

New subfamilies and a new genus and species of Melithaeidae (Coelenterata: Octocorallia: Alcyonacea) with comparative data on the structure of both melithaeid and subergorgiid axes

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Abstract

Asperaxis karenae, a new genus and new species of the gorgonian family Melithaeidae, is described. The coenenchymal sclerites of the new genus bear similarities to those of *Acabaria*, but the axis is quite different from that which is characteristic of the family. The axial sclerites are rods and sticks, often sinuous and branched, with simple, sparse, tubercles. The internodes may be whole or partial, and are not clearly delimited from the internodes. A new subfamily, Asperaxinae, is proposed to accommodate any taxa with the new axial characters, and the Melithaeinae for the existing nominal taxa. The structure of both axial forms and the subergorgiid axis are illustrated with scanning electron micrographs.

Key words: Coelenterata, Cnidaria, Octocorallia, Alcyonacea, Melithaeidae, *Asperaxis*, new genus, new species, Melithaeinae, Asperaxinae, *Subergorgia*, *Annella*, Tasmania, Australia

Introduction

Owing to a large overlap of spicular characters, delineation of generic boundaries in the gorgonian family Melithaeidae has troubled octocoral taxonomists for a very long time (eg. Wright & Studer, 1889: 172; Hickson, 1937: 89 [with some history]; and Bayer, 1981: 917–919 [who commented that four out of the five nominal “genera probably do not merit even subgeneric status”]). Since 1870, none of the new genera proposed to be included in the family (eg. *Psilacabaria* Ridley, 1884; *Berotulata* Nutting, 1911) have avoided becoming synonymised, with only five nominal genera (*Melithaea*, *Mopsella*, *Wrightella*, *Clathraria*, *Acabaria*) generally being recognised until Grasshoff (1999, p. 7) distinguished three genera and then (2000, p. 12) four genera. Grasshoff and Bargibant (2001, p. 83) also distinguished four.

The specimens upon which the new taxon is based are from the island state of Tasmania, off southeastern Australia, and the introduction of a new genus into the family is made possible by virtue of its distinct axial structure. Melithaeids are currently characterised as having an axis composed of alternating long internodes and short nodes, both of which include short, smooth, rod-shaped sclerites (commonly with a median girdle of tubercles), inseparably fused in the internodes and separable in the nodes. The new taxon also has an axis constructed of nodes and internodes that include sclerites, but the node/internode articulations are not discrete and the sclerites are very different from those found in the currently recognised genera. Branching, however, still occurs from the nodes as in the established genera, and there are a number of constructional characteristics of the axis that are similar to those of the nominal genera. For this reason the new genus is placed in the Melithaeidae, but because axial architecture is the main character on which scleraxonian families are separated, a division into two subfamilies is proposed.

Materials and methods

Most of the samples were collected by Karen Gowlett-Holmes and were loaned for this project by the South Australian Museum (SAM). Two other samples, one collected by Karen Gowlett-Holmes and one by Graham Edgar, were donated to the Museum and Art Gallery of the Northern Territory (MAGNT). Axial fragments were sputter-coated with gold and photographed on a Jeol 5610LV scanning electron microscope. The non-calcareous nodal material was totally or partially removed from the fragments using sodium hypochlorite solution. Decalcified colony fragments were prepared in a mixture of 50% formic acid and 15% sodium citrate. Mallory-Heidenhain rapid one-step stain was used to differentiate gorgonin (red) from mesogloea (blue) in hand-cut sections.

Unlike the nodes in the current nominal genera, those in the new taxon tend not to be conspicuously thicker than the adjoining internodes and are difficult to locate. Their presence can be detected without destructive decortication if the colony portions are immersed in clear fluid and viewed with a stereomicroscope using dark-field illumination. Care must be taken to avoid mistaking the silhouettes or shadows of polyps on the undersides of branches for nodal material.

The images of individual sclerites in figures 11–15 were made using the extended focal image software “Auto-Montage”, published by Syncroscopy. This software was previously trialled in Alderslade 2002 & 2003 and has proven to be an excellent illustration tool for octocoral taxonomy. It allows multiple images taken in different focal planes to be montaged into a single fully focussed image, so eliminating most depth-of-field problems. The software can be utilised manually to combine individually taken images, or it can be automated. In the automated mode, the software controls the digital camera (in this case, JVC KY-F1030) and a motorized focussing system (in this case, STY-Z-SYSCAN) to rapidly take and capture between 1 and 256 images over any set focal range. The method has

certain advantages over drawing and low-magnification scanning electron microscopy (SEM). With regards to drawing, it is independent of the researcher's artistic skill, and the results may be more similar to the view obtained via a light microscope—the latter may also apply to SEM images. When automated, the method is very time-efficient, and there is no need to wash, dry, and mount sclerites as is required for SEM—tissue samples macerated in bleach can be used straight away. There is arguably another major advantage over SEM, and that is the ability to more accurately reflect the range of variation of sclerite form. With a slide preparation and a light microscope, many hundreds of sclerites can easily and rapidly be assessed (repeatedly if needed) and selected for photography. The final images do require some adjusting and cleaning using digital image editing software (as do those from SEM).

MELITHAEIDAE Gray, 1870

Amended diagnosis. Fan-like or bushy gorgonians with a jointed axis of alternating flexible nodes and rigid internodes, both incorporating sclerites. Internodes constructed predominantly from sclerites embedded in a crystalline calcitic matrix and possessing a 3-dimensional lattice-like central core. Nodes whole or partial, containing sclerites held together with gorgonin to form a meshwork whose interstices are filled with mesogloea. Branching occurring predominantly from the nodes. Polyps monomorphic and able to completely retract into the coenenchyme or into prominent calyces. Polyps armed with collaret and points, and tentacles with crescentic “dragon-wing” scales. Coenenchymal sclerites include spindles, leaf clubs, foliate spheroids, double discs, birotulates, and capstans. Axis sclerites include short, straight rods that commonly have a median girdle of simple tubercles, or rods and sticks that are often sinuous and branched and possess simple, sparse, tubercles.

Type genus: *Melithaea* Milne Edwards & Haime, 1857

MELITHAEINAE new subfamily

Diagnosis. Melithaeids with axial sclerites in the form of short, straight rods that commonly have a median girdle of simple tubercles. Nodes generally conspicuous, even when covered in coenenchyme, and node-internode articulations relatively well delimited. Internodal sclerites longitudinally arranged and embedded in a matrix of subhedral calcite rods. Nodal sclerites each encased in a gorgonin sheath which bonds where the ends of the sclerites touch to form a relatively regular, polyhedral latticework whose multitudinous interstices are filled with mesogloea. Polyps with a well-defined collaret and points arrangement constructed from a relatively small number of large sclerites.

Type genus: Melithaea Milne Edwards & Haime, 1857, here designated.

ASPERAXINAE new subfamily

Diagnosis. Melithaeids with axial sclerites in the form of rods and sticks that are often sinuous and branched and possess simple, sparse, tubercles. Nodes whole or partial, inconspicuous when covered in coenenchyme, poorly delimited from the internodes, and soft and pale in colour owing to a low proportion of gorgonin relative to scleritic calcite. Sclerites within the internodes embedded in a matrix of subhedral calcite rods. Sclerites of the surface of the internodes (occasionally including a few coenenchymal sclerites) anastomosing and only partly embedded in the matrix, commonly forming longitudinal ridges. Outer nodal sclerites often forming continuations of the internodal ridges. Nodal sclerites each encased in a gorgonin sheath that is continuous where they come together, often in groups, forming a very irregular meshwork whose interstices are filled with mesogloea. Polyps armed with numerous small sclerites.

Type genus: Asperaxis new genus, here designated.

***Asperaxis* new genus**

Diagnosis. Internodes with a hollow central core containing a calcareous 3-dimensional latticework surrounded by a dense, thick, calcareous wall constructed from sclerites that are partially or totally embedded in a matrix of subhedral calcite rods. Nodes full or partial, not clearly delimited from the internodes but permeating the contiguous internodal structure, and consisting of sclerites united in an organic matrix of gorgonin and mesogloea. Internodal sclerite forms composed of rods, often sinuous and branched, with simple, sparse, tubercles. Nodes containing similar sclerite forms along with small irregular rods with thickened tuberculate ends.

Polyps retractile into prominent calyces, and armed with collaret and points; the collaret poorly developed and essentially formed from the merging of the of the near-horizontal proximal point sclerites. Pinnules and tentacle rachis containing scales. Calyces and coenenchyme with rods and spindles that are ornamented with large, complex tubercles.

Colonial branching from the nodes producing small bushy colonies that may have more than one point of attachment to the substratum. Branches commonly sinuous. Nodes rarely thicker than the internodes, sometimes crowded together and many occurring at places other than points of bifurcation.

Type species. Asperaxis karenae n.sp. by original designation.

Etymology. The generic name is derived from the Latin words *asper*, uneven or rough, and *axis* alluding to the very irregular form of the colonial axis. Gender masculine.

Remarks. It is important to note that *Asperaxis* could be mistaken for *Acabaria* if the detail of the axis is overlooked.

Asperaxis karenae new species (Figs 1–15)

Material examined. **Holotype:** NTM C14986, Mundy Island, Bathurst Channel, Port Davey, Tasmania, Australia, depth 4–6 m, K. Gowlett-Holmes, 13 April 2002.

Paratypes: NTM C13575, same data as holotype; NTM C14987, Sarah Island, Bathurst Channel, Port Davey, depth 8 m, G. Edgar, 20 March 1998; SAM H1397, Sarah Island, Bathurst Channel, Port Davey, depth 5–12 m, rock slope to mud bottom, WEB station 1, K. Gowlett-Holmes, W. Zeidler, F.A. Bavendam, 3 April 1993; SAM H1398, Schooner Cove, off Forrester Point, Bathurst Channel, Port Davey, steep wall, mud bottom, depth 3–18 m, WEB station 2, K. Gowlett-Holmes, W. Zeidler, F.A. Bavendam, 2 April 1993; SAM H1399, same data; SAM H1400, Cathedral Cave, Waterfall Bay, Tasman Peninsula, Tasmania, depth 15–18 m, growing over phidoloporid bryozoan on rock wall, K. Gowlett-Holmes, 29 October 1994; SAM H1401, Patersons Arch, Waterfall Bay, Tasman Peninsula, depth 10–13 m, on rock wall, K. Gowlett-Holmes, 17 September 1995.



FIGURE 1. *Asperaxis karenae* n. gen., n. sp., holotype NTM C14986 & paratype NTM C13575, *in situ* with a colony of the bryozoan *Triphyllozoon floribundum* (photo: K. Gowlett-Holmes).

Description. The holotype is a fragile, bushy, rather sparsely branched, 60 mm high colony (Figs 1–2A). The very short, slightly flattened main stem is of uneven thickness with broadest diameter of 4.4 mm. It arises from a small 13 x 6 mm holdfast and immedi-

ately divides into two major branches, 2.2 mm and 2.4 mm in diameter respectively. One of these gives rise to a lateral branch that is overgrown by sponge for most of its length.

