair); Bottom, Chamber wall showing filaments mineralized with coalesced microspheres of CHAp (SEM 2819, stereo pair).

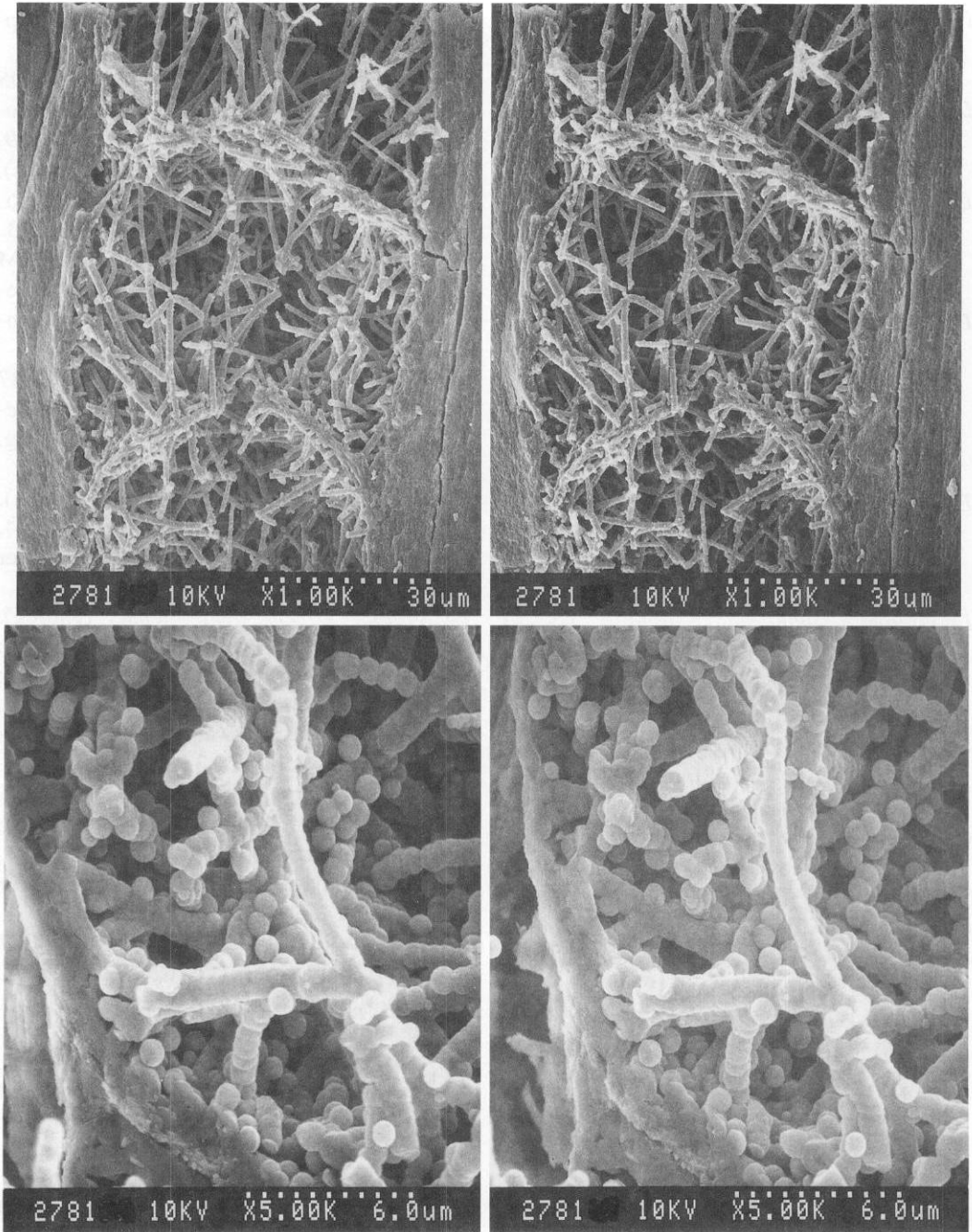


Fig. 6. Mineral component of gorgoniid axis. Longitudinal section of axis of *Leptogorgia cardinalis* after removal of gorgonin. Top, Chamber walls and filaments of core mineralized with CHAp; Bottom, Detail of chamber showing microspheres of CHAp coating filaments and chamber wall (SEM 2781—stereo pairs).

- Leptogorgia riodouroi* (Stiasny). USNM 82910 (SEM 2809). Taxonomic description: See Grasshoff 1988:116.
- Leptogorgia sanguinolenta* (Pallas). USNM 82904 (SEM 2793). Taxonomic description: See Grasshoff 1988:113.
- Leptogorgia setacea* (Pallas). USNM 43245 (SEM 2810–2812); USNM 43254 (SEM 2823); USNM 49777 (SEM 2822). Taxonomic description: See Bayer 1961:218.
- Leptogorgia stheno* (Bayer), pink colonies. USNM 49781 (SEM 2806–2807); USNM 50033 (SEM 2808); white colonies: USNM 49782 (SEM 2800, 2804). Taxonomic description: See Bayer 1961:220.
- Leptogorgia viminalis* (Pallas). USNM 82905 (SEM 2818, 2864, 2883). Taxonomic description: See Grasshoff 1988:102; 1992:60 (history, 97, 99, 102).
- Leptogorgia virgulata* (Lamarck). USNM 49690 (SEM 2753–2757, 2780, 2798). USNM 59331 (SEM 2796, 2798). Taxonomic description: See Bayer 1961:216.
- Leptogorgia styx* Bayer. USNM 98800 (SEM 2772–2775). Taxonomic description: See Bayer 2000:609.
- Olindagorgia marcgravii* (Bayer). USNM 73426 (SEM 2801–2803). Taxonomic description: See Bayer 1961:255.
- Pacifigorgia cribrum* (Valenciennes). USNM 49567 (fragment of holotype, MNHN Paris) (SEM 2870, 2871); USNM 49384 (SEM 2847–2849, 2851); USNM 1677 (SEM 2865, 2866); USNM 79433 (SEM 2867, 2868). Taxonomic description: Valenciennes 1846: pl. 13, figs. 1–3.—Verrill 1869:392, pl. 6, fig. 5 (*Leptogorgia rutila*); 391, pl. 5, fig. 5 (*L. adamsii* [part]).—Bielschowsky 1929:150. Although a detailed taxonomic evaluation has not been feasible in the present context, the specimens available suggest that most of the nominal species having fans consisting of fine, closely anastomosed networks may represent a single species.
- Pacifigorgia irene* Bayer. USNM 49365 (SEM 2855, 2856). Taxonomic description: See Bayer 1951:94, figs. 2, 3.
- Pacifigorgia media* (Verrill). USNM 57905 (SEM 2853, 2854, 2879). Taxonomic description: See Verrill 1864:33; 1869:389.
- Pacifigorgia stenobrochis* (Valenciennes). USNM 49366 (SEM 2767–2770). Taxonomic description: See Verrill 1869:393.
- Phycogorgia fucata* (Valenciennes). USNM 56886 (SEM 2776–2779). Taxonomic description: See Verrill 1869:413; Kükenthal 1919:921; Kükenthal 1924:360.
- Phyllogorgia dilatata* (Esper). USNM 5247 (SEM 2750–2752, 2758). Taxonomic description: See Verrill 1912:396, pl. 33, fig. 3; Bayer 1961:272, fig. 90, pl. 10, fig. 6.
- Pseudopterogorgia americana* (Gmelin). USNM 53582 (SEM 2761, 2763, 2764, 2771). Taxonomic description: See Bayer 1961:242.
- Pseudopterogorgia australiensis* (Ridley). USNM 82139 (SEM 2765, 2766); USNM 80952 (SEM 2873–2875); USNM 80593 (SEM 2859, 2860, 2863). Taxonomic description: See Ridley 1884:342, Kükenthal 1924:356.
- Pseudopterogorgia bipinnata* (Verrill). USNM 96216 (SEM 2826, 2876); USNM 50216 (SEM 2877, 2878, 2881, 2882). Taxonomic description: See Bayer 1961:229.
- Pterogorgia anceps* (Pallas). USNM 50057 (SEM 2655, 2656, 2676, 2732, 2857). Taxonomic description: See Bayer 1961:275.
- Pterogorgia guadalupensis* Duchassaing & Michelin. Material: USNM 52029 (SEM 2861); 51311. Taxonomic description: See Bayer 1961:277, fig. 92, pl. 9, fig. 6.
- Rumphella aggregata* (Nutting). Material: USNM 50275 (SEM 2660); USNM 86004 (SEM 2788, 2789). Taxonomic description: See Nutting 1910:4.

Results and Discussion

The order Gorgonacea of the subclass Octocorallia traditionally has been divided into two suborders: (1) Scleraxonia, with a

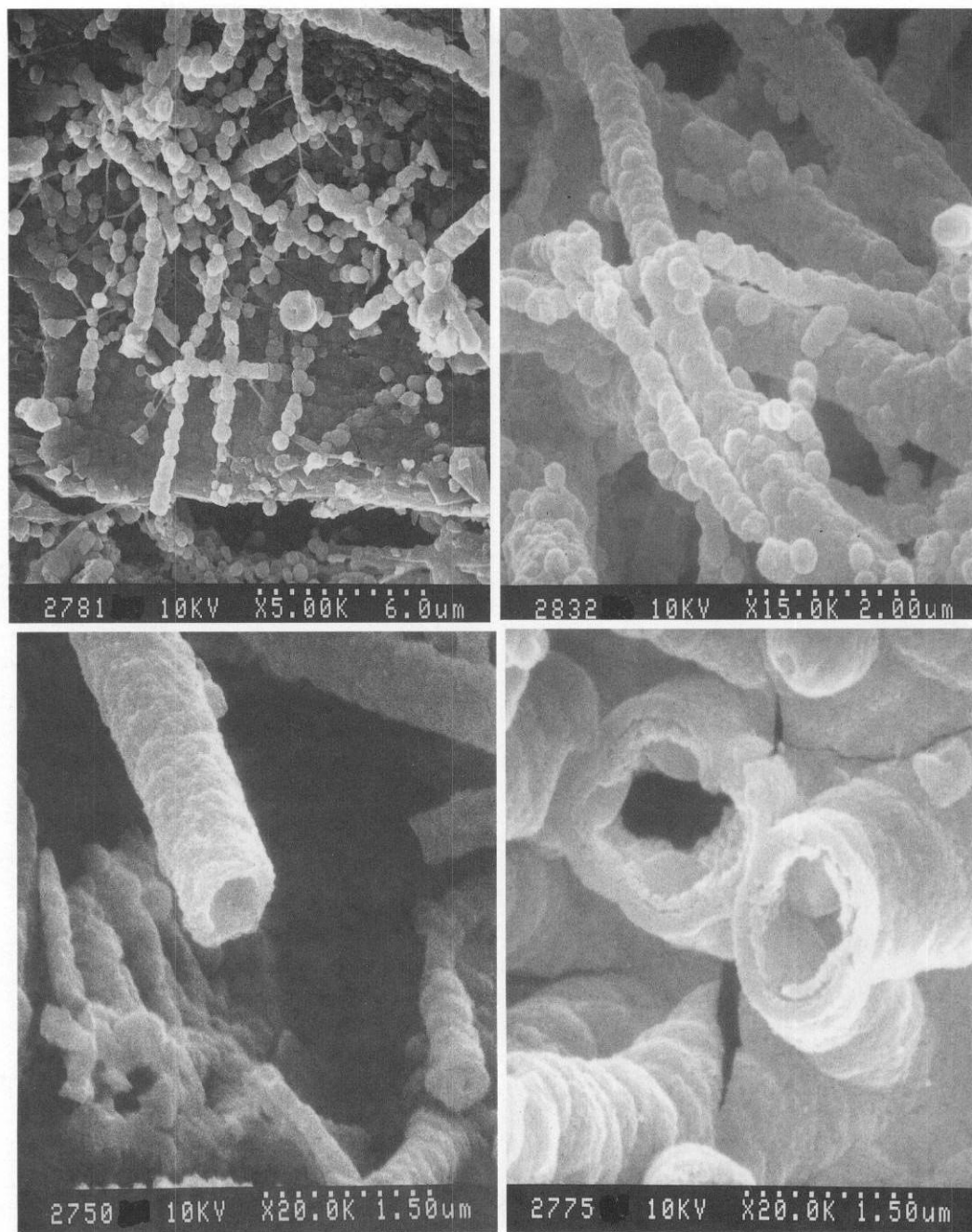


Fig. 7. Mineral component of gorgoniid supporting skeleton. Top left, Microspheres of CHAp in bead-like series covering organic filaments of *Leptogorgia cardinalis* holdfast (SEM 2781); Top right, Microspheres of CHAp fused to form rod-like coating on filaments of axial core of *Leptogorgia lemasti*, with some randomly located microspheres (SEM 2832); Bottom left, Mineral coating of filament of axial chamber of *Phyllogorgia quercifolia* consisting of CHAp microspheres fused to form rod-like structure with hollow core originally occupied by organic filament (SEM 2750); Bottom right, mineral coating of holdfast filaments of *Leptogorgia styx* showing deposition of CHAp in layers (SEM 2775).

