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Stylasteridae (Cnidaria, Hydrozoa, Filifera) from South Africa

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Abstract

We describe and figure the 20 species of stylasterid hydrozoans known from South Africa. These consist of seven new species, six range extensions, and seven species previously known from South African. Most of the specimens reported resulted from expeditions of the *Pieter Faure* (1898–1903) and *Meiring Naudé* (1975–1987), and are deposited primarily in the South African Museum (Cape Town). A replacement name (*Errina australis*) is proposed for the junior homonym *Errina hicksoni* Cairns, 1991. A brief history of species discovery of the South African stylasterids is presented. The new morphological term dactyloglossa is introduced to define a baffle-like structure found in dactylopores of some species. Of the 20 South African species, 12 (60%) are not yet known outside that area. Three patterns of distribution were noted: species confined to the tropical region of South Africa, those found in both the tropical and warm temperate regions of S. Africa, and those found only in the warm temperate regions, three in the latter group sharing their distribution with cold temperate southern South America and two with warm temperate New Zealand, representing a circum-southern temperate distribution.

Key words: Cnidaria, Stylasteridae, South Africa, new species, zoogeography, *Pedicularia*

Introduction

In her monumental work on the order Hydroida of southern Africa, Millard (1975) listed 286 species and subspecies from Africa south of 20°S (thus including southern Namibia and Mozambique). Ironically, she did not include the Stylasteridae because at that time they were placed in a different order, the Hydrocorallida. Of the 25 families of the order Hydroida reported by Millard, the 20 known species of Stylasteridae from South Africa would make it the fourth most species-rich hydroid family known from that region, following, Plumulariidae (85 species), Sertulariidae (67 species), and the Campanulariidae (21 species). The other major group of calcified corals, the Scleractinia, boasts at least 54 species for South Africa (Cairns & Keller 1993). Thus, whereas the Stylasteridae are not the most species-rich group of calcified corals known from off South Africa, they are a significantly diverse one, especially as the 14 new records reported herein suggest that a greater number may yet be found.

In addition to scientific (taxonomic, zoogeographic) interest, some of the South African stylasterids were once commercially harvested on a very limited scale to use as decorative objects, probably much as the tropical West African blue coral *Stylaster blatteus* was harvested as “akori” (Boschma 1961). According to Boonstra (1994), 382 kg of “*Allopora*” (probably *Stylaster nobilis*) was legally taken from Struis Bay to Quoia Point in 1991.

History of the Fauna

The first stylasterids reported from South African waters were three relatively shallow-water species described by Kent (1871): *Stylaster amphiheloides*, *S. nobilis*, and S. *subviolaceus*. Although the collection locality was not given for the last two species, they have subsequently been inferred to be from off South Africa, the type of *S. subviolaceus* coming from the collection of Sir E. Belcher, a British naval officer. These specimens are deposited at The Natural History Museum (BM). The next South African record was reported as *Allopora oculina* by Studer (1878) from off Cape of Good Hope, and is now regarded as an early record of the common *Stylaster bithalamus*, these specimens deposited at the Zoologisches Museum, Berlin (ZMB). Hickson (1900) reported *S. nobilis* from the Cape region, and England (1926) published histological sections of the male ampullae of the same species.

In a treatise on species of the genus *Stylaster*, Broch (1936) reported the new species *S. bithalamus* and additional records of *S. nobilis* and *S. subviolaceus* from T. Mortensen’s Java—South Africa Expedition of 1929–30. These specimens are deposited in the Zoologisk Museum, Copenhagen (ZMC).

The last person to contribute to this fauna was H. Boschma, who wrote five papers between 1956–1966 based primarily on specimens collected by the Ecological Survey of the University of Cape Town between 1947 and 1962. Each paper is an exhaustive description or re-description and discussion of one species: *Stylaster nobilis* (see Boschma 1956), *Gyropora africana* (see Boschma 1960a), *Stylaster bithalamus* (see Boschma 1960b), *Lepidopora diffusa* (see Boschma 1963b), and *Stylaster subviolaceus* (see Boschma 1966a). These specimens are deposited at The Naturalis Biodiversity Centre, Leiden. His final paper on the subject (Boschma 1966b) included a brief review of the seven species known from South Africa, concluding that the entire stylasterid fauna was endemic to that region.

Although not reporting stylasterids from South Africa, a number of papers from adjacent regions in the southwest Indian Ocean were compared, either from the literature or by examination of the specimens, to those from South Africa: Mauritius (Kirkpatrick 1887; Hickson & England 1909; Broch 1936, 1942; Boschma 1965); Providence Island (Hickson & England 1909); Kenya and Tanzania (Broch 1947; Boschma 1962; Cairns 1985); and on the other side of South Africa, the Discovery Seamount (southwest of South Africa) (Broch 1951a; Boschma 1966b). No stylasterids are yet reported from off Madagascar.

Material and Methods

Most of the newly reported specimens included in this paper were collected on the expeditions of the *Pieter Faure* (1898–1903) and *Meiring Naudé* (1975–1987), and are deposited at the South African Museum. A small voucher collection is also deposited at the NMNH. The expeditions of the *Pieter Faure* were organized by pioneer South African Naturalist John D. F. Gilchrist (1866–1926), who was charged with exploring the fisheries potential of the Cape region, but who also avidly studied whatever was collected in the trawls, as well as establishing an aquarium for the study of live specimens (Brown 1997). Background on the *Meiring Naudé* can be found in Lutjeharms & Shannon (1997). Specimens from several other vessels were also included (see Station List), as well as several privately collected specimens. Historically pertinent specimens were borrowed from The Naturalis Biodiversity Centre (Leiden), The Natural History Museum (London), the ZMB, and the ZMC. We examined original types or additional specimens of all 20 species.

In this paper one morphological term is resurrected and another is proposed. The resurrected term, once used by Broch (1936), is the **sphincter**, which pertains to the horizontal partitioning of the gastropore tube. Many gastropore tubes are simple cylinders, without partition, which may or may not contain a gastrostyle. Many other gastropore tubes contain a ring palisade (also once called a *cheval-de-frise*), which consists of an annular ring or girdle of small cylindrical elements that project from the wall of the gastropore tube near the level of the gastrostyle tip (Cairns 2011). Still other species in the genera *Conopora* and *Crypthelia* have a thin, solid (but medially perforate) sheet that divides the upper from lower gastropore chambers. Finally, in several species of South African *Stylaster* and *Stenohelia*, there is a solid continuous structure similar to a belt that encircles the gastropore tube at about the level of the gastrostyle apical spine, constricting the tube into a spherical lower portion and a cylindrical upper portion. This belt-like protrusion is called the sphincter.

The introduced term is the **dactyloglossa** (*dactyl* from dactylopore, + *glossa*, meaning tongue), and defines a structure found within the dactylopores of some species. In most species that have dactylostyles, they are composed of a row or multiple rows of small cylindrical elements, much like those of the ring palisade, that occur on the outer (and sometimes lateral) wall of the dactylopore tube (Cairns 2011). But, in several species of South African *Stylaster* and *Stenohelia*, each dactylopore has a series of horizontal, semi-circular (or broadly tongue-shaped) platforms, or baffles, that largely obscure the passage of the dactylopore tube. This structure is called a dactyloglossa, its function as yet unknown. It is similar to a structure termed pseudotabulae (Cairns 1991), but dactyloglossae are differently shaped and originate from only one side of the dactylopore tube.

Six species of South African stylasterids possess dactyloglossae: *Stylaster bithalamus, S. griseus, S. amphiheloides, S. kenti, Stenohelia venusta,* and *St. spinifera*. Five of these six species (not *St. spinifera*) also share the linked character states of having a similarly shaped gastrostyle with a sphincter constricting their gastropore chamber, and four of the six (not the two *Stenohelia*) have female efferent pores that open into the upper gastropore chamber. Whereas the sphincter may also be unique to this set of species, the efferent pore location is not. *Stenohelia spinifera* has a similarly shaped gastrostyle but no sphincter, and its female efferent pores are as yet unknown. Otherwise, these six species belong to two genera, and within the genus *Stylaster*, to two different species groups, and have widely divergent characteristics relating to positioning of the cyclosystems on the branch, curvature of the gastropore tube (both of genus level distinction), presence or absence of commensal polychaetes, number of dactylopores per cyclosystem (ranging from an average of 9 to 16), coenosteal microarchitecture, nematopore spines, and differently shaped male ampullae. To suggest that dactyloglossae resulted independently from convergent evolution in these six species (and at least 3 lineages) and that all of these taxa have remained endemic to South African waters, is highly unlikely. On the other hand, in the stylasterid molecular phylogeny of Lindner et al. (2008), the genus Stenohelia is not monophyletic, the three species analyzed grouping with other species of Stylaster, allowing for an interpretation that these six species may form a monophyletic clade and that

Stenohelia is not a discrete genus. Furthermore, to suggest a shared evolutionary history of this trait, perhaps originating in *Stylaster* (Group A) and then transmitting the trait to some South African species in *Stylaster* (Group C) and some South African species in *Stenohelia* is equally unlikely. Another possibility is that dactyloglossae are more common in the genera *Stylaster* and *Stenohelia* than currently thought, allowing the possibility of greater time and geographic range for this character to have evolved and spread. After all, the character is rather small, and obviously overlooked by Broch (1936) and Kent (1871) in their description of species having this trait. But, we have described many species of *Stylaster* and *Stenohelia*, always including SEM of the dactylostyles for each species, and we have never seen such a structure in any species heretofore. A final possibility is that it is a non-hereditary environmental reaction to an unknown local stimulus found only in this region. Regardless, the origin of this trait, its function, and its localized distribution off South Africa remain a mystery.

It should be noted at this point that the stylasterid type material designated by Hickson & England (1905) from the *Siboga* expedition was transferred from the Zöologisch Museum, Amsterdam (ZMA) to the Naturalis Biodiversity Centre (Leiden) in early 2012.

The numbers associated with the *Pieter Faure* collection (see Appendix) are sample numbers, not station numbers, and are often given in an archaic style bearing notation.

Descriptions and illustrations of the terminology used in this paper can be found in Cairns (2011).

The following abbreviations are used in the text:

BM	British Museum (Natural History), London (now The Natural History Museum)
L:D	Ratio of length to diameter of a structure, such as a gastrostyle or dactylostyle element
MN	R/V *Meiring Naudé*
MNHN	Muséum National d'Historie Naturelle, Paris
NIWA	National Institute of Water & Atmospheric Research, Wellington
NMNH	National Museum of Natural History, Smithsonian, Washington, DC
NZOI	New Zealand Oceanographic Institute, Wellington (now NIWA)
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden (now the Naturalis Biodiversity Centre)
PF	R/V *Pieter Faure*
SAM	South African Museum, Cape Town
SEM	Scanning Electron Microscopy
UCTES	University of Cape Town Ecological Survey (AFR = name of ship; FAL = False Bay; SCD = south coast dredging; WCD = west coast dredging)
USNM	United States National Museum (now the NMNH)
ZMA	Zöologisch Museum, Amsterdam
ZMB	Zoologisches Museum, Berlin
ZMC	Zoologisk Museum, Copenhagen

Systematic Account

Class **Hydrozoa**
Subclass **Athecatae**
Order **Filifera**
Superfamily **Hydractinoidea** Bouillon, 1978
Family **Stylasteridae** Gray, 1847
Genus ***Lepidopora*** Pourtalès, 1871

Lepidopora Pourtalès, 1871: 40.—Cairns, 1983a: 72; 1983b: 432—433; 1986a: 5; 1991: 21; 1992: 542, 545 (key).
Errina (Lepidopora): Boschma, 1963a: 336, 338.

Type Species. *Errina glabra* Pourtalès, 1867, by subsequent designation (Boschma 1963a).

Diagnosis. Colonies uniplanar or bushy. Coenosteal texture quite variable. Gastro- and dactylopores randomly arranged on branches, sometimes aligned, or sometimes with gastropores at branch axils; gastropore lips may occur. Both gastro- and dactylopores axial; gastrostyles present but dactylostyles not present. Dactylopores elevated on short, apically-perforate mounds (conical). Ampullae superficial and internal, with lateral efferent pores.

Discussion. The 16 species in the genus are listed and documented in Appeltans et al. (2012).

Holocene Distribution. Western and northeast Atlantic, western (including off New Zealand) and central Pacific (including Galápagos), off South Africa, Subantarctic, 60–2320 m.

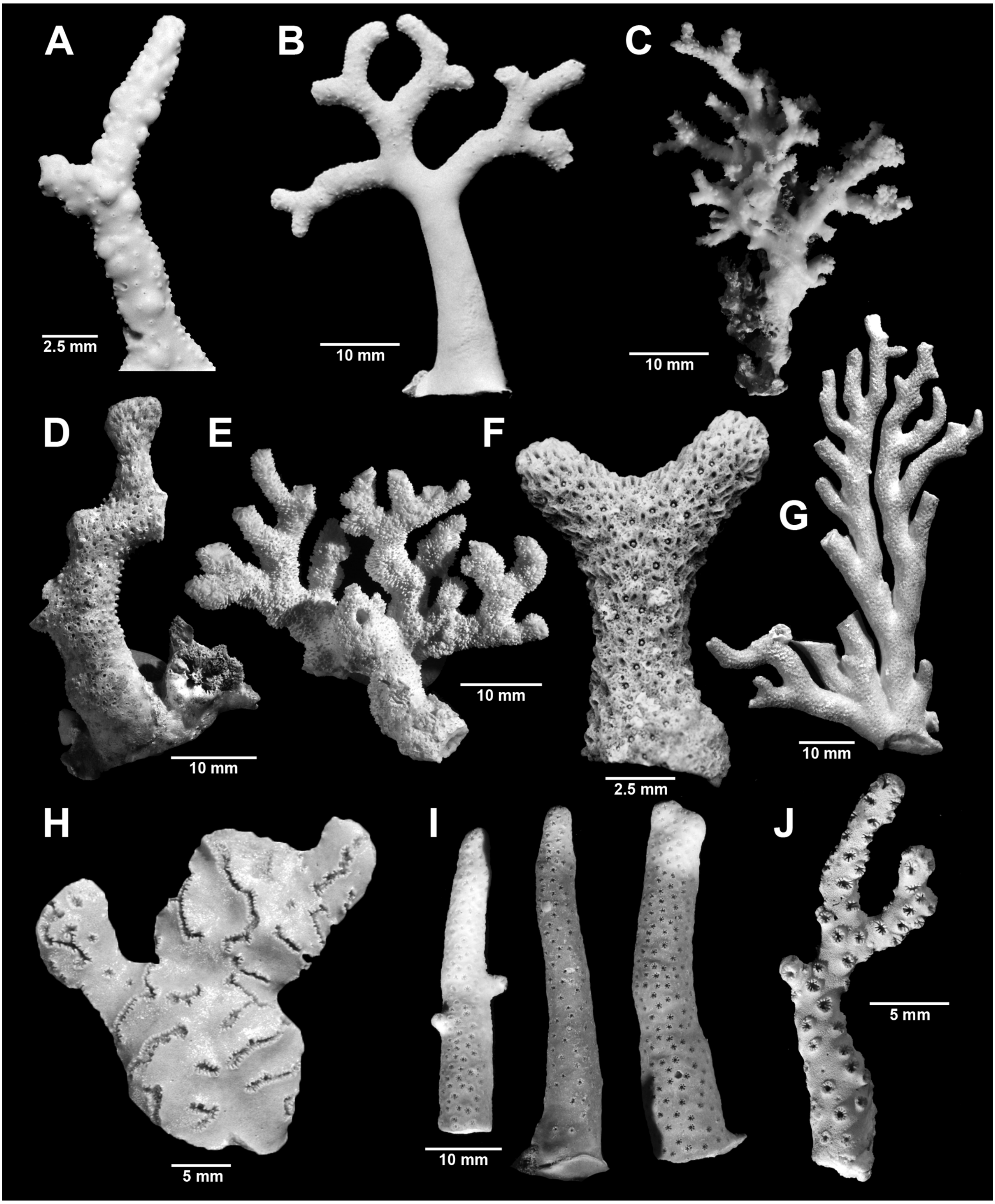

FIGURE 1. Colonies of various species: **A–B**, *Lepidopora diffusa*, *PF*13654. **C**, *Inferiolabiata africana*, holotype. **D**, *Inferiolabiata lowei*, *PF*907. **E**, *Inferiolabiata spinosa*, *Anton Bruun* 420A. **F**, *Errina capensis*, syntype, Manchester Museum. **G**, *Errina capensis*, *MN* XX129, female. **H**, *Gyropora africana*, BM 1977.8.5.1. **I**, *Stylaster nobilis*, *PF*7014, 3 distal branches. **J**, *Stylaster subviolaceus*, *PF*15675.

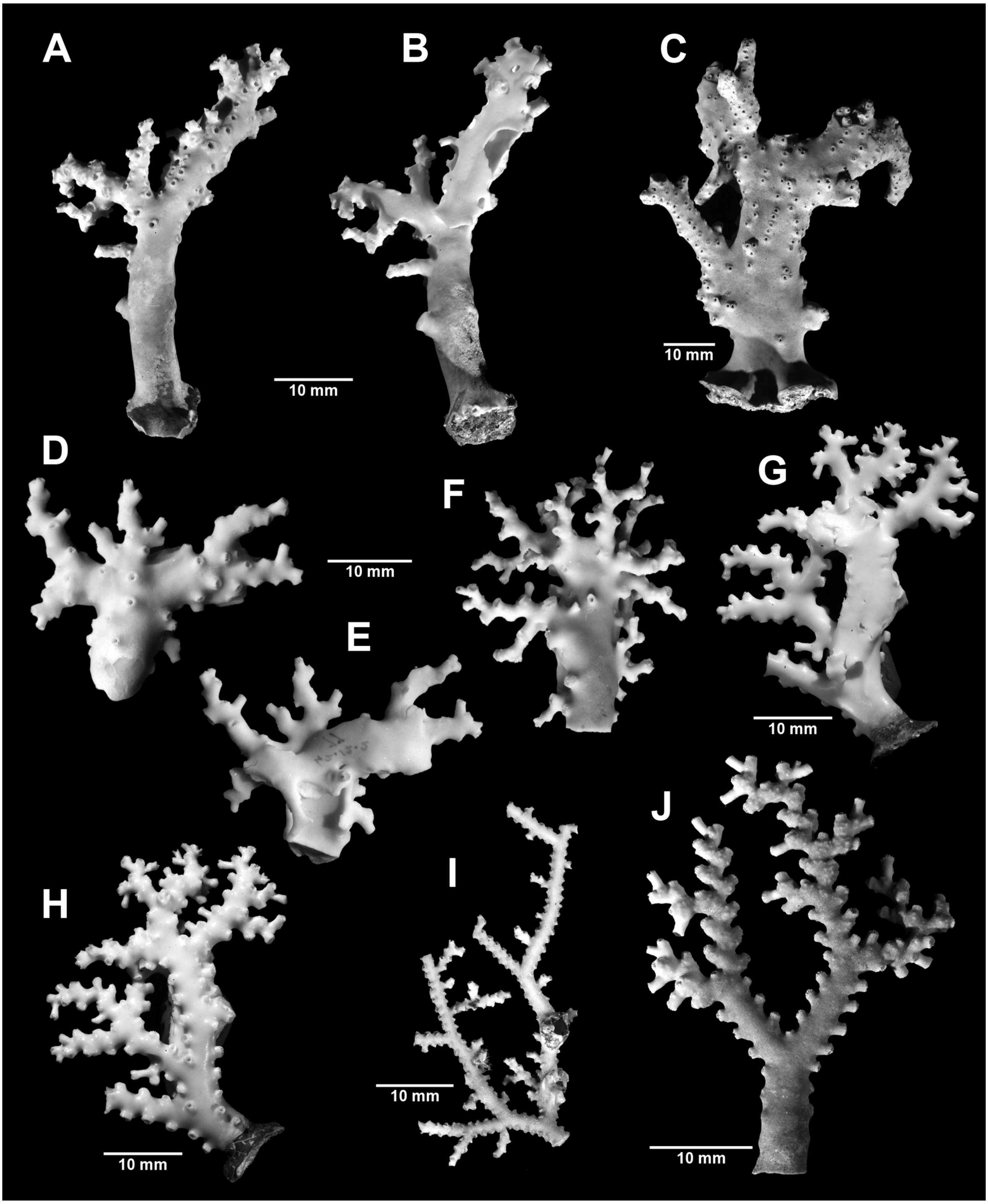

FIGURE 2. Colonies of various species: **A–B**, *Stylaster bithalamus*, *MN* SM185, male, anterior and posterior views of same colony, respectively. **C**, *Stylaster griseus*, holotype. **D–F**, *Stylaster amphiheloides*, syntypes, BM1842.12.2.79. **G–H**, *Stylaster amphiheloides*, *MN* SM228, posterior and anterior views of same colony. **I**, *Stylaster lonchitis*, Liltved specimen. **J**, *Stylaster kenti*, holotype.

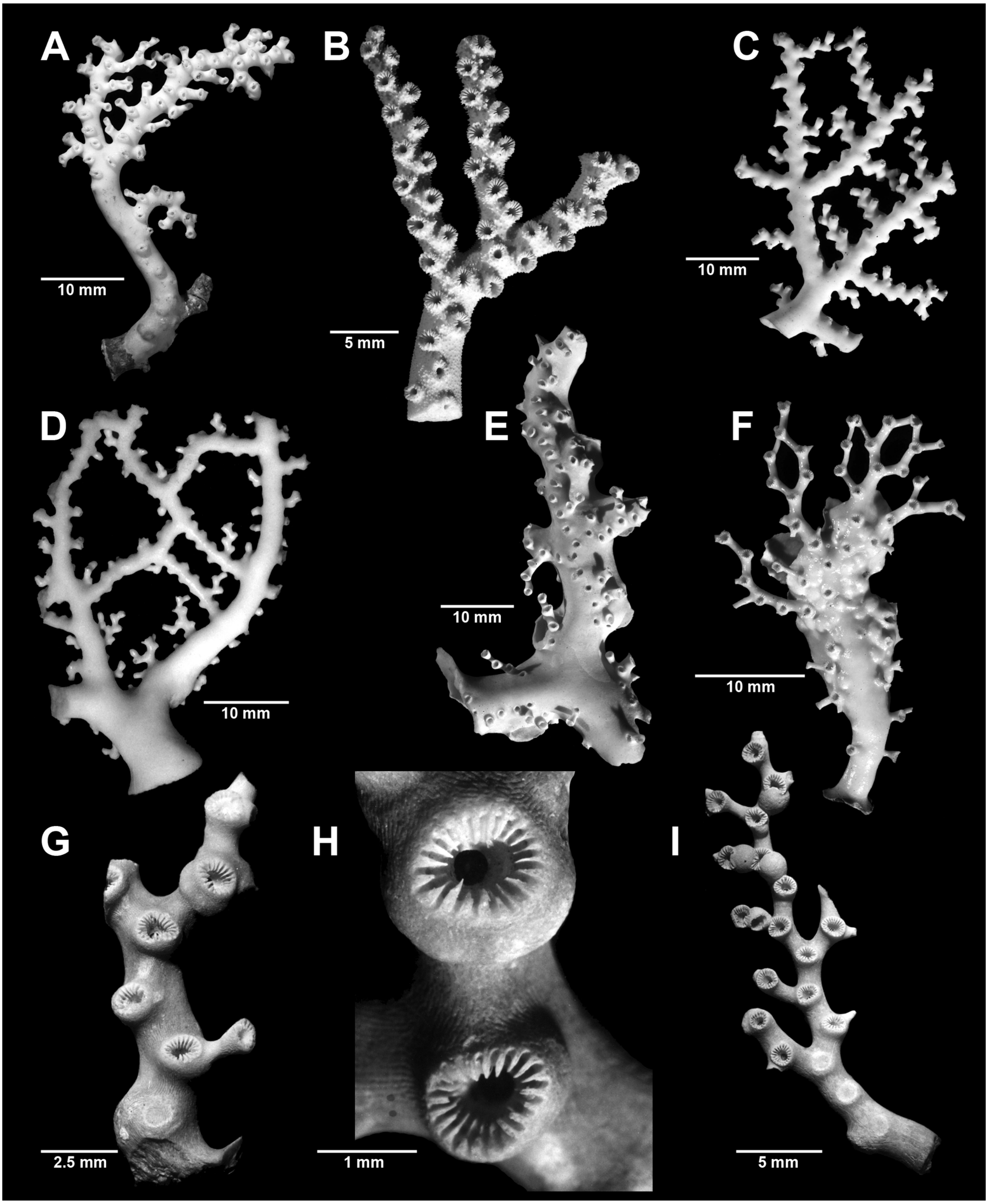

FIGURE 3. Colonies of various species: **A**, *Stenohelia venusta*, holotype. **B**, *Stenohelia spinifera*, holotype. **C**, *Conopora sola*, holotype. **D**, *Conopora verrucosa*, *Valdivia* 104. **E–F**, *Conopora tenuiramus*, **E**, female paratype from *PF*14306; **F**, holotype. **G–I**, *Crypthelia micropoma*, UCTES SCD301 (**H**, male; **I**, female).