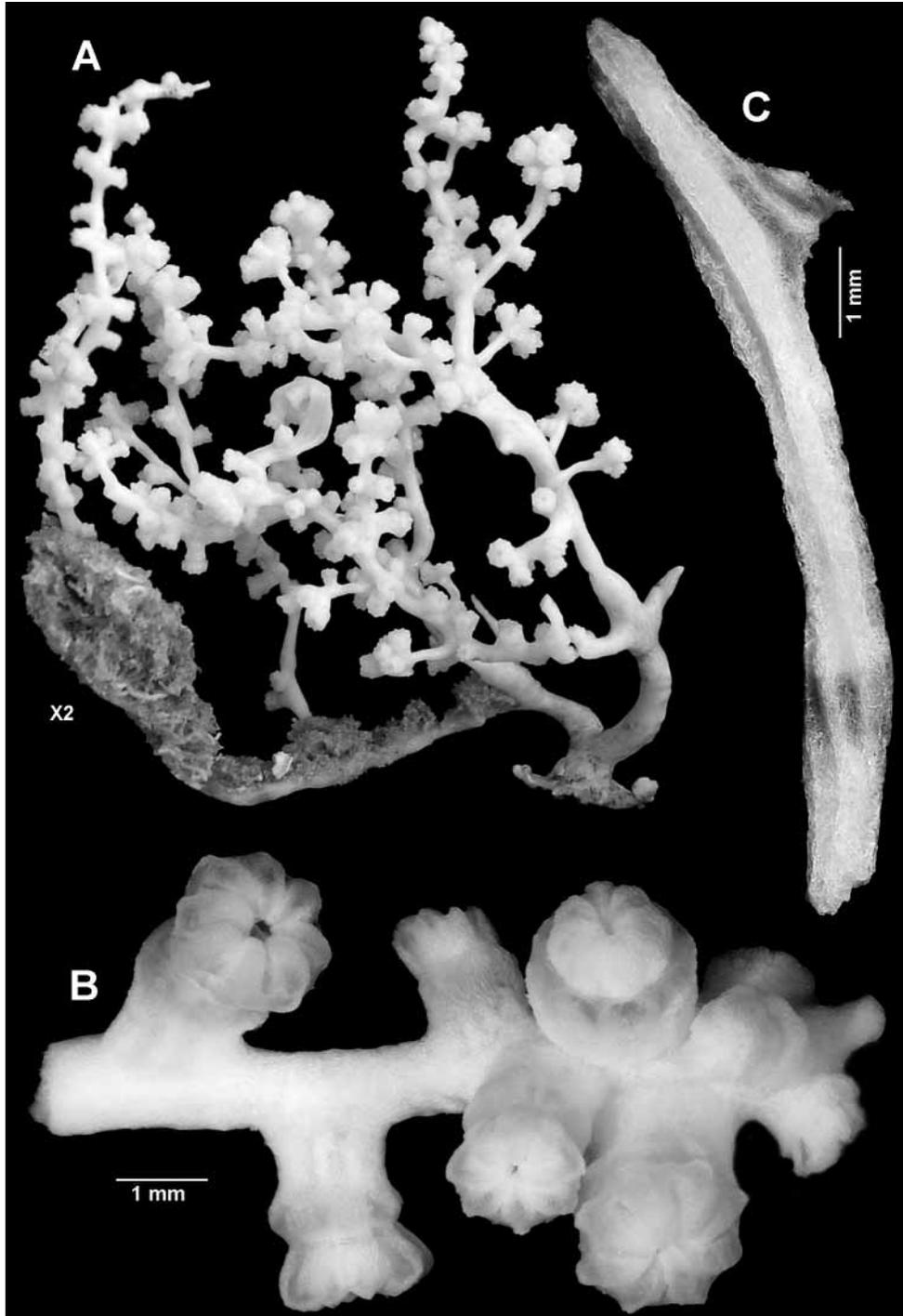


FIGURE 2. *Asperaxis karenae* n. gen., n. sp., holotype: A, colony; B, polyps clustered on twig tip; C, light photograph of decorticated axis fragment.

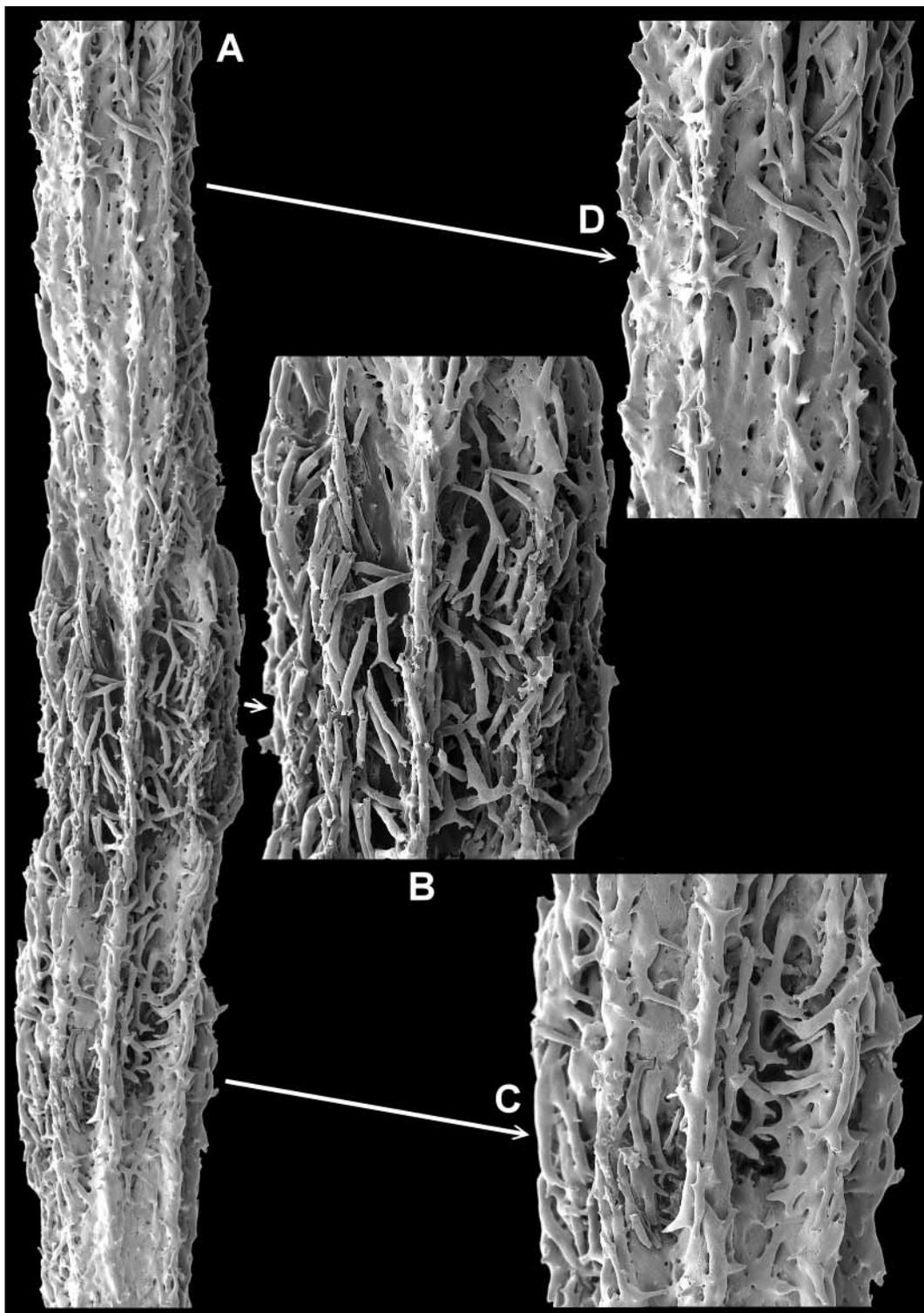


FIGURE 3. *Asperaxis karenae* n. gen., n. sp., holotype, axis: A, internodes and nodes; B, close-up of a whole node; C, close up of a partial node; D, close up of part of an internode.

Branching in the colony is irregularly lateral to the third order, with terminal twig lengths varying from about 5–35 mm in length and 0.75–1.6 mm diameter. Nearly every twig terminates in a cluster of polyps (Fig. 2A, B). Branching may arise at an acute angle or is more or less perpendicular, and the branches are sinuous.

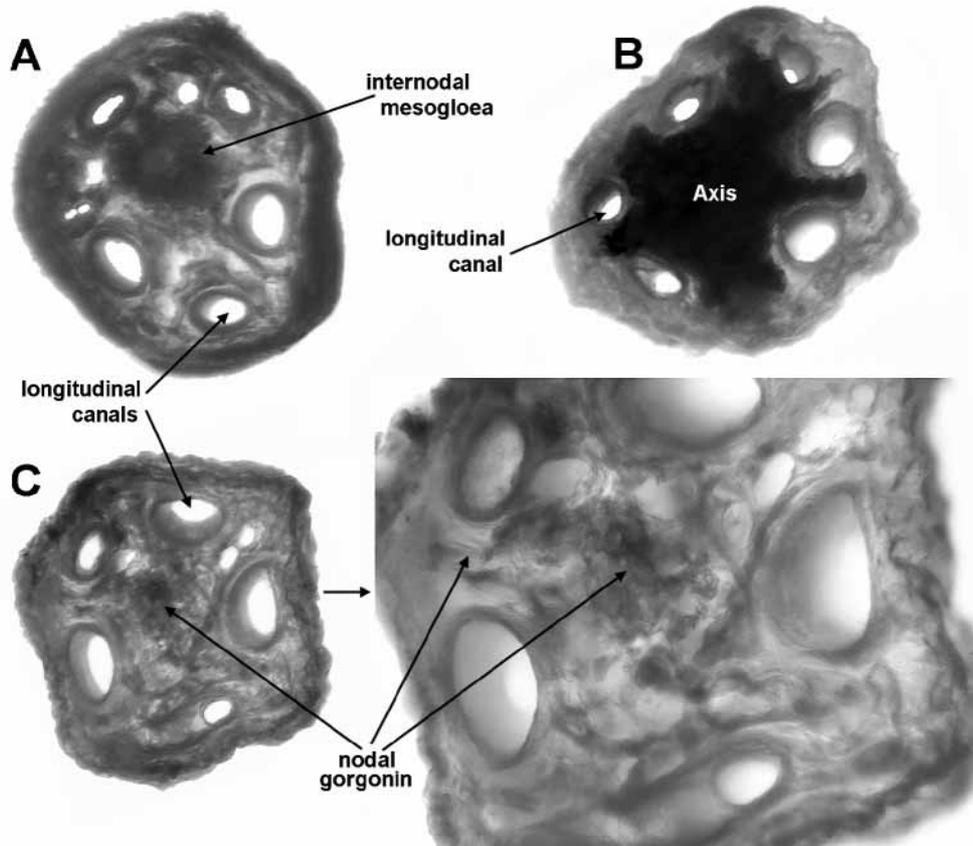


FIGURE 4. *Asperaxis karenae* n. gen., n. sp., holotype, decalcified twig cross-sections: A, internode region, showing mesogloea remnants; B, partially decalcified section through internode region showing axis and longitudinal canals; C, nodal region with close-up showing gorgonin remnants.

The axis consists of hard calcareous internodes and softer organic nodes, both of which incorporate sclerites (Figs 2C, 3). The internodes are formed from sclerites wholly or partially embedded in a matrix of subhedral calcite rods (Fig. 5). In some portions of the internodes, apparent imperfect or ongoing infilling with calcareous matrix has left the axis penetrated by numerous holes or canals. The internodal sclerites are mostly stick-like, sparsely tuberculated, often sinuous and often branched (Fig. 11A) (and coenenchymal sclerites are occasional included; see Fig. 6Ea). On the outside of the internode they are partially embedded, commonly anastomosing and usually gathered into longitudinal ridges although they may cover much of or all the surface (compare Figs 3 & 9A). Large

longitudinal canals run through the coenenchyme between the axial ridges, as can be seen in the thick, partially decalcified section in Fig. 4B. The interior of the internode is partly hollow and contains a 3-dimensional latticework of anastomosing tuberculate spindles that is penetrated by mesogloea (Figs 4A; 9C,D). Figure 5A depicts a longitudinal section through part of an internode, clearly showing part of the core lattice. The presence of embedded sclerites in the solid parts of the axis are not obvious from this aspect, as can be seen in the close-up (Fig. 5C), because the calcite rods from which they are constructed blend so well with those of the matrix. They can, however, easily be seen in a cross-sectional view, as depicted in Figure 9E, F.

Internodes begin in the tips of terminal twigs as an aggregation of both free and anastomosed sclerites. Infilling of the axis with the calcite matrix increases proximally. A growing terminal internode of a paratype is shown in Fig. 6A. The actual tip of this sample collapsed during processing with sodium hypochlorite to remove the coenenchyme. Figure 6F shows the tip of another twig axis processed for less time; the tuberculate spindles in the centre (Fig. 6Fa) were presumably destined to be incorporated into the trabecular core of the internode. Figure 6D shows the cavity left where a small partial node has been dissolved.