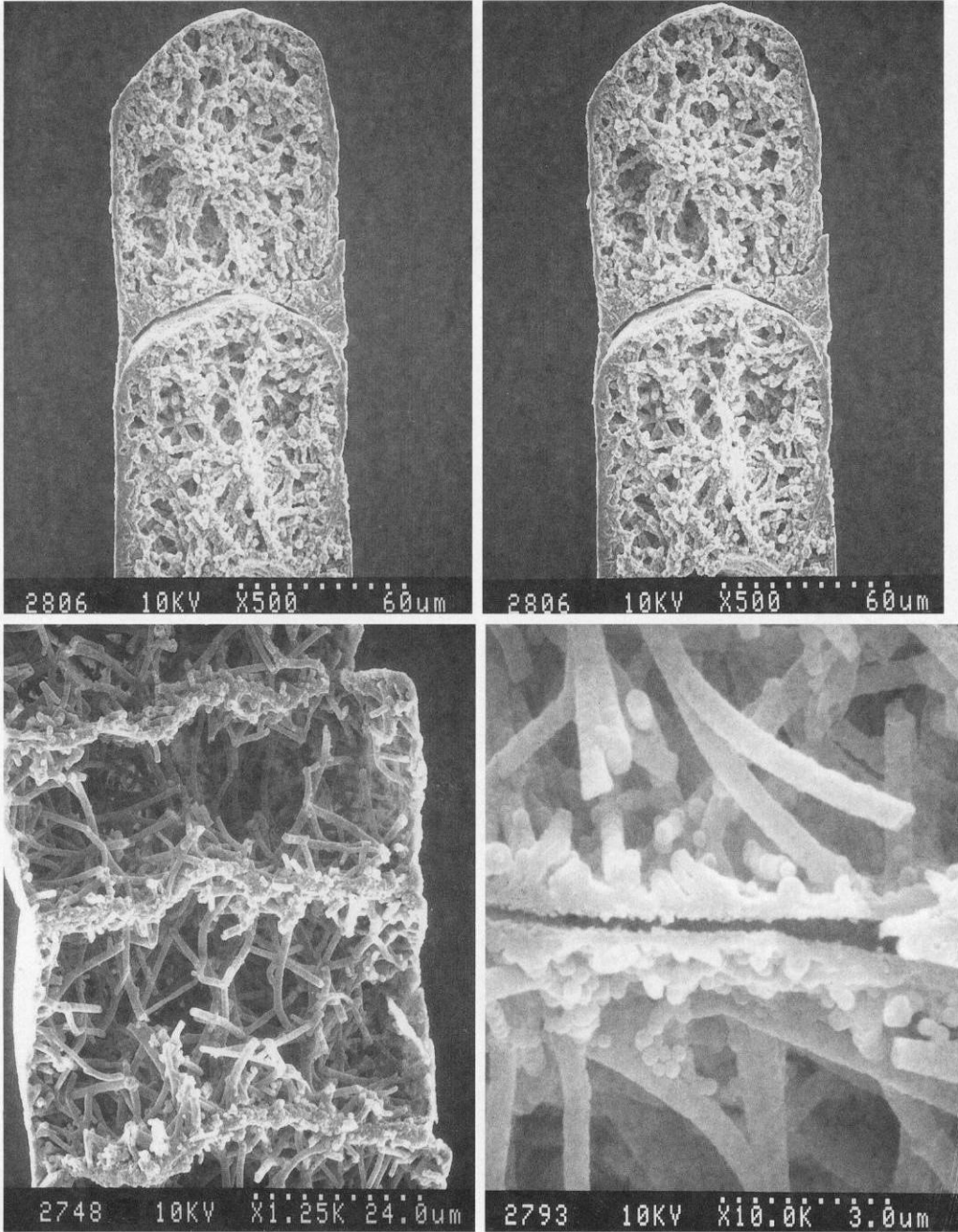


Fig. 8. Mineral component of gorgoniid axes. Top, Chambers of axial core of *Leptogorgia stheno* showing filaments coated with CHAp and space left after removal of organic partition by sodium hypochlorite (SEM 2806, stereo pair); Bottom left, Chambers of axial core of *Gorgonia mariae* showing filaments coated with CHAp (SEM 2748); Bottom right, Partition between chambers of axial core of *Leptogorgia sanguinolenta* showing space once occupied by organic lamella (SEM 2793).

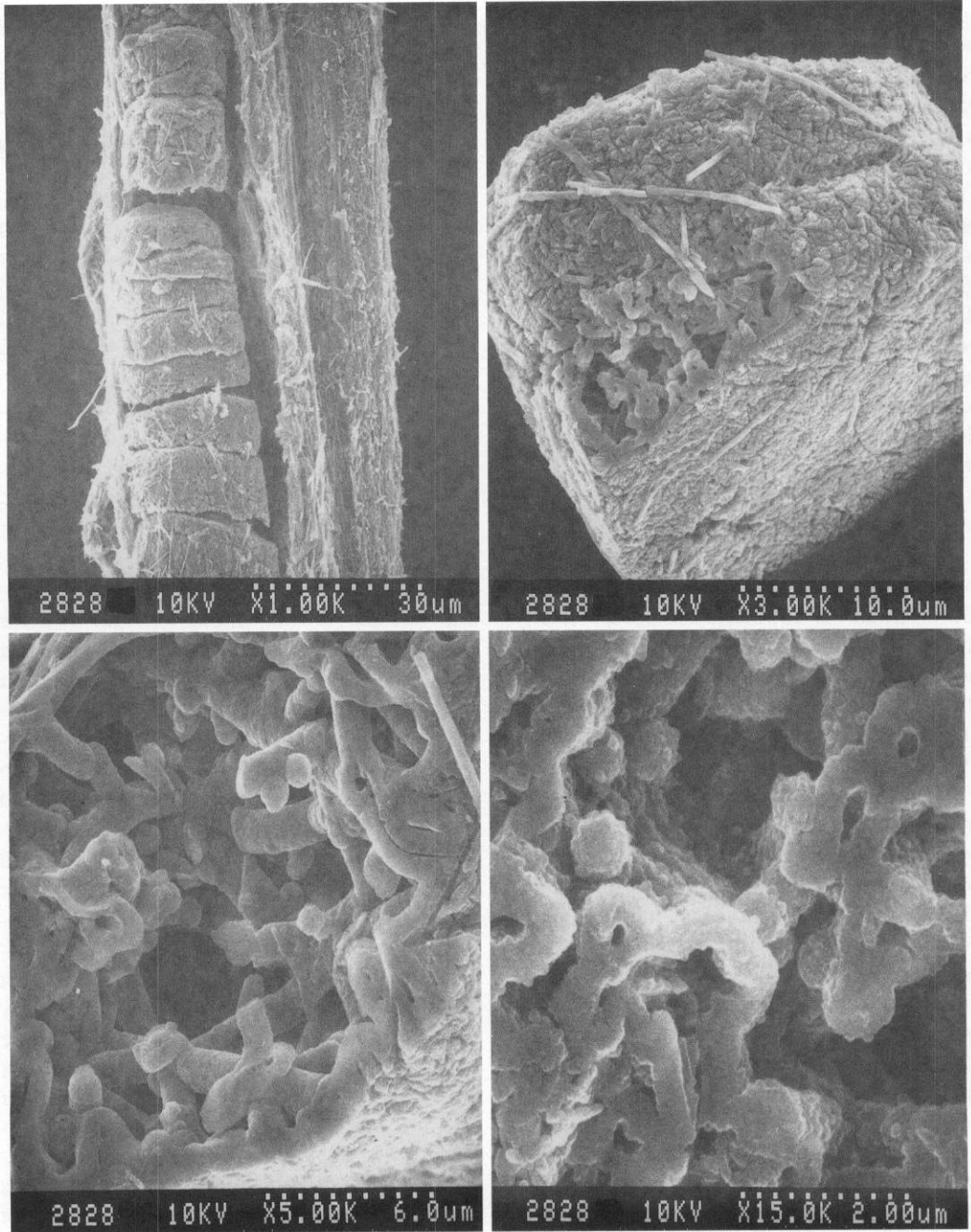


Fig. 9. Mineral component of gorgoniid axis. Top left, Heavily mineralized chambers of axial core of *Gorgonia ventalina* partially separated from axial cortex after maceration in sodium hypochlorite; Top right, Isolated chambers with break in wall showing internal structure; Bottom left, Filaments covered with CHAP in lumen of chamber; Bottom right, Filaments in lumen of chamber showing microspherulitic structure of mineral coating (SEM 2828).

supporting axis consisting of sclerites composed of magnesium calcite more or less completely bound together by gorgonin or crystalline calcite; and (2) Holaxonia, with a supporting axis consisting of gorgonin more or less heavily impregnated with CaCO_3 not in the form of sclerites. As mineralization of the axis has been considered of little practical taxonomic value, scant attention has been paid to its occurrence and distribution among holaxonian families. Recently, however, those families having a heavily calcified axis without a central core have been recognized as a separate suborder Calcaxonia (Grasshoff 1999:68), leaving those families with a chambered core in a flexible, poorly calcified or purely horny axis in the Holaxonia.

In the Holaxonia, the axis in the families Acanthogorgiidae, Paramuriceidae, and Gorgoniidae is reported as purely horny, that of the Plexauridae as containing some non-spicular calcareous matter, and that of the Keroeididae as containing smooth, fusiform calcareous sclerites (Aurivillius 1931, Bayer 1956).

When analyzed by X-ray diffraction, the mineral in the axis of all species of Calcaxonia proved to be CaCO_3 in the form of Mg-calcite or aragonite. In primnoids and chrysogorgiids, the holdfast may be a discoidal expansion firmly adherent to solid substrate or a branched, rootlike structure, either Mg-calcite or aragonite dependent upon species, embedded in soft substrate. The holdfast mineral of ellisellids was found to be Mg-calcite like that of the axis, and the holdfast mineral of ifalukellids proved to be aragonite like that of the axis, with possible contamination of Mg-calcite from the substrate.

In the chambered axial core in gorgoniids, CHAP is deposited in the form of "submicron spheres" (Macintyre et al. 2000) on the inner wall of the chambers and on the fine, organic fibrillar meshwork filling the chambers. In species having holdfasts containing CHAP, the mineral is similarly deposited as microspheres on the in-

terior wall and the fibrillar network filling the loculi in the gorgonin forming the lamellae of the holdfast. In gorgoniids having holdfasts reinforced with Mg-calcite or aragonite, the mineral is deposited between thin lamellae of gorgonin.

We found that the amount of MgCO_3 in the calcite of the axis ranges from 7.9 mole% in *Primnoella scotiae* to 15.7 mole% in *Plexaurella grisea* and *P. nutans*; and in the holdfast from 6.4 mole% in *Ainigmaptilon edisto* to 13.8 mole% in *Junceella gemmacea* (Table 1).

In no case did we find calcite with magnesium in the 33–42 and 71–85 mole% ranges as reported by Jeyasuria & Lewis (1987:218). In fact, we found that axes having the very high mole percentages of MgCO_3 reported by them, e.g., the species *Plexaura flexuosa* (72.0 mole%), *Muriceopsis flavida* (79.20 mole%), and *Swiftia exserta* (76.3 mole%)—have no mineral whatever, although the holdfasts of the first two are strongly mineralized with crystalline aragonite. Jeyasuria & Lewis's observations were made by atomic absorption spectrography of axial substance dissolved in HNO_3 . When samples of the axial substance of those same species are digested in 5.25% sodium hypochlorite, all organic components are dissolved, leaving no mineral framework for analysis by X-ray diffraction. Therefore, it can be concluded that the Ca and Mg concentrations found by Jeyasuria & Lewis (1987) were in ionic rather than mineral form. The amounts of MgCO_3 that they found in the calcite of *Plexaurella grisea* (18.1 mole%) and *Ellisella barbadensis* (14.6 mole%) are reasonably similar to our findings for *P. grisea* (15.7 mole%) and *Junceella gemmacea* (14.0 mole%).