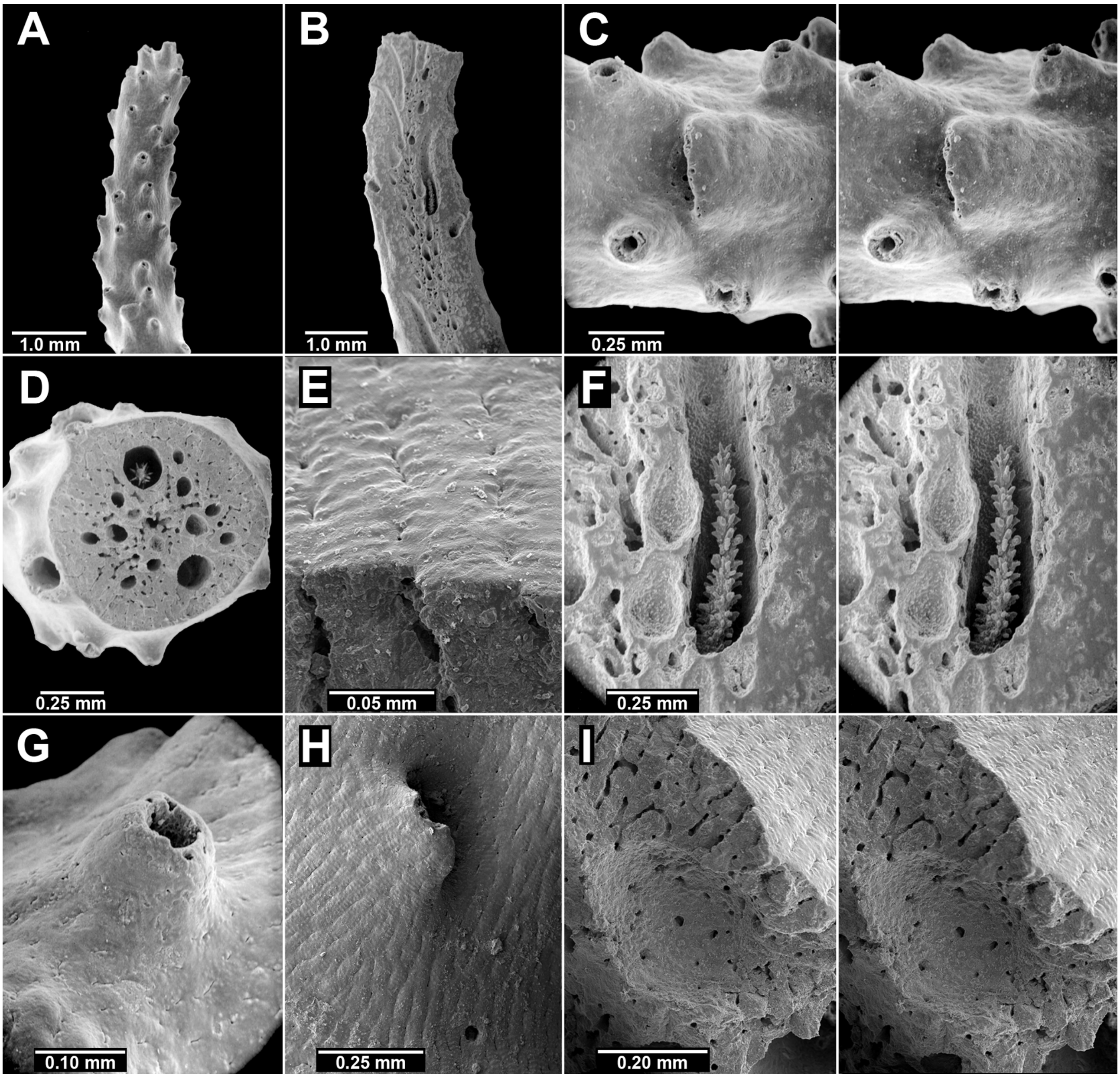

FIGURE 4. *Lepidopora diffusa* (**A–D, F–G**, paralectotype from UCTES SCD296, USNM 96200; **E, H–I**, *PF*13654, USNM 76395): **A**, branch tip. **B**, longitudinal section of branch showing axial gastro- and dactylopores. **C**, stereo view of gastropore lip and conical dactylopore spines. **D**, branch cross section showing axial gastro- and dactylopores. **E**, granular coenosteal texture. **F**, stereo view of a gastrostyle. **G**, a dactylopore spine. **H**, a gastropore lip. **I**, stereo view of an internal male ampulla.

Lepidopora diffusa (Boschma, 1963)
Figs. 1A–B, 4A–I, 22

Errina (Lepidopora) diffusa Boschma, 1963b: 391–396, 1 pl., 3 figs.; 1964: 61; 1966b: 112 (mention); 1967: 333; 1968, 207 (diagnosis)—Vervoort & Zibrowius, 1981:16, 27–28 (lectotype designation).
Lepidopora diffusa: Cairns, 1983b: 428 (new comb.).—Cairns et al., 1999: 44 (listed).

Types and Type Locality. The lectotype was designated by Vervoort & Zibrowius (1981: 28) as the figured specimen (Boschma, 1963b: pl. 1, fig. 2) from UCTES SCD296 (RMNH 13751). Fourteen additional paralectotypes from stations UCTES SCD254 and 296 are deposited at the Naturalis Biodiversity Centre (13801, 13802). Part of one paralectotype from UCTES SCD296 is also deposited at the NMNH as SEM stub 121 (USNM 96200). Type Locality: 33°07.3’S, 28°01’E (off East London, South Africa), 88 m.

Material Examined. Types; *MN* SM163, 25 fragments, SAM H3149; *MN* SM185, 2, SAM H3152; *PF*808, 4, SAM H1231; *PF*7023, 3, SAM H3088; *PF*12104, 1, SAM H1236; *PF*13061, 4 branches, SAM H3086; *PF*13654, 28 branches, SAM H1216, 1 branch, BM 1980.9.19.14, and 1 colony and SEM stub 1665 (USNM 76395); *PF*12312, 14 colonies, SAM H3089, and 1 branch, BM 1980.9.19.13.

Description. Colonies are bushy to planar (Fig. 1B), the largest corallum (the lectotype) 50 mm in height and 26 mm in width, with a basal branch diameter of 3–4 mm. Branching is sparse, dichotomous, and equal, the branching axils usually 90°. Branches are circular to slightly elliptical in cross section, terminating in slender tips about 1 mm in diameter, the tips blunt rather than pointed; there is no branch anastomosis. The coenosteum is linear-granular in texture, the coenosteal strips 40–65 µm in width, the granules arranged in transverse rows (about 95 rows/mm), each row consisting of 3–5 low rounded granules (Fig. 4E). The transverse rows of granules appear similar to a linear-imbricate structure. Colonies are dimorphic in colour, some being a light pink with white branch tips and branch cores, and others homogeneously white.

Gastropores uniformly distributed on branches, circular in shape (0.12–0.20 mm in diameter), and usually bordered abaxially by a broad, low lip (Figs. 4C, H), which causes the polyp to be directed anteriorly. Gastropore tubes are cylindrical and long, 3 to 4 times the length of the gastrostyle, often seen in branch cross section (Fig. 4D) to have the same diameter as the gastropore itself; a ring palisade is absent. The gastrostyle is cylindrical and elongate (L:W = 4.5–5.5), up to 0.7 mm long and about 0.12 mm in maximal diameter. Uniformly spaced blunt spines (up to 45 µm long and 14 µm in diameter) cover the style and are slanted in an upward direction. Dactylopore spines are also uniformly distributed over the branch surface and occasionally arranged in short linear series of 4–10 usually along the branch edge. They are low (up to 0.2 mm tall), apically perforate mounds (Fig. 4G), the circular apical pore about 85 µm in diameter and the dactylopore mound being about 0.20 mm in basal diameter and 0.12–0.14 mm in distal diameter. The tubular mounds are usually slanted anteriorly. Dactylopore tubes extend for long distances down the branch centre (axial dactylopores, Fig. 4B).

Internal cavities just below the branch surface 0.35–0.45 mm in diameter are common, some of which appear to communicate to the surface via very small efferent pores, these cavities presumed to be the male ampullae (Fig. 4I). Female ampullae were not observed.

Comparisons. Sixteen species and another two forms (see Zibrowius & Cairns 1992) are known in the genus *Lepidopora*, however none are known from the Indian Ocean or southeastern Atlantic. Given the insularity of stylasterid species, this is a good indication that *L. diffusa* is a discrete species. Nonetheless, only five species, including *L. diffusa*, have abcauline gastropore lips, but the other four species have linearly arranged gastro- and dactylopores, whereas those of *L. diffusa* are uniformly distributed. Conversely, of the ten species having uniformly distributed gastro- and dactylopores, including *L. diffusa*, none have gastropore lips.

Remarks. Boschma's (1963b) original description was fairly complete, the only contributions made herein relate to observations of the male ampullae, details of the coenosteal texture based on better preserved specimens, more detailed corallum illustrations made possible with the SEM, and several additional distributional records.

Distribution. Known from off southeastern South Africa between Richards Bay (Natal) and Sebastian Bluff, Agulhas Bank (Fig. 22), 47–101 m.

Genus *Inferiolabiata* Broch, 1951

Errina (Labiata) Broch, 1942: 39 (in part).
Errina (Inferiolabiata) Broch, 1951b: 125.—Cairns, 1983a: 107.
Inferiolabiata: Cairns, 1983b: 447—448; 1991: 40; 1992: 540, 544 (key).

Type Species. *Errina labiata* Moseley, 1979, by original designation.

Diagnosis. Colonies uniplanar or bushy, often modified by a commensal polynoid gall tube. Coenosteal texture **reticulate-imbricate.** Gastro- and dactylopores uniformly distributed, however dactylopore spines sometimes arranged in crescents. Gastrostyles elongate, often stabilized with transverse tabulae. Dactylopore spines horseshoe-shaped, the dactylotome facing upward (abcauline). Dactylostyles multiple per dactylopore. Ampullae superficial hemispheres.

Discussion. Only four species are known in the genus, this being the first record from off South Africa. The three previously described species were compared by Cairns (1991: Table 4).

Holocene Distribution. Antarctic and Subantarctic, cold temperate New Zealand and South Africa, tropical southwest Indian Ocean, 87–2100 m.

Inferiolabiata africana sp. nov.

Figs. 1C, 5A–K, 23

Spinipora echinata, Hickson & England, 1909: 352–353, pl. 44, fig. 8 (not *Spinipora echinata* Moseley, 1879 (=*Stellapora echinata*).

Etymology. Named for the continent from which the species was first collected.

Types and Type Locality. Holotype: *MN* SM134, 1 female colony, SAM, and SEM stubs 1676–77 (USNM). Paratypes: *MN* SM38, 2 female colonies, 1 male colony, 3 indet., SAM; *MN* SM103, 1 colony, SAM; *MN* SM107, 2 colonies, SAM; *MN* SM123, 1 dead colony, SAM; *MN* SM131, 1 male colony, SAM; *MN* SM134, 1 male colony, SAM, and SEM stubs 1678–79 (USNM); *MN* SM162, 70 dead fragments, SAM; *MN* SM165, 11 dead fragments, SAM; *MN* SM226, 19 colonies, SAM; *MN* SM228, 6 colonies (3 in alcohol), SAM; *MN* SM237, 2 colonies (1 in alcohol), SAM; *PF*14364, 1 colony, SAM H1441; *PF*2819A, 3 female, ex. SAM H1462; *Vema* 19–28, 5 branch fragments, SAM. Type Locality: 31°00.0’S, 30°27.2’E (off Margate, South Africa), 900 m.

Material Examined. Types; *Spinipora echinata* of Hickson & England (1909), *Sealark* D4, Providence Island, 137 m, MNHN (Paris).

Description. Colonies are roughly uniplanar to somewhat bushy, the latter condition amplified by the association with a commensal polychaete, which causes the coral to form an elongate, perforated tube up to 5 x 2 mm in diameter along its main stem. Colonies are relatively small, the largest (the holotype) only 4.8 cm in height and 3.5 cm wide, with a basal branch diameter of 4.1 mm. Branch tips are slender (about 1 mm in diameter) and pointed. The coenosteal texture is linear-imbricate, at least in the basal part of the colony and its thin basal encrustation. Higher on the colony this texture degenerates into a reticulate pattern, and the imbricate texture is covered with a smooth, dense, porcellaneous material (Fig. 5C), which largely obscures the slits between the coenosteal strips. The corallum is uniformly white.

Gastropores are equally distributed on all branch surfaces, circular in shape, and 0.24–0.38 mm in diameter; there is no bordering lip. The gastrostyle is elongate (L:D up to 6), the illustrated gastrostyle (Fig. 5I) 1 mm in length and 0.15 mm in diameter, the proximal portions stabilized by one or more horizontal tabulae (Figs. 5I, L). The style bears longitudinal ridges that in turn bear a series of blunt spines up to 40 µm in length. A diffuse ring palisade of short (about 35 µm) mushroom-shaped elements occurs in the upper third of the gastropore tube, often visible from an apical view of the gastropore (Fig. 5H) as is the gastrostyle tip, which sometimes extends even slightly above the coenosteal surface. The abcauline dactylopore spines are relative tall (up to 1 mm in height and 0.27–0.31 mm in width), the taller spines tubular proximally (Fig. 5E), the shorter spines having a slender dactylotome for their entire length. The dactylopore spines are perpendicular to the branch when positioned low in the colony, but slanted distally in the upper part of the colony, their exterior surface bearing longitudinal granular ridges, and their distal edges are finely serrate (Fig. 5D). Although many dactylopore spines occur individually, they also form crescents of 3–6 laterally placed spines below gastropores on distal branches. On the inner surfaces of the dactylopore spines, below the level of the coenosteal surface, are three rows of rudimentary dactylostyle elements (a central and two lateral dactylostyles, Fig. 5G), these elements up to 60 µm in height in the central row, and only about 30 µm in the lateral rows. These elements are difficult to see in an intact dactylopore spine, and must be viewed with high magnification (or SEM) in a broken structure.

Female ampullae are prominent superficial hemispheres 0.75–1.0 mm in diameter, each having a lateral efferent pore 0.2–0.3 mm in diameter (Fig. 5K). Male ampullae are irregular superficial protuberances 0.5–0.62 mm in diameter, each having a small apical efferent pore about 50 µm in diameter (Fig. 5J).

Comparisons. *Inferiolabiata africana* is similar to *I. lowei* in many aspects, especially coenosteal texture, dactylopore spine shape, ring palisade structure, and rudimentary dactylostyle structure, but differs consistently in several characters. It has a more delicate and finer colony shape (e.g., more slender branches), and consistently has

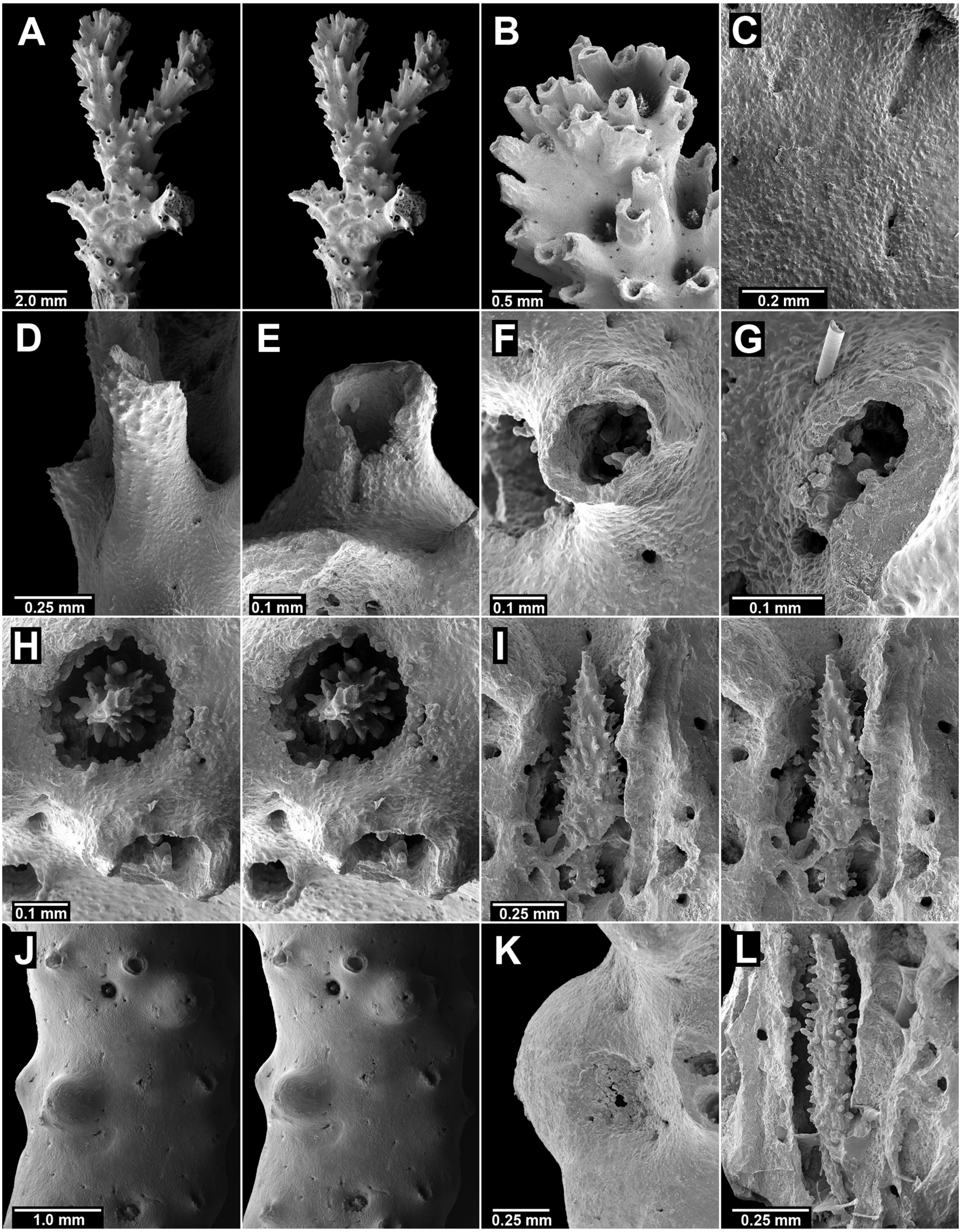

FIGURE 5. *Inferiolabiata africana* (**A–B, D–E, G–I, L**, male paratype from *MN* SM134, SAM; **C, F, J–K**, female holotype from *MN* SM134, SAM): **A**, stereo view of a distal branch. **B**, dactylopore spines surrounding a gastropore. **C**, coenosteal texture. **D–E**, individual dactylopore spines. **F–G**, cross sections of dactylopore spines showing multiple dactylostyles. **H**, stereo view of a gastrostyle tip and diffuse ring palisade**. I, L** view of a gastrostyles with stabilizing tabulae (**I** is a stereo view). **J**, stereo view of male ampullae. **K**, female ampulla and efferent pore.

a polychaete commensal; its gastropore tubes are slightly smaller, its gastrostyles slightly larger, and it does bear a ring palisade, which does not achieve the commodious aspect seen within the gastropore tubes of *I. lowei*; it often has its dactylopore spines arranged in abcauline crescents, and the spines are often cylindrical proximally, whereas those of *I. lowei* are rarely arranged in crescents and are rarely cylindrical. Finally, it has smaller female ampullae.

Distribution. Most of the southeastern coast of South Africa from Cape Peninsula to Richard's Bay (Natal Province) (Fig. 23), 165–1000 m; Providence Island, 137 m (Hickson & England 1909).

Inferiolabiata lowei **(Cairns, 1983)**

Figs. 1D, 6A–M, 24

Errina labiata: Boschma & Lowe, 1969: 15, pl. 5, map 2.
Errina (Inferiolabiata) lowei Cairns, 1983a: 113–117, figs. 22F–G, 28A–G.
Inferiolabiata lowei: Cairns, 1983b: 428, 451 (listed); 1991: 41, 43, pl. 25f–g, 26a–f.—Cairns et al., 2009: 97 (listed).

Types and Type Locality. The type series is housed primarily at the NMNH, with vouchers also deposited at Naturalis Biodiversity Centre and BM (see Cairns 1983a). Type Locality: 54°29'S, 39°22'W (west of South Georgia), 659–686 m.

Material Examined. *PF*907, 1 female colony, ex SAM 1489; *MN* SM185, 1 small fragment, SAM, and SEM stubs 1670–71, 1714 (USNM); type series.

Description (based on the larger South African specimen from PF907). The colony (Fig. 1D) is robust, uniplanar, and sparsely branched, not hosting a commensal polychaete. It measures 3.7 cm tall and 8.9 mm in basal branch diameter, having a somewhat flattened terminal branch 6 mm in greater width. The coenosteal texture is reticulate-imbricate, often covered with a dense smooth material on the upper parts of the corallum (Fig. 6C); the corallum is white.

Gastropores are equally distributed on all branch surfaces, circular in shape, and 0.35–0.40 mm in diameter. The gastrostyle is elongate and quite slender, only 0.11–0.14 mm in diameter, the proximal portions sometimes stabilized by tabulae (Fig. 6K, M). A rudimentary diffuse ring palisade occurs in the upper gastropore tube, composed of globular elements about 35 µm in height. Because of the slender nature of the gastrostyle and the rudimentary ring palisade, there is ample space surrounding the style within the gastropore tube. Although the ring palisade is visible from an apical view of the gastropore, the gastrostyle tip is slightly recessed below the coenosteal surface. The abcauline dactylopore spines (Figs. 6F–H) are up to 0.6 mm tall and 0.35–0.40 mm wide, in all cases the dactylotome occupying the entire length of the dactylopore spine (i.e., not proximally tubular). The exterior surface of the dactylopore spines is longitudinally ridged and spinose (Fig. 6E), and their distal edges are finely serrate; they are invariably independent, not grouped in abcauline crescents. Most dactylopore spines have multiple (1–3), rudimentary dactylostyles (Figs. 6G–J), the elements ranging from 35–45 µm in height.

The superficial female ampullae are 1.1–1.2 mm in diameter, although efferent pores were not observed.

Comparisons. See Comparisons of *I. africana* and Cairns (1991: Table 4) for comparisons of all species in this genus.

Remarks. The single South African specimen compares favorably with the South American type series, but differs in having slightly shorter dactylopore spines (those of the type series may be up to 1 mm), having a rudimentary ring palisade (those of the type series have none), and in having consistently independent, horseshoe-shaped dactylopore spines, whereas those from the type series sometimes have their spines arranged in crescents beneath the gastropores and are occasionally cylindrical proximally, not unlike the conditions found in *I. africana*. The South African specimen was also collected from slightly shallower than those from off South America and New Zealand.

Distribution. South Africa, continental shelf off Eastern Cape Province (Fig. 24), 90–155 m; Southwest Atlantic, off southern Argentina, Tierra del Fuego, Burdwood Bank, South Georgia, and Drake Passage, 250–960 m; New Zealand region, southern Norfolk Ridge, Three Kings Ridge, southwestern South Island, 164–751 m (Cairns 1991).

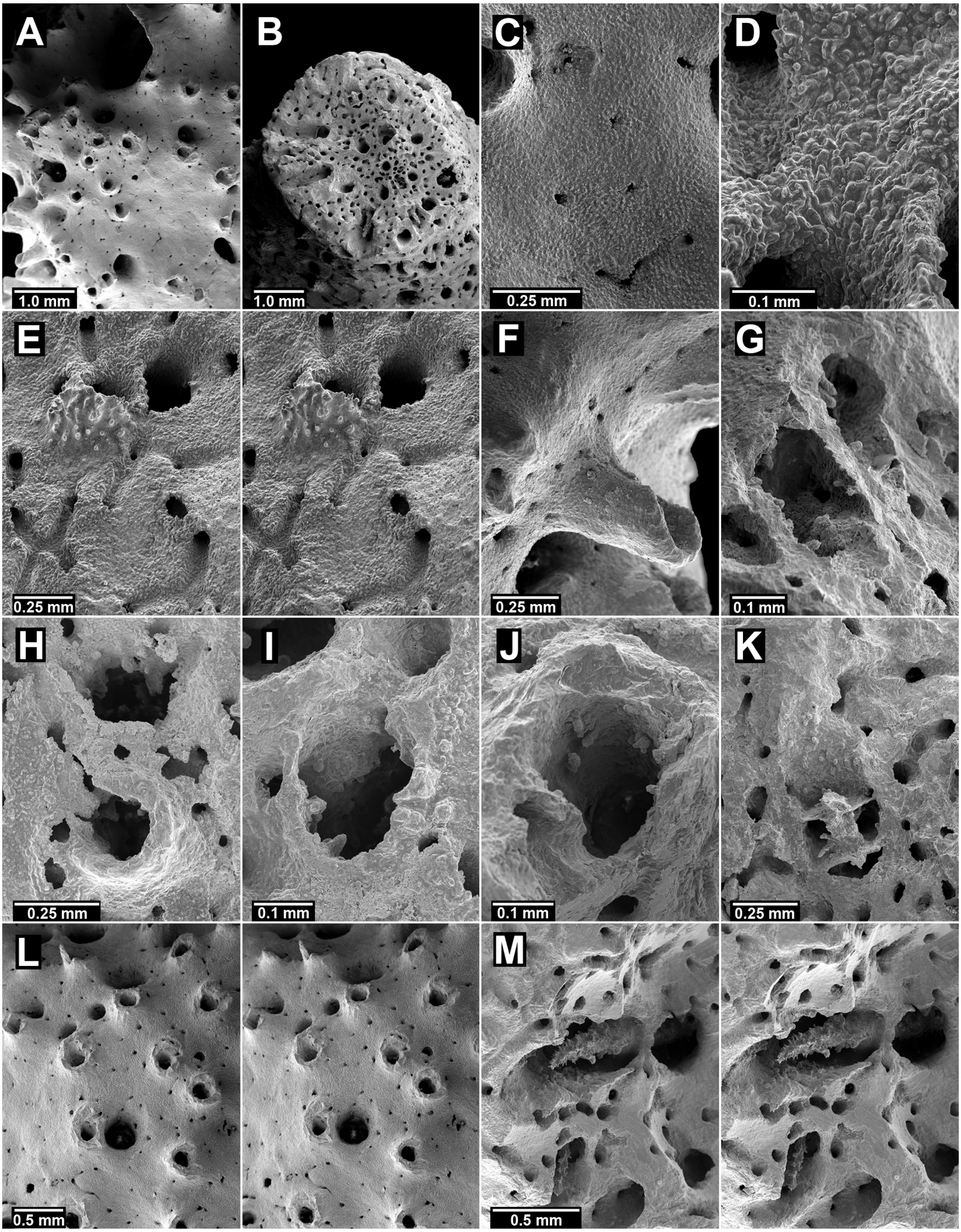

FIGURE 6. *Inferiolabiata lowei* from *PF*907, female, SAM: **A**, branch segment. **B**, branch cross section. **C–D**, coenosteal texture. **E–F**, dactylopore spines (E is a stereo pair). **G–J**, broken dactylopore spines showing rudimentary multiple dactylostyles. **K**, longitudinal section of a gastropore showing a broken gastrostyle, tabulae and a diffuse ring palisade. **L**, stereo view of a gastropore and several truncated dactylopore spines. **M**, stereo view of two gastrostyles, diffuse ring palisade, and tabula.

Inferiolabiata spinosa **Cairns, 1991**

Figs. 1E, 7A–H, 25

Inferiolabiata spinosa Cairns, 1991: 41, 42–43, pls. 24c–f, 25a–e.—Cairns et al., 2009: 97 (listed).

Types and Type Locality. The holotype and most paratypes are deposited at NIWA (=NZOI), and some paratypes are at the NMNH (see Cairns 1991). Type Locality: 32°25'S, 167°35'E (southern Norfolk Ridge, New Zealand), 318–383 m.

Material Examined. *MN* SM163, 10 dead fragments (2 female, 8 indet.), SAM, and SEM stub 1716 (USNM); *PF*13654, 1 fragment, SAM H2818, and SEM stub 1675 (USNM); *Anton Bruun* 420A, 2 female, 2 male, and 1 indeterminate colonies, and several smaller branches, USNM 1172363; type series.

Description. The South African colonies are small (largest only 2 cm in height) but are robust in form, the terminal branches being blunt, round in cross section, and 2–3 mm in diameter; there are no commensal polychaete tubes. Specimens reported from off Kenya (e.g., the illustrated specimen, Fig. 1E) are up to 7 cm in height. The coenosteal texture is imbricate (Fig. 7C) but the lateral borders of the coenosteal strips are poorly defined and the leading edges of the platelets are finely crenelate; the corallum is white.

Gastropores are equally distributed on all branch faces, circular in shape, and 0.25–0.40 mm in diameter. The gastrostyle is elongate, the illustrated one (Fig. 7D) 0.60 mm in height and 0.14 mm in diameter (L:D = 4.3), although no horizontal tabulae were noted. The style is covered with coarse cylindrical spines up to 50 µm in length. A well-developed, diffuse ring palisade, easily visible in apical view, occurs in the upper half of the gastropore tube, the globular elements up to 48 µm in diameter (Fig. 7D). The abcauline dactylopore spines (Figs. 7A, E, G) are up to 0.4 mm in height and 0.27–0.30 mm in width, having a dactylotome width of 0.13–0.15 mm. They are independent in placement (not laterally linked into crescents) and their outer surface is not ridged or spined, simply covered with fine, imbricate platelets. The multiple dactylostyles (3 per dactylopore spine, Figs. 7F, G) are robust and easily seen in apical view, as they occur within the dactylopore spine well above the coenosteal surface. The dactylostyle elements are pillar-shaped and up to 50 µm in height.