Nodes may be whole (ie. completely divide a branch portion into separate internodes as in Figs 3B; 7E) or they may be partial. Partial nodes vary from those that almost completely separate internodes to those that are exceedingly small and inset into the side of an internode (Figs 3C; 6D; 7A–D). There is no distinct boundary between nodes and internodes. At the juncture, the end of the internode consists of an irregular arrangement of partially embedded, protruding sclerites between which the nodal material has been deposited; figure 9B shows a very short, complete internode. Partial nodes are similar in that the solid internodal material gives way to partially embedded sclerites (Fig. 7A,B). Nodal sclerites appear to be the same as the stick-like internodal forms with the addition of short rods with thickened tuberculate ends (Fig. 7D). On the node surface these sclerites are often seen to be aggregated in such a way as to form continuations of the internodal sclerite ridges, and some anastomoses may occur; see Fig. 3B (whole internode) and Fig. 3C (partial internode). Within the node, sclerites are held in an organic matrix. The sclerites are sheathed in gorgonin, which binds them together leaving interconnected cavities containing mesogloea (Fig. 8A–C).

Branches arise from large, whole or partial nodes that are mostly inconspicuous (especially on thin branches) as they are commonly more or less the same thickness as the adjoining internodes. Nodes are also present in non-branching sections, and there may be a number of them crowded between points of bifurcation. They can be slightly swollen relative to the internodes, but this may not be reflected in a notable increase in branch thickness unless on thick basal branches. Internode length is estimated to vary from 0.75–10.00 mm, and nodes can be at least 1.5 mm long. The range of length of axial segments is difficult to accurately ascertain because the process is destructive.

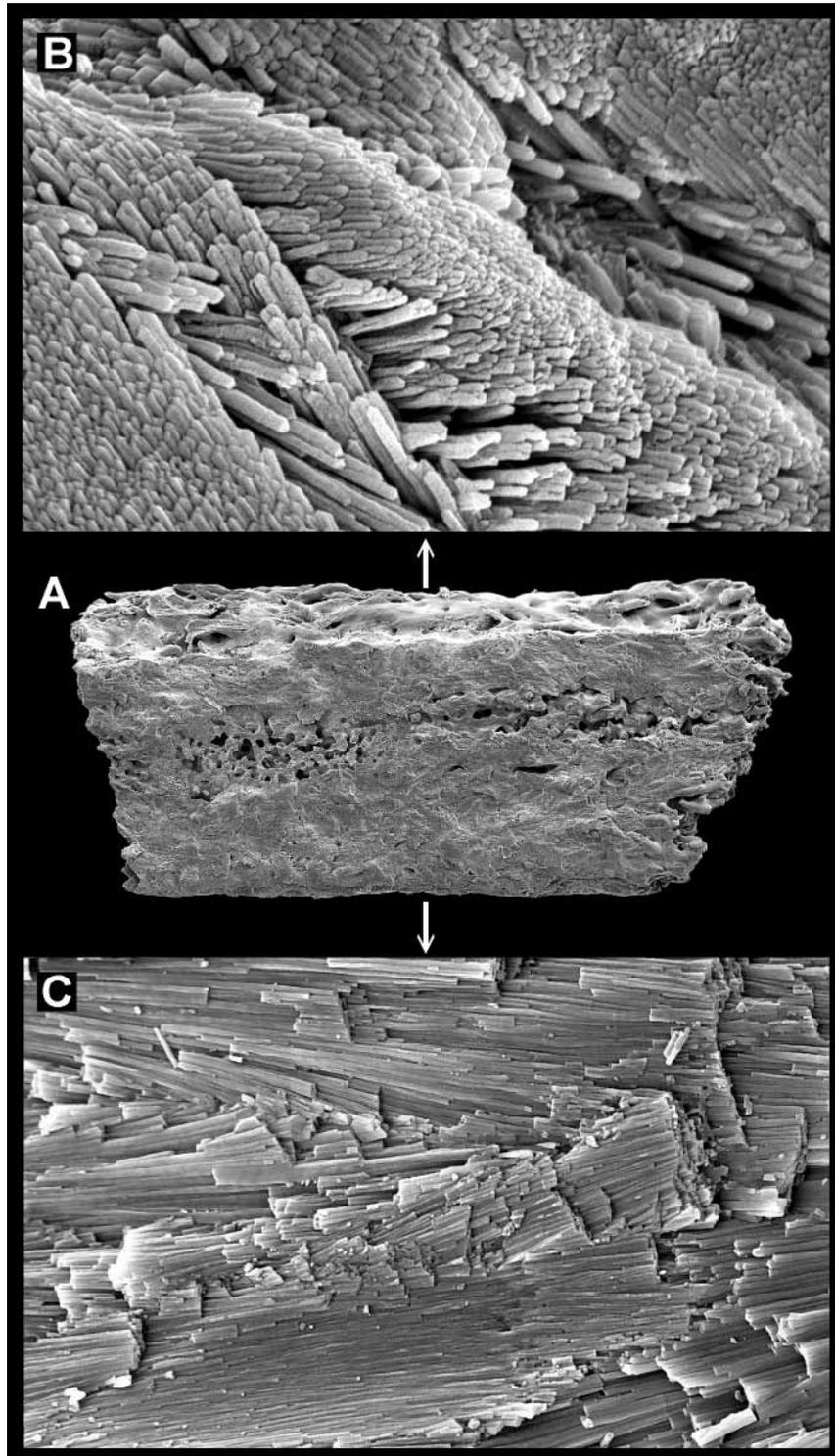


FIGURE 5. *Asperaxis karenae* n. gen., n. sp., holotype, axis: A, longitudinal section through internode fragment; B, close-up of calcite matrix on internode surface; C, close up of calcite matrix from internode interior.

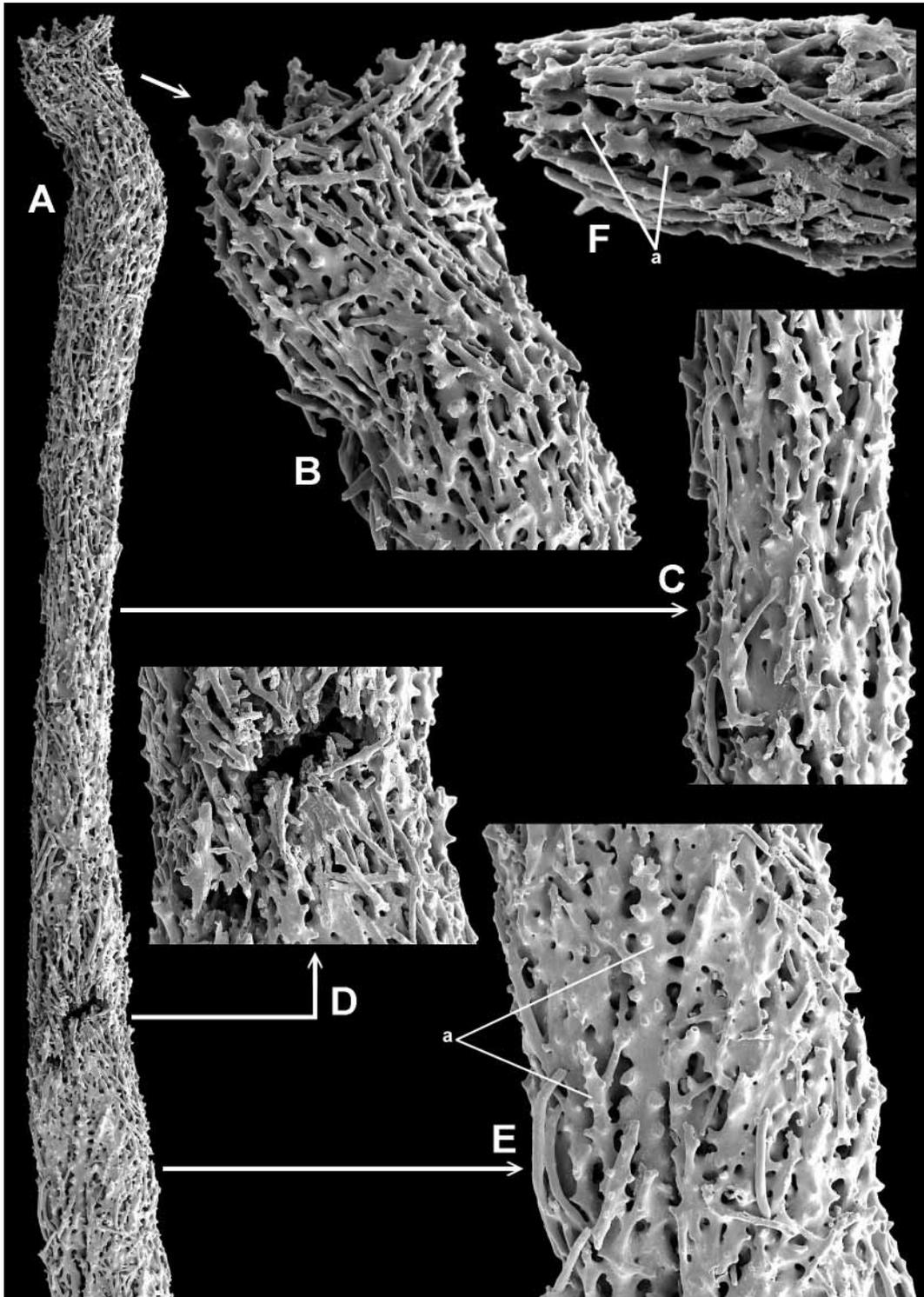


FIGURE 6. *Asperaxis karenae* n. gen., n. sp., developing axis: A–E, holotype; A, from distal portion of twig; B, close-up of region near tip; C–E, close-ups of older portions, with D showing cavity remaining from a dissolved partial node; F, paratype SAM H1398, axis tip.

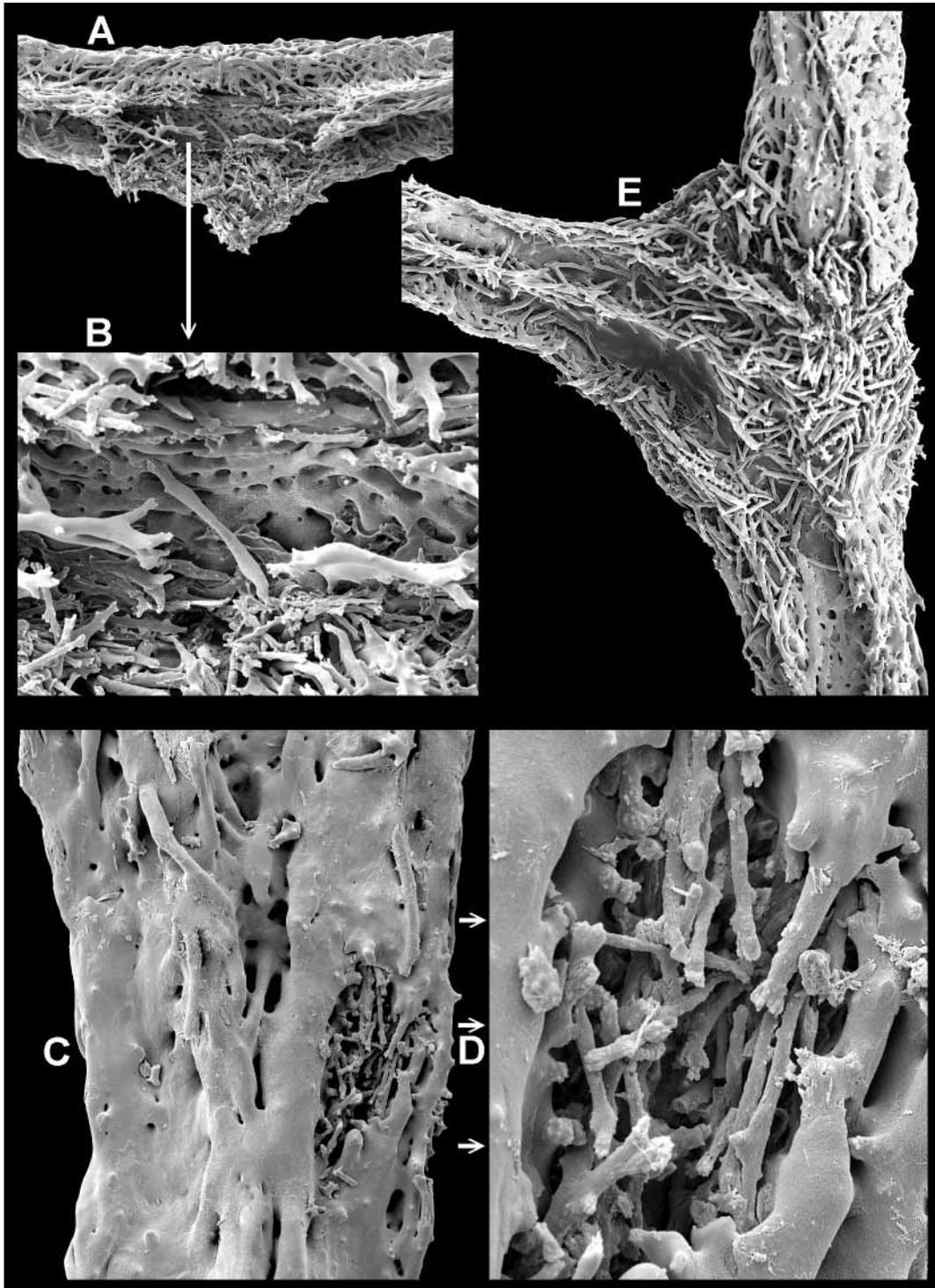


FIGURE 7. *Asperaxis karenae* n. gen., n. sp., holotype: A–B, C–D, cavities left by dissolved partial nodes; E, branching node.