We did not find crystals in the axis of *Muricea muricata*, *Plexaura flexuosa*, and *Eunicea tourneforti*, as reported by Lewis et al. (1992:281). However, after prolonged maceration (26–60 hours) in sodium hypochlorite, crystals similar to those they illustrated for *Plexaura flexuosa* (1992: fig. 1c)

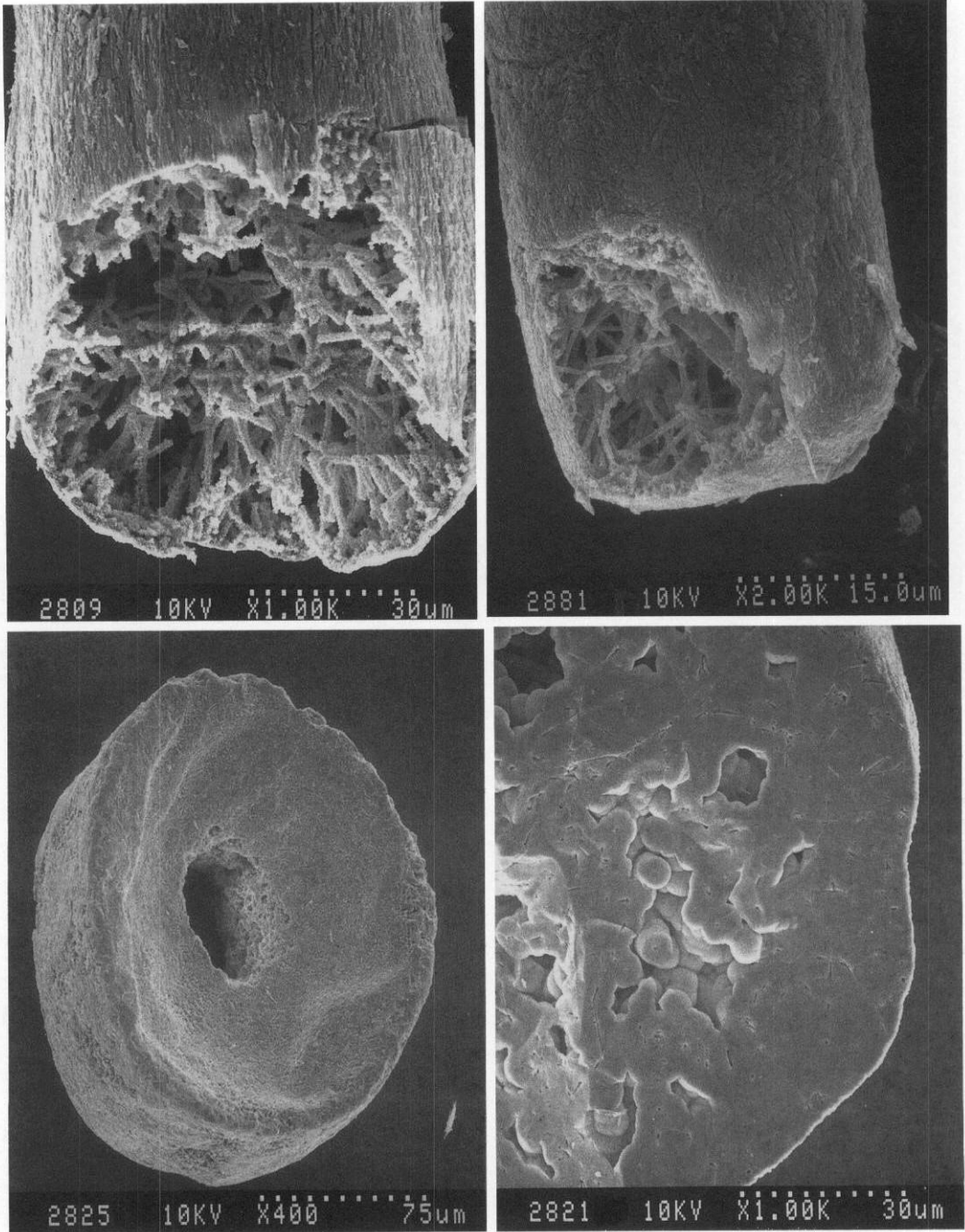


Fig. 10. Mineral component of gorgoniid axes. Top left, Core of axis of *Leptogorgia rioudouroi* (SEM 2809); Top right, Core of axis of *Pseudopterogorgia bipinnata* (SEM 2881); Bottom left, Heavily mineralized contents of chamber of axial core of *Leptogorgia setacea*, (SEM 2825); Bottom right, Coalesced spherulitic structure of heavily mineralized chamber of axial core of *Leptogorgia setacea* (SEM 2821).



Fig. 11. Mineral residue from holdfast of *Eugorgia ampla* after removal of organic matrix by maceration in sodium hypochlorite. View of aqueous preparation in transmitted light showing one nearly complete locus with mineralized internal filaments.

appeared on the lamellae of CHAp forming the axial cortex of *Leptogorgia virgulata* and *L. setacea*, but not on samples macerated for shorter periods (2–8 hours). X-ray diffraction showed those crystals to be calcium oxalate hydrate ($\text{Ca}_2\text{CaO}_4 \cdot 2\text{H}_2\text{O}$).

The holdfast of a few gorgoniid species is strengthened by Mg-calcite or aragonite, but the only axial mineral in the family Gorgoniidae worldwide is carbonate hydroxylapatite (CHAp). The axis and holdfast in a few members of the family are not mineralized. Neither axis nor holdfast of those *Eunicella* species examined, including those listed in Table 1, revealed any mineral residue after complete maceration in 5.25% sodium hypochlorite; colonies of a few species of *Eunicella* form no holdfast, being unbranched or scantily branched and lying prone on the seafloor.

The following situations were observed in the present study:

1. Neither axis nor holdfast mineralized: *Eunicella*, *Swiftia*, *Leptogorgia caryi*.

2. Axis not mineralized, holdfast aragonite: *Pterogorgia*, *Eunicea*, *Muriceopsis*, *Plexaura* and *Pseudoplexaura*.

3. Axis not mineralized, holdfast Mg-calcite: *Rumphella*.

4. Axis and holdfast mineralized with CHAp: *Eugorgia*, *Gorgonia*, *Leptogorgia*, *Pacifigorgia*, *Pseudopterogorgia*, *Phycogorgia*, *Phyllogorgia*.

5. Axis mineralized with CHAp, holdfast with aragonite: *Olindagorgia*, *Pseudopterogorgia bipinnata*.

6. Axis with "loculi" filled with Mg-calcite, holdfast aragonite: *Plexaurella*.

7. Axis and holdfast Mg-calcite: *Juncella*, *Ellisella*, *Chrysogorgia*, *Radicipes*, *Ainigmaptilon*, *Fanellia*, *Fannyella*, *Primoella*.

8. Axis and holdfast aragonite: *Narella*, *Candidella*.

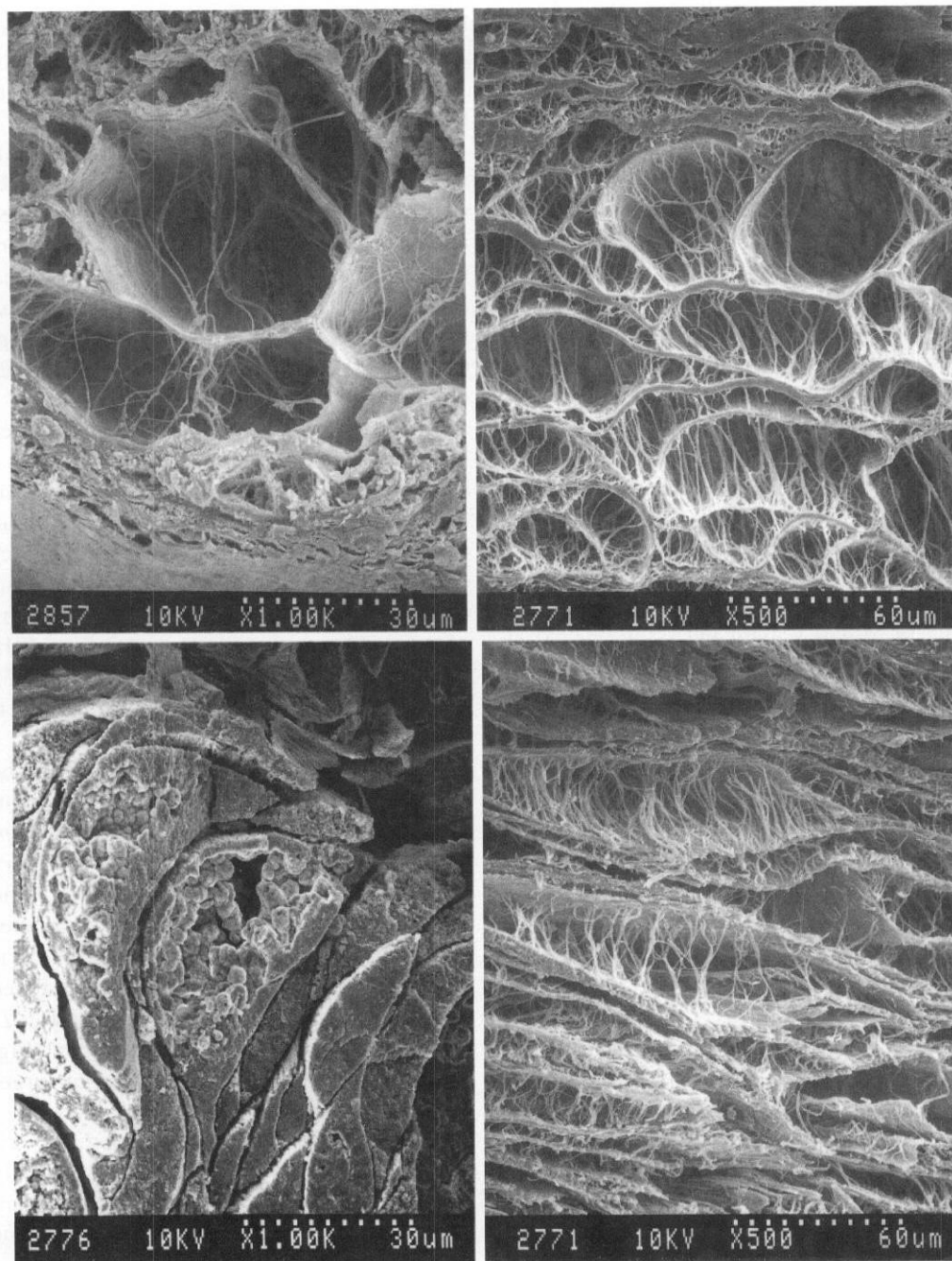


Fig. 12. Structure of gorgoniid holdfasts. Top left, *Leptogorgia alba*: Loculi polygonal in cross section (SEM 2857); Top right, *Pseudopterogorgia americana*: Loculi oval in cross section (SEM 2771); Bottom left, *Phycogorgia fucata*: Loculi crescentic in cross section (SEM 2776); Bottom right, *Pseudopterogorgia americana*: Loculi in longitudinal section (SEM 2771).

9. Axis aragonite, holdfast aragonite with Mg-calcite possibly as contamination from the substrate: *Plumigorgia*, *Ifalukella*.

Leptogorgia caryi and all species of *Eunicella* can be regarded as having the basic design of supporting skeletal structures of the Holaxonia (restricted sense) (Neumann 1911; Schimmbke 1914; Schneider 1905). Unlike all other species of the genus *Leptogorgia* examined in this study, the axis and holdfast *L. caryi* yield no mineral component upon complete maceration in sodium hypochlorite.

Examination by SEM demonstrates that the chambers comprising the central core of the axis are filled with a meshwork of fine organic filaments (Fig. 1, top). The partitions between the chambers (Fig. 1, bottom) as well as the walls clearly consist of a close meshwork of fine organic filaments some of which extend between successive partitions to form the network filling the chambers. This microstructure of the partitions was not observed in paraffin sections of histological preparations, perhaps owing to the small diameter of the filaments: 0.3 μm and less.

The lamellae of the holdfast are likewise composed of fine filaments. Successive layers of holdfast are separated by approximately fusiform spaces (Fig. 2, top) corresponding to the loculi between concentric layers of gorgonin in the axial cortex of Paramuriceidae, Plexauridae and Acanthogorgiidae. These holdfast loculi contain filaments extending from wall to wall in a network more open than that in the chambers of the axial core (Fig. 2, bottom).

Mineral Morphology

Axis.—The gorgonin of the axis cortex of most gorgoniid species is permeated by CHAp. After removal of the organic matrix, it has the form of slender, tapered strands aligned in irregular spirals and arranged in concentric layers around the axis core (Fig. 3, top). These strands are the “crescentic calcareous loculi” described and illustrated

by Lewis et al. (1992:291, fig. 6a, b) for *Lophogorgia cardinalis*, and comprise the “thin, crenulated layers or sheaths” mentioned by Macintyre et al. (2000).

The strands are in turn composed of fine mineral fibers (“crystals,” Lewis et al. 1992:292, fig. 6d) longitudinally oriented and showing minute, irregular surface granulations (Fig. 3 bottom left). In many cases, the fractured surface of longitudinally fractured axial cortex consists of narrow mineral fibers closely packed in longitudinal orientation (Fig. 3 bottom right).

Among all genera and species in which it has been observed by SEM, CHAp has a strikingly consistent morphology in the chambered core of the axis and in the loculi of the hold-fast. The mineral is precipitated on the fibrillar structure of the walls and the meshwork of organic filaments in the form of microspheres that range in size from 0.15 μm (or smaller) up to 0.3 μm (Figs. 4–7), but sometimes as much as 6.5 μm (Fig. 21, top left).