Female ampullae are superficial hemispheres up to 0.8 mm in diameter, each having a lateral efferent pore about 0.16 mm in diameter (Fig. 7H). Male ampullae are mammiform, about 0.50 in diameter, and have a large irregularly-shaped apical efferent pore up to 0.15 mm in diameter.

Comparisons. *Inferiolabiata spinosa* is most similar to *I. lowei*, in that both species have robust blunt branches, lack polychaete symbionts, and have independent dactylopore spines. *I. spinosa* differs in having a more pronounced and consistently imbricate coenosteal texture, much more robust ring palisade and dactylostyles (the latter of which continue to the distal end of the dactylopore spines), non-ridged dactylopore spines, and a less spacious gastropore tube. The South African specimens were also collected at a shallower depth than those from the New Zealand region. These two species are also compared by Cairns (1991: Table 4) in tabular form.

Remarks. Although only several small branches were available from South Africa, these specimens compare favorably to the New Zealand type series of *I. spinosa*, differing only in having slightly smaller gastropores and a larger male efferent pore. Larger specimens are reported herein from off Kenya.

Distribution. South Africa, continental shelf off Eastern Cape Province (Fig. 25), 90–93 m; off Kenya, 140 m; New Zealand region, southern Norfolk Ridge, southern Kermadec Ridge, off North Cape; off Auckland Island, 211–781 m.

Genus *Errina* Gray, 1835

Errina Gray, 1835: 85.—Cairns, 1983b: 459; 1986a: 49; 1991: 49–50; 1992: 542, 545.
Errina (Eu-Errina): Broch, 1942: 38.
Errina (Errina): Boschma, 1956a: F102.—Cairns, 1983a: 85.

Type Species. *Millepora aspera* Linnaeus, 1767, by original designation.

Diagnosis. Colonies uniplanar or bushy. Coenosteal texture usually reticulate-granular, but may be linear-imbricate, and occur in a variety of colours. Gastro- and dactylopores arranged uniformly on branches; gastropore abcauline lips may be present. Gastrostyles present. Dactylopore spines thick walled and horseshoe-shaped, the dactylotome facing downward (adcauline), sometimes clustered; dactylostyles absent. Ampullae usually superficial with lateral or apical efferent pores.

Discussion. There are 28 Recent and one fossil species known in the genus (Appeltans, et al. 2012), making it the third most species-rich in the family. Species are particularly common off New Zealand, Antarctica, Subantarctica, and in the Caribbean Sea.

In the course of this investigation it was noted that *Errina hicksoni* Cairns, 1991 is a junior primary homonym of *E. hicksoni* Boschma, 1963a, and thus the replacement name of *E. australis* (Latin for southern) is proposed for Cairns' name. *Errina hicksoni* Boschma, 1963 is a junior secondary synonym of *Lepidopora eburnea* (Calvet, 1903).

Holocene Distribution. New Zealand, Galápagos, N. Atlantic, Subantarctic, Antarctic, southwest Indian Ocean, 6–1772 m.

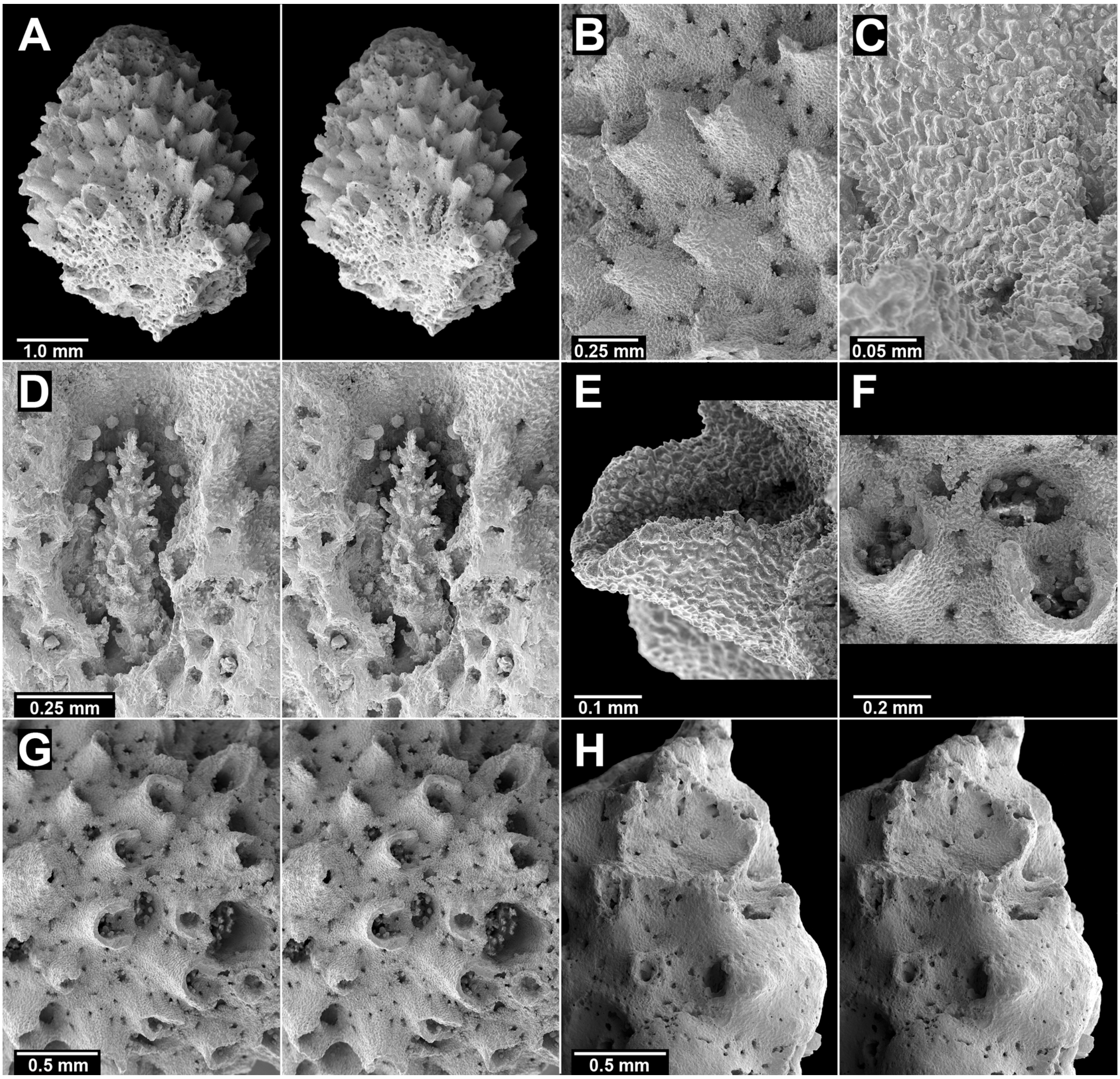

FIGURE 7. *Inferiolabiata spinosa* (**A–G**, male from *PF*13654, SAM; **H**, female from *MN* SM163, SAM): **A**, stereo view of branch tip showing dactylopore spines and a gastrostyle. **B**, dactylopore spines. **C**, imbricate coenosteal texture. **D**, stereo view of gastrostyle and diffuse ring palisade. **E**, dactylopore spine. **F**, dactylopore spines showing multiple dactylostyles. **G**, stereo view of dactylopore spines and a male ampulla with apical efferent pore (left). **H**, female ampullae and efferent pore, upper one ruptured.

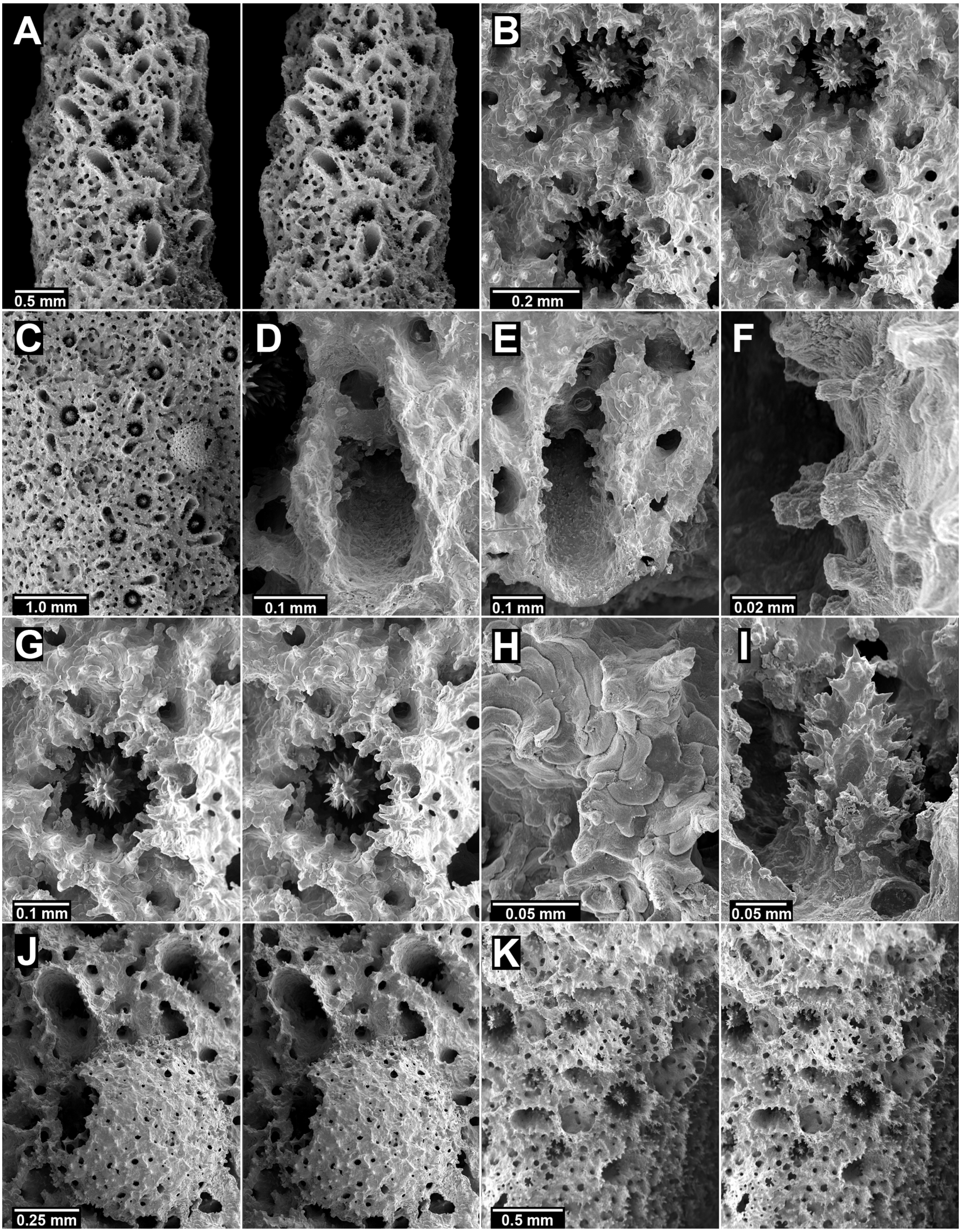

FIGURE 8. *Errina capensis* (**A, C–F, I–J**, female from *MN* XX129, SAM; **B, G–H, K**, male from *PF*13476, SAM H1228): **A**, stereo view of branch segment showing gastropores and dactylopore spines. B, stereo view of gastrostyle tips and diffuse ring palisade. C, female ampulla and branch surface. D–E, dactylopore spines showing basal platform and lateral dactylostyles. F, ring palisade elements. G, stereo view of gastrostyle tip, ring palisade, and imbricate coenosteal texture. H, radial-imbricate coenosteal texture. I, gastrostyle. J, stereo view of female ampulla and lateral efferent pore. K, stereo view of several male ampullae, and serrated edged dactylopore spines.

Errina capensis Hickson, 1912

Figs. 1G, 8A–K, 26

Errina (Labiopora) capensis Hickson, 1912: 886–887, 890, pl. 95, fig. 7, pl. 96, fig. 15.
Errina capensis: Hickson, 1912: 894 (listed).—Broch, 1942: 38, 40 (key).—Boschma, 1957: 52; 1963a: 337 (listed); 1966b: 112.—Cairns, 1983b: 428 (listed).—Williams, 1986: 14 (colour drawing).
Errina (Eu-Errina) capensis: Broch, 1942: 53–54, text-fig. 16, pl. 4, fig.15 (redescription).
Errina (Labiata) capensis: Broch, 1942: 91.

Types and Type Locality. Three female syntypes, preserved in alcohol, are deposited at the MNHN; one syntype branch (illustrated by Broch, 1942) is also deposited at the Zoological Museum, Oslo (B884); one syntype fragment is at the Manchester Museum; and one syntype fragment is at the BM (1950.1.11.90). Type Locality: off Cape of Good Hope, 30 fm (=55 m)(see Hickson 1912: 890).

Material Examined. Types; *MN* SM180, 1, SAM H3154; *MN* SM185, 1, SAM H3153; *MN* XX129, 1 male, 1 female, 1 indet. colonies, SAM, and SEM stubs 1607–609, USNM; *PF*503, 1, SAM H3090; *PF*808, 2, SAM H1221; *PF*11555, 1 colony, SAM H1237; *PF*12104, 1 female, 3 indet. colonies, SAM H3093; *PF*12314, 2 female branches, SAM H1219; *PF*13394, 24, SAM H1233; *PF*13465, 1 colony, SAM H1234; *PF*13476, 19 male branches, SAM H1228 and, and 3 female branches and SEM stub 1666, USNM 76521 and 76522, and four branches, BM1980.9.19.12; *PF*13599, 4 colonies, SAM H1232; *PF*13959, 9 colonies, SAM H1224; *PF*15614, 1, SAM H3092; *Valdivia* 100, 1, ZMB; off Cape of Good Hope, Manchester Museum.

Description. Colonies are uniplanar, having equal dichotomous branching, the axils between branches being fairly narrow; there is no branch anastomosis and no symbiosis with commensal polychaetes. The largest specimen (*MN* XX129) is 8.2 cm in height and 10.5 mm in basal stem diameter. Distal branches are blunt and slightly flattened to elliptical in cross section. The coenosteal texture is basically radial-imbricate, consisting of broad smooth platelets (Fig. 8H), but the coenosteal strips are narrow and poorly defined, bordered by rather large coenosteal pores (up to 58 µm in diameter), which confer a somewhat porous aspect to the branch surface. Furthermore, the coenosteum bears numerous small (up to 78 µm), sharp spines (Fig. 8G) that project perpendicular to the branch surface, giving it a spiny texture. Colonies are light orange in colour, the branch tips, cores, and ampullae usually being white.

Gastropores are uniformly distributed on all branch surfaces and are circular in shape, ranging from 0.20–0.30 mm in diameter; there are no bordering gastropore lips. The gastrostyles are stout and bullet-shaped (Fig. 8I), up to 0.24 mm in height, with a L:D of 1.6–2.0, and occupy the entire gastropore tube, the distal tip sometimes even rising slightly above the coenosteal surface (Figs. 8B, G). The gastrostyle is covered with tall (up to 34 µm) pointed spines, which are often fused into longitudinal or oblique ridges. The inner face of the upper half of the gastropore tube bears a wide diffuse ring palisade composed of blunt elements up to 44 µm in height. These elements continue to the uppermost part of the gastropore tube and are almost indistinguishable from the coenosteal spines (Figs 8B, G). The horseshoe-shaped dactylopore spines (Figs. 8D, E) are quite abundant, covering all surfaces of the branch, but better developed on one side (by definition, the anterior) and lateral branch edges. Near the branch tips the dactylopore spines are uniformly adcauline in orientation and discrete, but farther away from the tip the orientation of their dactylotomes may be lateral or oblique, and several dactylopore spines may be fused laterally into short rows. The dactylopore spines are fairly short (only 0.14–0.29 mm in height), and thin-walled (30–50 µm), about 0.20–0.25 mm in total width, and 0.4–0.5 mm long; the outer wall of the dactylopore spines are often buttressed with several thin ridges, which give the upper spine a serrate edge. Internally, each dactylopore spine has a single, thin, flat platform on its internal upper edge (Fig. 8D, E), which blocks about half of the dactylotome. Furthermore, each dactylopore spine has two lateral (but no medial) dactylostyles, the elements being 15–24 µm in height (Fig. 8E).

The female ampullae are prominent, hemispherical structures 0.6–1.0 mm in diameter, when mature having a circular lateral efferent pore about 0.30 mm in diameter (Fig. 8J). They occur on the anterior and lateral branch faces, sometimes in great abundance. Male ampullae are also superficial but smaller (0.45–0.50 mm in diameter), having a porous structure and small apical efferent pores (Fig. 8K). They concentrate on the anterior surface, often in clusters.

Comparisons. Among the 27 Recent species of *Errina* (Appeltans, et al. 2012; Cairns 1999), only two others are known from the Indian Ocean. *Errina capensis* is similar to the Subantarctic *E. kerguelensis* Broch, 1942 in gross colony shape and colour, but differs in almost all other characters (see Cairns 1983a). The other species, *E. aspera mascarina* Boschma, 1965, from Mauritius, differs in having a white corallum, much taller dactylopore spines, a longer gastropore tube and taller gastrostyles, although the styles do not reach the branch surface, and in lacking a ring palisade and coenosteal spines. Boschma (1965) gave convincing evidence that this subspecies (*Errina aspera mascarina*) was different from the Mediterranean nominal subspecies, although Zibrowius & Cairns (1992: 48) suggested that this specimen was collected in the Mediterranean, not off Mauritius.

Remarks. Despite several references to this species and a host of combinations (see synonymy), until now this species was known only from the type material. This is the first treatment that employs SEM, including the first description of the ampullae, as well as adding several new distributional records. Although no commensal polychaetes live with this species, it does commonly harbor attached barnacles.

Distribution. Known from coastal waters of South Africa from off the Cape of Good Hope to just north of Durban (Natal Province) (Fig. 26), 40–174 m.

Genus *Errinopsis* Broch, 1951

Errinopsis Broch, 1951b: 40.—Boschma, 1956a: F104.—Cairns, 1983a: 77–78; 1983b: 455–457; 1992, 540: 545;

Type Species. *Errinopsis reticulum* Broch, 1951b, by original designation.

Diagnosis. Colonies uniplanar to bushy, branching highly anastomotic (fenestrate), often with multiple attachments to substrate. Coenosteal texture a mixture of reticulate-granular and coarsely imbricate. Gastro- and dactylostyles uniformly arranged on branches. Gastrostyles present; dactylopore spines dimorphic, mound-like and horseshoe-shaped, the dactylotome facing downward (adcauline) as in *Errina*; dactylostyles absent. Ampullae superficial with lateral or apical efferent pores.

Discussion. This is a rarely reported genus consisting of only two species, previously known only from Subantarctic South America.

Holocene Distribution. Off southern South America and South Africa, 250–771 m.

Errinopsis fenestrata Cairns, 1983

Figs. 9A–I, 22

Errinopsis fenestrata Cairns, 1983a: 80–82, figs. 1I, 10A–G; 1983b: 428 (listed).—Cairns & MacIntyre, 1992: 98–99 (mineralogy).—Cairns, 2011: fig. 7A.

Types and Type Locality. The type series is deposited primarily at the NMNH, with vouchers also at the Naturalis Biodiversity Centre and BM (see Cairns 1983a). Type Locality: 59°49.4’S, 68°51.7’W (seamount in Drake Passage), 280–340 m.

Material Examined. *PF*13479, 1 colony, exSAM2817; 32°27.2’S, 28°55.9’E, 250 m, coll. William Rune Liltved, 12 July 1984, 1 colony and SEM stub 1672 (USNM 1189354); RV *Seidlecki* 601, 53°20’S, 42°42’W, 417–514 m, 1 colony, USNM 83591; type material.

Diagnosis. Colonies uniplanar and small (less than 11 mm in height), not yet forming anastomosing branchlets; branchlets rectangular in cross section, the longer axis perpendicular to plane of colony; coenosteal modification caused by commensal polychaete present. Coenosteal texture linear-granular (Fig. 9C–E), the strips being 52–90 µm in width and fairly smooth, covered with small (6 µm) sparse granules; coenosteum around and composing dactylopore spines imbricate (Fig. 9F); coenosteum light orange. Gastropores round (0.21–0.23 mm in diameter), occurring on anterior face and at branch axils; gastropore tubes cylindrical, without a ring palisade; gastropores bordered with a wide abcauline lip (Fig. 9B), which usually bears several dactylopore spines. Gastrostyle base thick and finely ornamented, capped by a coarsely ridged apical tip. Dactylopore spines dimorphic, one type consisting of short apically perforate cones (Figs. 9C, E), the pore being 27–33 µm in diameter, the second type being taller (up to 0.25 mm), slender (0.11–0.13 mm), cylindrical projections (Fig. 9D, F), usually with an pore or slit on its lower side, but not horseshoe-shaped as in *Errina*. Ampullae (?female) superficial and spiny due to coverage with dactylopore spines.

Remarks. Only a diagnosis is given above, as there is a complete description and illustrations in the original account. The South African specimens differ from the type material in two aspects: because the specimens are quite small (less than 11 mm tall), they have not yet developed a fenestrate colony form. Secondly, the South African specimens are light orange, not white as the type material.

Distribution. South Africa: known only from region near East London, Eastern Cape Province (Fig. 22), 174–250 m; Drake Passage and off Shag Rocks, 280–514 m.

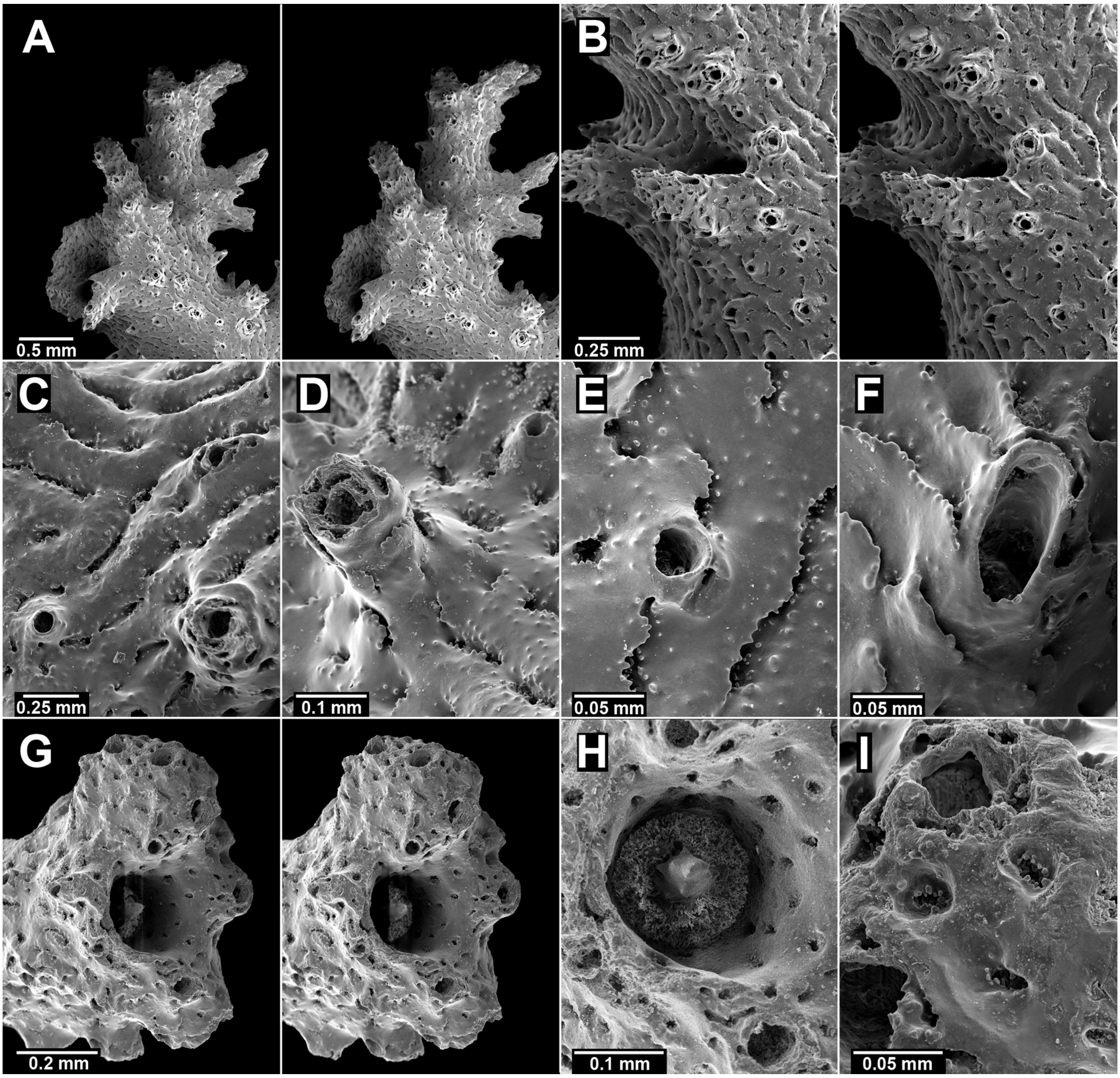

FIGURE 9. *Errinopsis fenestrata* from *PF*13479: **A**, stereo view of branch tips showing dactylopore spines. **B**, stereo view of prominent lower gastropore lip. **C–D**, dactylopore spines and linear-granular coenosteal texture. **E**, short conical dactylopore spine. **F**, taller dactylopore spine with slit-like dactylotome. **G**, stereo view of branch tip and gastrostyle tip. **H**, gastrostyle tip viewed from above. **I**, coenosteal texture (?ampullae).

Genus *Gyropora* Boschma, 1960

Gyropora Boschma, 1960a: 423–433.—Cairns, 1983b: 465–466 (redescription); 1992: 540, 545 (key to genus).

Type Species. *Gyropora africana* Boschma, 1960, by original designation.

Diagnosis. Colonies small, flabellate or columnar, the branches blunt and circular in cross section. Coenosteal texture reticulate-granular and pale reddish-purple in colour. Gastro- and dactylopores arranged in long, meandering, distichoporine rows, the row of gastropores sunken below coenosteal surface. Gastropore tubes short (peripheral), without a ring palisade, each having a gastrostyle covered with blunt spines. Dactylopore spines U-shaped, with common lateral walls, their dactylotomes directed toward the gastropore row; dactylostyles absent. Ampullae unknown.

Discussion. *Gyropora* differs from *Distichopora*, some species of which may also have meandering distichoporine pore rows, by having short (peripheral) gastropore tubes and blunt spines on the gastrostyle (see Cairns, 1983b, 1992). The genus is monotypic.

Holocene Distribution. Known only from off Cape Agulhas and Cape of Good Hope, South Africa, 22–80 m.