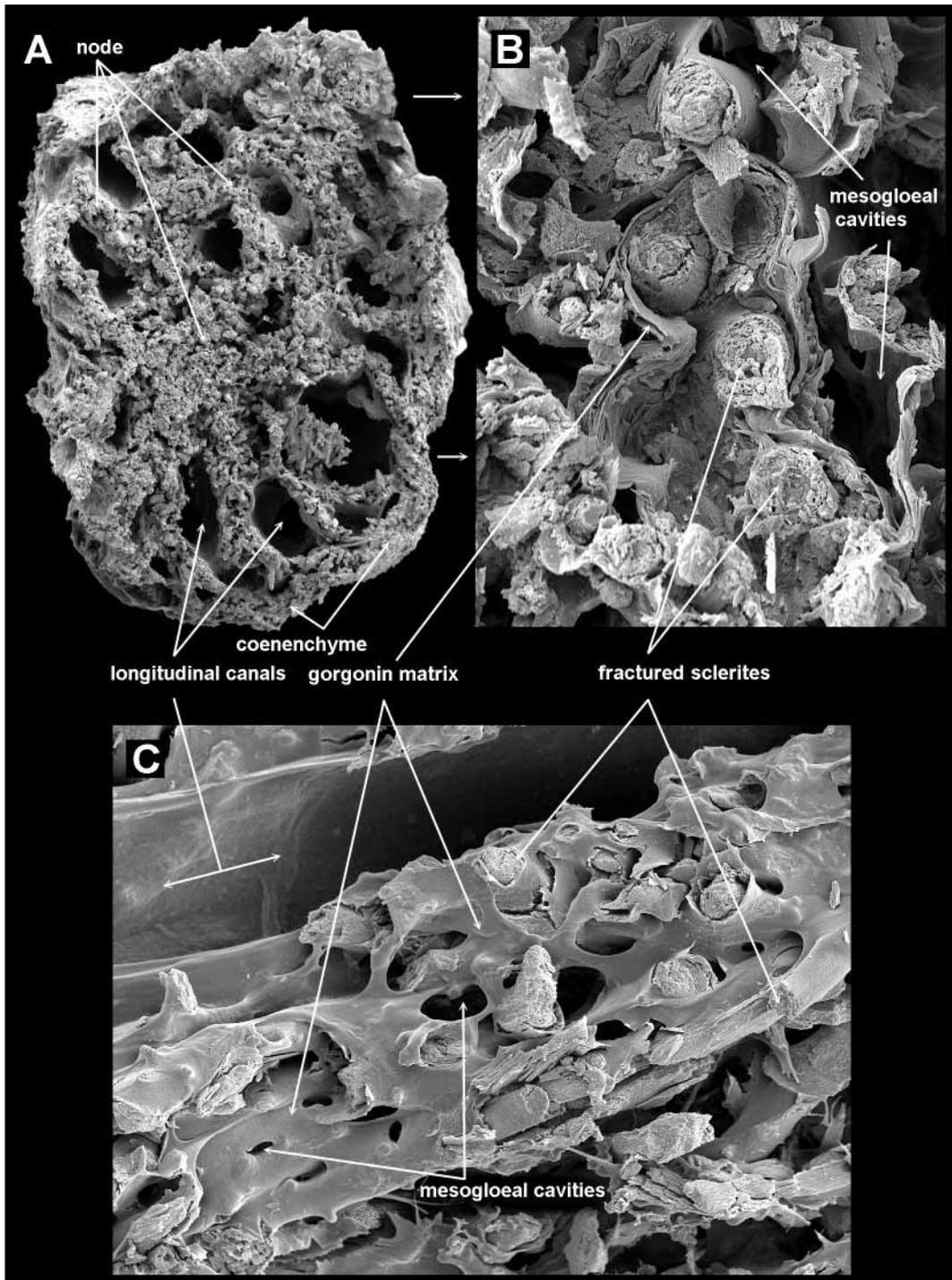


FIGURE 8. *Asperaxis karenae* n. gen., n. sp., paratypes: A–B, SAM H1400, cross section through node with close-up of nodal sclerites with gorgonin sheaths; C, NTM C14987, longitudinal section through a node showing nodal sclerites held within sheathing gorgonin.

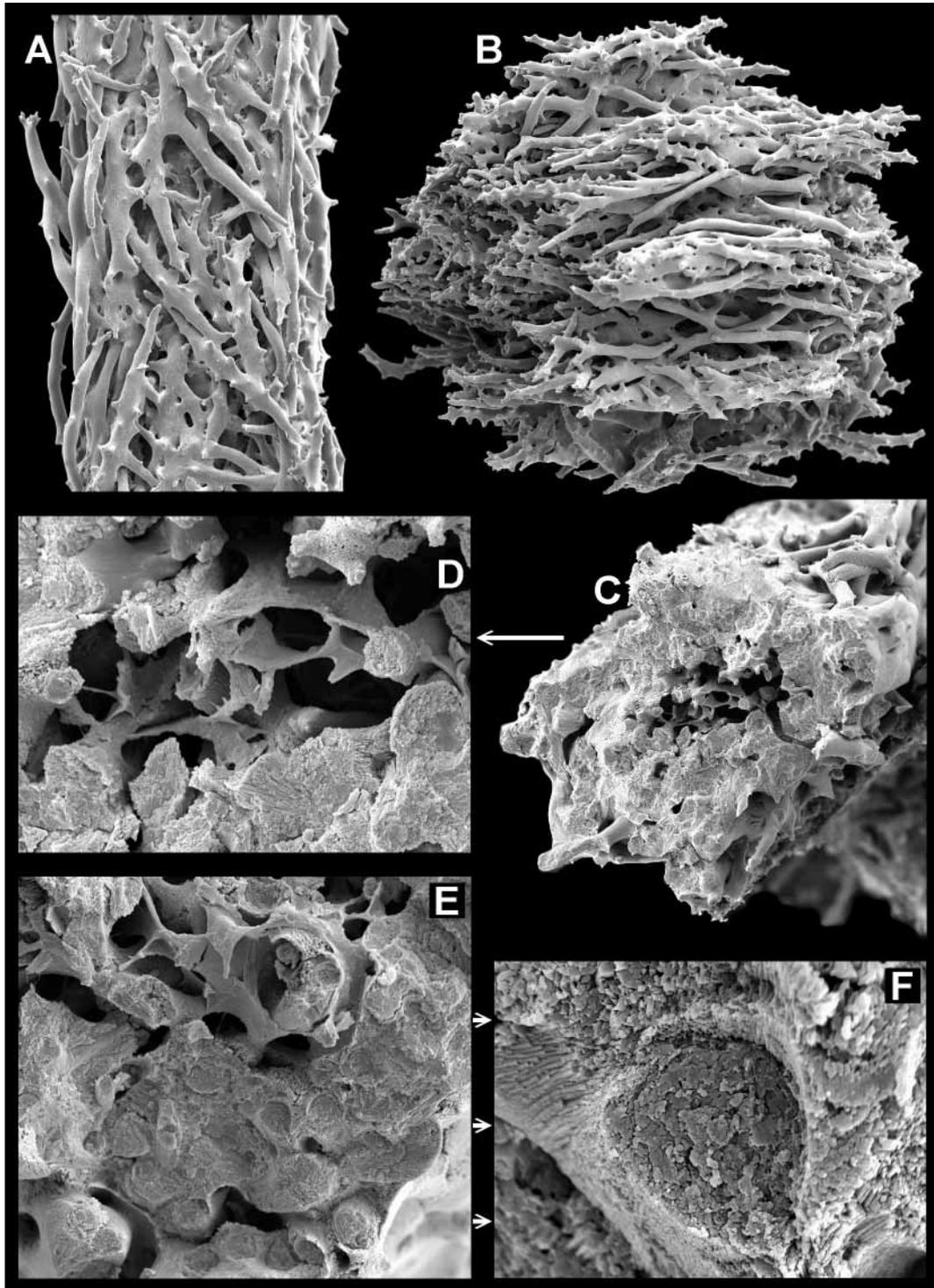


FIGURE 9. *Asperaxis karenae* n. gen., n. sp., holotype: A, partially embedded internodal surface sclerites; B, complete internode; CD, internode cross-section with close-up featuring the central core; EF, internode cross-section featuring sections through embedded sclerites.

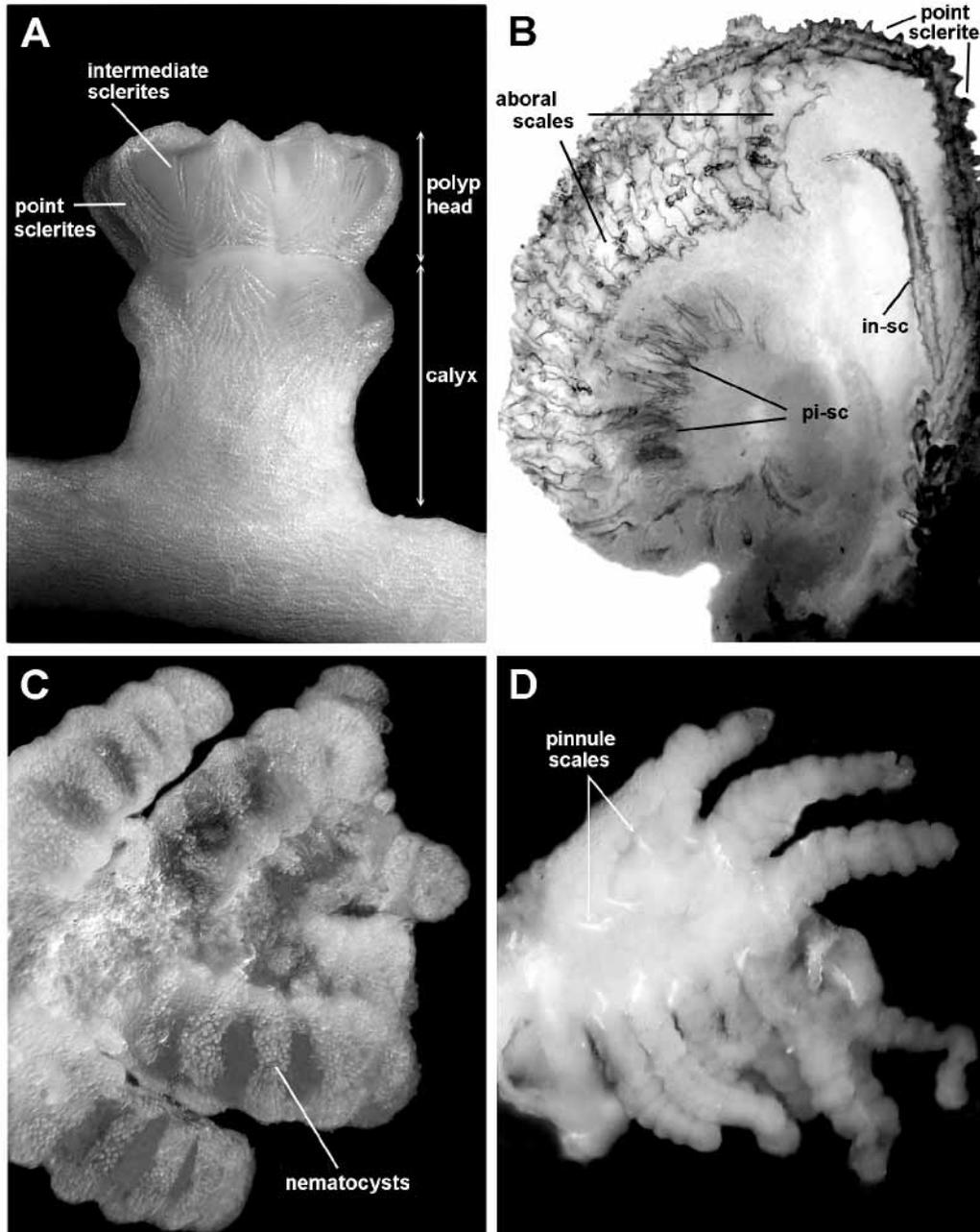


FIGURE 10. *Asperaxis karenae* n. gen., n. sp., holotype: A, polyp and calyx; B, side view of cleared tentacle, in-sc = intermediate sclerites, pi-sc = pinnule scales; C, tentacle tip showing nematocyst bands; D, tentacle tip showing position of pinnule scales.