The meshwork of filaments filling the chambers of the core varies greatly in complexity and extent of mineralization. In *Leptogorgia viminalis*, the filaments are very fine, only moderately anastomosed, and mineralized with very small microspheres (Fig. 4). In *L. lemasti*, the meshwork is dense and closely anastomosed, mineralized with small microspheres (Fig. 5), and in *L. cardinalis*, anastomosis is more open (Fig. 6) but the mineralization consists of larger microspheres.

Microspheres may be arranged uniseriably, bead-like along the filaments, usually with isolated microspheres located at random. The microspheres commonly become fused around the filaments to produce branching, anastomosing rods with irregular surfaces retaining vestiges of the initially bead-like structure (Fig. 7). The hollow core visible in broken ends of filaments represents the space originally occupied by the organic filament removed by maceration in sodium hypochlorite (Fig. 7, bottom left).

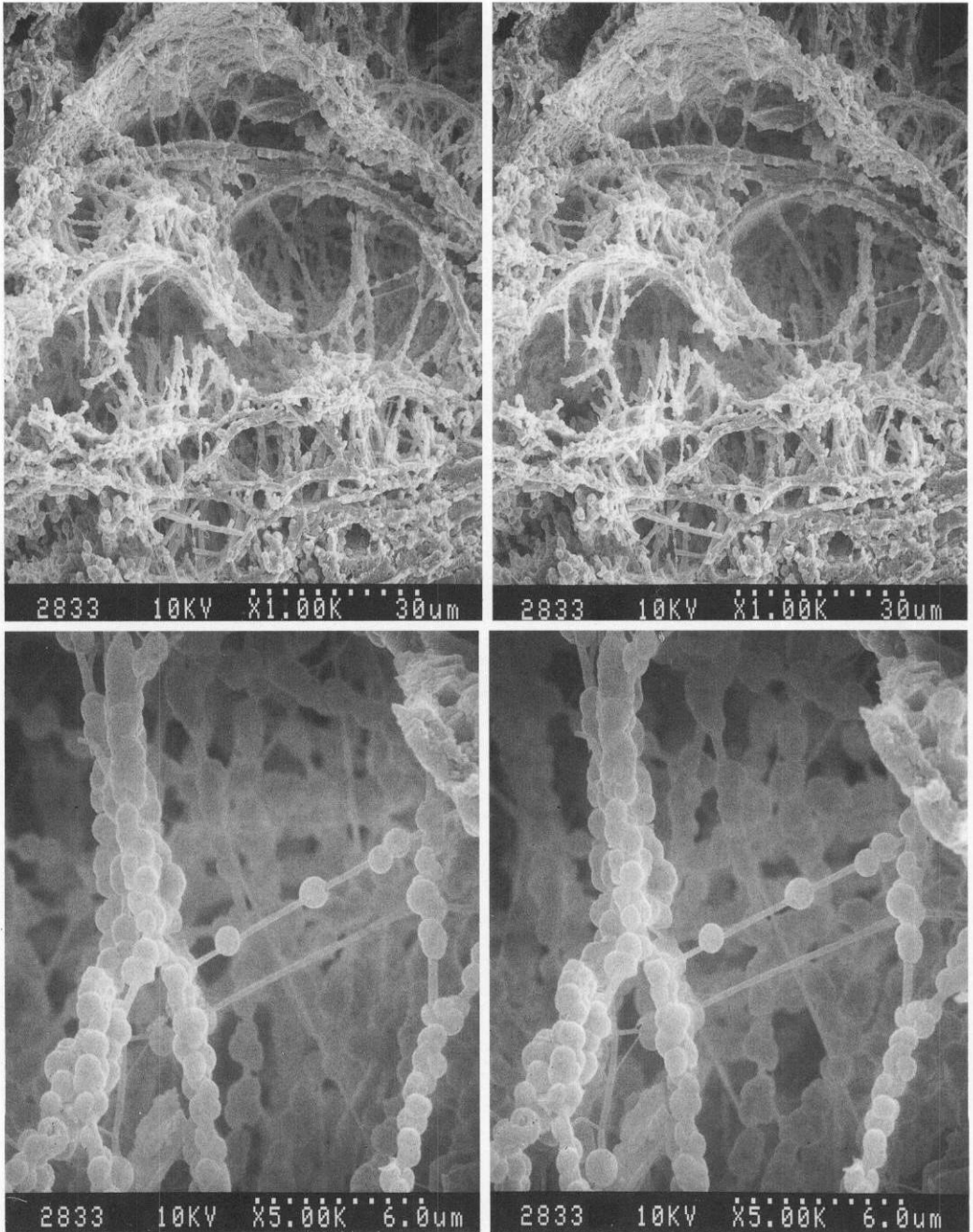


Fig. 13. Structure of gorgoniid holdfast. Cross section of loculi of *Leptogorgia lemasti* without maceration in sodium hypochlorite, leaving organic components in place, showing CHAp microspheres on organic filaments (SEM 2833, stereo pairs).

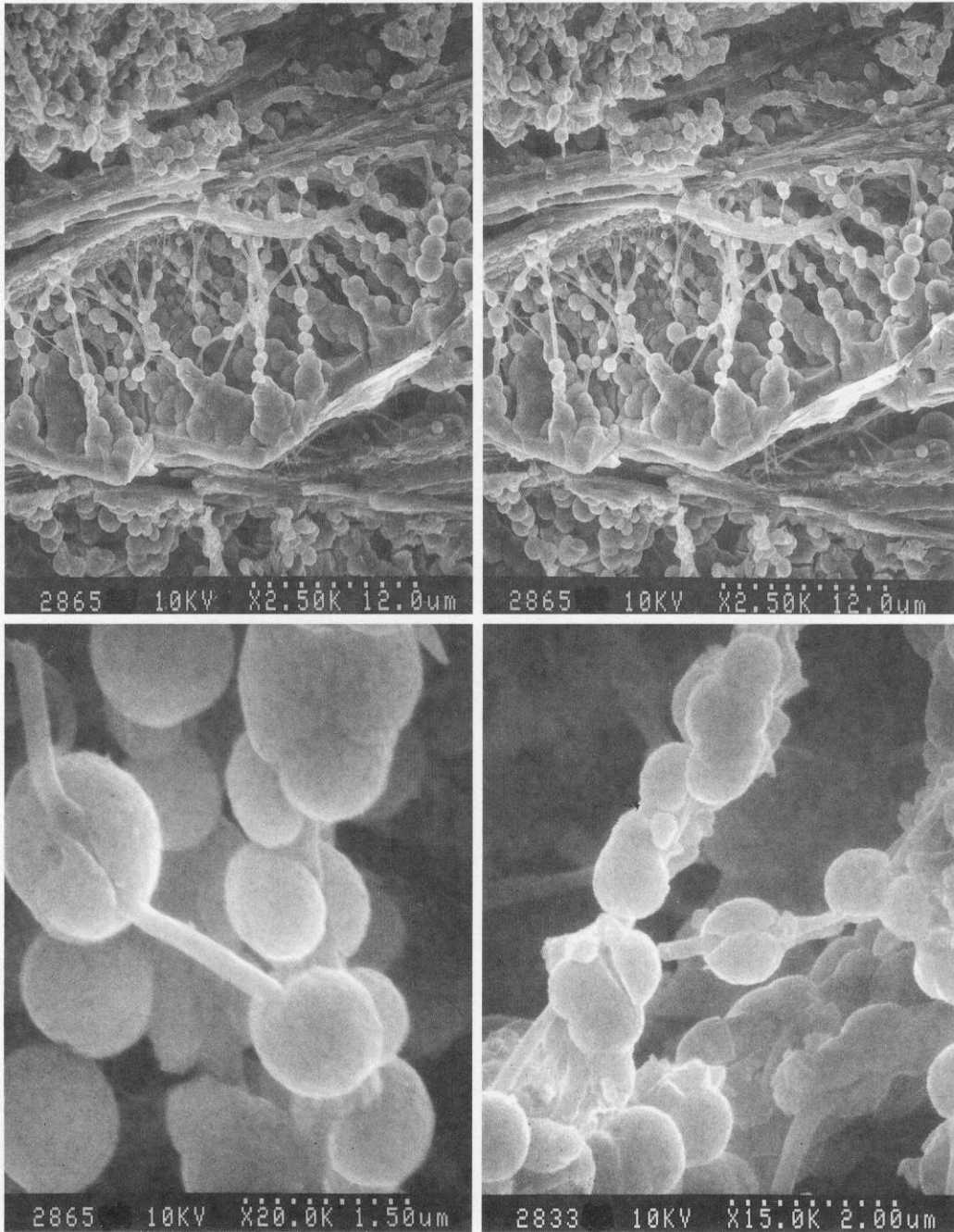


Fig. 14. Structure of gorgoniid holdfasts. Top, Longitudinal section of holdfast loculus of *Pacifigorgia cribrum* without maceration in sodium hypochlorite, leaving organic component intact (SEM 2865, stereo pair); Bottom left, Microspheres of CHAp on organic filaments of *Pacifigorgia cribrum* (SEM 2865); Bottom right, Microspheres of CHAp precipitated around filaments of holdfast loculi of *Leptogorgia alba* (SEM 2833).

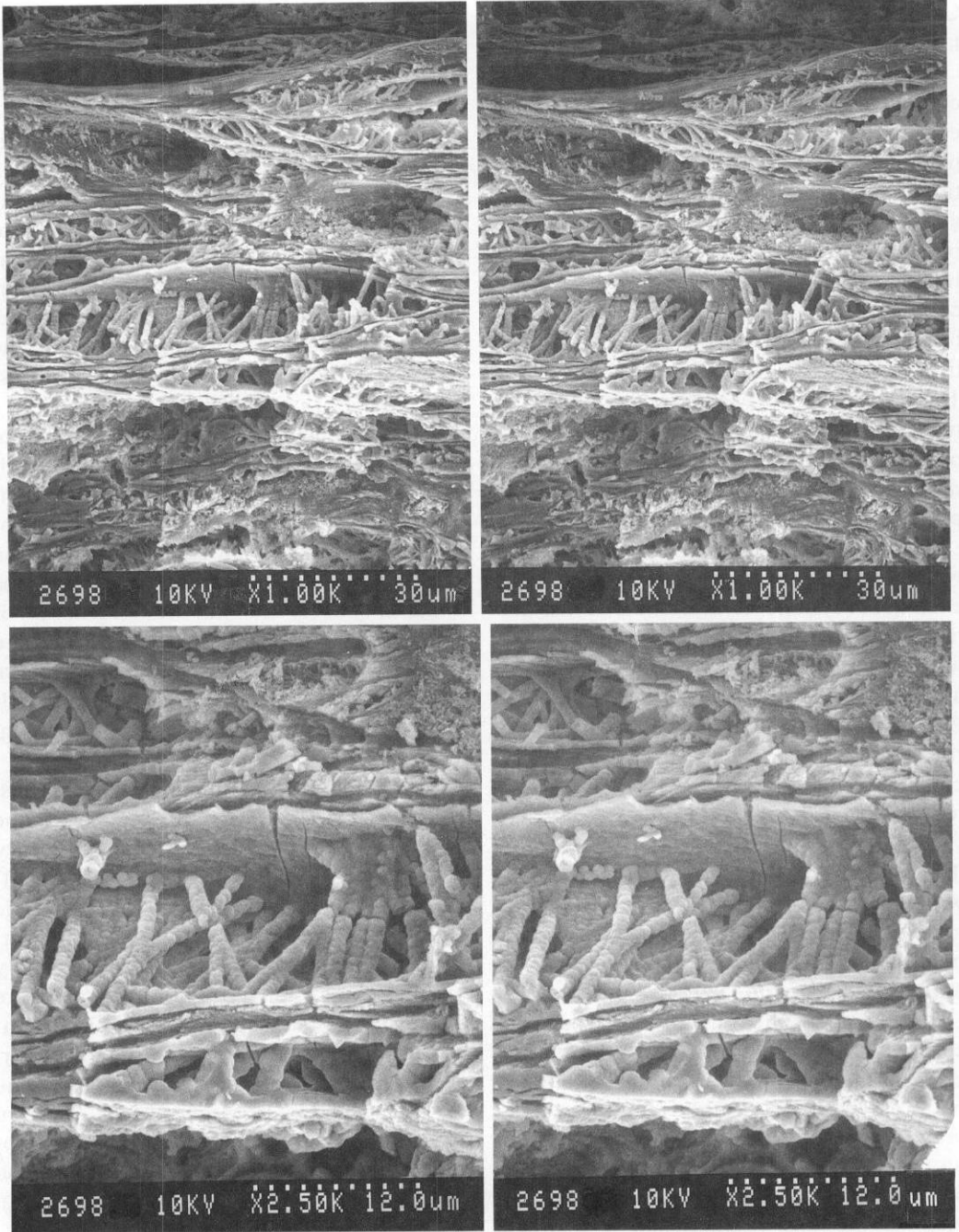


Fig. 15. Structure of gorgoniid holdfasts. Top, Longitudinal section of holdfast of *Gorgonia mariae* showing mineralized loculi; Bottom, Detail of above with filaments coated with microspheres of CHAp fused to form columns (SEM 2698, stereo pairs).