Gyropora africana Boschma, 1960

Fig. 1H, 23

Gyropora africana Boschma, 1960a: 423–433, pl. 1, figs. 1–9, text-figs. 1a–d; 1966b: 112 (listed).—Vervoort & Zibrowius, 1981: 13, 26–27 (lectotype designation).—Cairns, 1983b: 466, figs. 13A–H, 24J, 25L (redescription).—Cairns & Macintyre, 1992: 100–101 (mineralogy).

Types and Type Locality. A lectotype was designated from the syntype series of two specimens by Vervoort & Zibrowius (1981) UCTES TRA151, which is now cut in two pieces and deposited at Naturalis Biodiversity Centre (Coel. 13749). The smaller paralectotype cannot be found. Type Locality: 34°51’S, 19°35’E (off Cape Agulhas, South Africa), 22 m.

Material Examined. Lectotype; specimen from BM 1977.8.5.1, Cape of Good Hope (Cairns 1983b); *Valdivia* 95, 6 branches, ZMB; *PF*2675, 1, SAM H1235.

Remarks. This species is known from only four locations, two of them reported herein, all from shallow water off South Africa. The *Valdivia* specimen, collected 62 years before the original description, was only a km from the type locality. The species was adequately described and figured by Boschma (1960a) and Cairns (1983b), and thus no additional SEM illustrations are included. Being a monotypic genus, the generic diagnosis is sufficient for its identification.

Distribution. As for the genus (Fig. 23).

Genus *Stylaster* Gray, 1831

Stylaster Gray, 1831: 37.—Boschma, 1956a: F99.—Cairns, 1983a: 136; 1983b: 476–479; 1986a: 54; 1991: 60–61; 1992: 540, 544.—Cairns & Lindner, 2011: 36.
Allopora Ehrenberg, 1834: 303, 371.
Stylaster (Eustylaster): Broch, 1914: 7.

Type Species. *Madrepora rosea* Pallas, 1766, by subsequent designation (Milne Edwards & Haime 1850: xxii).

Diagnosis. Colonies uniplanar, bushy, or lamellate. Coenosteal texture variable, including reticulate-granular and linear-imbricate; coenosteum expressed in a variety of colours. Gastro- and dactylopores arranged in cyclosystems arranged on the branch edges (Species group C), uniformly on all branch surfaces (Species group A), or irregularly on three sides of the branches (Species group B). Gastropore tube single-chambered but may be partitioned by a ring palisade or a sphincter; gastrostyles present. Dactylostyles present, some species having dactyloglossae. Ampullae usually superficial with exterior efferent pores, but sometimes opening into upper gastropore tube.

Discussion. Eighty-two Recent (and 7 fossil) species are now recognized in the genus (Appeltans, et al. 2012), making it by far the most species-rich and morphologically diverse genus in the family. Cairns (1983b) divided the species of the genus into three groups based on the arrangement of their cyclosystems in an effort to facilitate comparisons among species. These groups were not implied to have phylogenetic significance.

Holocene Distribution. Cosmopolitan, 1–2010 m.

Stylaster (Species group A)

Diagnosis. Species of *Stylaster* having cyclosystems arranged on all surfaces of the branch; branch tips usually blunt. Formerly called *Allopora*.

Stylaster nobilis (Kent, 1871)

Figs. 1I, 10A–L, 24

Allopora nobilis Kent, 1871: 279–280, no fig.—Moseley, 1879: 480 (listed); 1881: pl. 2, figs. 10–12; 1892: 460–461, text-figs. 2–3.—Hickson, 1900: 93–94.—Gilchrist, 1921: 31, 72.—Boschma, 1956b: 154–164, pl. 1, figs. 1–4, pl. 2, figs. 1–4, pl. 3, figs. 1–9, 4 text figs. (complete redescription and discussion of previous records); 1957: 23–24 (complete synonymy); 1961: 220–221; 1966a: 271; 1966b, 112.—Rudd, 1978: 1–36.—Vervoort & Zibrowius, 1981: 38.—Williams, 1986: 11, 13.

Allopora explanata Kent, 1871, 280, pl. 25, figs. 2, 2a–c.—Moseley, 1879: 480 (listed).

Stylaster (Allopora) nobilis: England, 1926: 267, 273–275, text figs. 9–11 (observations of male gonophore).—Broch, 1936: 11, 13, 63–65, pl. 11, fig. 28, text-figs. 20–21 (redescription).

Stylaster nobilis: Best, Faure & Pichon,1980: 623 (listed).—Cairns, 1983b: 429 (listed).

Types and Type Locality. Fragments of the male holotype of *A. nobilis* are deposited at the BM (1893.6.1.1). Type Locality: Boschma (1957) "fixed" the type locality of this species as False Bay, South Africa, 30 fms, the locality of the specimen reported by Hickson (1900), however this is not based on a type specimen and thus cannot serve as the type locality. The type locality was unrecorded in the original description and thus remains unknown, but is probably in the region of the Cape of Good Hope.

Material Examined. *PF*393, 1 colony, SAM H1239; *PF*503, 1 colony, SAM H1238; *PF*559, 2 colonies, SAM H1227; *PF*622, 1 colony, SAM H1230; *PF*808, 1 colony, SAM H1231; *PF*7014, 1 female, 1 male colony, and SEM stubs 1695–96, USNM 76531, and 34 colonies, SAM H1229; *PF*7023, 11 colonies, SAM H1243; *PF*13476, 1 indet. colony, SAM H1228; *PF*15607, 2 colonies, SAM H1220; *PF*15614, 1 colony, SAM H1218; *PF*15618, 2 colonies, SAM H3054; *PF*15675, 2 colonies, SAM H1217; *PF*18347, 1 colony, SAM H1494; UCTES AFR801, 1 colony, RMNH 15833; UCTES AFR801, 1 male colony, RMNH 15876; UCTES FAL332, 1 colony, RMNH 15838; UCTES FAL573, 5 colonies, RMNH 15831; UCTES FAL582, 1 colony, RMNH 15832; UCTES SCD56, 1 colony, RMNM 15834; UCTES SCD311, 1 colony, RMNH15837; UCTES TRA 23, 1 male and 1 female colony, RMNH 15835, and 2 male colonies and SEM stub 1694 (USNM 76532); UCTES WCD36, 1 colony, RMNH 15830; *Valdivia* 95, 5 fragments, ZMB; off Cape Town, 9–22 m, 1 female colony, coll. Branko Velimirov, Senckenberg Museum, Frankfurt; Mossel Bay, 1 colony, SAM H1510; off Cape of Good Hope, 2 colonies, BM1977.8.7.1; five fragments of holotype (BM 1893.6.1.1); specimens reported by Hickson (1900) MHNHP; specimens reported by Boschma (1956a, 1966b (reported herein)), the Naturalis Biodiversity Centre; specimens reported by Broch (1936), ZMC.; specimen reported by Best et al. (1980), Musée Royal de l'Afrique Centrale, Tervuren (Belgium), #968.

Description. Colonies are large, robust, uniplanar, and sparsely branched, not uncommon for colonies up to 5 cm being unbranched (Fig. 1J). The largest known colony (the holotype) is 30 cm tall and 23 cm wide, having a massive basal branch diameter of 5 cm. Branching is dichotomous, resulting in U-shaped axils; branch tips are blunt, 2–4 mm in diameter; there is no branch anastomosis. There are no polynoid gall tubes. The coenosteal texture is reticulate-smooth, the strips being 22–41 µm in width and fairly short, but quite tall, standing as pillars up to 0.2 mm in height (Fig. 10D); the bordering coenosteal slits are quite narrow, about 2 µm. Small, shallow cylindrical depressions are scattered over the coenosteum, each about 50 µm in diameter and only 20–30 µm in depth, these assumed to be nematopores (Fig. 10B, K, L). The colonies are light pink to rose colour, but branch tips and the central core of large diameter branched are white.

Cyclosystems are homogeneously arranged on all branch surfaces, although occasionally several appear to be arranged in a short row, and in some cases 2 or 3 cyclosystems are fused together. Cyclosystems are round, 0.7–0.8 mm in diameter, and usually flush with or only slightly raised above the coenosteum (Fig. 10B). Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 4–8; the average is 6.14 ($\sigma = 1.05$); and the mode is 6 (but see Remarks). Diastemas (Fig. 10B) are not uncommon, especially in cyclosystems near the base of the colony.

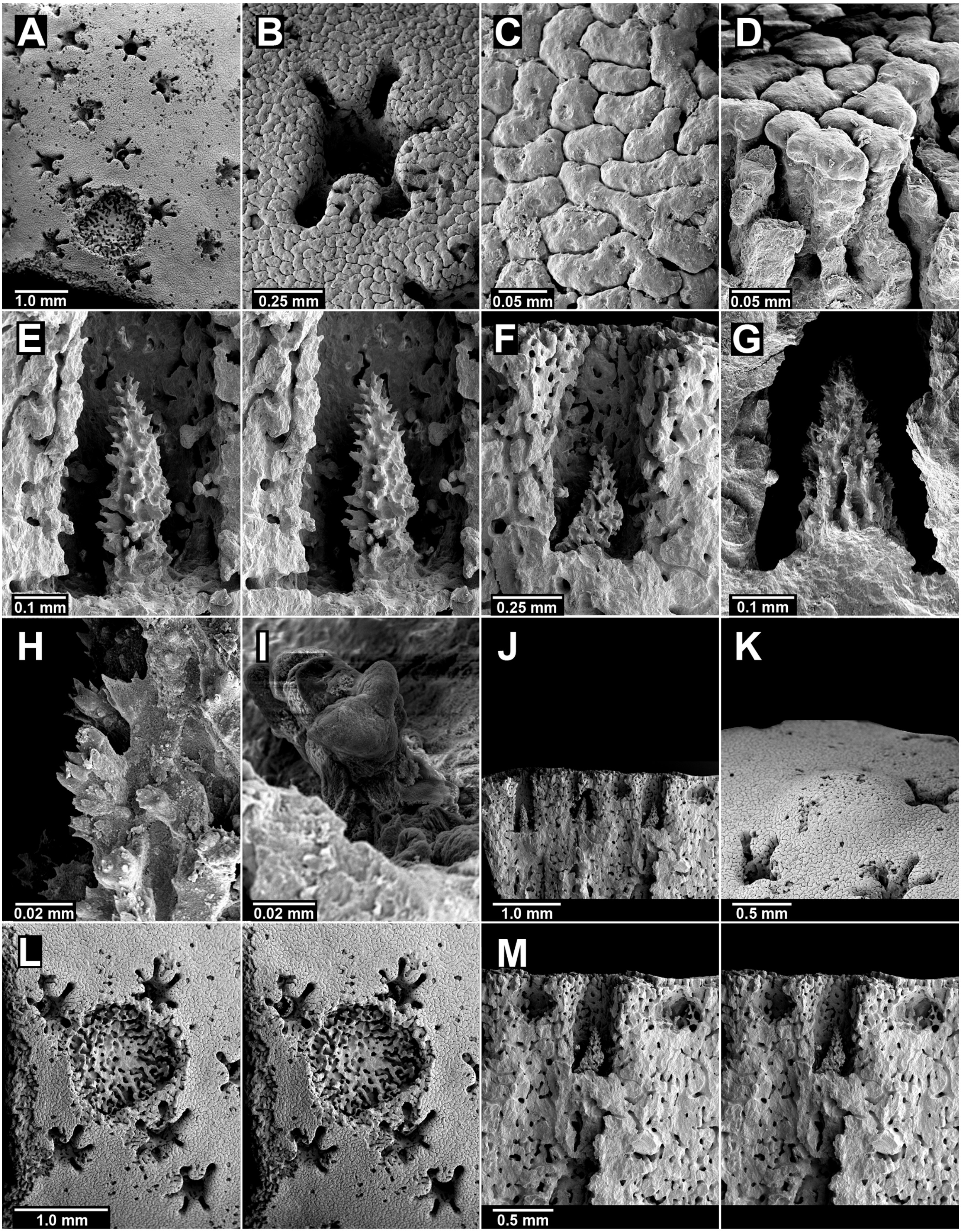

FIGURE 10. *Stylaster nobilis* (**A–C, I, K, L**, female form *PF*7014, USNM 76531; **E–F, J, M**, male from UCTES TRA32, USNM 76532; **D, G, H**, male from *PF*7014, USNM 76531): **A**, branch segment with numerous cyclosystems, a ruptured female ampulla, and numerous nematopores. **B**, a cyclosystem. **C–D**, reticulate-smooth coenosteal texture. **E–G**, gastrostyles and diffuse ring palisade (**E** is a stereo pair). **H**, spines on gastrostyle. **I**, dactylostyle elements. **J, M**, branch cross section with gastrostyles and internal male ampullae (**M** is a stereo pair). **K**, superficial female ampulla. **L**, stereo view of ruptured female ampulla.

The gastropore is circular and the gastropore tube cylindrical, each having a diameter of 0.28–0.35 mm, the tube as deep as 1 mm. The gastrostyle is lanceolate and pointed, up to 0.45 mm in height and 0.25 mm in diameter, having a L:D ratio of 1.5–3.2. The style is covered with sharp spines up to 21 µm in length. There is a discrete ring palisade near the tip of the gastrostyle (Fig. 10E), the clavate elements up to 65 µm in height. The dactylotomes are 60–100 µm in width, the pseudosepta being wider and variable in size. Dactylostyles (Fig. 10I) are well developed, often unilinear rows of clavate elements up to 50 µm in height, easily seen in apical view.

Female ampullae are primarily internal, only low superficial mounds visible in an intact corallum (Fig. 10K), but these cavities are easily seen in branch cross section, ranging from 1.2–1.5 mm in diameter. Efferent pores are never seen, although it is not unusual to observe spent female ampullae, seen as large craters in the coenosteum (Figs. 10A, L). It is likely that the entire top of the ampulla disintegrates to release the planula. Male ampullae are also primarily internal, about 0.34– 0.41 mm in diameter, and also best seen in branch cross section (Figs. 10J, M). They are very abundant in colonies, manifested as very low superficial mounds having apical efferent pores, the pores irregular in shape and about 50 µm in diameter.

Comparisons. See Comparisons in the account of *S. subviolaceus* and Table 1.

Remarks. Although relatively few specimens are known of this species, it is one of the best-described stylasterids thanks to the exhaustive account of Boschma (1956b), the redescription of Broch (1936), and the observations of male gonophores by Hickson (1900). For instance, Boschma summarized the results of counting 600 dactylopores per cyclosystem, resulting in a range of 2–8, an average of 5.09, and a mode of 5, slightly less than reported herein, and he illustrated no less than 21 gastrostyles.

Distribution. Common on South African continental shelf from Saint Helena Bay (Western Province) to Sandy Point (near Cape Morgan), Eastern Cape Province (Fig. 24), 3–174 m.

Stylaster subviolaceus (Kent, 1871)

Figs. 1J, 11A–L, 25

Allopora subviolacea Kent, 1871: 280.—Moseley, 1879: 480 (listed).—Boschma, 1957: 28–29 (in part, not tropical records, which are *S. blatteus*); 1961: 206–210, 218–219 (comparison to *S. blatteus*); 1966a: 267–271, pl. 1, text-figs. 1–2 (complete redescription); 1966b: 112.—Vervoort & Zibrowius, 1981: 38.—Williams, 1986: 12, fig. 1.

Not *Allopora subviolacea*: Greeff, 1886: 11.—Bauer, 1896: 696.—Monod, 1928: 175.—Eguchi, 1941: 1183 (most being S. *blatteus*).

Stylaster (Allopora) subviolaceus: Broch, 1936: 13, 17, 66–69, pl. 11, fig. 29, text fig. 21 (redescription, in part, not West African specimens).

Stylaster subviolaceus: Cairns, 1983b: 429 (listed).—Zibrowius & Cairns, 1992: 76.

Types and Type Locality. Male holotype deposited at the BM (1851.11.14.27); 3 small fragments of holotype also deposited at the Naturalis Biodiversity Centre (RMNH 15364). Type Locality: Unknown, although Boschma (1966a) attempted to “restrict” the type locality to the southern coast of South Africa.

Material Examined. *PF*15607, 12 colonies, SAM H3053–54; *PF*15614, 4 colonies, SAM H3051; *PF*15618, 2 male colonies, SAM 1225; *PF*15675, 8 colonies, SAM 3052, and SEM stub 1697 (USNM); *PF*15745, 5 colonies, SAM H3055; UCTES TRA120, 5 colonies, Naturalis Biodiversity Centre; UCTES FAL303, 1 colony, Naturalis Biodiversity Centre; TRA151, 1 male fragment and SEM stub 1698, USNM 76533; portion of holotype deposited at the Naturalis Biodiversity Centre; holotype (BM 1851.11.14.27); specimen reported by Broch (1936), ZMC; specimen reported by Boschma (1966a), Naturalis Biodiversity Centre.

Description. Colonies are moderately large, uniplanar, and sparsely branched, not having branch anastomosis. The largest known colony (the holotype) is 8.9 cm in height and 1.3 cm in basal branch diameter. Branching is dichotomous, with U-shaped axils, the branch tips about 2.5 mm in diameter. There are no polynoid gall tubes. The coenosteal texture is reticulate-smooth (Figs. 11 C–E), the strips being 60–80 µm in width and somewhat convex in shape, also having a vertical dimension, as in *S. nobilis*; the coenosteal slits are only 2–3 µm in width. Nematopores were not observed. The colonies are light violet or purple in colour, the central core and tips of branches being white to light yellow.

Cyclosystems are homogeneously arranged on all branch surfaces. They are elliptical to irregular in outline and 0.9–1.3 mm in greater diameter; their edges are slightly raised above the coenosteum, especially on the lower

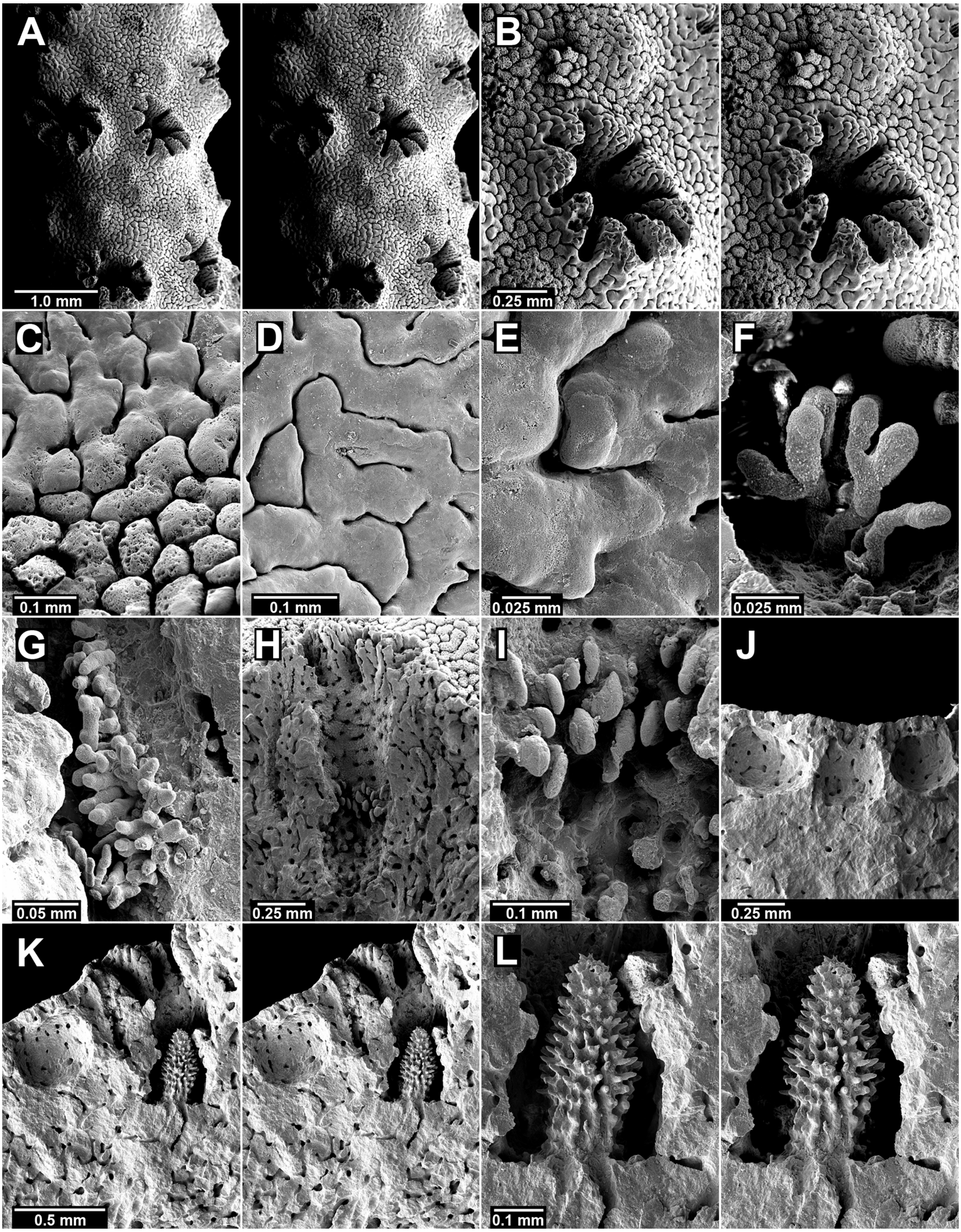

FIGURE 11. *Stylaster subviolaceus* (**A–F, H–I**, male from *PF*15675, SAM; **G, J–L**, male from UCTES TRA151, USNM 76533): **A**, stereo view of branch segment with cyclosystems and male ampullae. **B**, stereo view of a cyclosystem and adjacent male ampulla. **C–E**, reticulate-smooth coenosteal texture. **F–G**, dactylostyle elements. **H**, gastropore tube missing its gastrostyle but showing the ring palisade. **I**, elongate ring palisade elements. **J,** branch cross section showing internal male ampullae. **K**, stereo view of gastrostyle and internal male ampulla. **L**, stereo view of a gastrostyle.

TABLE 1. Distinguishing Characteristics of the South African species of *Stylaster* (Group A).

	S. nobilis (Kent, 1871)	*S. subviolaceus* (Kent, 1871)	*S. blatteus* (Boschma, 1961)	*S. bithalamus* Broch, 1936	*S. griseus* n. sp.
Branch Tips	Blunt	Blunt	Blunt	Sympodial	Blunt
Commensal Polynoid Tube	Absent	Absent	Absent	Present	Absent
Coenosteal Colour	Rose-pink	Rose (white interior)	Dark purple	White	Gray or light brown
Coenosteal Texture	Reticulate-Smooth, deep strips	Reticulate-Smooth, deep strips	Reticulate-Granular	Reticulate-Granular (irregular granules)	Reticulate-Granular (irregular granules)
Cyclosystems: Prominence and Diameter	Flush, 0.7–0.8 mm	Raised, 0.9–1.3 mm	Slightly raised, 0.8–0.9 mm	Slightly raised, 1.0–1.4 mm	Raised, 0.9–1.1 mm
Dactylopores/Cyclosystem: Range, Average, Mode	2–8; 6.1; 5 and 6	3–12; 8.67; 8	6–12; 8.88; 9	1–19; 11.0; 10 and 11	7–12; 9.22; 9
Isolated Dactylopores	Common	Rare	Very common	Absent	Absent
Dactylostyles	Unilinear, 50 µm tall	Multilinear, 80 µm tall	Rudimentary elements	Dactyloglossae	Dactyloglossae
Female Ampullae	Primarily internal, 1.2–1.5 mm, no efferent pore	Unknown	Superficial, 0.5–0.65 mm	Primarily internal, with efferent pore into gastropore tube	Internal, with efferent pore into upper gastropore tube
Male Ampullae	Partially internal, 0.4 mm	Primarily internal, 0.38–0.50 mm, efferent pores unknown	Superficial, 0.3–0.45 mm	Superficial, 0.3–0.5 mm	Low mounds, 0.4 mm
Other Characters		Ring palisade elements elongate	Ring palisade elements elongate	Gastrostyles variable in shape	Gastrostyles variable in shape
Distribution	Southwestern S. Africa, 3–174 m	Southwestern S. Africa, 22–88 m	Gulf of Guinea, 0–10 m	South Africa, 11–131 m	Southeastern S. Africa, 80–155 m

(abcauline) side. Based on 30 cyclosystems, the range of dactylopores per cyclosystem is 6–12; the average is 8.67 (σ = 1.56); and the mode 8. Other counts made by Broch (1936) and Boschma (1961, 1966a) yielded slightly lower averages of 6.78, 6.97, and 8.06, modes of 7 and 8, and a range as low as 3. Diastemas are rare.

The cylindrical gastropore tube is 0.32–0.39 mm in diameter and up to 1.3 mm long. The gastrostyles are lanceolate (Fig. 11 K, L), up to 0.58 mm in height and 0.23 mm in diameter, having a H:D ratio of 1.7–3.6. The gastrostyle is covered with spines, each up to 40 µm in length. The ring palisade consists of elongate (not cylindrical) elements, each up to 60 µm in length and 22 µm in width, the greater axis aligned with the gastropore tube (Fig. 11H, I), each elongate about 50 µm in height. The dactylotomes are 70–75 µm in width. Dactylostyles are well developed (Fig. 11F, G) and often in a crowded arrangement, each slightly clavate element up to 76 µm in height and about 15 µm in diameter.

Female ampullae are unknown. Male ampullae are primarily internal (Figs. 11 B, J, K), visible on the surface as only a slight swelling and apical efferent pore. The diameter of the internal cavity is 0.38–0.50 mm.

Comparisons. *Stylaster subviolaceus* is quite similar to *S. nobilis*, both species sympatric in range and depth. However, when scrutinized (Table 1), *S. subviolaceus* appears to differ in: having a higher range and average number of dactylopores per cyclosystem, a coarser coenosteal texture composed of wider and slightly convex coenosteal strips, raised cyclosystems (vs flush), elliptical to irregularly-shaped (vs round) and larger cyclosystems, lacking isolated dactylopores, and in having distinctively shaped ring palisade elements.

Stylaster subviolaceus has also been confused with *S. blatteus* (Boschma, 1961) in the past, as chronicled by Boschma (1961). *S. blatteus*, the so-called “West African blue coral” or “akori” has been used to manufacture ornamental beads at least since the sixteenth century. This species occurs exclusively in shallow water (0–10 m) in the tropical Gulf of Guinea region. Perhaps because of the similarity of colour and belonging to the same genus, the tropical species was called *Allopora subviolacea* by several authors (see synonymy) until Boschma (1961) recognized the mistake and named the tropical species *A. blattea*. *S. subviolaceus* differs from *S. blatteus* (Table 1, and Zibrowius & Cairns 1992) in having a less intense colouration (not dark purple) that fades in the branch axis and tips, reticulate-smooth coenosteal texture (not reticulate-granular), larger cyclosystems, lacking isolated dactylopores (which are very common in *S. blatteus*), and in having much larger dactylostyles. Iro nically, both species share the same morphology of the elongate elements composing their ring palisades.

Remarks. Although the species has been well described and figured (Broch 1936, Boschma 1966a, and herein), it must be kept in mind that it is known from relatively few records, most of that material consisting of small branches.