One of the reasons this colony has been selected as the holotype is that the polyps are slightly distended. The tentacles are folded over the mouth, and the polyp head generally sits just above the calyx (Fig. 10A). Polyps are scattered irregularly along the branches, either singly or in groups of 2 or 3, and are gathered in terminal clusters of 4–15 (Fig. 2B).

A few calyces are cylindrical but most are slightly expanded distally showing the contracted introvert between the rim and the polyp head. The largest calyx is 1.2 mm tall, 1.2 mm basal diameter, and 1.9 mm distal diameter. The largest polyp head is 1.2 mm tall and 2.0 mm across. Juvenile polyps occur here and there on branches, but are most commonly found in the terminal clusters where they can be as short as 0.4 mm.

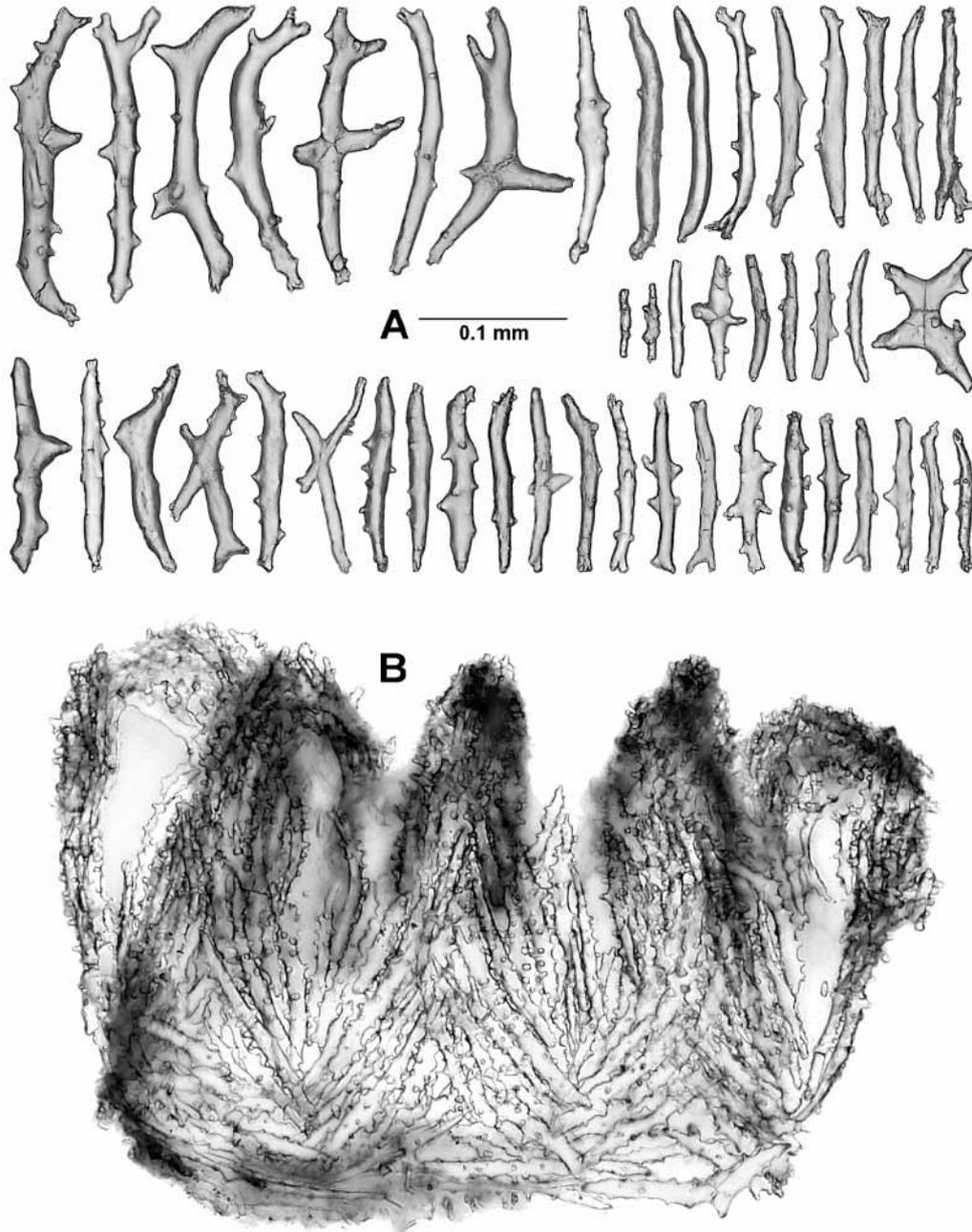


FIGURE 11. *Asperaxis karenae* n. gen., n. sp., holotype: A, axial sclerites; B, points and collaret arrangement.

The calicular sclerites are sticks, spindles, and clubs about 0.15–0.28 mm in length (Fig. 12). The tubercles are mostly large, complex, and irregularly arranged. The sclerites are oriented longitudinally in the lower half of the calyx, becoming formed into 8 chevrons in the upper half, and forming 8 teeth on the calyx rim (Fig. 10A).

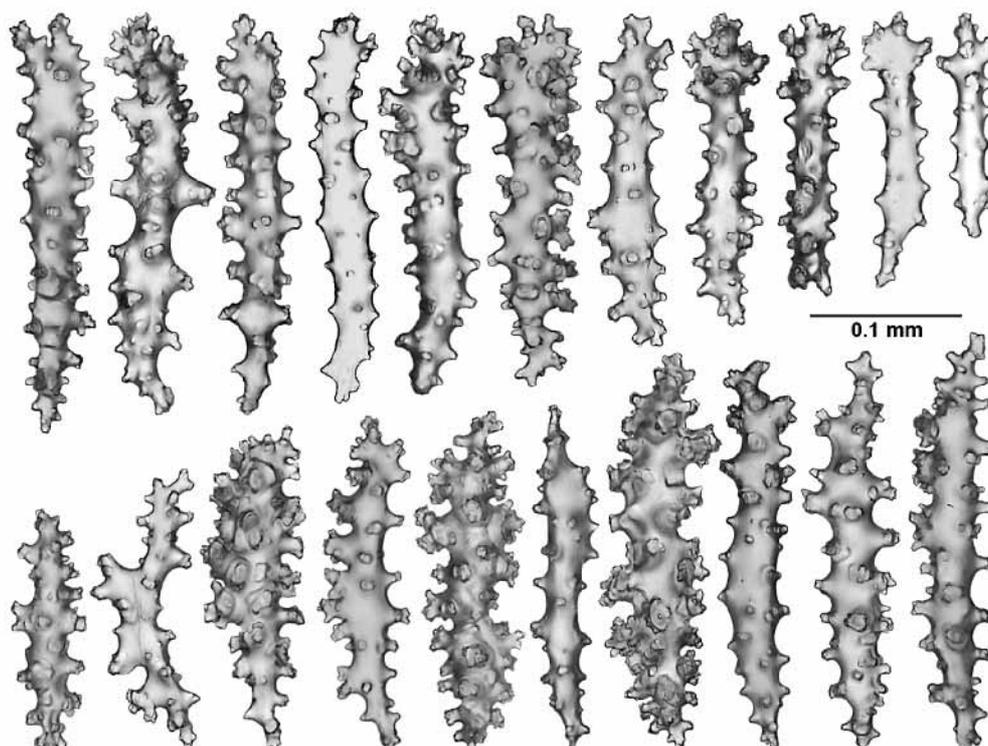


FIGURE 12. *Asperaxis karenae* n. gen., n. sp., holotype, calicular sclerites.

The polyp head is heavily armed with numerous point sclerites (Fig. 10A). At the base of each point the sclerites are more or less horizontally arranged and these combine with a small number of long bow-shaped sclerites to constitute a weak collarlet. Above this region the sclerites are in chevrons, becoming longitudinal as they encroach on the base of each tentacle. Between each set of points there is a group of 2–7 (usually about 2) lower, intermediate, stick-like sclerites of various sizes, and above this there are 0–2 small, upper, intermediate sclerites (Fig. 10B in-sc, 11B). The point sclerites are sticks and clubs. A few clubs (Fig. 13Aa) occur in the distal part of each of the points. They have large tubercles and branched heads and are about 0.12–0.20 mm long. The remainders of the point sclerites are flattened sticks c. 0.07–0.29 mm long with simple tubercles (Fig. 13Ab). In the pharynx there are small rods about 0.036–0.066 mm long that have two medial girdles of knob-like tubercles (Fig. 13B).

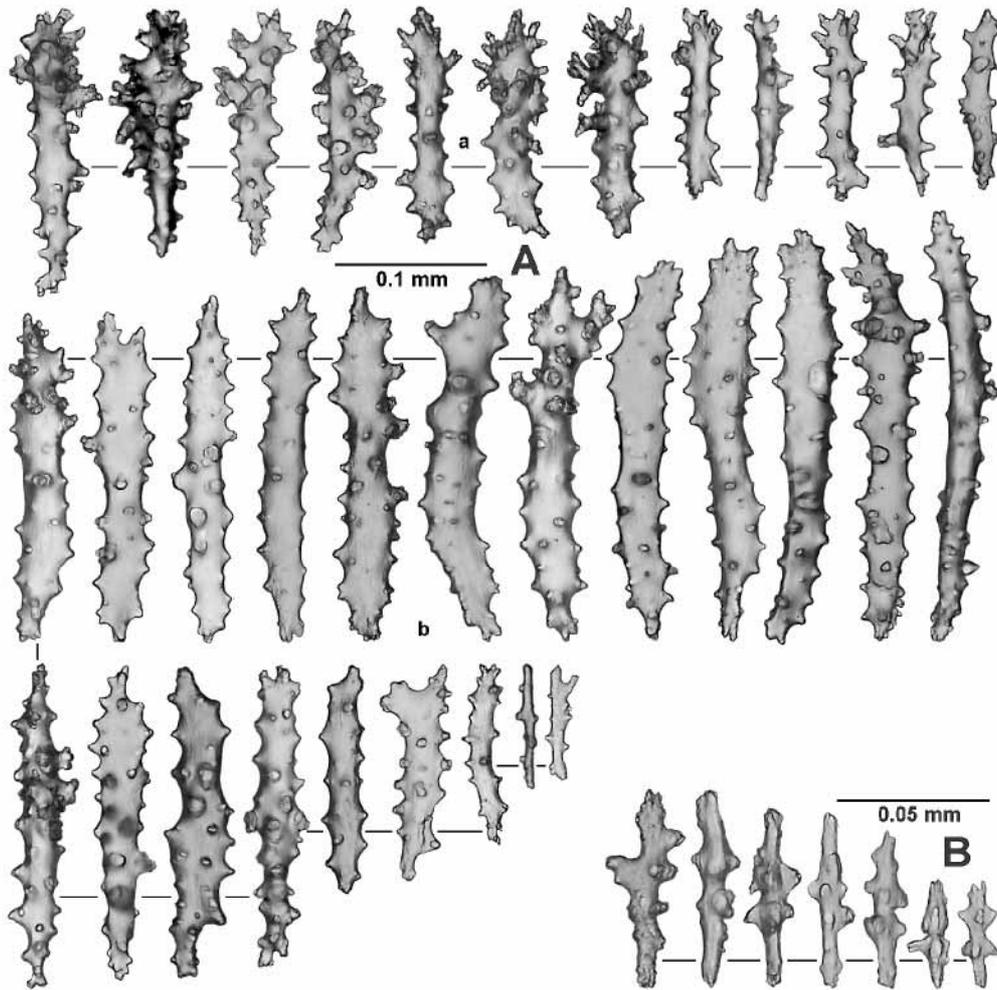


FIGURE 13. *Asperaxis karenae* n. gen., n. sp., holotype, anthocodial sclerites: A, points; B, pharynx.