CHAp sometimes is deposited in distinct layers (Fig. 7, bottom right).

In weakly mineralized axes, the mineral component of the cortex separates from the core in delicate concentric sheets that break up into minute fragments during preparation. Depending upon the extent of mineralization, the core may remain more or less intact but in extremely fragile form, breaking up into longer and shorter fragments composed of a variable number of chambers that may expose the mineralized partitions and filaments within (Fig. 8 top). The partitions between chambers consist of two layers separated by a narrow space originally occupied by the organic lamella removed during maceration in sodium hypochlorite (Fig. 8 bottom).

The wall of the axial core may be so weakly mineralized that the contents of the chambers separate as individual disks, distally convex and basally concave (Fig. 9 top left). These disks are composed of the filamentous network so heavily mineralized that it is nearly solid CHAp (Fig. 9 top right), composed of the rodlike mineral coating of the organic filaments (Fig. 9 bottom left); greater magnification clearly shows the submicrospherulitic structure of the CHAp (Fig. 9 bottom right). When its wall is more strongly mineralized, the axial core may emerge from maceration as a cylinder of CHAp filled with a network of mineralized filaments (Fig. 10 top).

The greatest mineralization of the axial core was observed in the western Atlantic species *Leptogorgia setacea* and *L. stheno*, both of which form unbranched or weakly branched flagelliform colonies living prone on the seafloor. CHAp is precipitated more or less uniserially along the organic filaments in the form of microspheres that fuse together on the interior wall of the chambers, sometimes leaving a central lumen where incompletely fused microspheres were lost during preparation (Fig. 10 bottom left).

Holdfast.—At the base of the colony, the coenenchyme extends outward over the

substrate and the basal axial epithelium secretes successive layers of gorgonin that form a spreading holdfast. The lamellae of the holdfast are partially separated by small open spaces of roughly fusiform shape, about 30 μm in diameter and undetermined length, analogous to the loculi between the layers of axial cortex present in the Paramuriceidae, Plexauridae and Acanthogorgiidae. These holdfast loculi contain fine organic filaments similar to those of the chambers of the axial core, secreted by the holdfast epithelium as it produces successive layers of gorgonin.

Maceration of holdfast tissue in sodium hypochlorite dissolves the gorgonin lamellae, leaving a finely divided residue consisting of the CHAp that lined the walls of the holdfast loculi. An aqueous preparation viewed under a petrographic microscope consists mostly of minute fragments of CHAp. Although the mineralized loculi are extremely fragile, a few may remain more or less intact, showing the fine, mineral-coated filaments filling the interior (Fig. 11).

Free-hand sections of untreated holdfast cut transversely and radially show the shape of the loculi. In cross section, loculi vary in shape from polygonal (Fig. 12 top left) to oval (Fig. 12 top right) and crescentic (Fig. 12 bottom left), often more or less irregular. In longitudinal section roughly along a radius of the holdfast, loculi are elongate, tapering, interdigitating with others at roughly the same level, separated vertically from those above and below by one or more layers of gorgonin (Fig. 12 bottom right). In the Gorgoniidae, CHAp is precipitated on the interior walls of the loculi and on the organic filaments, as is the case in the chambers of the axial core.

If not treated in sodium hypochlorite, the fine organic filaments remain essentially intact (Figs. 13, 14). Microspheres of CHAp are precipitated on the filaments apparently at random, as some filaments have none and others a few, while some are completely covered with mineral. The shape of the mi-

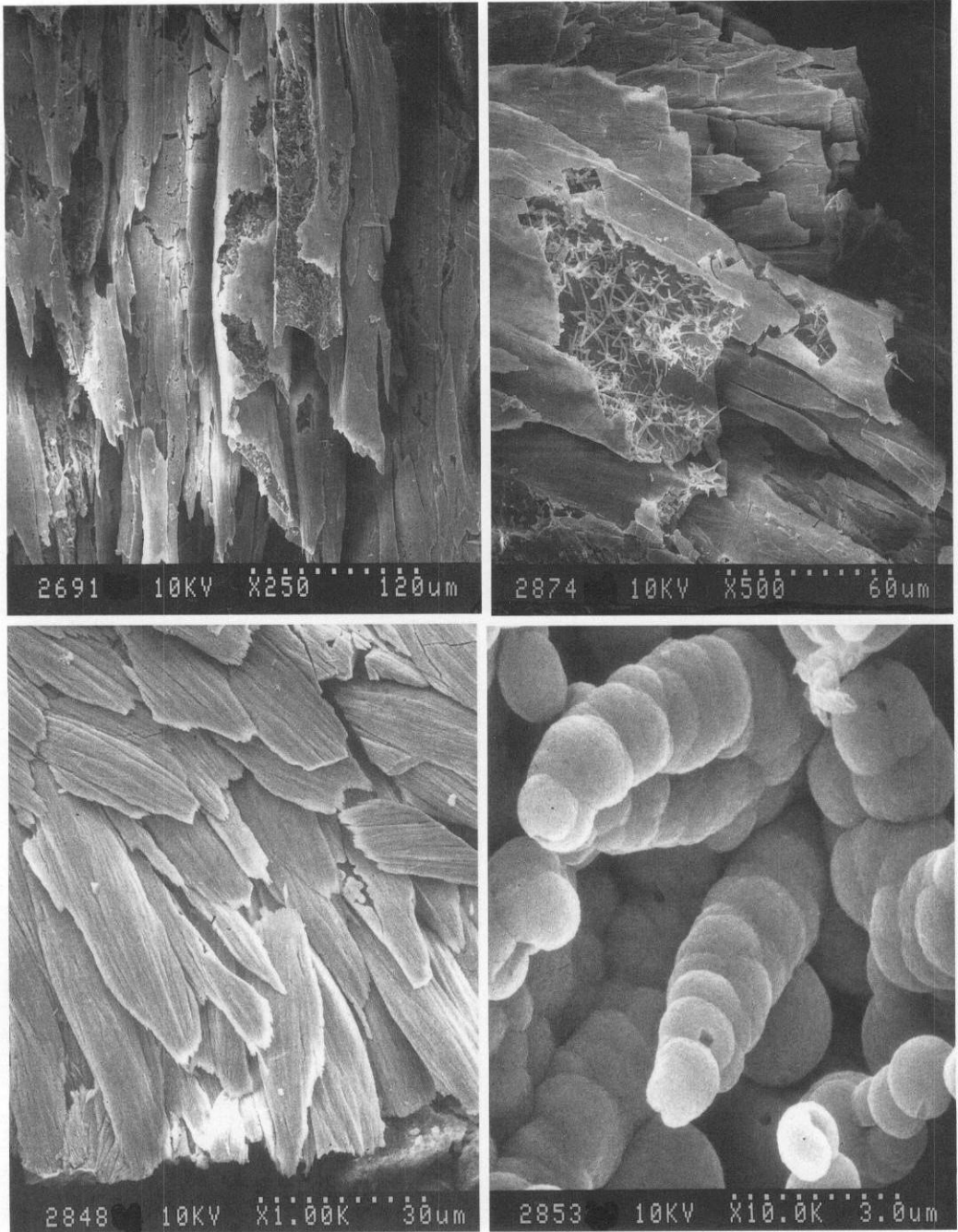


Fig. 16. Structure of gorgoniid holdfasts. Top left, *Eugorgia aurantiaca*, Mineralized loculi of holdfast partly etched from organic matrix (SEM 2691); Top right, *Pseudopterozorgia australiensis*: Mineralized loculi of holdfast partly etched from organic matrix (SEM 2874); Bottom left, *Pacifigorgia cribrum*: Mineralized loculi of holdfast partly etched from organic matrix (SEM 2848); Bottom right, *Pacifigorgia media*, Spherules of CHAP in lumen of holdfast loculus showing decrease in size along filament (SEM 2853).

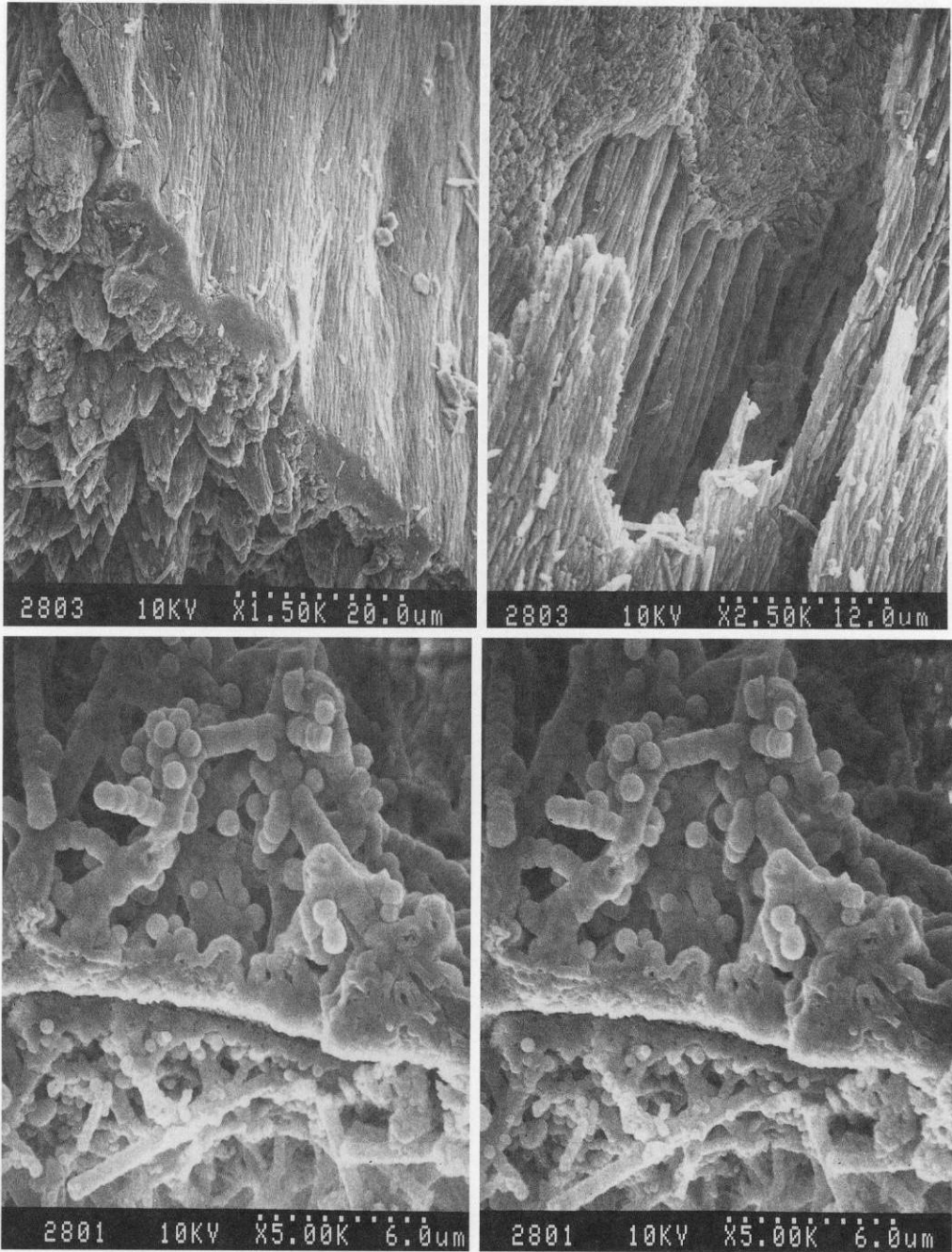


Fig. 17. Mineral components of gorgoniid supporting skeleton. Top, Crystalline aragonite of holdfast of *Olindagorgia marcgravii* (SEM 2803); Bottom, Coalesced microspheres of CHAp on filaments and partition between chambers of axial core of *Olindagorgia marcgravii* (stereo pair).