Distribution. Known from a small region off southwestern South Africa from the Cape of Good Hope to Cape Agulhas (Western Cape Province)(Fig. 25), 22–88 m.

Stylaster bithalamus Broch, 1936

Figs. 2A–B, 12A–I, 27

Allopora oculina: Studer, 1878: 636.—Hickson, 1900: 94.—Boschma, 1966b: 112.
Stylaster (Allopora) bithalamus Broch, 1936: 13, 18, 74–76, pl. 12, fig. 34, text-fig. 25.
Allopora bithalamus, Boschma, 1957: 18; 1960b: 435–445, pls. 1–3, text-figs. 1–4 (redescription).—not Eguchi, 1964: 7 (=*S. eguchii*).—Boschma, 1966b: 110–112, figs. 1e–h (comparison to *A. eguchii*).—Vervoort & Zibrowius, 1981: 38.
Stylaster bithalamus: Broch, 1936: 75.—Cairns, 1983b: 429 (listed).

Types and Type Locality. Holotype, ZMC. Type Locality: 33°57’S, 18°15’E (Table Bay, South Africa), 93 m.

Material Examined. *MN* SM185, 1 male colony, SAM, and SEM stub 1702 (USNM); UCTES SCD 316, 1 male colony, RMNH 15821; UCTES SCD289, 1, SAM; UCTES SCD316, 1, SAM; UCTES AFR801, RMNH 15827, and SEM stub 1703 (USNM 76534); *Valdivia* 93, 1, ZMB 7040; *Valdivia* 104, 7 colonies, ZMB 7042; specimens mentioned by Boschma (1960b), Naturalis Biodiversity Centre; *Allopora oculina* reported by Studer (1878) from *Gazelle* station 16, ZMB 1654.

Description. Colonies are of moderate size, robust, uniplanar, and sparsely branched, the largest colony (UCTES AFR801 described by Boschma 1960b) 6 cm in height and 8 x 12 mm in basal branch diameter. Branching is dichotomous and somewhat irregular, the distal branches being fairly slender (2–3 mm in diameter), not blunt, but usually terminating in an apical cyclosystem. Commensal polynoid tubes are present in all specimens examined (Figs. 2B, 12A), including the type, all eight specimens reported by Boschma (1961), and the specimens reported herein (see Remarks). The polynoid gall tubes are fairly large, up to 6 x 3 mm in cross section, and dominate the posterior face of larger coralla. The coenosteal texture is reticulate-granular (Fig. 12C), the strips ranging from 52–67 µm in width, covered with irregularly-shaped granules. Nematopores were not observed. The colonies are uniformly white.

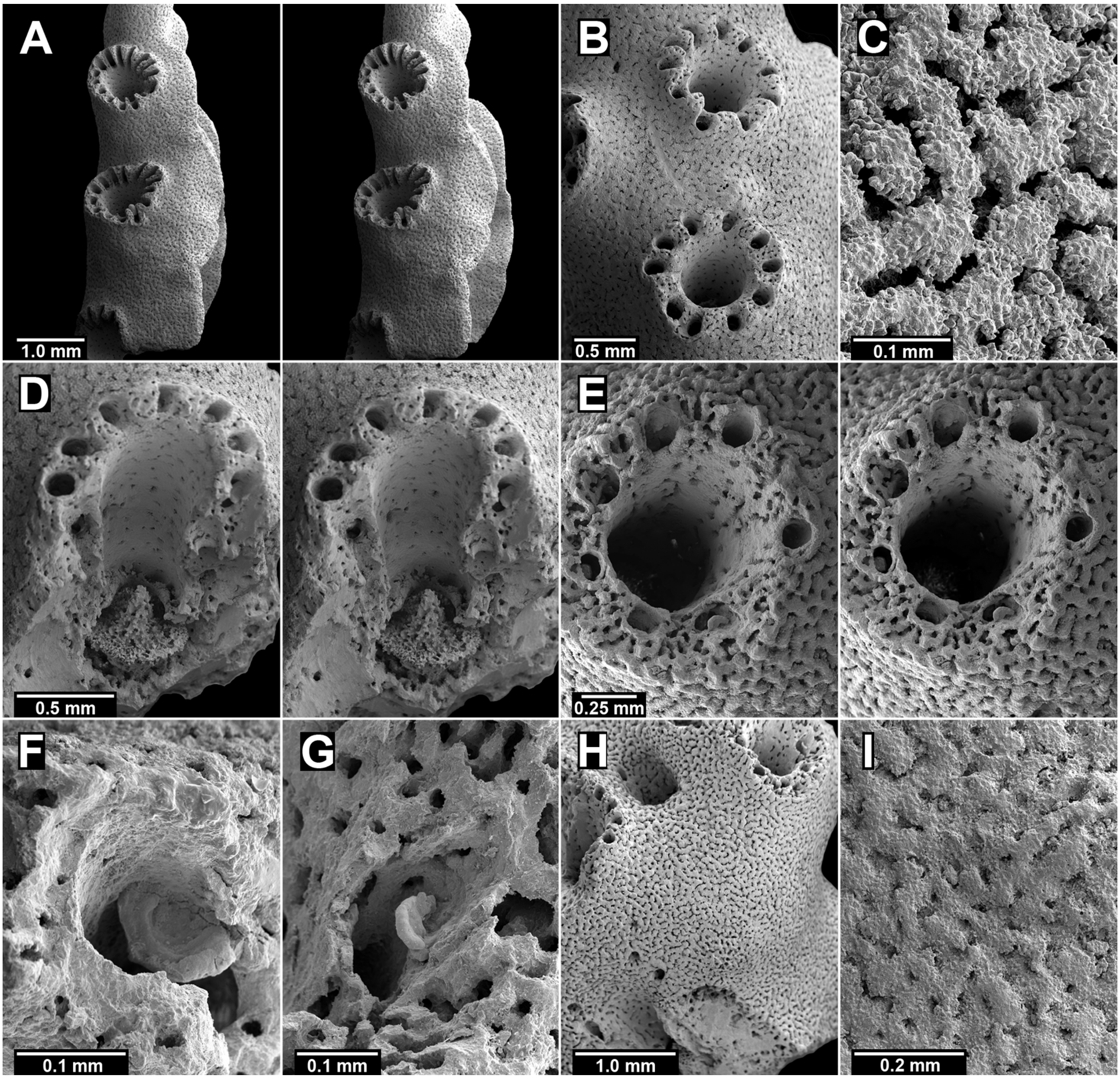

FIGURE 12. *Stylaster bithalamus* (**A–B, D, F–I**, *MN* SM185, SAM; **C, E**, female from UCTES AFR801, USNM 76534): **A**, stereo view of branch segment bearing lateral cyclosystems, polynoid gall tube to right. **B**, cyclosystems. **C**, reticulate-granular coenosteal texture. **D**, stereo view of gastropore tube, gastrostyle, and sphincter. **E**, stereo view of a cyclosystem showing one small dactyloglossa. **F–G**, large and small dactyloglossae, respectively. **H–I**, ?male ampullae.

Cyclosystems are homogeneously arranged on the anterior and lateral surfaces of most branches; the polynoid gall tube occupying the posterior face does not bear cyclosystems. Distal branches tend to have a sympodial arrangement of cyclosystems (Fig. 12A), like those *Stylaster* species in Group B. Cyclosystems are circular to slightly elliptical in shape, 0.85–1.5 mm in diameter, and flush to slightly raised above the coenosteum. Cyclosystems are never arranged in rows. Based on 25 cyclosystems, the range of dactylopores per cyclosystem is 7–16; the average is 11.0 ($\sigma = 0.85$); and the mode is 10. Even though based on a low number of cyclosystems these numbers are consistent with those reported by Broch (1936) based on much larger numbers, range, 9–16; average, 11.5; and mode, 11, and Boschma (1961), range,1–19; average, 10.8; and mode, 10. Diastemas are common but not very wide.

The gastropores are circular (about 0.45 mm in diameter), and the gastropore tube may be as deep as 1.6 mm. As explained in detail by Boschma (1961), the gastrostyles are variable in shape, Boschma describing four distinct but intergrading shapes. In general, the style has a short cylindrical to discoidal base that supports the mid-section of the style, which is the widest part of the structure. Above this middle section, which can be torus-shaped, the elongate apical spine either gradually or abruptly diverges from the lower section, ending in a pointed tip (Fig. 12D). The entire gastrostyle may be as tall as 0.55 mm and occupy the lower third to half of the gastropore tube. At the level of the lower gastrostyle apical spine is a solid constriction of the tube (analogous to a ring palisade, see Fig. 12D), called a sphincter by Broch (1936), and thus suggesting a comparison to the double-chambered gastropore tubes of *Conopora*. This belt-like structure is similar to that described for *S. griseus*. The dactylotomes are about 0.1 mm wide, and the pseudosepta are thick (0.15–0.27 mm in width) with convex upper surfaces. Each dactylopore contains several dactyloglossae (Figs. 12E–G), which occlude most of the tube.

Female ampullae are primarily internal, hardly seen in apical view except as low bulges about 1.2 mm in diameter. They communicate to the upper chamber of an adjacent gastropore tube via an efferent pore. Male ampullae are partially internal, seen in apical view as small (0.3–0.5 mm in diameter) mounds (Fig. 12I), with apical efferent pores.

Comparisons. *Stylaster bithalamus* is compared to the morphologically similar *S. griseus* in the account of that species. Among the other South African *Stylaster* species in Group A (Table 1), *S. bithalamus* differs in having dactyloglossae, internal female ampullae with efferent pores that open into gastropore chambers, and non-lanceolate gastrostyles.

Remarks. Although Boschma (1961) stated that polynoid gall tubes were often associated with this species, but that they were not associated with his specimen from UCTES AFR801, examination of a specimen from UCTES AFR801 (RMNH 15827) did show evidence of polynoid gall tubes.

Distribution. Continental shelf of southern South Africa from Saint Helena Bay (most of Western and Eastern Cape Provinces)(Fig. 27), 11–155 m.

Stylaster griseus sp. nov.

Figs. 2C, 13A–M, 28

Etymology. Named *griseus* (Latin, meaning grey), for the colour of the coenosteum.

Types and Type Locality. Holotype: *PF*13063, colony of indeterminate gender, SAM H1459. Paratypes: *MN* SM163, 3 poor fragments, SAM; *MN* SM179, 1 female colony (in alcohol), SAM, and SEM stub 1701 (USNM); *MN* SM180, 1 colony base, SAM; *MN* SM184, 22 worn fragments, SAM; *MN* SM185, 1 male and 3 indet. colonies (in alcohol), SAM, and SEM stub 1715 (USNM); *PF*808, 1 colony, indet., SAM H1231; *PF*907, 1 male and 3 indet. colonies, SAM H1467; *PF*13654, 2 female and 1 male colonies, SAM H1460, and SEM stub 1699–1700 (USNM); UCTES SCD289, 1 female colony, RMNH 15820; UCTES SCD296, 1 male colony, RMNH 15826. Type Locality: off Hood Point Lighthouse (Eastern Cape Province), South Africa, 90 m.

Material Examined. Types.

Description. Colonies are of moderate size, robust, uniplanar, and sparsely branched, the largest colony (the holotype, Fig. 2C) 7 cm tall and 6 cm wide, with a basal branch diameter of 14.1 mm. Branching is dichotomous but not regular, the blunt, cylindrical branch tips 2–4 mm in diameter. There are no polynoid commensals. The coenosteal texture is a fine reticulate-granular, the strips ranging from 53–72 µm in width, each covered with small, irregularly-shaped granules (Fig. 13D, F). Nematopores were not observed. The colonies are light grey to light brown in colour, and chalky white when dead.

Cyclosystems (Fig. 13B) are uniformly arranged on all branch surfaces, although sometimes arranged in longitudinal rows up to 15 cyclosystems in length. Cyclosystems are slightly raised above the coenosteum and circular in shape, 0.9–1.13 mm in diameter. Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 7–12; the average is 9.22 ($\sigma = 1.30$); and the mode is 9. Diastemas occur occasionally but are rarely wider than two pseudosepta.

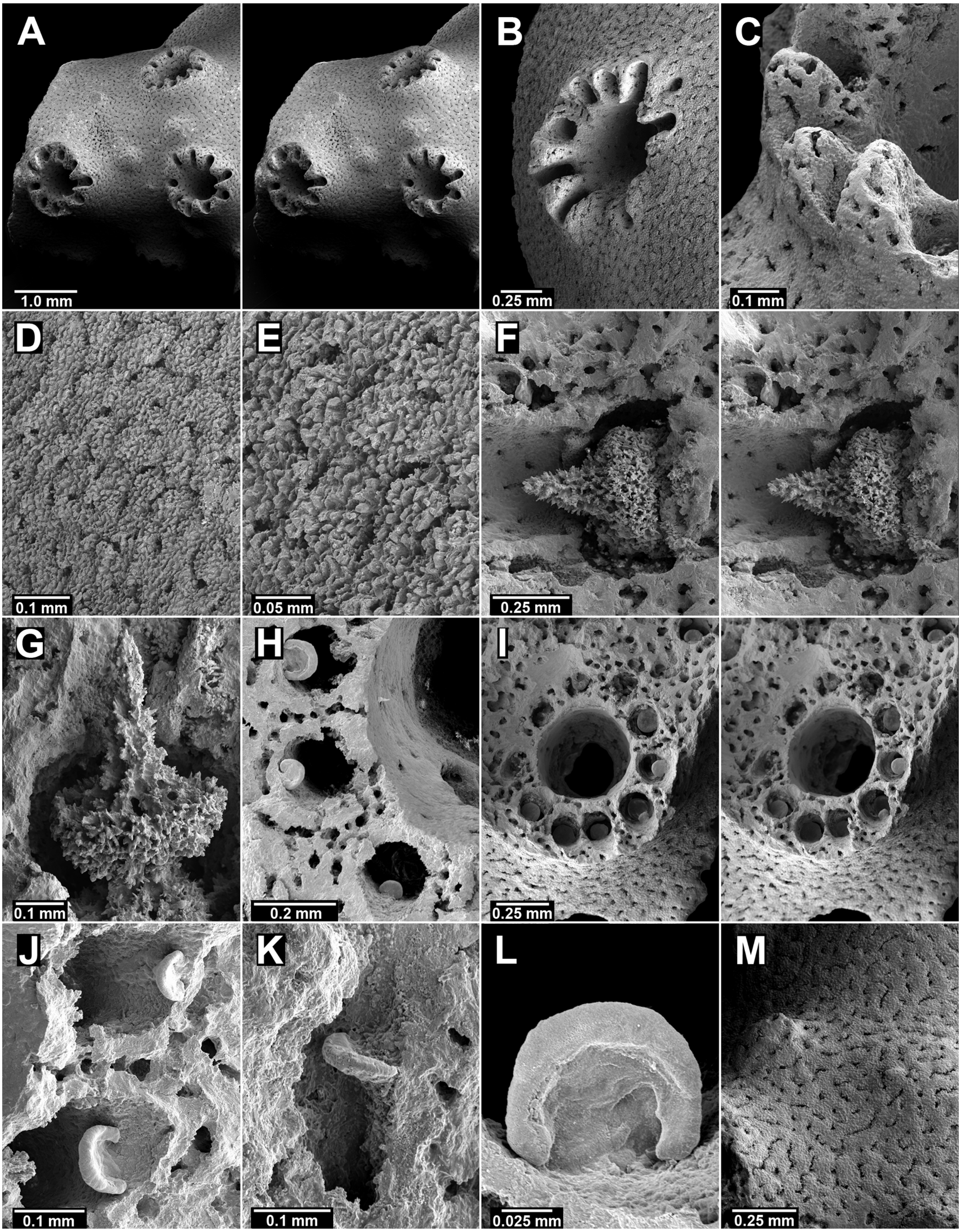

FIGURE 13. *Stylaster griseus* (**A, C, F, H, J, L–M**, male paratype colony from *PF*13654, SAM H1460; **B, D–E, G, K**, indet. gender from *PF*13654, SAM H1460; I, female from *MN* SM179, SAM): **A**, stereo view of cyclosystems and male ampulla. **B**, a cyclosystem with a narrow diastema. **C**, several pseudosepta. **D–E**, reticulate-granular coenosteal texture. **F**, stereo view of gastrostyle and sphincter. **G**, gastrostyle. **H–L**, cross-section of dactylopore tubes showing various sizes of dactyloglossae. **M**, male ampullae.

The gastropore is circular (about 0.43 mm in diameter), and the deep gastropore tube is cylindrical, as much as 1.4 mm in depth. The base of the gastrostyle is a short cylinder about 0.35 mm in diameter, which supports a discoidal torus that is 0.40–0.50 mm in diameter. Above the torus is a tall slender apical spine, the entire gastrostyle measuring up to 0.64 mm in height (Figs. 13F, G). At the level of the base of the apical spine the gastropore tube constricts as a sphincter (a continuous in structure like a low belt about 68 µm in width and 36 µm in height, not composed of discrete cylindrical elements, Figs. 13F, G). The dactylotomes are 0.09–0.13 mm in width, and the pseudosepta are 0.07–0.25 in width, their upper surfaces convex (Fig. 13C). Each dactylopore contains 1–3 dactyloglossae, usually getting larger with greater depth in the pore. The dactyloglossae are semi-circular (or broadly tongue-shaped), about 0.08–0.10 mm wide and 0.09 mm in height, and about 20 µm thick, although their outer margins appear to be the thickest (Figs. 13H–L). The larger uppermost dactyloglossae occlude about one-third of the dactylopore.

Female ampullae are primarily internal, hardly seen in surface view, and are about 0.9 mm in internal diameter, opening via an efferent pore into the upper chamber of an adjacent gastropore tube. Male ampullae are also primarily internal, but can be seen in apical view as small (0.35–0.40 mm in diameter) mounds, each with a small apical efferent pore (Figs. 13A, M).

Comparisons. *Stylaster griseus* is quite similar to *S. bithalamus* in many characters, and, after examination of more specimens, may prove to be a subspecies or just a distinctive form of the latter. The species are similar in coenosteal texture, in lacking nematopores, their female and male ampullar shapes, gastrostyle shape, and presence of dactyloglossae, as well as overlapping in distribution and depth range. *S. griseus*, however, seems to consistently differ (Table 1) in having, a gray to light brown corallum, blunt branch tips, a slightly higher average and modal number of dactylopores per cyclosystem, and in lacking polynoid gall tubes.

Distribution. Known only from off the continental shelf off the Eastern Cape Province (Fig. 28), 80–155 m.

Stylaster (Species group C)

Diagnosis. Species of *Stylaster* having cyclosystems arranged only on branch edges; branch tips usually slender, ending in one cyclosystem.

Stylaster amphiheloides Kent, 1871

Figs. 2D–F, 14A–L, 29

Stylaster amphiheloides Kent, 1871: 277–278, pl. 24, figs. 1a–c.—not Hickson & England, 1905: 13.—Boschma, 1957: 2; 1966b: 112.

Stylaster ampheliodes: Cairns, 1983b: 430 (listed, misspelled).

Types and Type Locality. The primary syntypes are deposited at the BM (1842.12.2.74–80). Three syntype fragments are also at the Naturalis Biodiversity Centre (RMNH 15319) and a fragment and SEM stub 1709 at the NMNH (USNM 85785). Type Locality: Cape of Good Hope, depth not recorded.

Material Examined. *Galathea* 196, fragments, ZMC*;* *Galathea* 197, 1 colony, ZMC; *MN* SM38, 38 colonies, SAM; *MN* SM85, 3 colonies, SAM; *MN* SM86, 2 colonies, SAM; *MN* SM90, 3 colonies, SAM; *MN* SM92, 1 colony, SAM; *MN* SM94, 5 colonies, SAM; *MN* SM103, 7 colonies, SAM; *MN* SM107, 27 colonies, SAM; *MN* SM123, 2 colonies, SAM; *MN* SM129, 5 colonies, SAM; *MN* SM131, 4 colonies, SAM; *MN* SM162, 30+ fragments, SAM; *MN* SM165, 30+ fragments, SAM; *MN* SM226, 5 colonies (including 3 in alcohol), SAM; *MN* SM228, 27 colonies (including 18 in alcohol), SAM, and SEM stub 1713 (USNM); *MN* SM232, 14 colonies (2 in alcohol), SAM; *MN* SM234, 2 colonies, SAM; *MN* SM237, 2 colonies (1 in alcohol), SAM; *PF*907, 2 colonies, SAM H2816; *PF*1915, 4 colonies, SAM H1463; *PF*2819A, 10 colonies, SAM H1462, and SEM stub 1711–12 (USNM); *PF*12729, 1 colony, SAM H1457, and SEM stub 1710 (USNM); *PF*14743, 1 colony, SAM H1504; *PF*17995, 1 colony, SAM H1464; syntypes from BM, NMNH and Naturalis Biodiversity Centre. Reference Material: specimens reported by Hickson & England (1905).

Description. Colonies are relatively small, rarely exceeding 3.5 cm in height, but may be equally or as wide as their height; colonies are uniplanar or bushy. Branching is dichotomous, the distal branches quite delicate, terminating

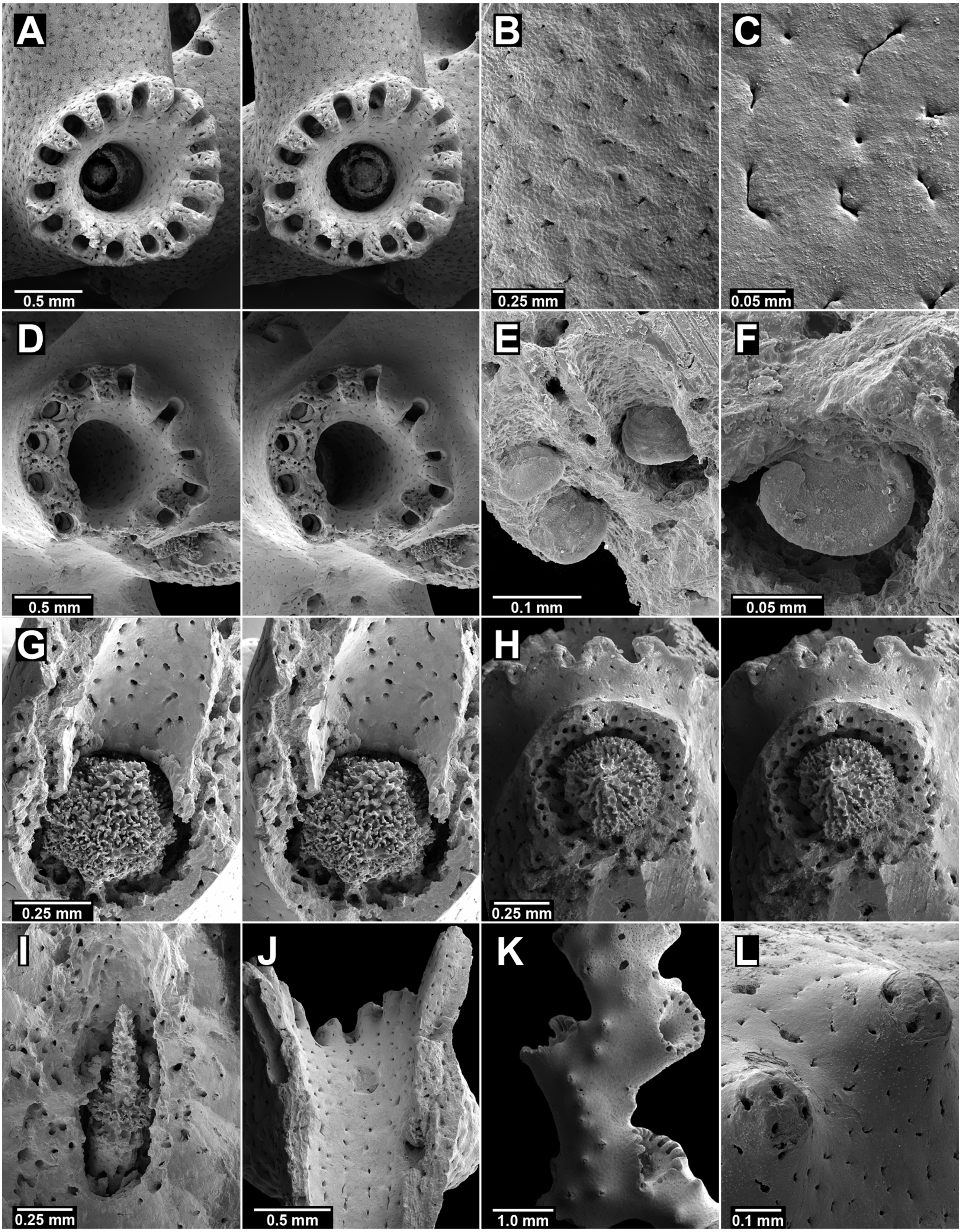

FIGURE 14. *Stylaster amphiheloides* (**A,** male syntype, USNM 85785; **B, E–F, H–J**, female from *PF*2819A, SAM H1462; male from **K–L**, *MN* SM328, SAM): **A**, stereo view of a cyclosystem. B–C, reticulate-granular coenosteal texture. **D**, stereo view of a damaged cyclosystem showing some dactyloglossae. **E–F**, dactyloglossae. **G**, stereo view of a gastrostyle from above. **H**, stereo view of a gastrostyle and sphincter. **I**, elongate gastrostyle and sphincter. **J**, longitudinal fracture of gastropore tube showing a female efferent pore. **K–L**, male ampullae.

in a terminal cyclosystem. Commensal polynoid tubes present in all colonies, starting at a very small colony size, the tubes being rectangular in cross section, about 5 x 2.5 mm in cross section (Figs. 2E, F). The tube is interpreted as occurring on the posterior side of the colony. The coenosteal texture is reticulate granular (Figs. 14B, C), the strips 75–120 µm in width, and covered with low rounded granules. In some colonies the coenosteum is flat, almost porcellaneous, the granules covered by smooth coenosteal deposits. The colonies are uniformly white.

Cyclosystems are arranged exclusively on the branch edges, characteristic of Group C species, and only in rare cases having some cyclosystems on the anterior face. Delicate distal branches have cyclosystems arranged in a regular sympodial manner. Cyclosystems are circular to slightly irregular in shape (Fig. 14A), and 1.3–2.0 mm in greater diameter. Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 9–21; the average is 13.9 ($\sigma = 2.46$); and the mode is 13. Diastemas are rarely present, but only in cyclosystems on the main branch.

The gastropores are circular (about 0.6 mm in diameter), and the gastropore tube is straight and cylindrical. The gastrostyle has a short cylindrical base, a toroidal mid-section, and a tall slender apical spine, which projects through a belted sphincter (Figs. 14G–I). The gastrostyles range from 0.5 to 0.8 mm in height, occupy 1/3 to ½ of the gastropore tube, and have a L:D ratio of 1.1–2.6, those parameters depending on the length of the apical spine. The dactylotomes are 0.10–0.12 mm in width, and the pseudosepta are 0.15–0.16 mm in width, with convex upper faces. Each dactylopores contains a series of dactyloglossae (Figs. 14D–F), each up to 0.11 mm in width, which occlude most of the dactylopore tube.