Along each edge of the tentacles is a single row of about 10 pinnules that are ringed with nematocyst batteries (Fig. 10C–D). The aboral aspect of the tentacle is covered with two rows of transversely placed scales (Figs 10B, 14A) that are about 0.09–0.28 mm long. Proximally, the scales are crescent-shaped to fit the curvature of the tentacle surface and they are complexly branched or have branched tubercles. Distally the scales become shorter and simpler in design. On the adoral face there is a single small scale associated with the base of each pinnule (Fig. 10B pi-sc, D). These scales are asymmetrical foliaceous crescents (Fig. 14B), 0.09–0.16 mm long and they lie curved around the proximal side of the pinnule base. The narrow tail of the scale seems to lie on the lateral edge of the tentacle rachis, the crescent curves around the pinnule base, and the foliaceous portion lies on the oral face of the pinnule base.

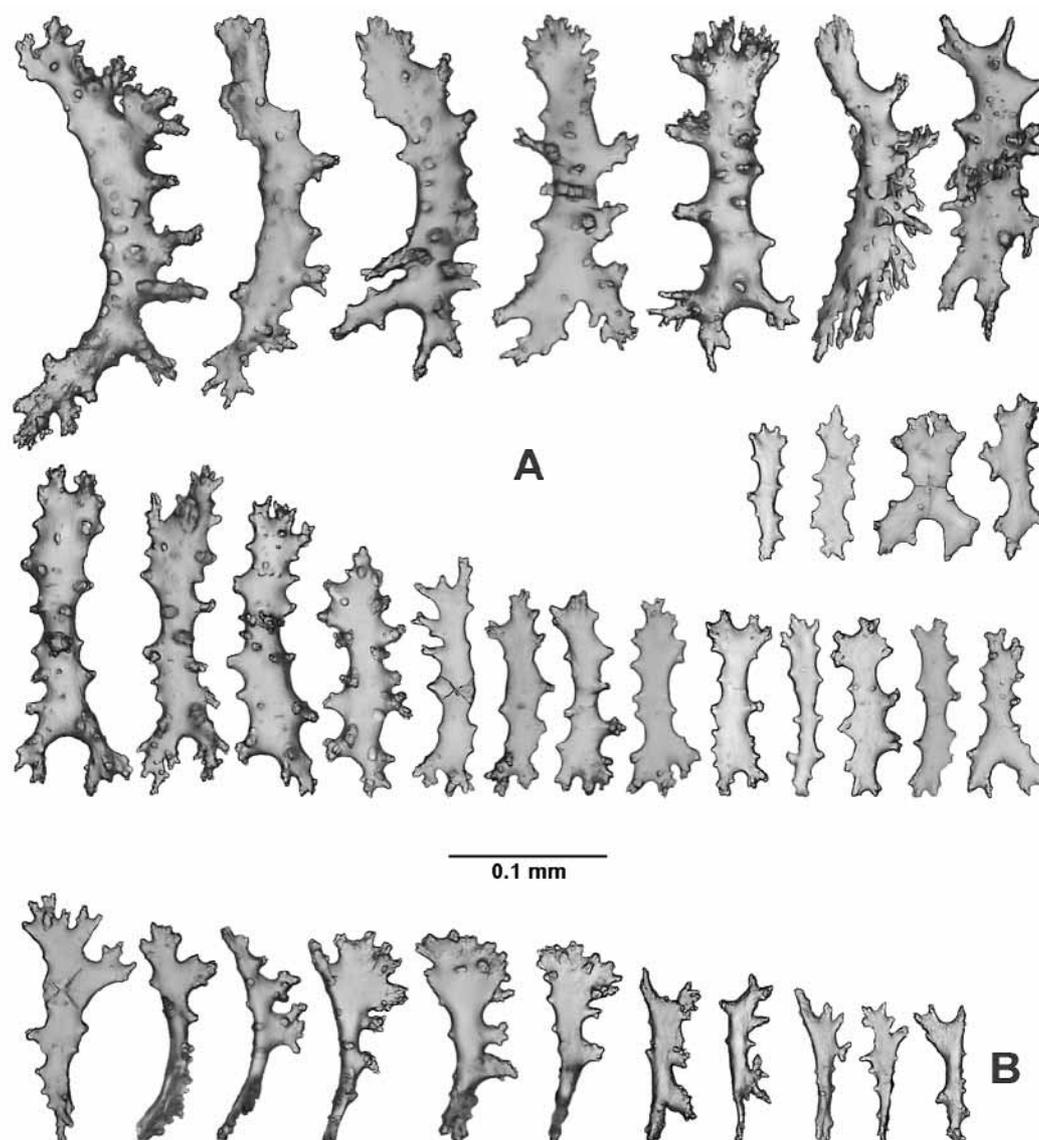


FIGURE 14. *Asperaxis karenae* n. gen., n. sp., holotype, tentacular sclerites: A, rachis; B, base of pinnules.

The sclerites of the twigs and branches are complexly tuberculated sticks and spindles, occasionally branched, 0.05–0.28 mm in length (Fig. 15).

Colour. Live colonies are pale pink. Preserved colonies are white to pale brown with white internodes and pale yellow nodes.

Variability: Several of the paratype lots consist of colonies or colony fragments that are noticeably thinner than the holotype.

- a) Polyp density can be quite variable, with some colonies having long branches with very few polyps
- b) Clusters of polyps are very common, and do not only occur at the end of terminal branches.
- 3) Club-like sclerites may be few or even rare in the tip of the points arrangements.
- 4) Several lots show signs of initial preservation in acidic formalin.

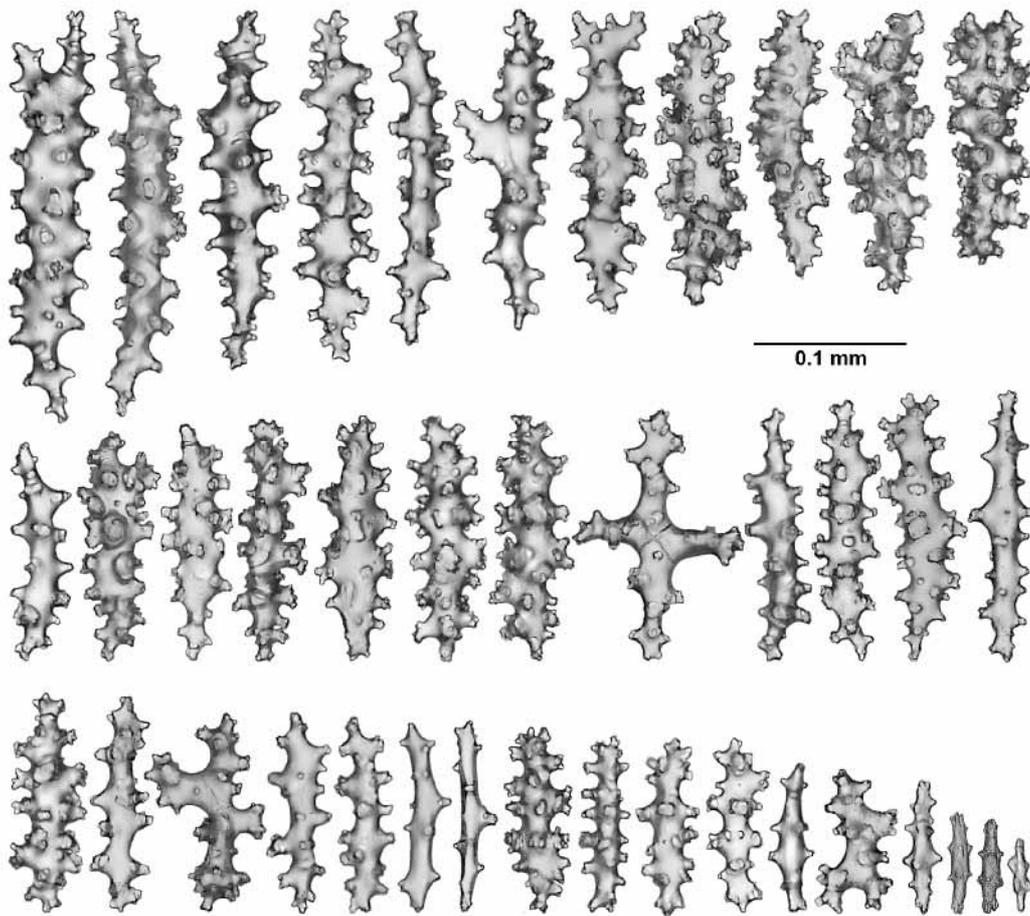


FIGURE 15. *Asperaxis karenae* n. gen., n. sp., holotype, coenenchymal sclerites.

Etymology. The species is named for my good friend and colleague Karen Gowlett-Holmes, Marine Collection Manager, CSIRO Tasmania, and multi-award winning underwater photographer. Karen is a regularly donator of material to the MAGNT collected during her many private expeditions.

Remarks. The species is known from two types of habitat. The following comments are those of Karen Gowlett-Holmes:

“Both habitats are extremely low-light, and both have other taxa usually found in much deeper environments. In the Waterfall Bay caves, the low light is similar to about 50+ m deep, and much of the fauna is the same as that seen at this depth or deeper. The Bathurst Channel, on the other hand, appears to be an isolated water body with regards to the open ocean, and has a strong pycnocline across the mouth of the channel. The area is a drowned river valley, flooded sometime about 12,000 to 15,000 years ago, and it is likely that the current sessile fauna invaded the area at that time and has been virtually isolated for about 10,000 years. What makes the region most unusual is that the upper two to four metres of the water column is a distinct layer of virtually fresh, darkly tannin-stained water (like very strong black coffee). The transition into the marine layer below is very sharp and the marine layer is very clear and very dark. The fauna of the Bathurst Channel most closely resembles that of the shelf break and upper slope, for example 80 to >120 m depth. I therefore think the new taxon is probably a deepwater emergent species. Further evidence for this is that the new taxon is always associated with various bryozoan species and these species are also known from deep water. It occurs predominantly with *Triphyllozoon floribundum* (Phidoloporidae), a fenestrate bryozoan that forms small colonies in the caves but very large colonies (up to at least 60 cm in diameter) in deeper water and in the Bathurst Channel. Sometimes the gorgonian is found with *Schizoretepora tessellata* (Phidoloporidae), a poorly known fenestrate species found in the caves and the Bathurst Channel, and occasionally dredged on the shelf break. Less commonly, the new gorgonian is found associated with *Idmidronea* sp. (Cyclostomata: Tubuliporidae), an undescribed, finely branching, arborescent species found in the caves, on rock walls, and common out to the shelf break. On one occasion the new gorgonian was found with *Adeonellopsis* sp. (Adeonidae), a possibly undescribed branching species that is one of the dominant species found on the outer shelf, shelf break, and upper slope, and is common in dark areas in the caves and in the Bathurst Channel.