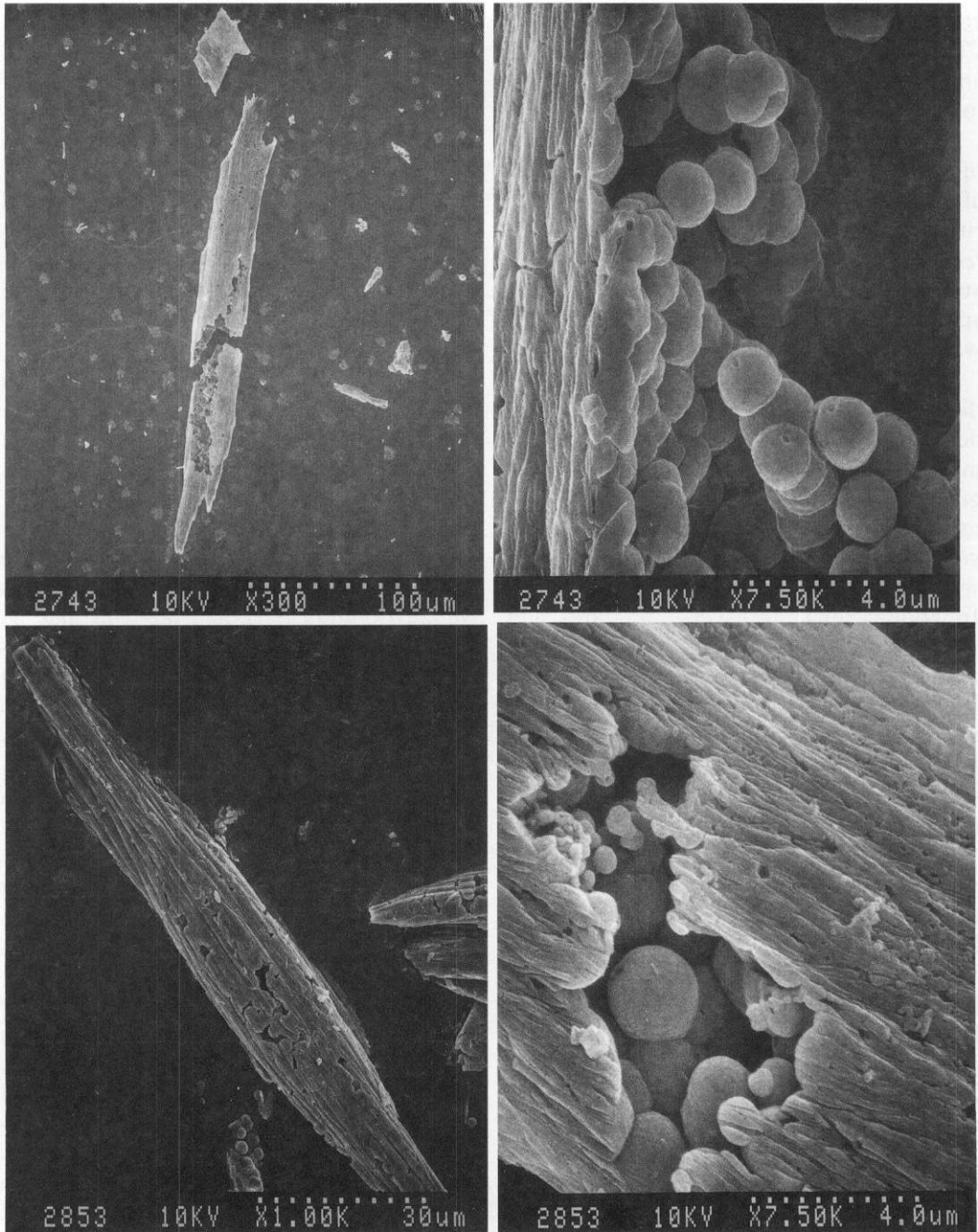


Fig. 18. Morphology of CHAp in Gorgoniidae. Top, *Eugorgia rubens*: Left, Single mineralized holdfast locusus isolated after maceration in sodium hypochlorite; Right, Microspheres of CHAp in lumen of locusus seen through break in wall (SEM 2743). Bottom, *Pacifigorgia media*: Left, Mineralized holdfast locusus isolated after maceration in sodium hypochlorite; Right, Microspheres of CHAp in lumen of locusus seen through break in wall (SEM 2853). The outer surfaces of the locular walls exhibit linear cast patterns of the gorgonin that surrounded them. These outer wall cast patterns can be seen also in Figs. 19 and 20.

crosspheres indicates that precipitation of CHAp begins at a nucleation site on a filament and grows around it (Fig. 14, bottom).

The mineral component of the holdfast of *Gorgonia mariae* remains almost intact after brief treatment in sodium hypochlorite, as mineralization is stronger than in *L. lemasti*. The mineral lining of the loculi is strong, and uniseriably arranged microspheres covering the filaments extend from wall to wall like columns (Fig. 15).

Partial removal of the organic surface of the holdfast reveals the surface of the underlying mineral. The mineralized loculi may be partially intact, fusiform as in *Eugorgia aurantiaca* (Fig. 16 top left), polygonal in cross section as in *Pseudopterogorgia australiensis* (Fig. 16 top right), or even scale-like as in *Pacifigorgia cribrum* (Fig. 16 bottom left). Transverse fractures and breaks in the locular walls provide a view of internal structure. The decreasing size of microspheres from the locular wall toward the interior (Fig. 16 bottom right) suggests a time element in formation of CHAp microspheres along the organic filaments during holdfast formation (also Fig. 13, top).

The holdfast loculi of *Phycogorgia fucata* are more strongly mineralized than in any other species examined in this study. Distinctly crescentic in cross section, they are filled more or less completely with partially fused microspheres (Fig. 12 bottom left).

Although the filaments and walls of the chambers of the axial core of *Olindagorgia marcgravii* are mineralized with microspherular CHAp of typical form (Fig. 17, top), the holdfast is mineralized with crystalline aragonite (Fig. 17, bottom), a combination unique so far in the family Gorgoniidae.

Complete removal of the gorgonin matrix frees the mineralized lining of the loculi, which retain more or less of their shape according to the degree of mineralization. Although fragile and extensively broken during preparation, the mineralized loculi in

some cases may remain more or less intact, revealing their fusiform shape (Figs. 11, 18 top and bottom left). The microspheres of CHAp coating the wall and interior filaments can be seen through breaks in the wall (Fig. 18 top and bottom right). In species having a less extensively mineralized wall, the loculi and their interior microspheres break down into a fine white sediment composed of minute fragments, some of which retain traces of their original structure.

The outer surface of the locular wall is a cast of the surface of the gorgonin matrix upon which it was precipitated. In many cases the spheroidal form of the CHAp is distinctly retained (Figs. 19 top, and 20 bottom left), but in others it may be more or less completely obliterated owing to the small size of the component microspheres (Fig. 19 bottom left), and the wall may be composed of microspheres 0.6 μm in diameter fused to form a solid sheet (Fig. 19 bottom right). Typically, the microspheres comprising the locular wall are 1.1–1.4 μm in diameter, often but not always with a distinct central opening indicating the location of the organic filament that extended from the organic surface into the interior of the loculus (Fig. 19 top right) upon which it was deposited and which formed one of the "strings" for the bead-like microspheres filling the interior.

The surface of the microspheres of CHAp varies from smooth, even at high magnification (Fig. 20 top left, 21 top left) to sharply prickly (Fig. 21 top right and lower left) and coarsely thorny (Fig. 21 bottom right). In many species the surface is nearly smooth at moderate magnification (Fig. 21 top left), appearing finely granular or more coarsely granular at higher magnifications (Fig. 20 top right and bottom right).

The axes of *Pterogorgia anceps*, *P. citrina*, and *P. guadalupensis* reveal no mineral component upon maceration in sodium hypochlorite, but holdfasts are reinforced with dense crystalline aragonite (Table 1)

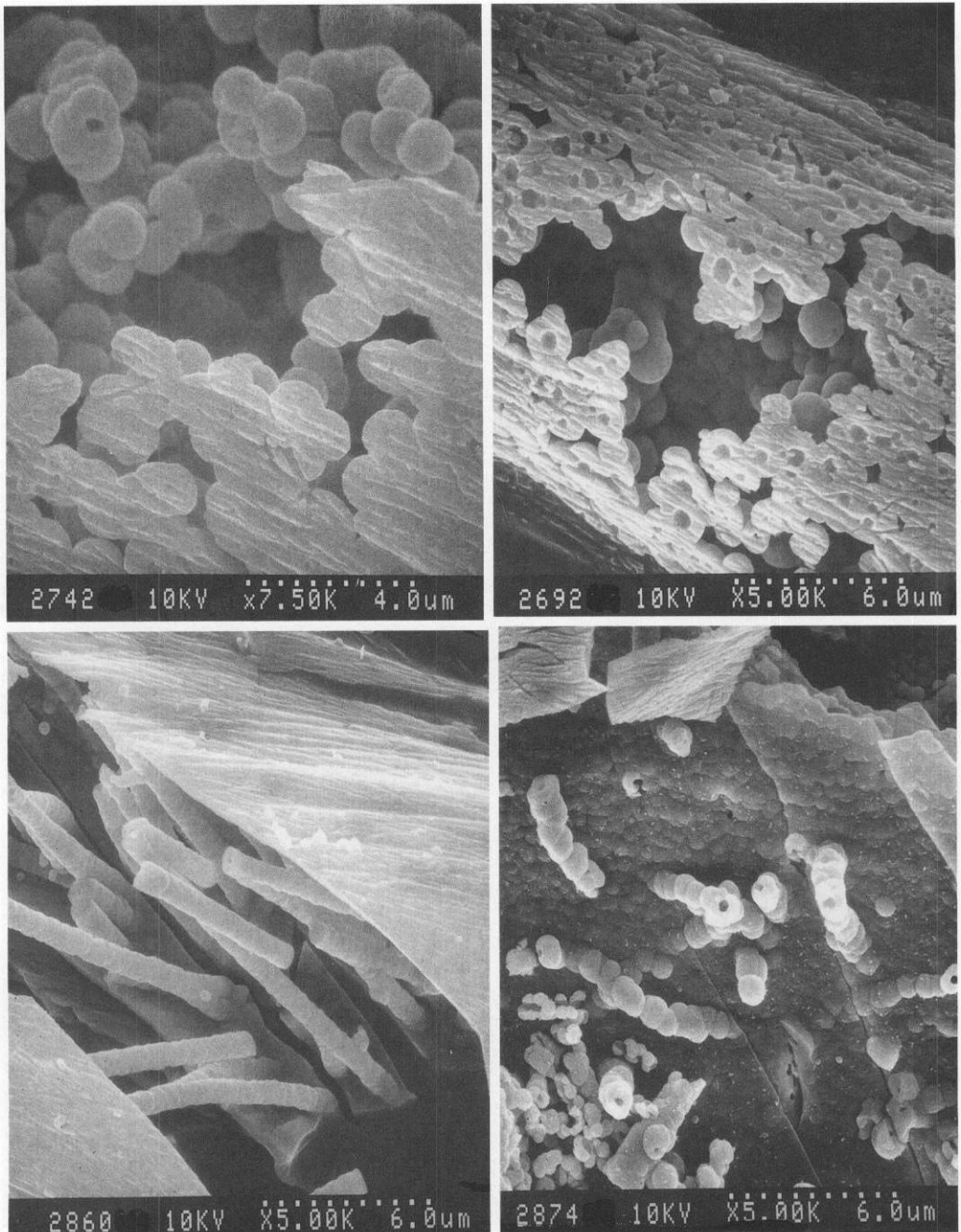


Fig. 19. Morphology of CHAP in Gorgoniidae. Top left, Surface of wall of holdfast locus of *Eugorgia rubens* showing component hemispheres near gap in incompletely mineralized wall and microspheres of interior filaments (SEM 2742); Top right, Surface of wall of holdfast locus of *Eugorgia aurantiaca* showing component hemispheres near gap in incompletely mineralized wall and microspheres of interior filaments (SEM 2692); Bottom left, Break in wall of mineralized holdfast locus of *Pseudopterogorgia australiensis* showing filaments coated with fused microspheres of CHAP forming rod-like structures (SEM 2860); Bottom right, Interior of broken holdfast locus of *Pseudopterogorgia australiensis* showing small microspheres of CHAP forming wall, and strands of uniserial microspheres extending from wall surface (SEM 2874).