Female ampullae are visible externally as low swellings 1.1–1.2 mm in diameter that are invariable located in clusters around a cyclosystem; their efferent pores open into the adjacent upper gastropore tube (Fig. 14J) through a pore 0.17–0.22 mm in diameter. Male ampullae are scattered over the coenosteum and occur even on the polynoid gall tube. They are shaped as small cones, up to 0.35 mm in height, 0.15 mm in distal diameter, and 0.4–0.6 mm in basal diameter, giving these colonies a spiny appearance (Figs. 14K, L). Each bears 1–3 tiny (25 µm diameter), irregularly-shaped efferent pores.

Comparisons. Even though they are placed in different species groups, *S. amphiheloides* and *S. bithalamus* are quite similar. *S. amphiheloides* can be distinguished by having its cyclosystems relegated only to its branch edges, having a higher number of dactylopores per cyclosystem (average 13.98 vs 11.0), and in having conical male ampullae. Furthermore, *S. amphiheloides* is thus far known only from 155–1000 m, whereas *S. bithalamus* appears to be a shallower water species at 11–155 m.

Remarks. As Boschma (1966b) suggested, the deeper-water records reported by Hickson & England (1905) from Indonesia are not *S. amphiheloides*, those specimens similar only in having a commensal polynoid worm.

Distribution. From Cape Town to Richards Bay (Natal)(Fig. 29), 155–1000 m, although most records deeper than 500 m.

Stylaster lonchitis Broch, 1947

Figs. 2I, 15A–J, 30

?Stylaster eximius facies *dentatus, irregularis, minor:* Hickson & England, 1905: 10–11, pl. 1, figs. 4–8.

Stylaster (Eu-Stylaster) lonchitis Broch, 1947: 309–311, pl. 1, fig. 2, text-fig.2a–c.

Stylaster lonchitis: Boschma, 1957: 12; 1962, 287–293, 2 pls., 2 text-fig. (complete redescription).—Vervoort & Zibrowius, 1981: 40.—Cairns 1983b: 430 (listed).

Stylaster sp. Liltved, 1989: fig. 227 (with *Pedicularia* scar).

Types and Type Locality. Holotype, BM 1950.5.22.6; fragment of holotype, USNM 85786. Type Locality: 4°57’S, 39°13’18”E (Pemba Channel, Tanzania), 113 m.

Material Examined. *Anton Bruun* 8—420A, several colonies, USNM 1104251 and 1174691; *MN* SM163, 10 small dead branch fragments, SAM; 33°01.8’S, 28°04.4’W (off Gonubie), 85 m, 17 July 1984, coll. William Rune Liltved, 1female colony now in 11 pieces, SAM, and 1 colony and SEM stubs 1704–05 (USNM 1189355); holotype; specimens reported by Boschma (1962).

Description. Colonies are uniplanar and relatively small, the largest specimen examined (Gonubie specimen) only 4.5 cm in height. Branching is dichotomous and usually at right angles; branches are straight, not geniculate, even though the cyclosystems are closely arranged in an alternating manner (sympodially) on either side of the branches (Fig. 2I). The coenosteal texture is linear-granular, the coenosteal strips ranging from 57–72 µm in width, and are often sharply convex, almost ridged (Fig. 15D, E). The strips are covered with low rounded granules, as well as numerous nematopore tubes in the shape of truncated cones, the cones up to 100 µm in height and about 85 µm in basal diameter (Fig. 15F). The colony is a salmon orange, whereas the branch tips are white.

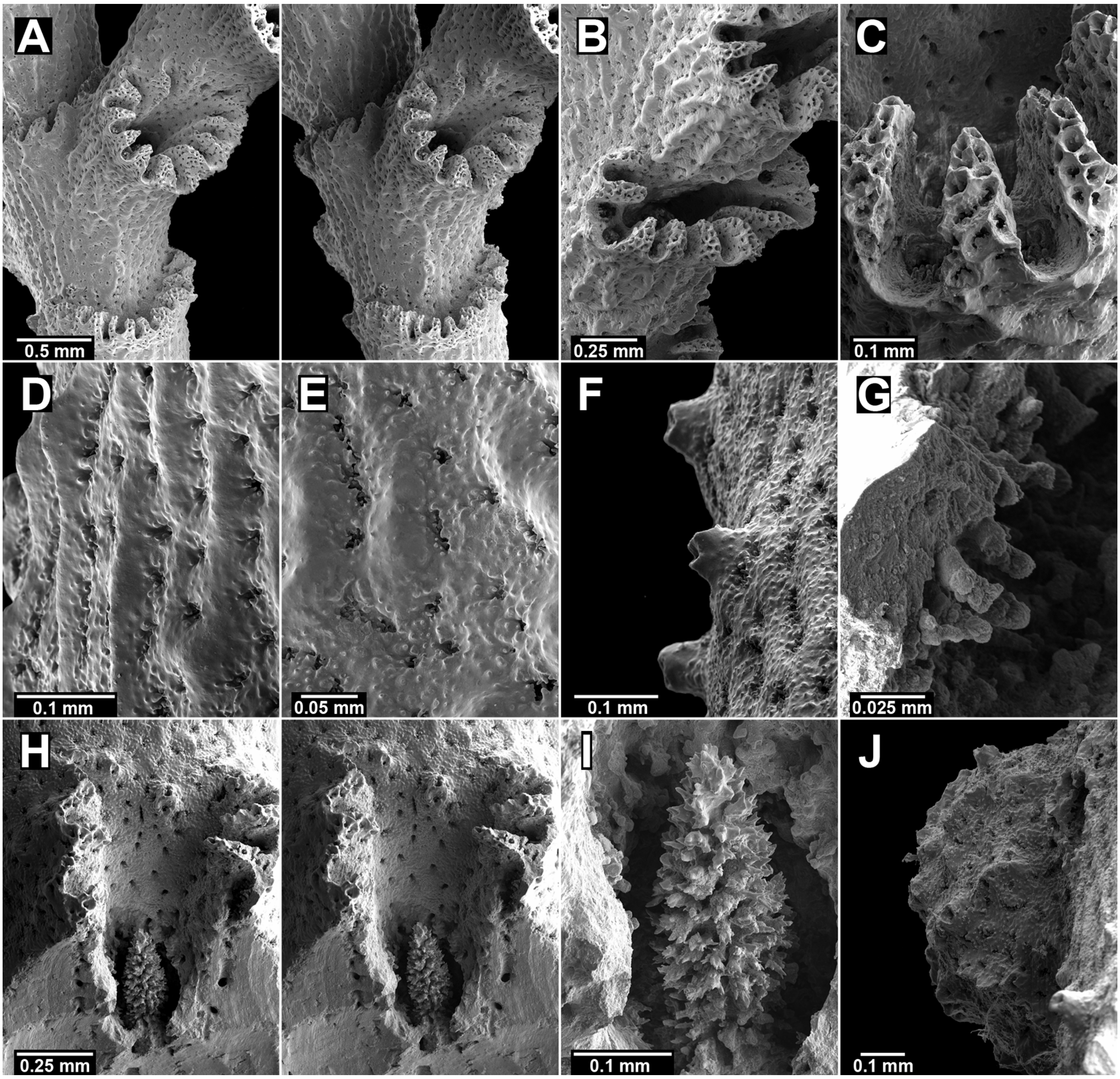

FIGURE 15. *Stylaster lonchitis* collected by Liltved, female, USNM 1189355: **A**, stereo view of two cyclosystems. **B**, cyclosystem with a broad diastema. **C**, porous pseudosepta. **D–E**, ridged linear-granular coenosteal texture. **F**, conical nematopore tubes. **G**, dactylostyle elements. **H**, stereo view of gastropore tube and gastrostyle. **I**, gastrostyle and ring palisade. **J**, female ampulla.

Cyclosystems are exclusively arranged on the branch edges and are very closely spaced; they are circular near the branch tips, but somewhat horizontally elongate or irregular in shape on the majority of branches (Figs. 15A, B). Dactylopores are missing from the entire upper edge of the cyclosystem, resulting in a crescent-shaped tier of abcauline dactylopore spines (Figs. 15A, B), and with the coenosteal strips seeming to flow directly into the upper diastemate region of the gastropore tube. Cyclosystems are 0.8–1.2 mm in greater diameter. Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 7–14; the average is 10.38 (σ = 1.56); and the mode, 10. Based on the same number of cyclosystems, Broch (1947) reported a range of 7–12, an average of 9.54 and a mode of 10, whereas Boschma (1962) reported a range of 6–12, a weighted average of 9.21, and a mode of 9. Cyclosystems near the branch tips tend to be complete, lacking the diastema (Fig. 15A, upper), and thus have slightly more dactylopores per cyclosystem, which might explain the slight discrepancy on the reported averages and ranges.

The gastropore tube is straight and cylindrical, about twice the length of the gastrostyle. The gastrostyle is lanceolate, up to 0.35 mm in height and about 0.14 mm in diameter; a diffuse ring palisade is present, the cylindrical elements being about 19 µm in height (Figs. 15H, I). The dactylotomes are about 0.9–1.1 mm in width, the pseudosepta range from 0.11–0.18 mm in width, the latter being quite porous (Fig. 15C). Dactylostyles are composed of a linear row of clavate elements, each about 27 µm in height (Fig. 15G).

Female ampullae are usually clustered on one side of the branches, and are prominent hemispheres 0.70–0.75 mm in diameter; nematopores tubes also cover the ampullae, making them prickly in appearance (Fig. 15J). Efferent pores are rarely observed, but when present are quite small, about 0.10 mm in diameter. Male ampullae are not known.

Comparisons. Although the identity of the South African specimens are undoubtedly the same as *S. lonchitis*, it is possible that this species is a junior synonym of the taxa reported from Indonesia as *Stylaster eximius* facies *dentatus*, *irregularis*, and *minor*, by Hickson & England (1905), and if so, one of these names would have nomenclatural priority, e.g., *dentatus*. This possibility was hinted at by Boschma (1962) when he compared *S. lonchitis* to *S. duchassaingi*, which he thought similar to *S. eximius*. Although the types of these facies and of *S. lonchitis* have been examined by the authors, there is simply not enough material at hand to make a definitive synonymy. The unifying characters of this taxon are its crescent-shaped cyclosystems with broad diastemas, prominent nematopores tubes, straight branches, and closely spaced cyclosystems.

Distribution. Continental shelf off the Eastern Cape Province of South Africa (Fig. 30), 85–90 m; off Kenya and Tanzania (Pemba Canal and Zanzibar Channel), 55–140 m.

Stylaster kenti sp. nov.

Figs. 2J, 16A–G, 22

Etymology. Named in honor of W. Saville Kent, in recognition of his description of the first stylasterids from the South African coast (Kent 1871).

Types and Type Locality. Holotype: *MN* SM43, 1 male colony, SAM, and SEM stubs 1706–07 (USNM). Paratypes: *MN* SM43, 1 male branch fragment and 3 female branch fragments, SAM, and SEM stub 1708 (USNM). Type Locality: 28°45.5'S, 32°24.5'W (off Richards Bay, Natal), 360–420 m.

Material Examined. Types.

Description. Colonies are relatively small and uniplanar in shape, the largest colony (the holotype, Fig. 2J) measuring 4.1 cm in height and 3.1 cm in width, having a broken basal branch diameter of 5.0 mm. Branching is dichotomous. The coenosteal texture is reticulate-granular (Fig. 16C), the strips ranging from 50–70 µm in width, and are covered with low rounded granules. Nematopores and commensal worms are not present. The corallum is light brown, fading to off-white near the branch tips.

The cyclosystems are closely spaced and arranged linearly on all branch edges, alternating in a sympodial manner (Fig. 2J). Cyclosytems are elliptical to elongate in shape, the greater axis being up to 1.4 mm in length (Fig. 16B). Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 8–15; the average is 12.42 (σ = 1.25); and the mode is 13. Diastemas are not present.

The gastropores are circular (0.30–0.40 mm in diameter), and the gastropore tube is long (up to 1.6 mm) and cylindrical, about three times the length of the gastrostyle, widening into a spherical gastropore chamber proximally. The gastrostyle has a short cylindrical base, which supports a toroidal middle section, topped by a vertical spine, the entire style being about 0.5 mm in height, the distal spine constituting about 60% of that height. The middle and upper portions are covered with spines, those on the distal spines being much coarser (Fig. 16F). At the level of the upper gastrostyle spine the tube is constricted by a belt-like sphincter (Fig. 16F), which is about 90 µm in width. The pseudosepta range from 0.10–0.22 mm in maximum width, whereas the dactylotomes are 0.90–0.10 in width. Each dactylopore contains several linearly arranged dactyloglossae (Figs. 16D, E) that serve as baffles that occlude most of the dactylopore tube.

Female ampullae are low swellings about 1.2 mm in diameter that always occur near cyclosystems (Fig. 16B). Their efferent pores open into the upper gastropore tube. Male ampullae are considerably smaller (0.3–0.5 mm in diameter), irregular in shape, and occur in clustered on all branch surfaces (Figs. 16A, G). They have small apical efferent pores. Both types of ampullae often have a single small (0.09–0.10 mm diameter) round pore that appear to have been drilled through their surface, perhaps by a gastropod predator as noted in the genus *Adelopora* (see Cairns 1982).

Comparisons. As mentioned in the Material and Methods section, only six stylasterid species are known to have dactyloglossae, and only one other than *S. kenti* belonging to *Stylaster* (Group C): *S. amphiheloides*. Although similar, *S. kenti* differs from that species in lacking commensal polynoid gall tubes, having a brown corallum, and having irregularly-shaped (not conical) male ampullae. And, although somewhat similar in colour, gastrostyle morphology, and dactyloglossae, *S. kenti* differs from *S. griseus* in cyclosystem placement, number of dactylopores per cyclosystem, and depth range.

Stylaster kenti is also similar *S. brunneus* Boschma, 1970 in coenosteal colour and colony shape, but differs in almost every other character, including placement of cyclosystems, dactylostyle morphology, coenosteal texture, and female ampullae size and efferent pore location. Furthermore, *S. brunneus* is known only from the New Zealand/New Caledonian region (Cairns 1991).

Distribution. Known only from the type locality (Fig. 22).

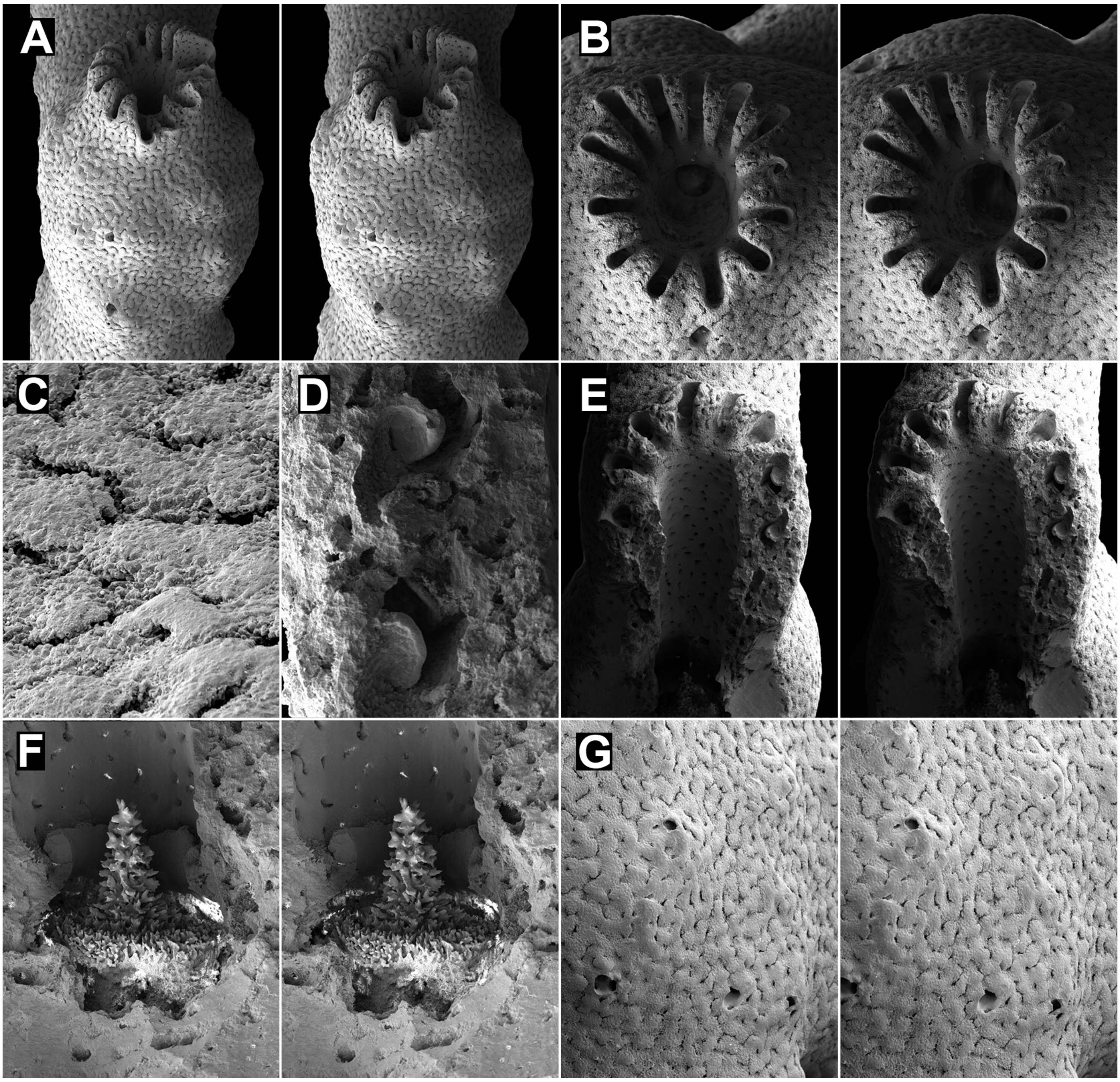

FIGURE 16. *Stylaster kenti* (**A, C, F–G**, male holotype, *MN* SM43, SAM; **B, D–E**, female paratype from *MN* SM43, SAM): **A**, stereo view of a cyclosystem and several male ampullae. **B**, stereo view of a cyclosystem. **C**, reticulate-granular coenosteal texture. **D–E**, various dactyloglossae (**E** a stereo pair). **F**, stereo view of a gastrostyle and sphincter. **G**, male ampullae.

Genus *Stenohelia* Kent, 1870

Stenohelia Kent, 1871: 121.—Boschma, 1956a: F100.—Cairns, 1983b: 486–487; 1986a, 94; 1986b: 19; 1991: 70; 1992: 540–541 (key).

Type Species. *Allopora maderensis* Johnson, 1862, by subsequent designation (Broch 1936).

Diagnosis. Colonies uniplanar and usually quite delicate, often living in association with commensal polynoid polychaetes. Coenosteal texture usually linear-imbricate, reticulate-imbricate, or finely imbricate; usually white or yellow in colour. Gastro- and dactylopores arranged in cyclosystems, which occur exclusively on anterior branch faces. Gastropore tubes usually elongate and curved 90°, such that the gastrostyle tip cannot be seen in surface view. Gastrostyle encircled by a ring palisade or a sphincter. Dactylostyles usually well developed, although some species have dactyloglossae instead. Ampullae superficial, often clustered, with discrete efferent pores.

Discussion. Ten valid Recent species are recognized in the genus and another putative fossil species from the Eocene of Tonga (see Cairns 1991; Cairns et al. 1999; Appeltans et al. 2012). Representatives of all but two of these species (the Japanese species *S. yabei* and *S. echinata*) were examined for comparisons. The two new species described below bring the total to 12 Recent species in this genus, including the second and third southern hemisphere species.

Holocene Distribution. Atlantic, Pacific and Indian Oceans, 91–2021 m.

Stenohelia venusta sp. nov.

Figs. 3A, 17A–K, 30

?*Stylaster minimus*, Hickson & England, 1909: 346 (Mauritius).

Etymology. From the Latin *venustus*, meaning beautiful, elegant, and graceful, a name that could be given to virtually any stylasterid.

Types and Type Locality. Holotype: *MN* SM232, female colony (in alcohol), SAM, and SEM stubs 1682–83 (USNM). Paratypes: *MN* SM226, 1 male colony, SAM; *MN* SM232, 3 female and 3 male colonies, SAM, and SEM stub 1681 (USNM); *PF*1915, 1 male colony, SAM H1463; *PF*13395, 2 branches, SAM H2820; *PF*13476, 3 male branches, SAM H1228; *Anton Bruun* 8—420A, 1 male colony (dry) and 1 male colony (in alcohol), USNM 76773. Type Locality: 32°14.9'S, 29°10.4'E, 620–650 m (off Umtata, northern Eastern Cape Province).

Material Examined. Types. Reference Material, fragment of male syntype of *S. tiliatus*, *Siboga* 105, USNM 77280.

Description. Colonies are uniplanar and relatively small, the largest specimen (the holotype, Fig. 3A) only 4.6 cm in height and 2.6 cm in width, with a basal branch diameter of 4.5 mm; branch anastomosis occurs occasionally. The coenosteum is covered with reticulate strips 50–60 µm in width, each strip covered with small irregularly-shaped granules (Figs. 17D, E). The coenosteum is white.

Cyclosystems are unifacial in arrangement, unilinearly positioned on the anterior face (Fig. 17A). They are elliptical to irregular in shape, up to 1.3 mm in greater diameter and about 0.8–0.9 mm in lesser diameter, the greater diameter usually oriented perpendicular to the branch axis (Figs. 17B, C). Based on 50 cyclosystems, the range of dactylopores per cyclosystem is 13–20; the average is16.46 (σ = 1.74); and the mode is 16.

Gastropores are also elliptical in shape, up to 0.35 mm in greater diameter and about 0.3 mm in lesser diameter. The gastropore tube is long (up to 1.6 mm) and invariably bent about 90° just beneath the gastropore. The gastrostyle occupies only the lower 30% of the tube, and is composed of a lower section about 0.21 mm in diameter that supports a cylindrical distal portion, which is approximately 0.10 mm in diameter. A solid inner ring (the sphincter) constricts the tube at the transition point of the basal to distal portion of the style (Figs. 17H, I). The illustrated style is 0.45 mm in height, and is covered with small spines. The dactylotomes are fairly consistent in width (60–70 µm), whereas the pseudosepta are somewhat irregular in width, ranging from 64–145 µm wide (Fig. 17F). The tops of the pseudosepta range from slightly convex to slightly concave. Each dactylopore contains 1–3 dactyloglossae, the uppermost being at the level of the coenosteal surface, and thus most easily seen in damaged cyclosystems (Fig. 17J). The dactyloglossae are tongue-shaped, about 60–70 µm in surface dimensions, and about 8–10 µm thick, each blocking approximately 70–80% of the dactylopore tube.

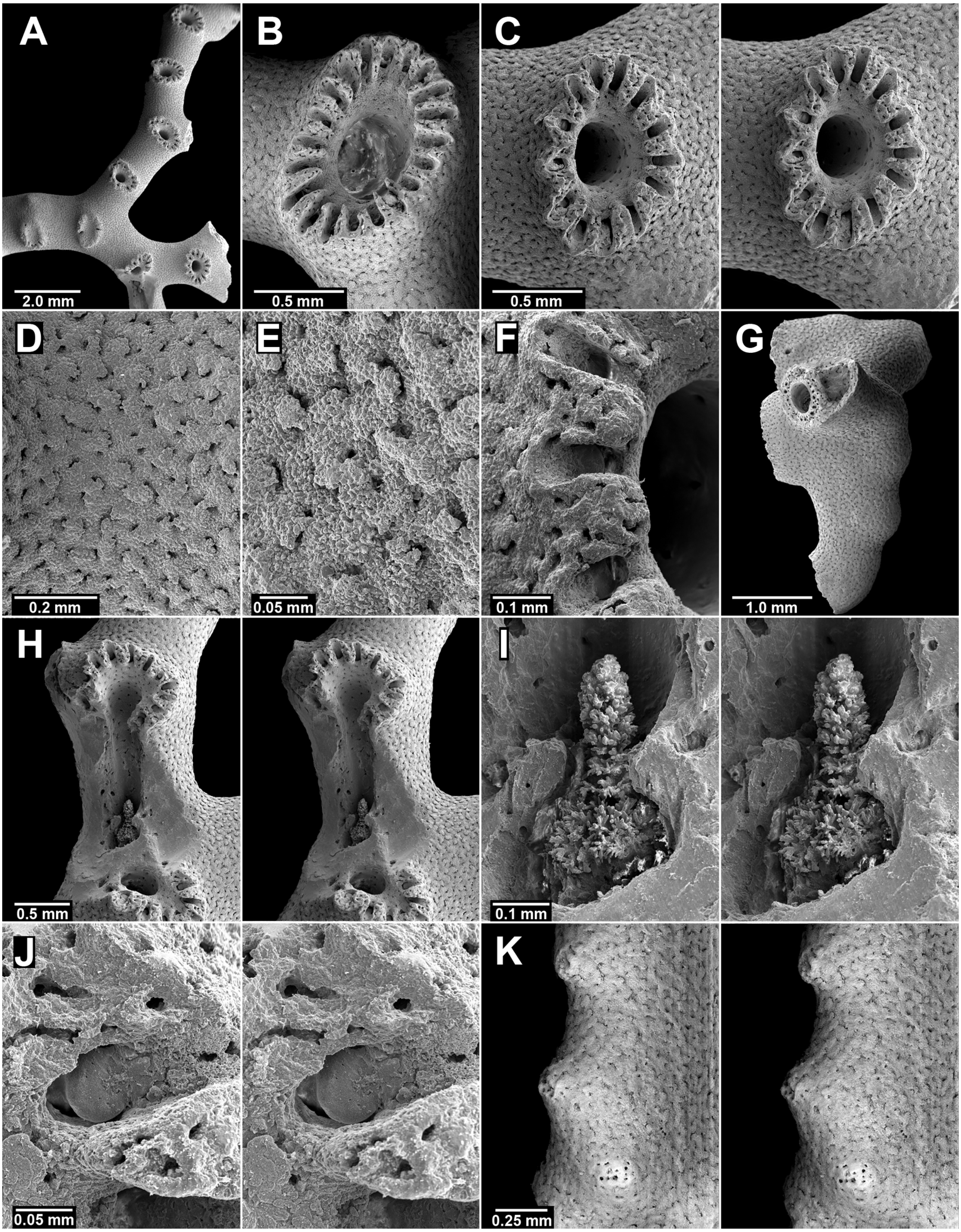

FIGURE 17. *Stenohelia venusta* (**A–J**, female holotype, *MN* SM232, SAM; **K**, male paratype, *MN* SM232, SAM): **A**, unifacially arranged cyclosystems; **B**, a cyclosystem. **C**, stereo view of a cyclosystem showing some dactyloglossae. **D–E**, reticulate granular coenosteal texture. **F**, several pseudosepta. **G**, female ampullae. **H**, stereo view of an elongate gastropore tube and its gastrostyle. **I**, stereo view of a gastrostyle and its massive sphincter. **J**, stereo view of a dactyloglossa. **K**, stereo view of male ampullae.