Bryozoans in this part of the world are rarely overgrown by anything (at least for long), as they produce deterrent secondary metabolites and have other means of defence as well. It may be worth noting, therefore, that it is quite common to find small colonies of *Mopsella zimmeri* growing on *Triphyllozoon munitum* in South Australia, so perhaps some groups of melithaeids have an affinity with phidoloporids in particular.”

Comparative Comments. Although the axis of the new genus has obvious morphological differences to that found in a nominal melithaeid genus such as *Acabaria* or *Melithaea*, the basic constructional scheme is very similar.

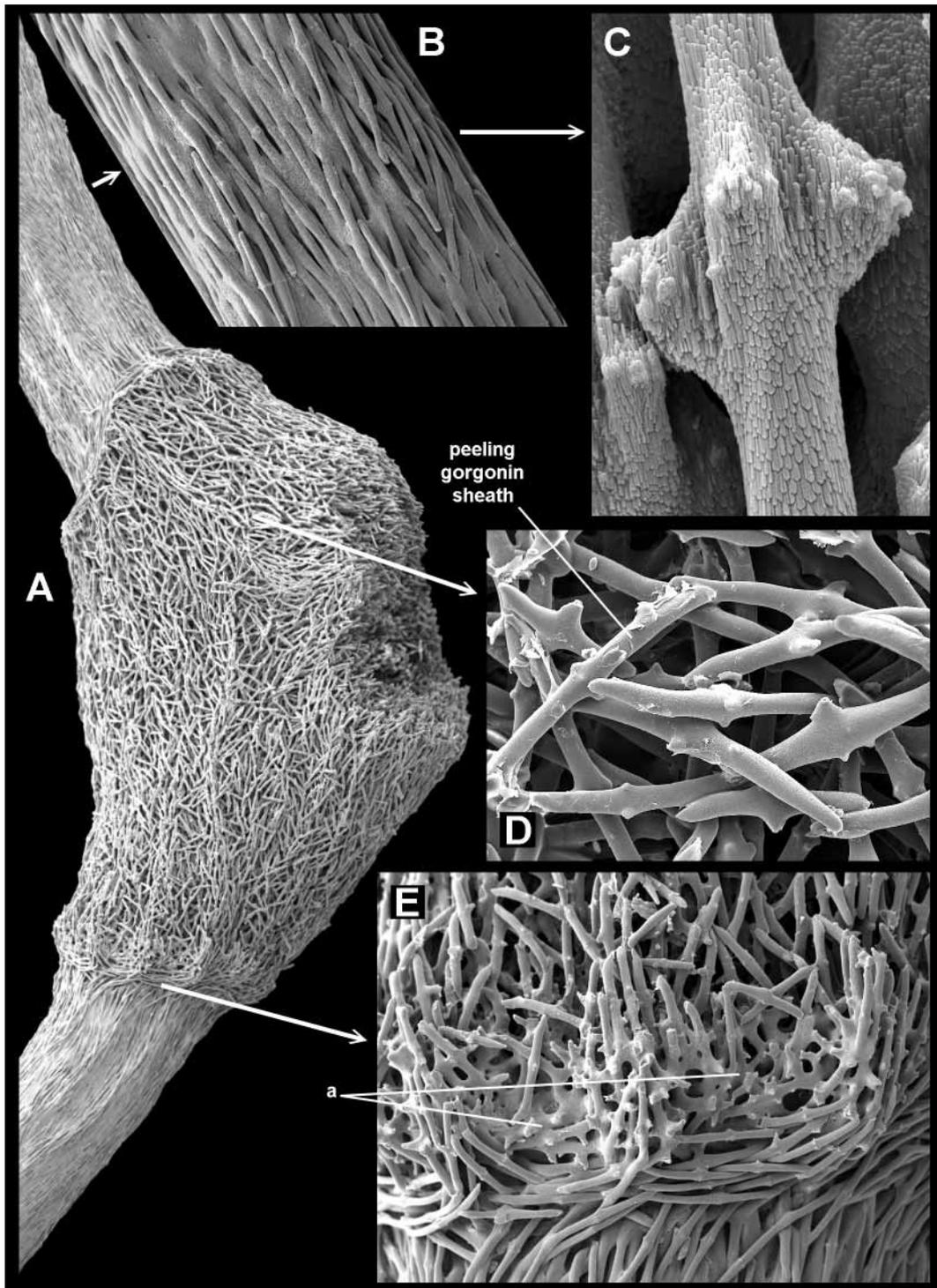


FIGURE 16. *Acabaria* sp. axis: A, decorticated node-internode articulation; B–C, serial close-ups of internode surface; D, close-up of nodal sclerite network showing sclerites with peeling gorgonin sheaths; E, close-up of internode-node boundary region showing the edge of the underlying fused latticework.

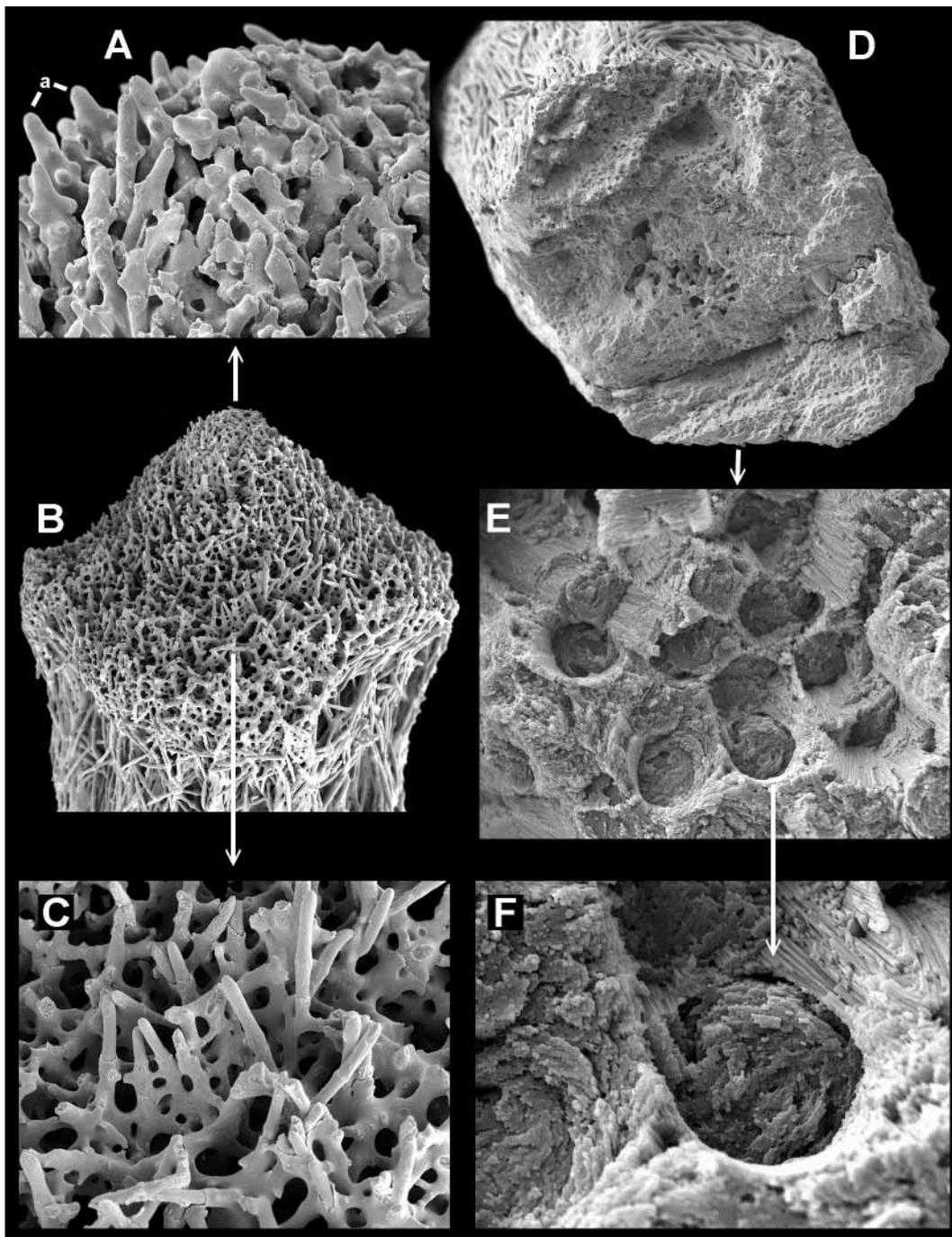


FIGURE 17. *Acabaria* sp. axial internodes: A–C, tip of internode with indicated close-ups; D–F, cross-section of internode showing central core, and serial close-ups showing sections through embedded sclerites.

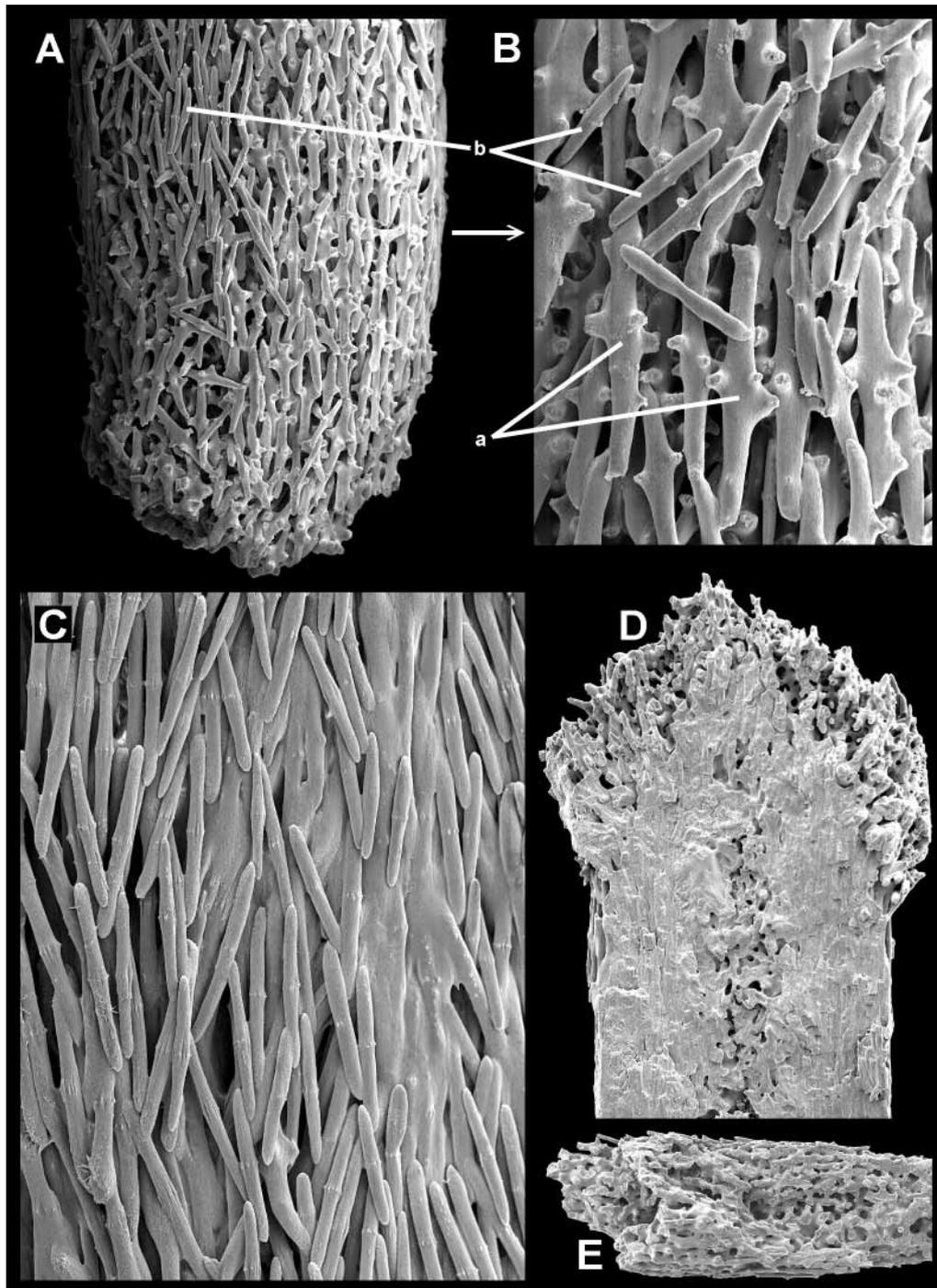


FIGURE 18. *Melithaea* sp. axial internodes: A–B, developing tip with associated close-up; C, surface of older internode; D, longitudinal section featuring central core and terminal laticework; E, longitudinal section through part of young internode almost wholly consisting of core structure.