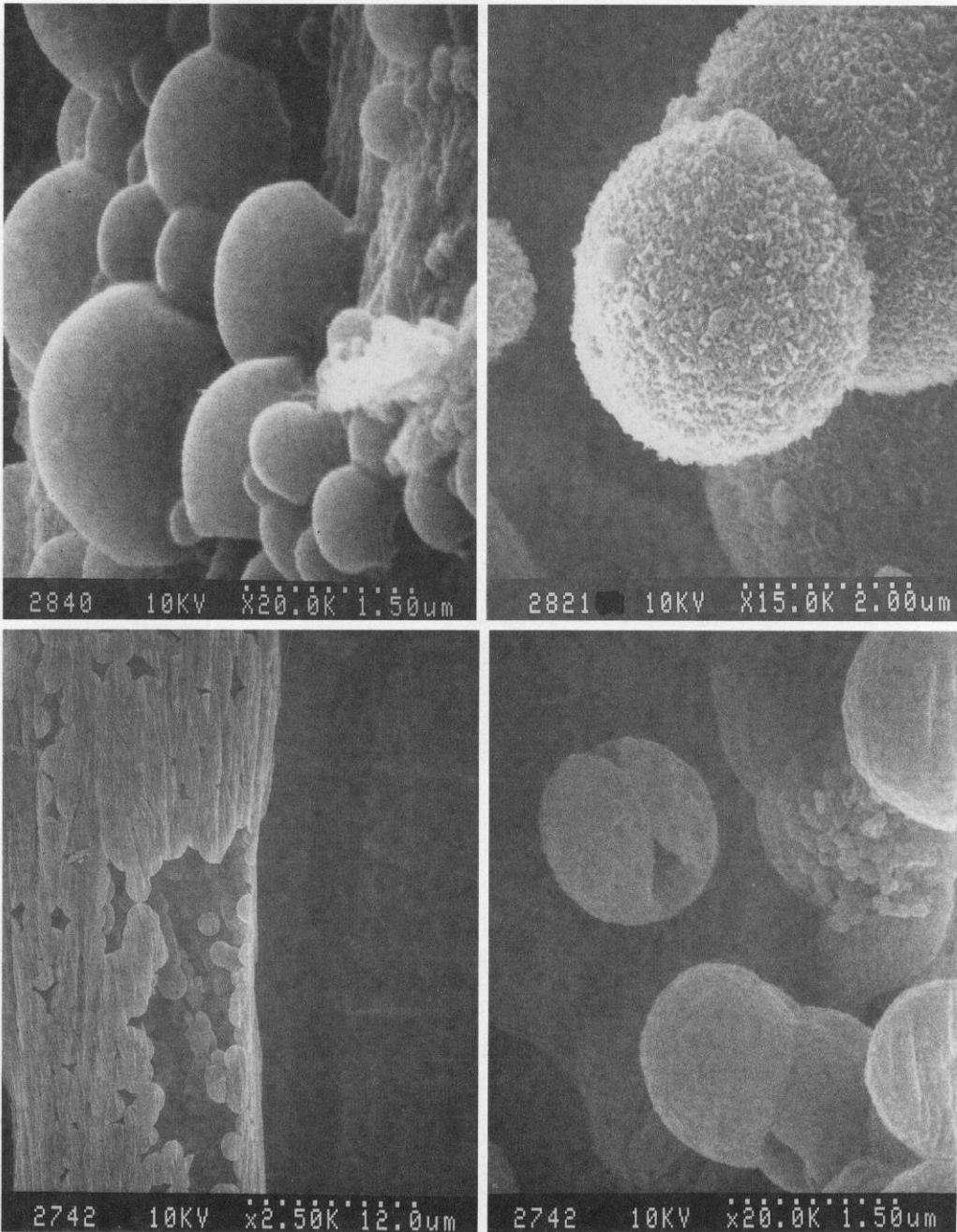


Fig. 20. Morphology of CHAp in Gorgoniidae. Top left, Microspheres of CHAp on wall of axial chamber of *Leptogorgia africana* (SEM 2840); Top right, Microsphere in axial chamber of *Leptogorgia setacea* (SEM 2821); Bottom left, Mineralized loculus of holdfast of *Eugorgia rubens* with incomplete wall consisting of hemispherical microspheres (SEM 2742); Bottom right, Microspheres of *Eugorgia rubens* at higher magnification to show surface texture and spaces formerly occupied by organic filament (SEM 2742).

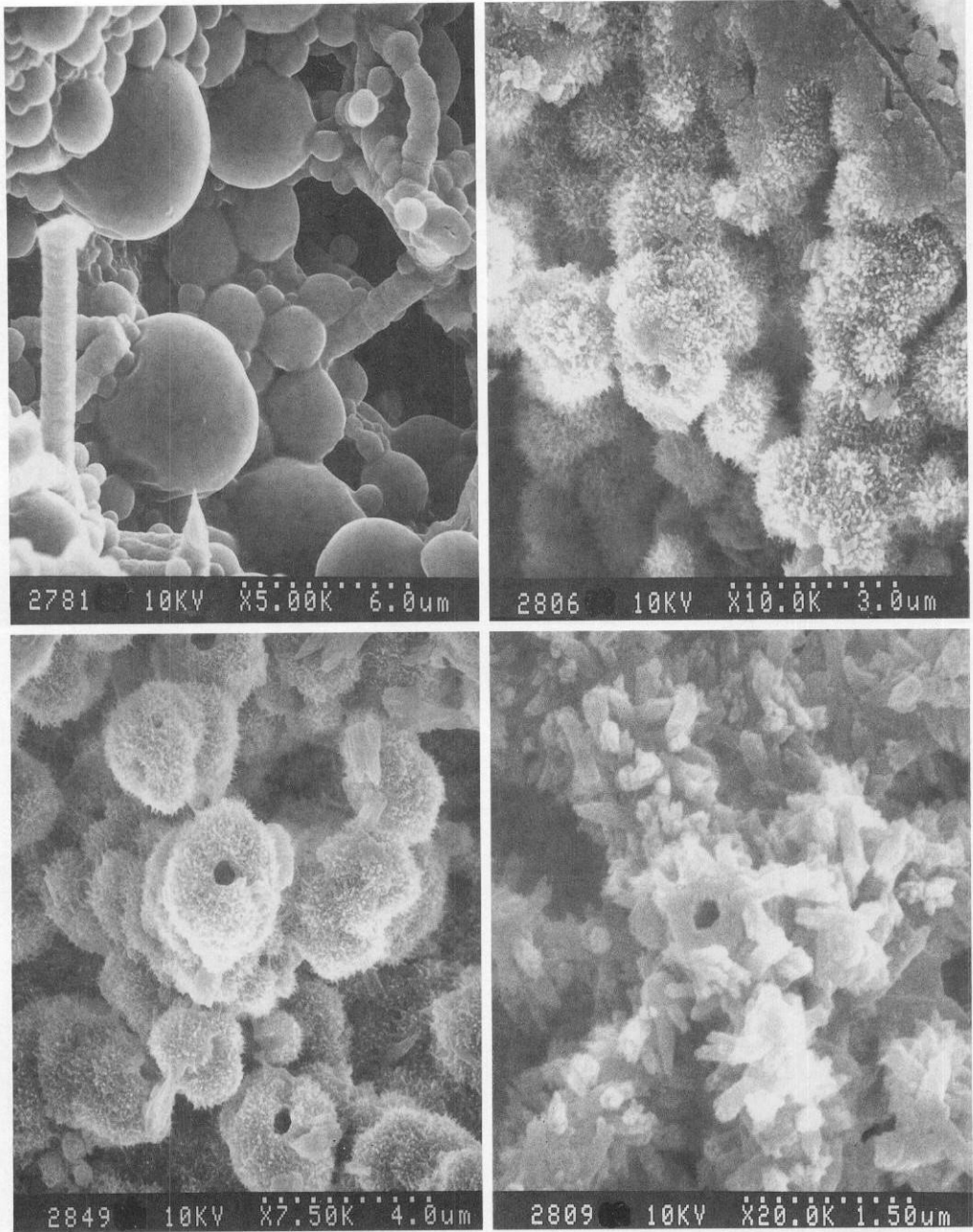


Fig. 21. Surface texture of CHAP in Gorgoniidae: Top left, Smooth microspheres in axial core of *Leptogorgia cardinalis*; Top right, Prickly microspheres in axial core of *Leptogorgia steno*; Bottom left, prickly microspheres in axial core of *Pacifigorgia cribrum*; Bottom right, Thorny surface of CHAP coating filaments of axial core of *Leptogorgia rioudouroi* (SEM 2809).

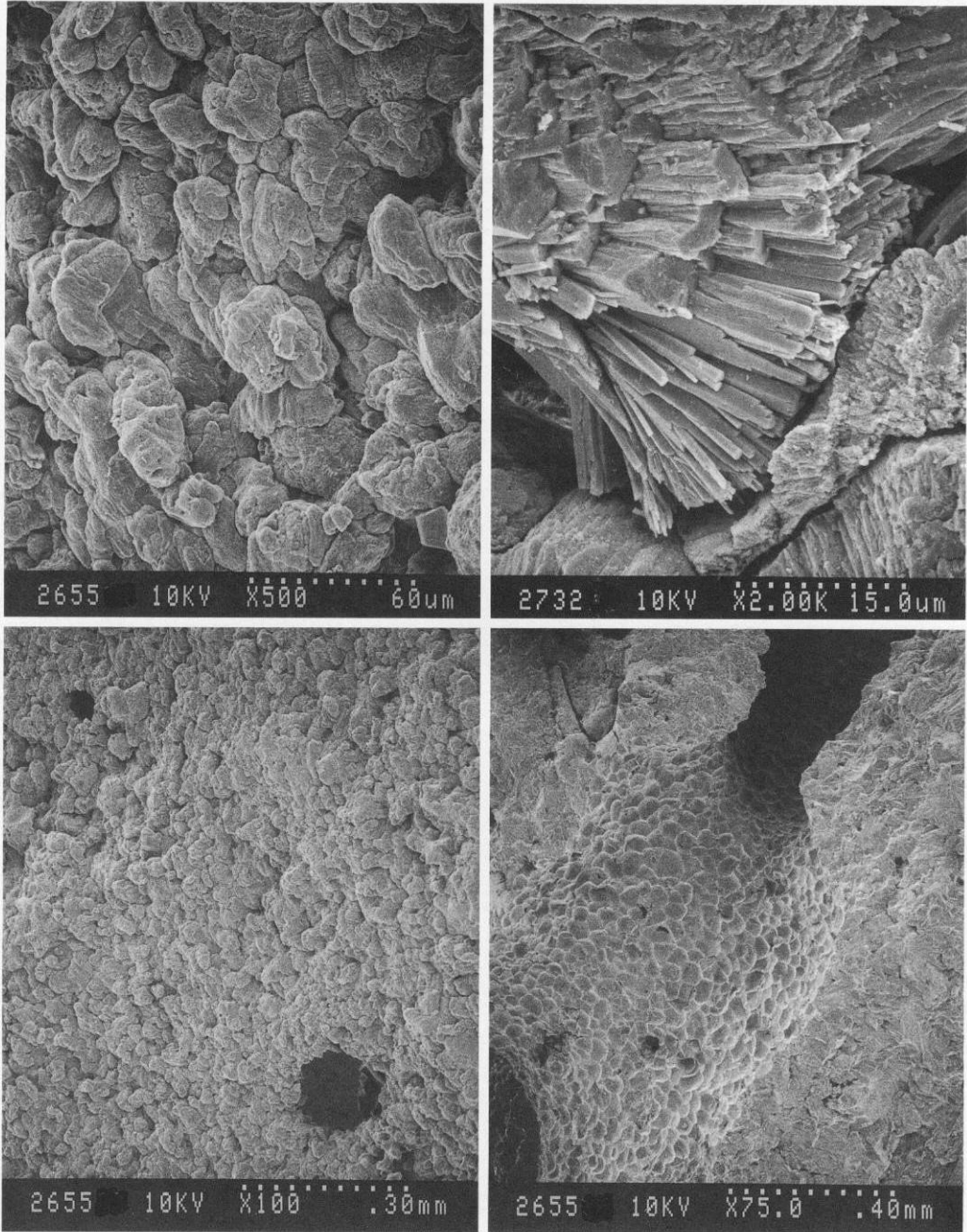


Fig. 22. Mineral of holdfast of *Pterogorgia anceps*: Top left, Surface of holdfast (SEM 2655); Top right, Fracture surface showing aragonite crystals (SEM 2732); Bottom left, Surface of holdfast showing entrance to sponge gallery (SEM 2655); Bottom right, fracture surface showing inner surface of sponge gallery (SEM 2655).