Female ampullae are superficial hemispheres 0.6–0.8 mm in diameter, arranged in close proximity on the posterior faces of terminal branches (Fig. 17G); efferent pores are inconspicuous but are lateral in position, not opening within the gastropore tube. The male ampullae are smaller (0.35–0.50 mm diameter) and conical in shape, with a small (about 35 µm diameter), irregularly-shaped apical efferent pore. The male ampullae tend to cluster on the posterior side of the branches (Fig. 17K).

Comparisons. Among the 11 other species in the genus, *Stenohelia venusta* is most similar to *S. tiliata* (Hickson & England, 1905), originally described and still known only from the Sulu Sea at 275 m. Examination of the syntype of *S. tiliata* shows it to have15–16 dactylopores per cyclosystem, irregularly-shaped cyclosystems, a rough reticulate coenosteal texture, lacking a ring palisade, and male ampullae about 0.5 mm in diameter. The only difference detectable between the two species is that *S. venusta* has dactyloglossae, whereas *S. tiliata* has typical dactylostyles composed of aligned pillars. One must keep in mind, however, that *S. tiliata* is known only from one specimen, and the taxonomic value of dactyloglossae is yet to be determined. Regardless, these two species would appear to be sister species, if not conspecific.

Stenohelia venusta also bears a resemblance to *S. conferta* Boschma, 1968, known only from the Antipodes Islands at 1335 m. They are similar in coenosteal texture, cyclosystem shape, and in lacking a typical ring palisade, but *S. venusta* differs in having a higher number of dactylopores per cyclosystem, and in having dactyloglossae.

Hickson & England (1909) reported *Stylaster minimus* from Mauritius, which heretofore was the only record of this genus in the Indian Ocean, the type locality for *Stylaster (=Stenohelia) minimus* being the Philippines at 1089 m. They did not supply any substantive description or illustrations for this specimen.

Distribution. Known from the continental shelf and slope off South Africa from Cape Blaize to northern Eastern Cape Province (Fig. 30) (159–710 m); off Kenya (140 m), ?Mauritius (Hickson & England, 1909), 140–710 m.

Stenohelia spinifera sp. nov.

Figs. 3B, 18A–M, 31

Etymology. From the Latin *spiniferus*, meaning spine bearing, an allusion to the prominent and densely packed nematopore tubes.

Types and Type Locality. Holotype: *PF*13479, 1 male colony, SAM H1461, and SEM stub 1692 (USNM). Type Locality: off Sandy Point (near Cape Morgan, northern Eastern Cape Province), 174 m.

Material Examined. Type.

Description. The holotype (Fig. 3B) is uniplanar, 2.8 cm tall and 1.95 cm wide, with a basal branch diameter of 3.8 mm. Branch anastomosis does not occur. The coenosteum is composed of reticulate strips 40–60 µm in width, each strip covered with bundles of slender rods, the rods 9–10 µm in length and about 2 µm in diameter, producing a rough microtexture (Fig. 18E, F). The coenosteum, as well as the sides of the cyclosystems and ampullae, are densely covered with tall (up to 0.26 mm), slender papillae (nematopore tubes, Figs. 18A–C, G, H), each with an apical pore 19–27 µm in diameter, sometimes 2 or 3 papillae fusing into a wider ridge having 2 or 3 apical pores. Altogether these nematopores spines produce a characteristically spiny aspect. The coenosteum is white.

Cyclosystems are unifacial in placement, positioned in a staggered arrangement on the anterior branch face (Fig. 3B). Cyclosystems are circular to slightly elliptical in shape, with a somewhat sinuous outer edge due to the high concavity of the pseudosepta; cyclosystems are up to 1.6 mm in greater diameter. The holotype bears 45 cyclosystems. Based on 26 cyclosystems, the range of dactylopores per cyclosystem is 12–15; the average is 13.35 ($\sigma = 0.098$); and the mode is 14.

Gastropores are round and about 0.40 mm in diameter; the gastropore tube is elongate and curved 90°, characteristic of the genus, such that the tip of the gastrostyle is not visible. The gastrostyle occupies the lower spherical portion of the gastropore tube, which is about 70 µm in diameter. It is supported by a short. cylindrical (about 0.3 mm in diameter) pedestal that supports a toroidal middle section about 0.55 mm in diameter and 0.2 mm tall (Fig. 18K, L). Above this section is an apical spine of unknown dimensions (Fig. 18K); there is no ring palisade or sphincter. The middle and upper portions are densely covered with laterally fused spines, the spines up to 0.13 mm in length (Fig. 18M). The dactylotomes are consistently 0.09–0.10 mm in width, whereas the pseudosepta (measured at their outer edge) are wider and somewhat more variable in width, ranging from 0.15–0.24 mm in

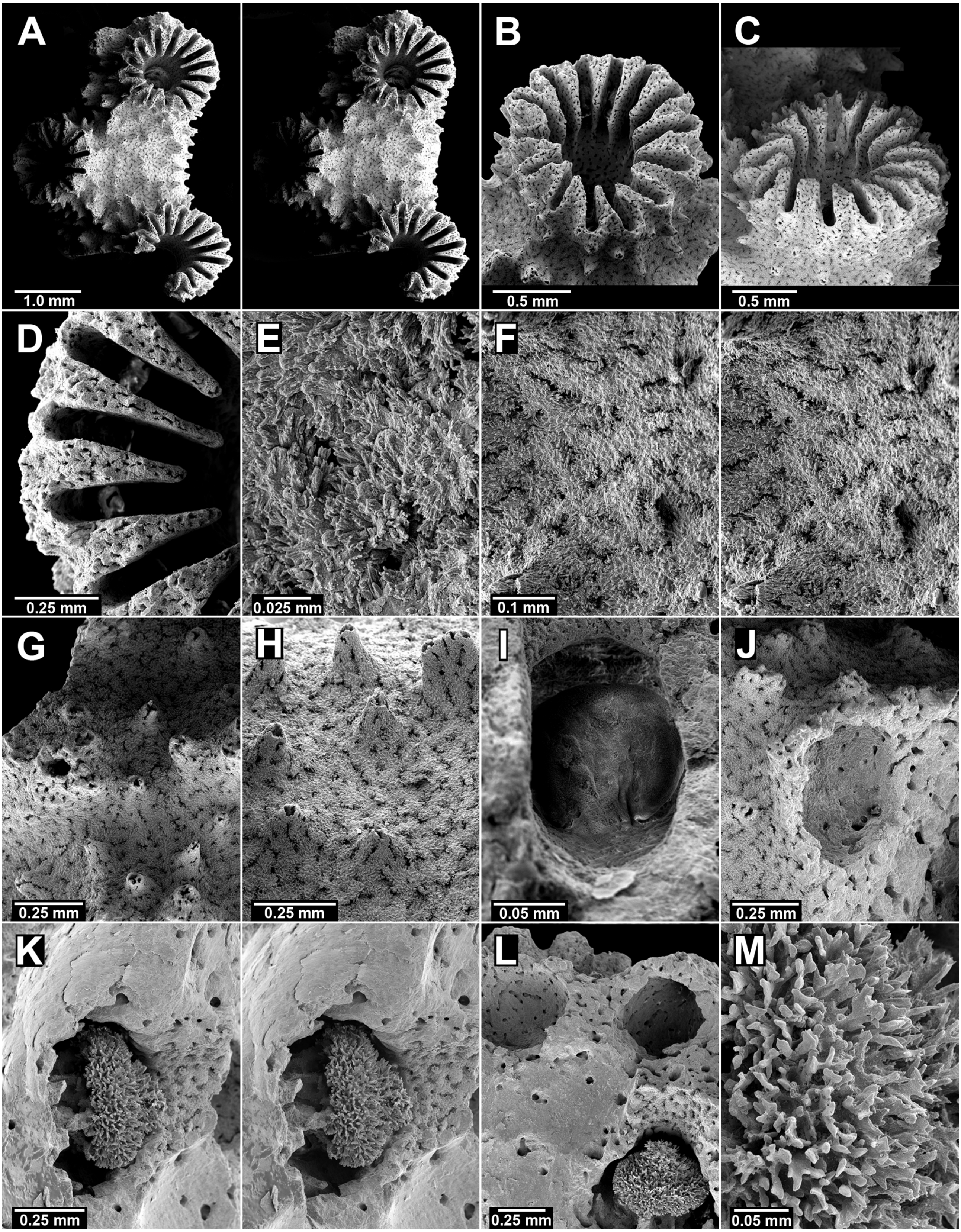

FIGURE 18. *Stenohelia spinifera*, male holotype from *PF*13479, SAM H1461: **A**, stereo view of cyclosystems and tall nematopore tubes. **B–C**, individual cyclosystems and tall nematopore tubes. **D**, pseudosepta. **E–F**, rough reticulate coenosteal texture. **G–H**, nematopore tubes. **I**, a dactyloglossa. **J**, cross section of an internal male ampulla. **K**, stereo view of a gastrostyle, but with a broken tip. **L**, cross section of male ampullae, and a broken gastrostyle. **M**, spination on the gastrostyle.

width. The upper faces of the pseudosepta are highly concave. Each dactylopore contains at least one dactyloglossa, roughly level with the coenosteal surface, seen best in damaged cyclosystems (Fig. 18I). The dactyloglossae are roughly circular in shape, about 0.11 mm in diameter, and block about 80% of the dactylopore tube.

Male ampullae are superficial, irregularly-shaped mounds 0.6–0.7 mm in diameter (Figs. 18J, L), and occur primarily on the anterior branch surface; each has an apical efferent pore about 60 µm in diameter. Each male ampulla is covered with 5–10 tall nematopores spines, making them look quite spiny. Female ampullae are unknown.

Comparisons. Although two other species (*S. umbonata* (Hickson & England, 1905) and *S. echinata* Eguchi, 1968) have coenosteal papillae (either nematopore tubes or ridges), *S. spinifera* differs in having dense, uniformly arranged papillae. It is also distinctive in having dactyloglossae, a character shared with only one other species in the genus, *S. venusta*.

Remarks. *Stenohelia spinifera* was collected at the precise locality and depth as *S. venusta* but ten days later. Although they are the only two species in the genus to have dactyloglossae, *S. spinifera* can be distinguished by bearing large coenosteal papillae, having a rough coenosteal texture, having on average less dactylopores per cyclosystem, and in having irregularly shaped male ampullae primarily on the anterior branch faces.

Distribution. Known only from one record, the type locality (Fig. 31).

Genus *Conopora* Moseley, 1879

Conopora Moseley, 1879: 503.—Boschma, 1956a: F100.—Cairns, 1983a: 128; 1983b: 489–490; 1991: 71; 1992, 540, 544 (key).

Type Species. *Conopora tenuis* Moseley, 1879 (=*C. laevis* (Studer, 1878)), by monotypy.

Diagnosis. Colonies usually uniplanar and firmly attached, however one species (*C. adeta* Cairns, 1987) is bushy and free living. Corallum shape often influenced by commensal polynoid gall tube. Coenosteal texture usually linear-imbricate but may be linear-granular, and invariably white. Gastro- and dactylopores arranged in cyclosystems, which are sympodially arranged on branch edges, uniformly distributed on all branch surfaces, tetraserially arranged, or unifacially arranged on anterior face. Gastropore tubes double-chambered, the chambers partitioned by a gastropore ring constriction. Gastro- and dactylostyles absent. Ampullae both superficial and internal, efferent pores apical or opening within upper gastropore chamber.

Discussion. The genus was revised and a table of comparisons of most species was given by Cairns (1991). There are now known to be 11 Recent species in the genus (Appeltans, et al. 2012), including the two new species described herein, and two fossil species. These are the first records of this genus from South Africa.

Holocene Distribution. Indo-West Pacific, Subantarctic, Antarctic, 110–2355 m.

Conopora sola sp. nov.

Figs. 3C, 19A–J, 24

Etymology. From the Latin *solus* (meaning alone or solitary), a reference to the absence of a commensal polynoid polychaete.

Types and Type Locality. Holotype: female colony, *MN* SM237, SAM, and SEM stubs 1685–86 (USNM). Paratypes: *MN* SM86, 1 female, SAM; *MN* SM232, 3 female colonies (1 in alcohol), SAM; *MN* SM237, 1 female colony in alcohol, SAM; *PF*14356–62, 1 female colony, SAM H1465; UCTES AFR950, 1 female colony, SAM; *Valdivia* 104, 2 female colony, ZMB 7039. Type Locality: 32°15.4’S, 29°09.7’E (continental slope off northern Eastern Cape Province, South Africa), 600–650 m.

Material Examined. Types.

Description. Colonies are uniplanar and relatively small, the holotype (Fig. 3C) measuring 4.0 x 2.8 cm, with a broken basal branch 4.4 mm in diameter. Branching axils vary between 60–90°; branch anastomosis does occur. Distal branches are round in cross section, but the thicker, more proximal branches are rectangular in cross section, the longer axis of the rectangle being perpendicular to the plane of the colony; there are no polynoid tubes. The coenosteal texture is a well defined linear-imbricate (Figs. 19G–I), the strips being 50–60 µm in width, with approximately 55–70 platelet leading edges per mm. Each platelet bears 4–7 low longitudinal ridges, which terminate in a sinuous distal edge. The coenosteum, ampullae, cyclosystem sides, and pseudosepta are densely covered with low nematopore mounds, each mound about 40 µm in diameter, the apical pore being 8–9 µm in diameter, and the height only about 15 µm (Fig. 19J). The coenosteum is white.

Cyclosytems are sympodially arranged on the branch edges, 1.0–1.2 mm in diameter, and circular to slightly irregular in shape. Based on 40 cyclosystems, the range of dactylopores per cyclosystem is 9–13; the average is 10.90 (σ = 1.13); and the mode is 11. There are no diastemas, even in basal branches.

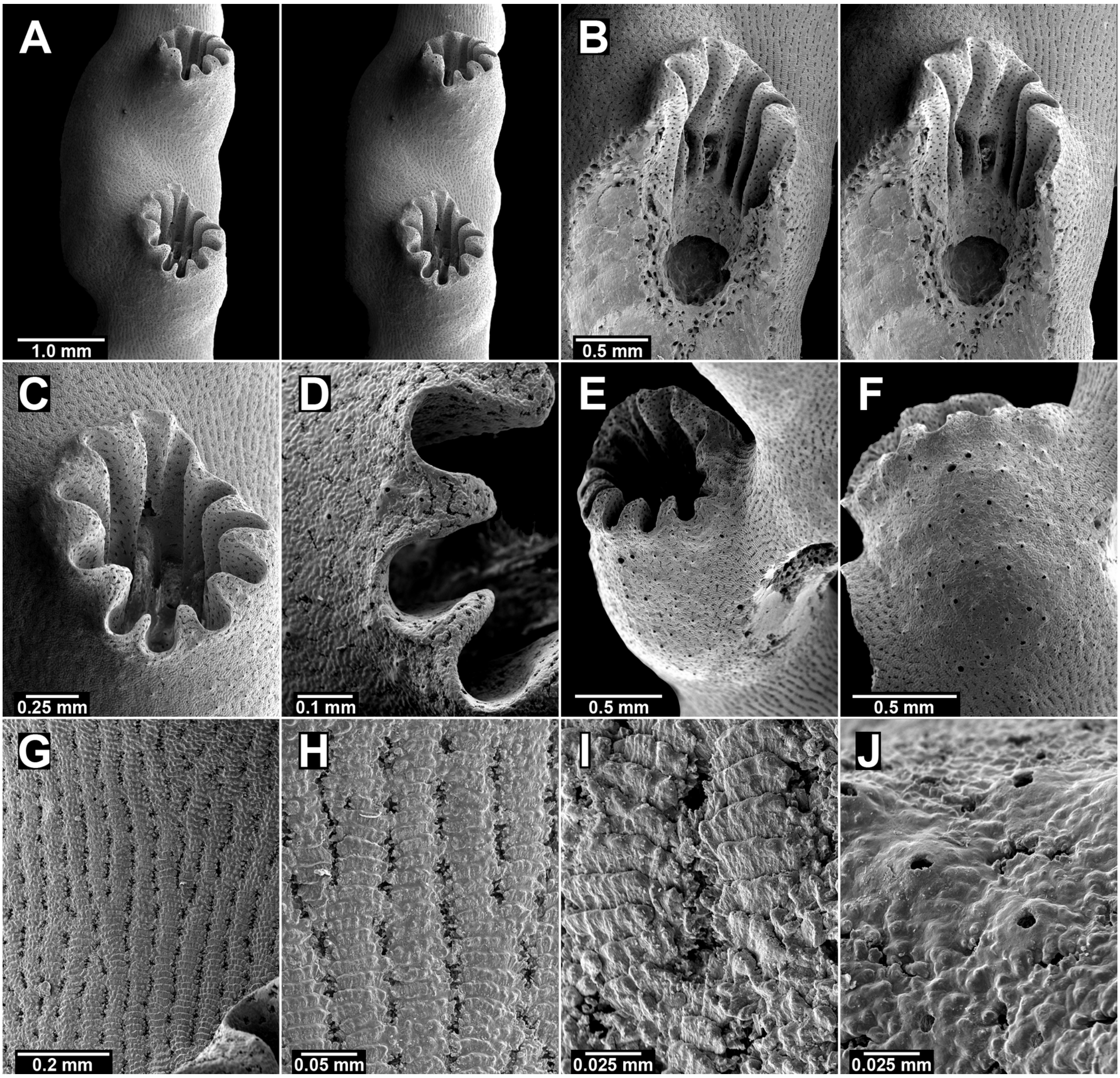

FIGURE 19. *Conopora sola*, female holotype from *MN* SM237, SAM: **A**, stereo view of cyclosystem, with female efferent pore visible in gastropore tube of lower polyp. **B**, longitudinal fracture of gastropore tube, with two female efferent pores visible in dactylotome region. **C**, a cyclosystem. **D**, pseudosepta. **E–F**, large female ampulla adjacent to a cyclosystem, covered with nematopore mounds. **G–I**, linear-imbricate coenosteal texture. **J**, nematopore mounds.

The gastropore is double chambered (Fig. 19B), but consists of three sections. The lower chamber is hemispherical, about 0.50 mm in diameter. The upper chamber is about the same size and shape, the two chambers separated by a thin gastropore ring constriction of about 0.4 mm diameter. Above the upper chamber is a roughly cylindrical tube that is flanked by the dactylotomes. The dactylotomes range from 0.10–0.15 mm in width, the pseudosepta (Fig. 19D) being slightly wider and more variable in width, ranging from 0.09–0.25 mm wide. The tops of the pseudosepta are flat to slightly convex.

Female ampullae are massive (up to 1.9 mm in diameter) swellings (not hemispherical) that occur adjacent to cyclosystems (Figs. 19A, B, E, F). They must be close to a cyclosystem as their efferent pores open into an adjacent upper gastropore tube, usually in a dactylotome region (Figs. 19A, B). Male ampullae are unknown.

Comparisons. Among the ten other Recent *Conopora* species, *C. sola* is clearly most similar to *C. verrucosa*, and indeed, may in the future prove to be merely a subspecies or population of that species. It is similar to *C. verrucosa* in its colony shape, nematopore distribution, coenosteal texture, and female ampullar structure (i.e., efferent pores leading to gastropore chamber), but does differ consistently in several characters. *Conopora sola* does not have a symbiosis with polychaete worms (but then the type of *C. pauciseptata* Broch, 1951, a purported junior synonym of *C. verrucosa* from Discovery Seamount southwest of South Africa, also does not host a polynoid commensal). It does not have diastemate cyclosystems, even in the base of the colony, which gives it a higher range and average number of dactylopores per cyclosystem (average of 10.9 and mode of 11 compared to an average of 6.59 and mode of 8 for the type of *C. pauciseptata* according to Broch, 1951b). Finally, its female ampullae are larger than those of *C. verrucosa*.

Distribution. Off southeastern South Africa from southern Agulhas Bank to off Cape Saint Lucia, Natal (Fig. 24), 155–620 m.

Conopora verrucosa **(Studer, 1878)**

Figs. 3D, 27

Stylaster verrucosus Studer, 1878: 635, figs. 6a–b.
Conopora pauciseptata Broch, 1951b: 41–44.—Cairns, 1983a: 128–130, figs. 31C–D, 36A–G; 2011: fig. 8L.
Conopora verrucosa: Zibrowius, 1981: 275.—Cairns, 1983b: 490, figs. 21E–H, map 11; 1991: 72–73, pls. 57e–g, 58a–d (complete synonymy).

Types and Type Locality. The holotype of *S. verrucosus* is deposited at the ZMB (#1764). Type Locality: 35°02'S, 175°40'E (off northern North Island, New Zealand), 1092 m.

The holotype of *C. pauciseptata* (female colony) is deposited at the BM (2012.1). Type Locality: 42°03.9'S, 00°03.5'E (Discovery Seamount), 472 m.

Material Examined. *MN* SM129, 1 female colony, SAM; *Valdivia* 103, 1 colony, ZMB Cni 14537; holotypes of *S. verrucosus* and *C. pauciseptata*.

Remarks. Since so few specimens are reported herein, and this species is well described and illustrated elsewhere (see synonymy), a redescription is not provided. In brief, the specimen from *MN* SM129 is a female colony 24 mm in height, 21 mm in width, and 5.1 mm in basal branch diameter (Fig. 3D). Even at this stage the commensal polychaete tube is well developed. Cyclosystems are arranged sympodially, and are about 1.4 mm in diameter. Based on 8 cyclosystems there is a range of 3–11 dactylopores per cyclosystem, and an average of 7.12. Adcauline diastemas are common, especially in cyclosystems near the colony base. The colony has one female ampulla, with an efferent pore that opens into the adjacent gastropore chamber.

The type of *C. pauciseptata* is identical to typical *C. verrucosa* except that it does not have a symbiosis with a commensal polynoid, which even Broch (1951b) suggested was "fortuitous", or somewhat unusual.

Distribution. Off southeastern South Africa from off Margate (Natal) and eastern Agulhas Bank (Fig. 27), 500–850 m. Elsewhere: widespread in Subantarctic South America and off Antarctica (see Cairns 1983a: map 11), New Zealand from Kermadecs to the Antipodes (Cairns 1991), Discovery Seamount, 198–2355 m.

Conopora tenuiramus **sp. nov.**

Figs. 3E–F, 20A–N, 25

Etymology. From the Latin *tenuis* (thin) and *ramus* (branch), an allusion to the slender terminal branches of this species; treated as a noun in apposition.

Types and Type Locality. Holotype: *MN* SM228, female colony, SAM, and SEM stubs 1690, 1693 (USNM).

Paratypes: *MN* SM162, 4 branch fragments, gender indeterminate, SAM; *MN* SM228, 2 male branches, SAM; *MN* SM232, 2 dead male branch fragments, SAM, and SEM stub1690 (USNM); *PF*14306, 1 female colony, SAM H1455. Type Locality: 32°29.5'S, 28°57.1'E (continental slope north of East London, off northern Eastern Cape Province), 650–700 m.

Material Examined. Types. Reference Material: Broch's (1936) Mauritius specimen of *C. tenuis* and *C. major* (ZMC).

Description. Colonies are uniplanar and relatively small, the holotype (Fig. 3F) only 3.8 cm tall and 2.4 cm broad, with an intact basal branch having a diameter of 2.75 mm. However, larger colonies are known (*PF*14306), which are up to 6 cm long and 1.1 cm in diameter, most of the main branch diameter consumed with a polynoid gall tube. Regardless of the size of the colonies, the distal branches are invariable delicate and thin, usually less in diameter than the cyclosystems they support. All colonies support a commensal polynoid gall tube (Figs. 3E, F), which is prominent in the basal part of the main branches, often forming a web-like membrane that seems to envelope the lower branches. Branching is dichotomous, nodes occurring at almost every cyclosystem, producing a highly ramified and often anastomotic colony. The coenosteal texture is a well-defined linear-imbricate (Figs. 20G–I), the strips being 70–80 µm in width, with about 65 platelet leading edges per mm, although parts of some colonies appear to have a smooth (worn?) texture (Fig. 20J). The platelets are somewhat roughened by having low longitudinal ridges. The branch and polynoid gall tube coenosteum, ampullae, and pseudosepta are densely covered with low nematopore mounds, the pores on the coenosteum and ampullae 20–40 µm in diameter (Fig. 20K) and the mounds up to 30 µm in height, whereas those on the pseudosepta are usually slightly larger (35–45 µm in diameter) and flush with the coenosteum, and arranged one to a pseudoseptum (Fig. 20C, E). The colonies are white.

Cyclosystems are unifacially arranged on all branches in a linear manner, elliptical to slightly irregular in shape (Figs. 20B–D), and 1.0–1.4 mm in greater diameter. Based on 40 cyclosystems, the range of dactylopores per cyclosystem is 13–19; the average is 16.0 ($\sigma = 1.13$); and the mode is 15.

The gastropore tube is double chambered (Fig. 20F), the lower chamber flattened, about 0.45 mm in diameter and 0.15 mm in height, separated from the upper spherical chamber by a delicate gastropore ring constriction of about 0.26 mm diameter. The upper chamber is about 0.35 mm in diameter, above which the gastropore tube is flanked with dactylotomes. Dactylotomes range from 75–80 µm in width, the pseudosepta being slightly wider and more variable in width, ranging from 0.10–0.21 mm. The tops of the pseudosepta are flat to slightly convex.

Female ampullae are massive swellings (up to 1.6 mm in diameter), sometimes even hemispherical, but often partially submerged in the coenosteum, most clustered in the coenosteum forming the polynoid gall tube (Fig. 20L). Efferent pores are well defined, lateral in position, and about 0.25–0.30 mm in diameter. Male ampullae are also clustered in the polynoid gall tube coenosteum and frequently internal, only seen in a cross sectional break of the polynoid gall tube coenosteum (Figs. 20M, N). They are about 0.4–0.7 mm in internal diameter; their efferent pores were not observed.

Comparisons. Only one other species of *Conopora* has unifacially-arranged cyclosystems (but see below), *C. unifacialis* Cairns, 1991 (from New Zealand). *Conopora tenuiramus* is easily distinguished from that species by its thicker pseudosepta, lesser number of dactylopores per cyclosystem, polychaete commensalism, and gastropore tube shape. But, *Conopora tenuiramus* is also similar to *C. laevis* (Studer, 1878), especially in its delicate colony shape, polychaete commensalism, nematopore distribution, and ampullar shape, but *C. tenuiramus* can be distinguished by having unifacially arranged cyclosystems, more dactylopores per cyclosystem, and thinner branches.

Although similar, the specimen reported from Mauritius by Broch (1936) as *C. tenuis* Hickson & England, 1905, has smaller cyclosystems and female ampullae, hemispherical female ampullae, and a mixture of unifacial and sympodially arranged cyclosystems.

Conopora tenuiramus was also compared to Broch's (1936) *C. major* Hickson & England, 1905, also collected from off Mauritius. Both species have unifacial cyclosystems, a polynoid commensal, and similarly-sized cyclosystems and ampullae, but Broch's specimens differ in having female efferent pores that open within the gastropore tube, and frequently having enlarged (widened) pseudosepta in the abcauline position of the cyclosystem, resembling incipient lids characteristic of *Crypthelia*.

Distribution. Continental shelf and slope off southeastern South Africa from Cape Seal (Western Cape Province) to northern Eastern Cape Province (Fig. 25), 146–650 m.