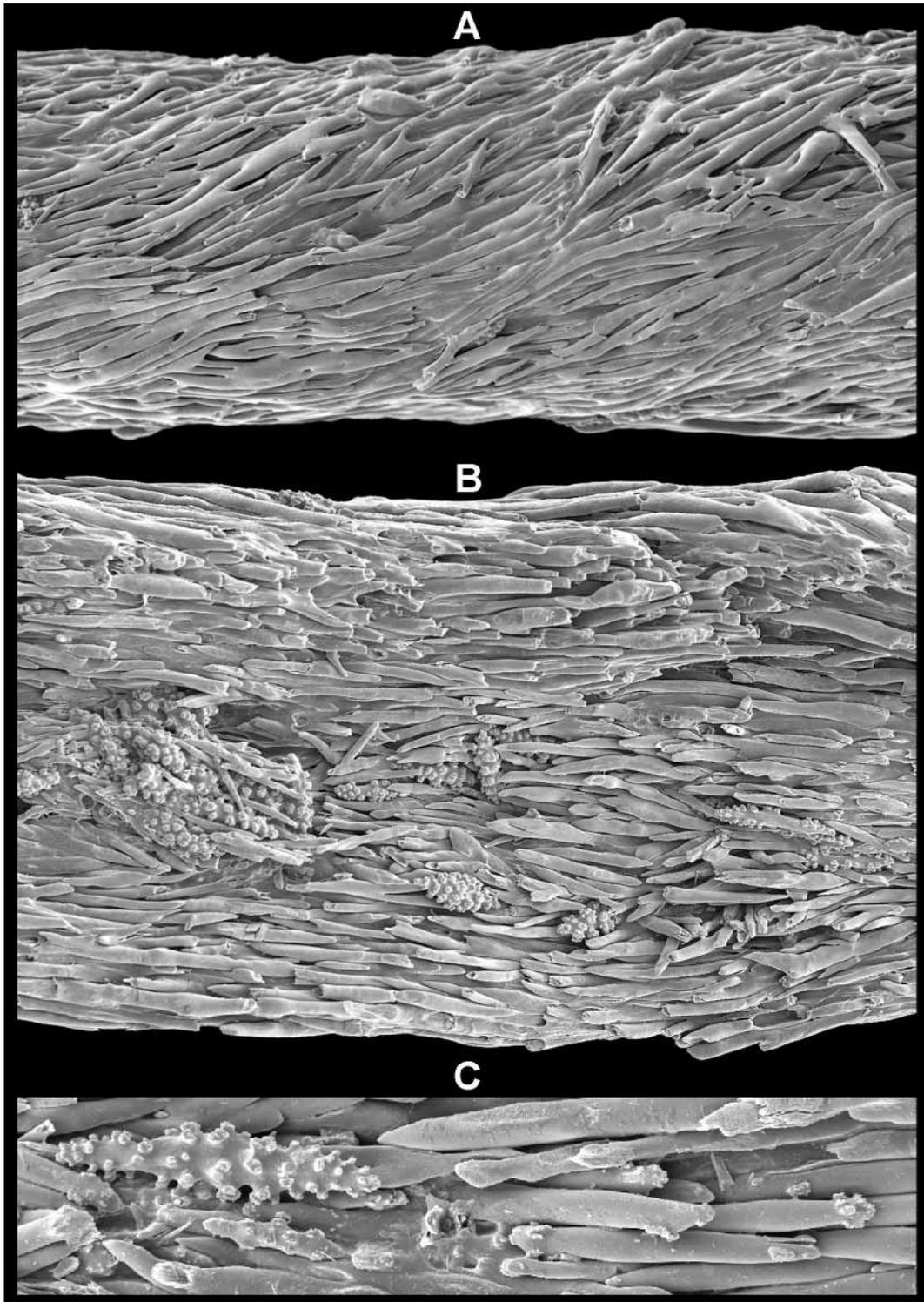


FIGURE 19. *Annella reticulata* axis: A, anastomosed surface sclerites; B–C, longitudinal section with close-up of central region featuring free sclerites.

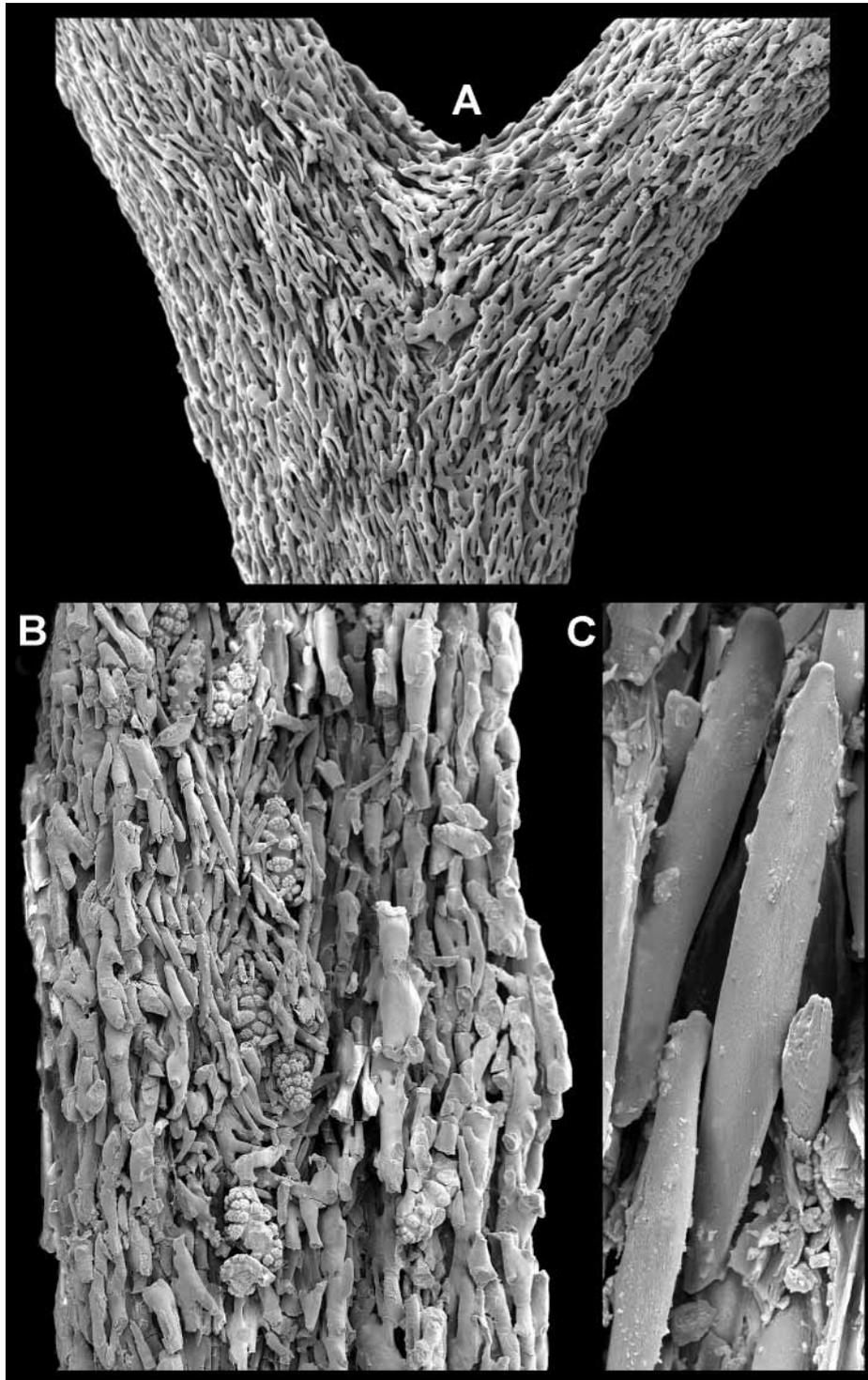


FIGURE 20. *Subergorgia suberosa* axis: A, anastomosed surface sclerites; B–C, longitudinal section with close-up of central region featuring free sclerites.

One of the obvious differences is that in current nominal genera the node-internode articulation is relatively well defined. The node of a species of *Acabaria* is depicted in Fig. 16A. The overlying coenenchyme has been removed, revealing the typical melithaeid axial sclerites partially cemented together on the internodal surface (Fig. 16B, C) and forming a 3-dimensional meshwork in the node (Fig. 16D). An enlargement of the region where the hard internode material abuts the softer nodal substance is shown in part E of that figure. Across the centre of this image, part of a latticework can be seen where sclerites are anastomosing or linked by calcite bridges (Fig. 16Ea). If all the soft nodal material and loose sclerites are removed from the end of an internode, this latticework is shown to be covering its conoid end in a shallow layer (Figs 17B, C; 18D). The sclerites in the rounded tip of the internode, however, are different (Fig. 17Aa). These are larger spindles with a number of rounded tubercles, somewhat similar to those that can be found in the axis that is forming in the tips of *Asperaxis* twigs, which presumably become incorporated into the latticework of the internodal core. The formative melithaeinid axis appears to be similar to that of *Asperaxis*. Figure 18A depicts a decorticated twig tip of a *Melithaea* species. As in *Asperaxis*, an internode begins as an aggregation of loosely bound tuberculate spindles (Fig. 18Ba), the rod-shaped sclerites by which the melithaeid axis has usually been characterised occurring only on the outside (Fig. 18Ab, Bb). Figure 18C shows the surface of an older internode; cavities are still present where the calcite infilling is not yet complete. In the early stages of sclerite fusion, an internode is mainly just a cylindrical latticework (the future core), with a layer of small, loose, rod-like sclerites on the outside (Fig. 18E). As the internode ages, the core becomes surrounded by large numbers of these rods embedded in a matrix of subhedral calcite rods (Fig. 17D–F). The core continues right into the tip of the conoid end of the internode (Fig. 18D) and, according to Koelliker (1865, pl. XV, fig. 8), the mesogloea of the core (his “Centralstrang”) is continuous from internode to internode through the node.

Axes from specimens having the characters of classical species of *Melithaea*, *Mopsella*, and *Acabaria* were examined in the course of this research and all were found to have the same basic construction. Additionally, because the sparsely tuberculate axial sclerites of *Asperaxis* (eg. Fig. 9A) have similarities to those in the axes of *Subergorgia* and *Annella*, species of these genera were also examined. The axis of *Annella reticulata* (Ellis & Solander, 1786) and that of *Subergorgia suberosa* (Pallas, 1766) are illustrated in figures 19 and 20 respectively. The presence of free tuberculate sclerites in a subergorgiid axis (sclerites like those in the outer coenenchyme) is not well documented despite being discovered by Koelliker 140 years ago (1865, p. 144 and pl. XV, fig. 2). Indeed, it was overlooked by López-González and Gili (2001, p. 122), who used the presence of these sclerites in the axis of the new genus *Rosgorgia* as a major character distinguishing that genus from *Annella* and *Subergorgia*. Fabricius and Alderslade followed suit pending further investigation (2001, p. 56). In the several samples of *Annella* and *Subergorgia* that were analysed for this paper, tuberculate sclerites were commonly found in the centre of

the axes, but they are not restricted to this region (Figs 19B, 20B). However, the simple, non-anastomosing spindles (with or without a few terminal tubercles) reported and figured by a few authors (eg. Aurivillius 1931, p. 21, fig 2 (centre); Bayer 1956, p. F198, 2c) do seem to be restricted to the centre of the axes (Figs 19B,C, 20B,C). At least in the few samples examined, this central section is certainly not composed solely of tuberculate coenenchymal-style sclerites as stated by Kinoshita (1910, p. 224–225) and seemingly implied by Muzik and Wainwright (1977, p. 321).

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