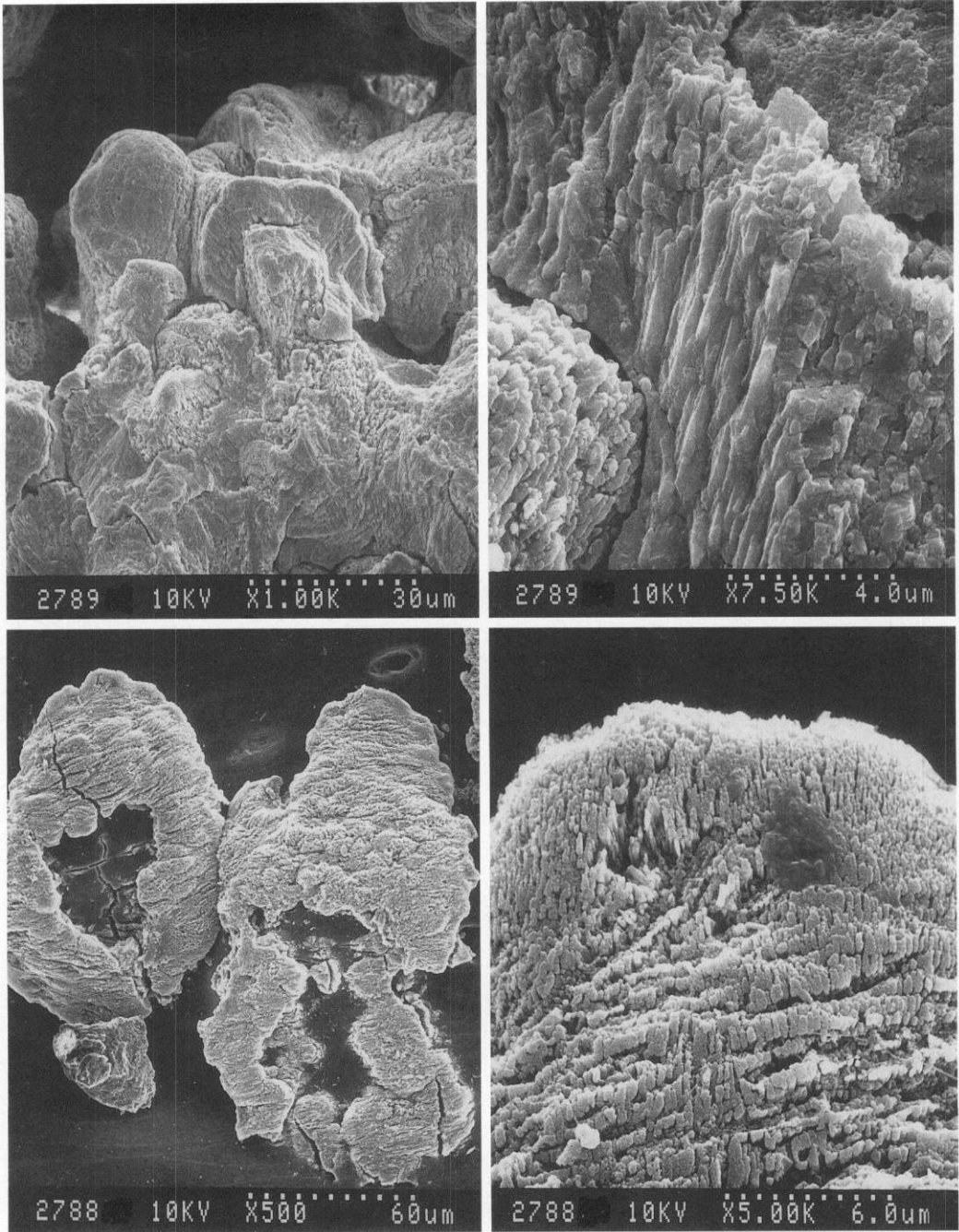


Fig. 23. Mineral of holdfast of *Rumphella aggregata*. Top left, Fracture surface of component granules of Mg-calcite (SEM 2789); Top right, Fracture surface showing calcite crystals (SEM 2789); Bottom left, Incompletely formed granules of calcite on surface of organic lamella near edge of holdfast (SEM 2788); Bottom right, calcite crystals of incomplete granule of holdfast (SEM 2788).

Table 1.—Gorgonian skeletal mineralogy.

Species	Locality/depth	HOLAXONIA	Holdfast	Axis
<i>Keroeides pallida</i> 25366	Hawaii/252–256 m	Keroeidae	not collected	calcite 9.2 mole% MgCO ₃
<i>Acanthogorgia armata</i> 17239	Newfoundland/380 m	Acanthogorgiidae	no mineral	no mineral
<i>Paramuricea placomus</i> 14491	Georgia/644 m	Paramuriceidae	no mineral	no mineral
<i>Swiftia exserta</i> 94393	Bahamas/180–190 m		no mineral	no mineral
<i>Eunicea tourneforti</i> 50275	Florida/reef	Plexauridae	aragonite	no mineral
<i>Muricea muricata</i> 50314	Curacao/reef		not analyzed ²	no mineral
<i>Muriceopsis flavida</i> 14374	Nassau/reef		aragonite	no mineral
<i>Plexaura flexuosa</i> 51769	Yucatan/reef		aragonite	no mineral
<i>Plexaura homomalla</i> 50689	Andros/reef		aragonite	no mineral
<i>Plexaurella grisea</i> 6917	Florida/reef		aragonite	calcite 15.7 mole% MgCO ₃
<i>Plexaurella nutans</i> a/c 322031	Florida/reef		aragonite	calcite 15.7 mole% MgCO ₃
<i>Pseudoplexaura porosa</i> 1629	Florida/reef		aragonite	no mineral
<i>Eugorgia ampla</i> 8967	Baja California/shallow	Gorgoniidae	CHAp	CHAp
<i>Eugorgia aurantiaca</i> 52317	California/shallow		CHAp	CHAp
<i>Eugorgia aurantiaca</i> a/c 16679	Panama/shallow		CHAp	CHAp
<i>Eugorgia rubens</i> 50032	LaJolla, Cal./31–37 m		CHAp	CHAp
<i>Eunicella cavolini</i> 89285	Genoa/39 m		no mineral	no mineral
<i>Eunicella filiformis</i> 82909	Mauretania/35–50 m		no holdfast ¹	no mineral
<i>Gorgonia flabellum</i> 51766	Cozumel/reef		CHAp	CHAp
<i>Gorgonia mariae</i> 93965	Grenada/13 m		CHAp	CHAp
<i>Gorgonia ventalina</i> 55027	Dominican Rep./17–22 m		not analyzed ²	CHAp
<i>Leptogorgia cardinalis</i> 50052	Off Captiva/80 m		not analyzed ²	CHAp
<i>Leptogorgia cardinalis</i> 49711	Off Palm Beach/37 m		calcite ³ 11.4 mole% MgCO ₃	CHAp
<i>Leptogorgia caryi</i> 57157	Str. Juan de Fuca/73 m		no mineral	no mineral
<i>Leptogorgia gilchristi</i> 59824	Mozambique/55 m		not analyzed ²	CHAp
<i>Leptogorgia lemasti</i> 52730	W. Mexico/shallow		CHAp	CHAp

Table 1.—Continued.

Species	Locality/depth	Holdfast	Axis
<i>Leptogorgia rioudouroi</i> 82910	Mauretania/35–50 m	no holdfast ¹	CHAp
<i>Leptogorgia sanguinolenta</i> 82904	Off Ivory Coast/20 m	CHAp	CHAp
<i>Leptogorgia setacea</i> 43245	Virginia/24 m	no holdfast ¹	CHAp
<i>Leptogorgia sihenoi</i> (white) 49781	Off Louisiana/64 m	no holdfast ¹	CHAp
<i>Leptogorgia sihenoi</i> (pink) 49782	Off Louisiana/49 m	no holdfast ¹	CHAp
<i>Leptogorgia sihenoi</i> (pink) 50033	Off Louisiana/55–70 m	no holdfast ¹	CHAp
<i>Leptogorgia styx</i> 98800	NE of Clipperton I/1900 m	CHAp	CHAp
<i>Leptogorgia viminalis</i> 82905	Off Liberia/46–49 m	not collected	CHAp
<i>Leptogorgia virgulata</i> 49690	Apalachee Bay/6 m	CHAp	CHAp
<i>Olindagorgia marcravii</i> 73426	Brazil/3 m	aragonite	CHAp
<i>Pacificigorgia cribrum</i> 1677	C. San Lucas/shallow	CHAp	CHAp
<i>Pacificigorgia media</i> 57905	I. Maria Magdalena/10–12 m	CHAp	CHAp
<i>Pacificigorgia stenobrochis</i> 49366	Panama/shallow	CHAp	CHAp
<i>Pacificigorgia fucata</i> 56886	Chile/45 m	CHAp	CHAp
<i>Phyllogorgia dilatata</i> 5247	Brazil/shallow	CHAp	CHAp
<i>Pseudopterogorgia americana</i> 53582	Belize/4–5 m	not collected	CHAp
<i>Pseudopter. australiensis</i> 82139	W. Australia/8 m	not collected	CHAp
<i>Pseudopter. australiensis</i> 80952	Darwin/weed reef	not collected	CHAp
<i>Pseudopter. australiensis</i> 80953	NW Shelf Australia/37–39 m	CHAp	CHAp
<i>Pseudopterogorgia bipinnata</i> 96216	Eleuthera/7.63 m	aragonite	CHAp
<i>Pterogorgia anceps</i> 50057	Sarasota/2 m	aragonite	no mineral
<i>Pterogorgia guadalupensis</i> 51311	Aruba/reef	aragonite	no mineral
<i>Pterogorgia guadalupensis</i> 52029	St. John, V.I./reef	not collected	no mineral
<i>Pterogorgia citrina</i> 51028	Aneгада/1 m	aragonite	no mineral
<i>Rumphella aggregata</i> 86004	Gilbert Is./2–5 m	calcite 12.7 mole% MgCO ₃	no mineral
CALCAXONIA			
Ellisellidae			
<i>Junceella gemmacea</i> not cat.	Philippines/shallow	calcite 13.8 mole% MgCO ₃	calcite 14.0 mole% MgCO ₃
<i>Ellisella barbadensis</i> 50610	Off Pensacola/75 m	calcite 11.2 mole% MgCO ₃	calcite 11.1 mole% MgCO ₃
Ifalukellidae			
<i>Ifalukella yanii</i> 50142	Caroline Is./3 m	aragonite	aragonite
<i>Plumigorgia hydroides</i> 59811	Cuyo Ids, Sulu Sea/15 m	calcite ³ 11.2 mole% MgCO ₃	aragonite
		calcite ³ 12.3 mole% MgCO ₃	aragonite

Table 1.—Continued.

Species	Locality/depth	Holdfast	Axis
<i>Chrysogorgia spiculosa</i> 52851	Key West/1281 m Georges Bank/3259 m	calcite 6.4 mole% MgCO ₃ calcite 8.3 mole% MgCO ₃	calcite 11.7 mole% MgCO ₃ calcite 8.3 mole% CO ₃
<i>Radictypes gracilis</i> 11913			
<i>Ainigmipatilon edisto</i> 54491	Ross Sea/611 m	calcite 6.4 mole% MgCO ₃ calcite 5.9 mole% MgCO ₃ aragonite	calcite 10 mole% MgCO ₃ calcite 9.8 mole% MgCO ₃ aragonite
<i>Ainigmipatilon antarcticum</i> 82871	S. Shetland Is./88–112 m		
<i>Calyptrophora trilepis</i> 57445	Blake Plateau/814 m	aragonite calcite 9.9 mole% MgCO ₃ calcite 6.3 mole% MgCO ₃ aragonite	calcite 13.8 mole% MgCO ₃ calcite 7.9 mole% MgCO ₃ aragonite
<i>Candidella</i> sp. 56774	Hawaii/374 m		
<i>Fanella tuberculata</i> 30029	Japan/187 m	calcite 6.9 mole% MgCO ₃	calcite 7.9 mole% MgCO ₃
<i>Fanyella rossii</i> 77360	Antarctic Peninsula/110 m		
<i>Narella</i> n. sp. a/c 272779	Hawaii/ca. 250 m		
<i>Primmoeella scottiae</i> 77370	Argentina/ca. 400 m		

¹ Colonies lie prone on soft substrate, not forming a holdfast.

² Not analyzed because holdfast could not be separated from substrate.

³ Probably contamination from substrate.

which, in some cases, is extensively perforated by a boring sponge. The mineral is deposited in the form of irregular granules that fuse into a solid mass (Fig. 22 top left); fracture surfaces clearly reveal the aragonite crystals of the component granules (Fig. 22 top right). The outer surface of the mineralized holdfast is granular, with pores opening into the sponge galleries (Fig. 22 bottom left), the walls of which show the usual pitted surface characteristic of sponge borings (Fig. 22 bottom right).

The axis of the Indo-Pacific genus *Rumphella* has no mineral component but the holdfast is reinforced with massive crystalline CaCO_3 . Unlike the case in *Pterogorgia*, the mineral form is Mg-calcite containing 12.7 mole% magnesium carbonate. The surface of the mineralized holdfast is coarsely granular as is the case in *Pterogorgia* but the individual granules are more distinctly separated, stacked one upon another and fusing proximally (Fig. 23 top left); fracture surfaces reveal the orientation of the calcite crystals (Fig. 23 top right). The surface of a holdfast near what must have been an actively thickening margin shows incompletely formed nodules (Fig. 23 bottom left) composed of crystalline Mg-calcite (Fig. 23 bottom right) on the surface of the organic lamella.

Conclusion

This detailed study of the skeletal mineralogy of axes and holdfasts of 58 species of Gorgonacea further documents the presence of aragonite (Lowenstam 1964), amorphous carbonate hydroxylapatite (Macintyre et al. 2000), and Mg-calcite (Lowenstam 1964) in these structures. In contrast, octocoral sclerites as far as known are composed of Mg-calcite (Chave 1954, Lowenstam 1964, Milliman 1974). Apatite, though unusual in modern invertebrates, is said to be common in invertebrates in the fossil record. Hence, Macintyre et al. (2000) interpreted its occurrence in the family Gorgoniidae to be a vestige of an earlier history

of phosphatic skeletal mineralization among coelenterates.

The distribution of skeletal minerals in the various octocoral species studied suggests that the patterns are taxonomically rather than environmentally controlled. This is particularly well demonstrated by the enigmatic occurrence of carbonate hydroxylapatite, which is found only in the family Gorgoniidae over its entire geographic and bathymetric ranges. It also raises the question about the significance of mineralogical differences among genera and species in one family traditionally defined on the basis of morphological characteristics.

The possible relationship between skeletal mineralogy in the axes and holdfasts of octocorals and their taxonomy could prove to be useful in resolving problems in octocoral systematics. Future descriptions of octocoral species should therefore consider the mineralogy that may exist in axes or holdfasts.

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