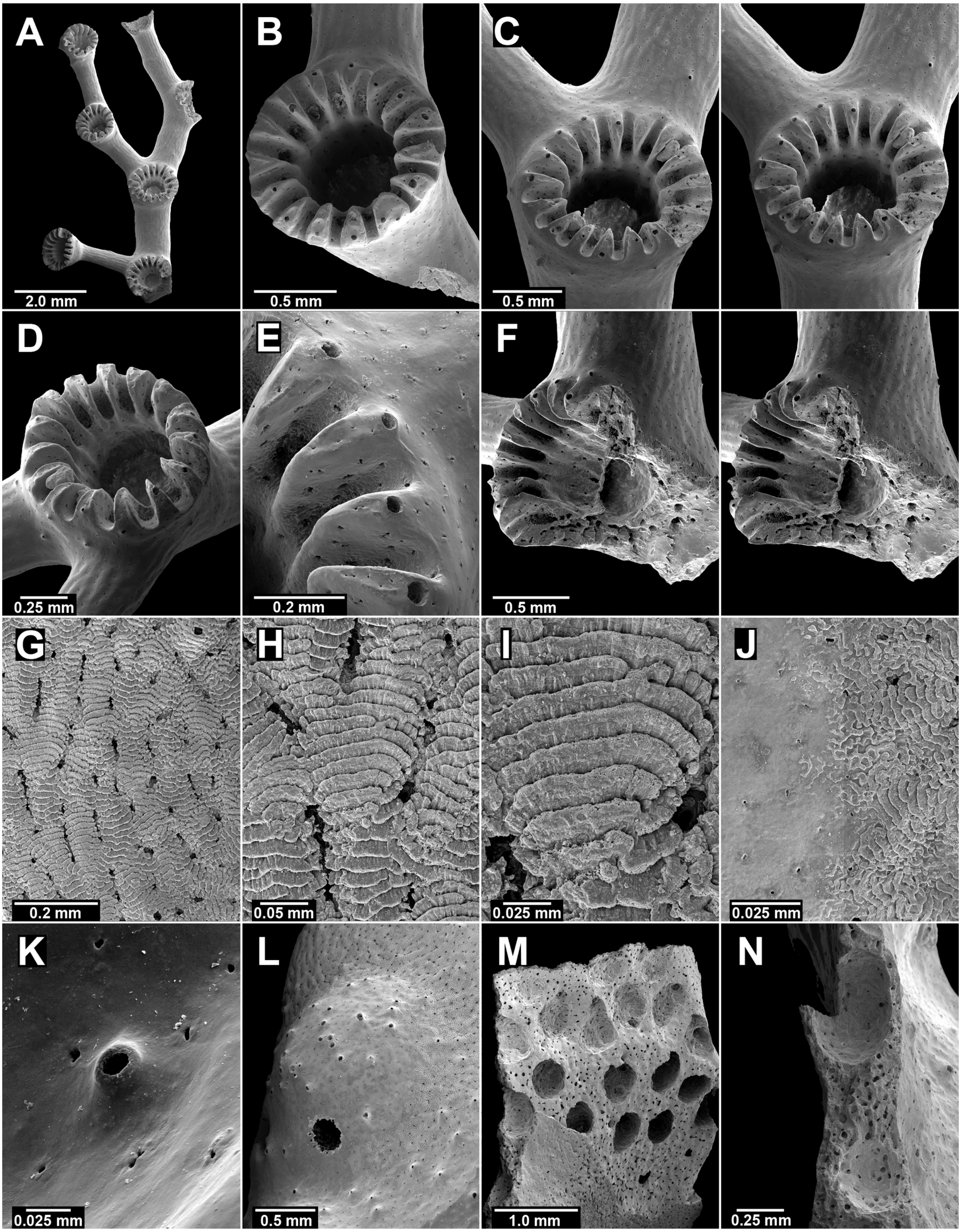

FIGURE 20. *Conopora tenuiramus* (**A–L**, female holotype, *MN* SM228, SAM; **M–N**, male paratype, *MN* SM232, SAM): **A**, unifacially arranged cyclosystems. **B–D**, cyclosystems showing the regular placement of one nematopore per pseudoseptum (**C** is a stereo pair). **E**, nematopores on outer edges of each pseudoseptum. **F**, stereo view of double-chambered gastropore tube. **G–I**, linear-imbricate coenosteal texture. **J**, transition of linear-imbricate to smooth coenosteal texture. **K**, a single nematopore mound. **L**, female ampulla and efferent pore. **M**, transverse section though several male ampullae lodged in polynoid gall tube coenosteum. **N**, longitudinal section of male ampullae in polynoid gall tube coenosteum.

Genus *Crypthelia* Milne Edwards & Haime, 1849

Crypthelia Milne Edwards & Haime, 1849: 69.—Boschma, 1956a: F100.—Cairns, 1983a: 130; 1983b: 492–493; 1986a: 100–101; 1991: 82; 1992: 540, 544 (key).—Cairns & Lindner, 2011: 81.

Type Species. *Crypthelia pudica* Milne Edwards & Haime, 1849, by monotypy.

Diagnosis. Colonies usually uniplanar, with delicate branches; commensal polynoid polychaete tubes common. Coenosteal texture usually linear-imbricate; nematopores common. Gastro- and dactylopores arranged in cyclosystems, which usually occur exclusively on anterior branch face (in one species bifacial). Gastropore tubes double chambered, divided by a gastropore ring constriction; gastro- and dactylostyles absent. Gastropores covered by a lid of variable length and width. Ampullae usually superficial, female ampullae occurring in lid or proximal cyclosystem wall; male ampullae usually clustered in ring around cyclosystem wall or in lid. Efferent pores of both genders open apically or within upper gastropore chamber.

Discussion. This genus is similar to *Conopora*, but distinguished by having a lid that covers all or part of the cyclosystem. There are 31 Recent and one fossil species in the genus (Appeltans, et al. 2012), making it the second most species-rich genus in the family.

Holocene Distribution. Atlantic, Indo-West Pacific, North Pacific, Galápagos, Subantarctic, 85–2789 m.

Crypthelia micropoma Cairns, 1985

Figs. 21A–K, 31

Crypthelia micropoma Cairns, 1985: 736–739, figs. 23–31.

Types and Type Locality. Holotype deposited at the NMNH (USNM 72354), and paratypes at the NMNH and BM. Type Locality: 2°42’S, 40°53’E (off Malindi, Kenya), 140 m.

Material Examined. *MN* ZF2, SAM, and SEM stub 1687–1689 (USNM); *MN* SM162, 2 branch fragments SAM, and SEM stub 1684 (USNM); *MN* SM185, 4 branch fragments, male and female, SAM; UCTES SCD301, 1 female and 1 male colonies, Naturalis Biodiversity Centre. Types.

Description. Colonies are uniplanar and small, the holotype only 22.7 mm in height, and 17 mm in width, with a 2.8 mm basal branch diameter. Branching is dichotomous, the distal branches usually of lesser diameter than the cyclosystems they support. There is no evidence of polychaete commensalism. The coenosteal texture is a well-defined linear-imbricate (Fig. 21F), the strips being 65–70 µm in width and bordered by rather large coenosteal pores 20–25 µm in diameter; there are about 70 platelets per mm. The platelets are somewhat convex and slightly roughened by low longitudinal ridges. There are no nematopores.

Cyclosystems are unifacially arranged on all branches in a linear manner, circular to irregular in shape, and up to 1.3 mm in greater diameter (Figs. 21A, B). Based on 30 cyclosystems, the range of dactylopores per cyclosystem is 15–21; the average is 18.80 ($\sigma = 1.32$); and the mode is 19. There are no diastemas.

The gastropore tube is double chambered (Figs. 21C, G), the lower chamber flattened, about 0.5 mm in diameter and 0.11 mm in height. The base of the lower chamber sometimes bears numerous slender spines (needles), each up to 59 µm in height and about 8 µm in diameter (Fig. 21G, H), not to be confused with a true gastrostyle. The delicate gastropore ring constriction (Figs. 21C, G) is about 0.41 mm in diameter, and the roughly spherical upper chamber is about 0.80 mm in diameter. Dactylotomes are relatively short, and are 0.08–0.10 mm in width. Pseudosepta are of variable width, and sometimes narrower than the dactylotomes, ranging from 0.08–0.10 mm. The tops of the pseudosepta are highly porous and concave (Figs. 21D, E). Female cyclosystems with well-developed ampullae have a short and narrow lid, whereas male cyclosystems do not have lids at all.

Female ampullae are large (up to 1.9 mm in diameter), globular superficial masses invariable placed adjacent to a cyclosystem (Figs. 21A, B, I, J). Efferent pores were not observed in the limited material at hand, but open within the gastropore tube beneath the lid in the type material. Male ampullae are clustered as 4–6 irregular swellings around part of the perimeter of the cyclosystems; each has a small apical efferent pore (Fig. 21K).

Remarks. Already known as the shallowest of the *Crypthelia* species at 140 m, the South African records are found shallower still, at 85 m.

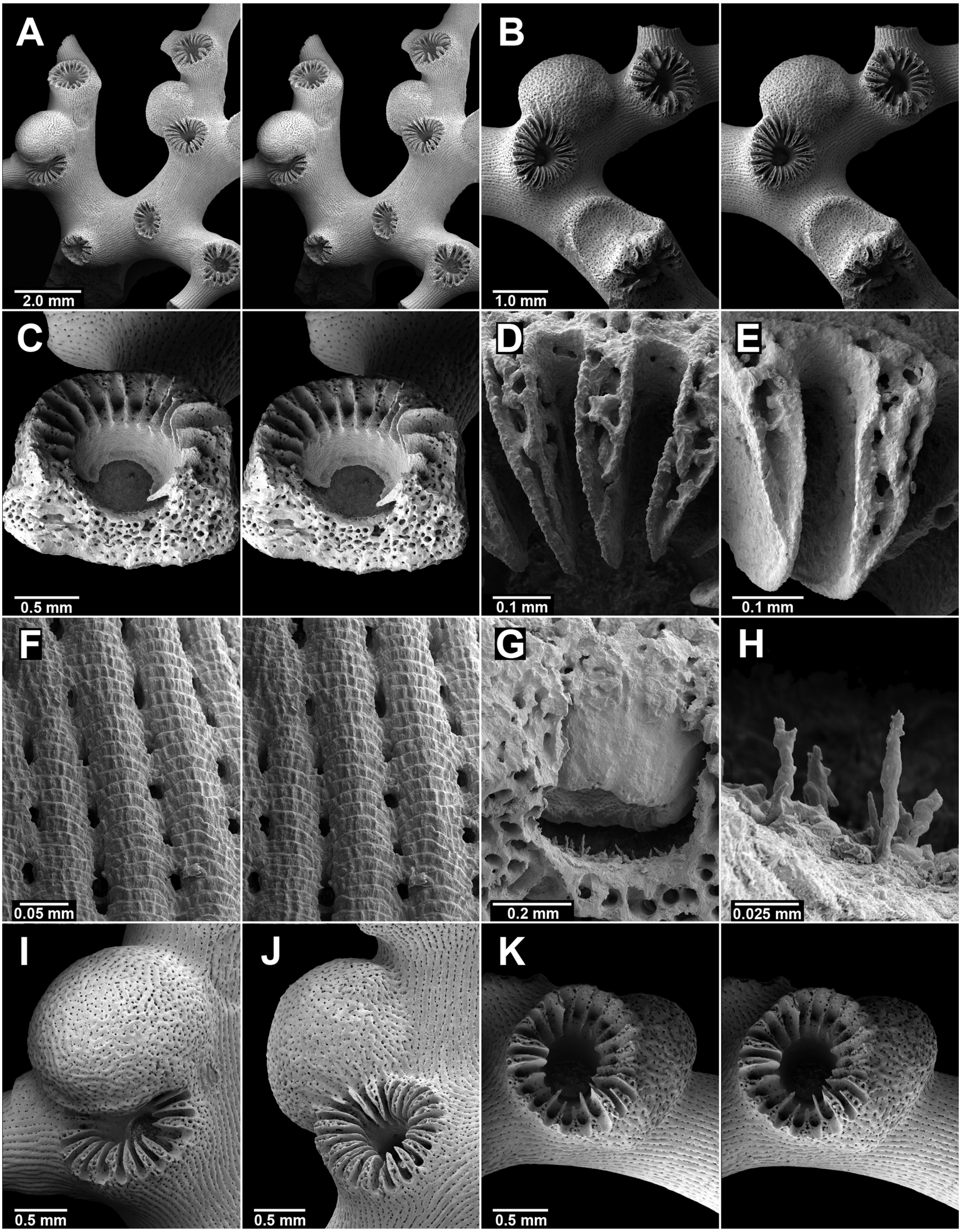

FIGURE 21. *Crypthelia micropoma* (**A–B, D, I–J**, female from *MN* ZF2, SAM; **C, E–H, K**, male from *MN* ZF2, SAM): **A**, stereo view of unifacial cyclosystems, some with female ampullae. **B**, stereo view of one intact and one spent female ampullae. **C**, stereo view of double-chambered gastropore tube. **D–E**, porous pseudosepta. **F**, stereo view of linear-imbricate coenosteal texture. **G**, longitudinal section of lower gastropore chamber. **H**, small spines in lower gastropore chamber**. I–J**, female ampullae adjacent to cyclosystems. **K**, stereo pair of male ampullae adjacent to a cyclosystem.

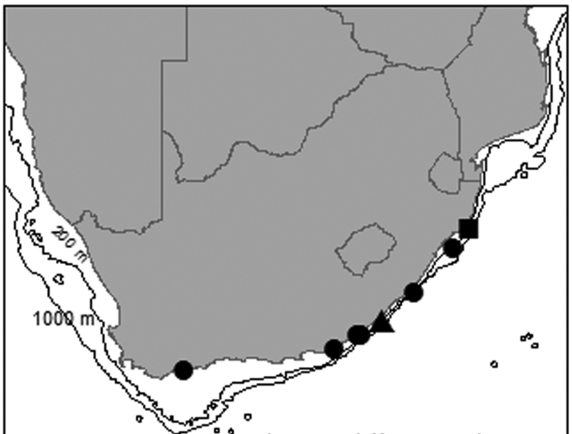

FIGURE 22. *Lepidopora diffusa* (circles), *Errinopsis fenestratus* (triangle), *Stylaster kenti* (square)

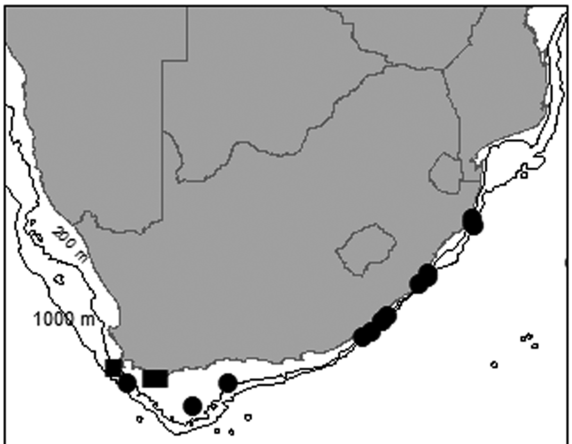

FIGURE 23. *Inferiolabiata africana* (circle), *Gyropora africana (*square)

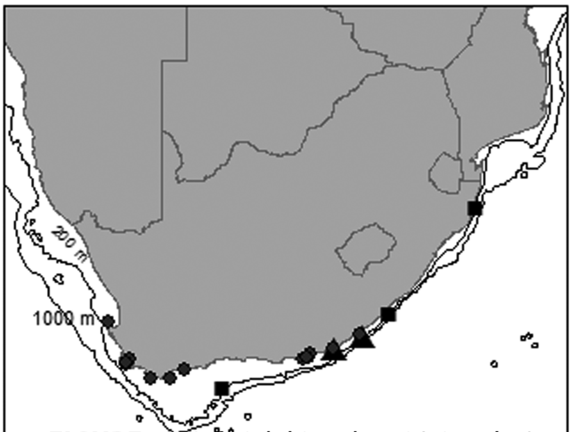

FIGURE 24. *Inferiolabiata lowei (*triangles*),* *Stylaster nobilis* (circles)*, Conopora sola (*squares)

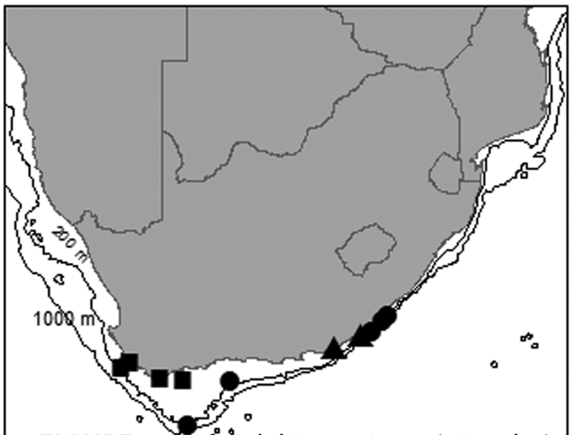

FIGURE 25. *Inferiolabiata spinosa* (triangles), *Stylaster subviolacea (*squares), *Conopora tenuiramus (*circles)

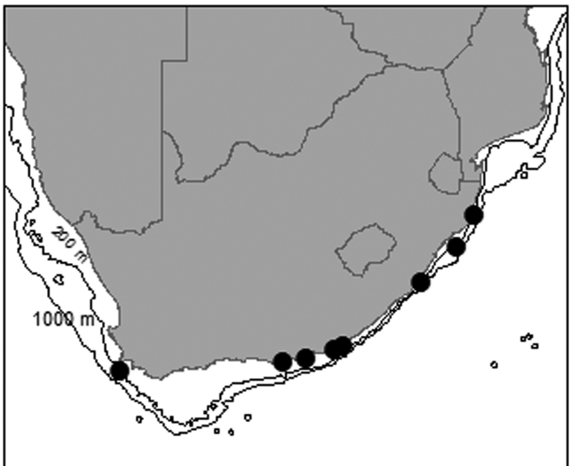

FIGURE 26. *Errina capensis*

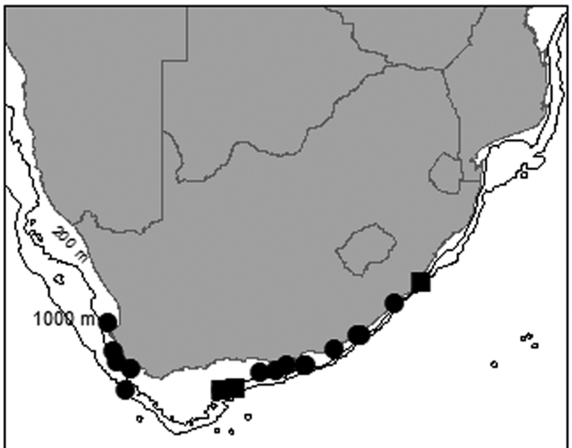

FIGURE 27. *Stylaster bithalamus* (circles). *Conopora verrucosa* (squares)

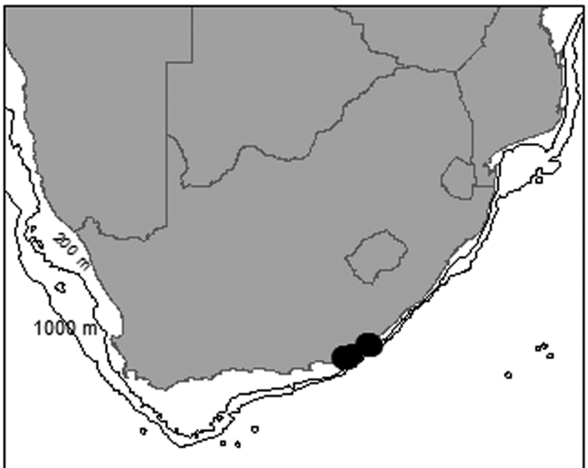

FIGURE 28. *Stylaster griseus*

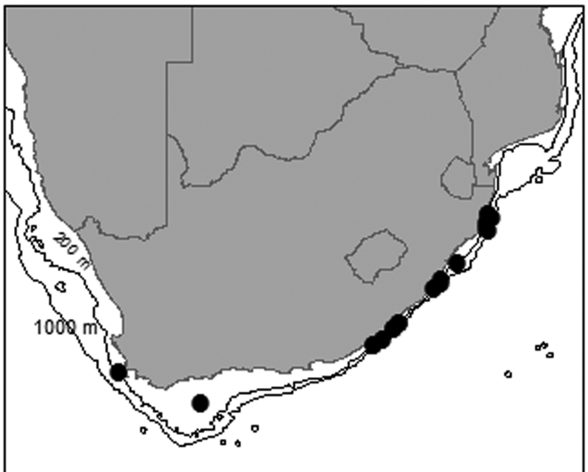

FIGURE 29. *Stylaster amphiheloides*

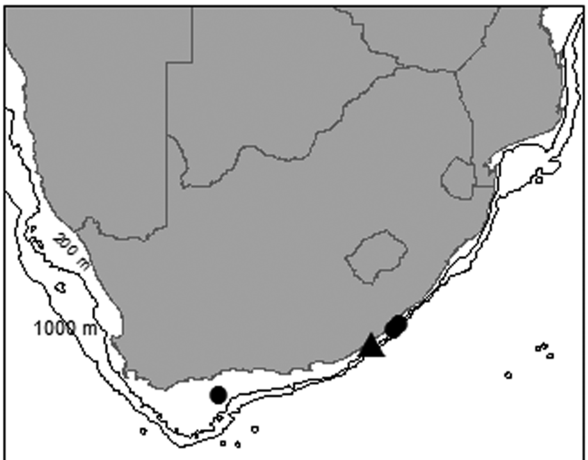

FIGURE 30. *Stylaster lonchitis* (triangle), *Stenohelia venusta* (circles)

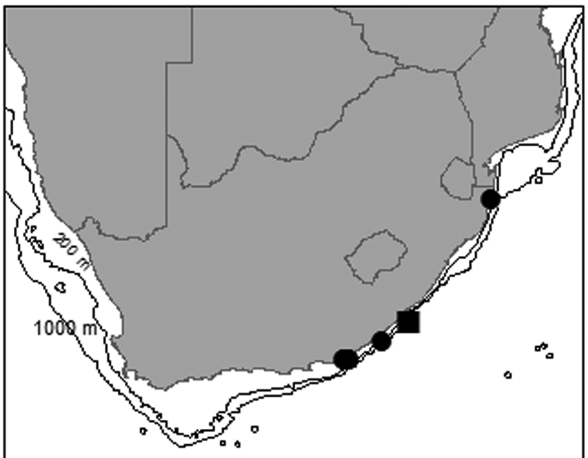

FIGURE 31. *Stenohelia spinifera* (square) *Crypthelia micropoma* (circles)

The male of this species is the only one in the genus to lack cyclosystem lids, and as such may be confused with the genus *Conopora*.

Distribution. Off South Africa, from Port Elizabeth to northern Natal, 85–630 m (Fig. 31); off Kenya, 140 m.

Zoogeography

The warm southern flowing Agulhas Current on the southeastern African coast and the cold northern flowing Benguela Current on the western coast combine to produce a variety of zoogeographic provinces for the African coastline (Briggs 1974; Spalding 2007; Griffiths, et al. 2010). The region of Africa north of the Cape of Good Hope, in the Atlantic, is generally considered to be the cold temperate Namaqua Province (although Briggs considers it to be warm temperate). No stylasterids are known from this region, and thus it is not discussed further. The region between the Cape and approximately the Great Kei River (East London) is considered to be the warm temperate Agulhas Province, although its northern border is controversial, definitions ranging from Algoa Bay to

TABLE 2. Stylasteridae known from South Africa (* previously reported from S. Africa). E = Endemic; distributional patterns explained in text; Agulhas zoogeographic province (warm temperate), Natal zoogeographic province (subtropical), Transitional region (former Transkei).

	Endemic	Distribution Pattern	Agulhas Province	Trans-itional	Natal Province	Elsewhere	Depth (m)
**Lepidopora diffusa* (Boschma, 1963)	E	2	X		X		47–101
Inferiolabiata africana , n. sp.		2	X	X	X	Providence I.	165–1000
I. lowei (Cairns, 1983)		3c	X			southern S. Amer., NZ	90–155
I. spinosa Cairns, 1995		3d	X			Kenya, NZ	90–93
**Errina capensis* Hickson, 1912	E	2	X		X		40–174
Errinopsis fenestrata Cairns, 1983		3c	X			southern. S. America	174–250
**Gyropora africana* Boschma, 1960	E	3a	X				22–80
Stylaster (Group A)							
**Stylaster nobilis* (Kent, 1871)	E	3a	X				3–174
**S. subviolaceus* (Kent, 1871)	E	3a	X				22–88
**S. bithalamus* Broch, 1936	E	3b	X	X			11–155
S. griseus , n. sp.	E	3a	X				80–155
Stylaster (Group C)							
**S. amphiheloides* Kent, 1871	E	2	X	X	X		155–1000
S. lonchitis Broch, 1947		2	X			Kenya, Tanzania	85–90
S. kenti , n. sp.	E	1			X		360–420
Stenohelia venusta, n. sp.		2	X	X		Kenya	159–710
St. spinifera , n. sp.	E	3a	X				174
Conopora sola , n. sp.	E	2	X	X	X		155–620
C. verrucosa (Studer, 1878)		3c	X	X		southern S. Amer., NZ	500–850
Crypthelia tenuiramus , n. sp.	E	3b	X	X			146–650
C. micropoma Cairns, 1985		2	X		X	Kenya	85–630

Natal (see Briggs 1974). For the purposes of this paper, the region between Great Kei River and Margate (the former Transkei region) is considered to be a transitional region between the warm temperate and subtropical Natal Province to the north.

Among the 20 South African stylasterid species, there are essentially three patterns of distribution (Table 2): 1, restricted to the tropics (1 species); 2, occurring in both the warm temperate and subtropical provinces without regard to the zoogeographic border between them (8 species); and 3, occurring only in the warm temperate region of South Africa, some species also occurring in other parts of the world (11 species). *Stylaster kenti* is the only species in pattern 1, which may be an artifact, as it is known from only one record so far. The second pattern (Table 2: pattern 2) consists of four species endemic to South Africa, and another four that have extended distributions in the tropical regions of the Southwest Indian Ocean as far as Providence Island or Kenya. The third pattern (Table 2: patterns 3a–d) consists of five species endemic to the warm temperate region of South Africa (pattern 3a), two species (pattern 3b) that also occur in the transitional region (former Transkei), three species that also occur off cold temperate South America and sometimes New Zealand (pattern 3c), and a final species (*I. spinosa*) that occurs off warm temperate New Zealand and the tropical Southwest Indian Ocean (pattern 3d). Thus, whereas the statement made by Boschma (1966b) that all South African stylasterids were endemic to that country, while true at that time, it is now known that only 12 of 20 species (60%) are endemic, and that the distribution of the remaining eight occur in tropical regions to the north, and more interestingly, have shared distributions with the cold temperate regions of southern South America and New Zealand in a southern circum-temperate distribution pattern. In this regard, the circum-temperate genera *Inferiolabiata* and *Errinopsis* are reported for the first time off South Africa.

Pedicularia as a symbiont of South African stylasterids

The cypraeoid gastropod genus *Pedicularia* Swainson occurs worldwide from shallow to deep water. The highest latitude occurrences presently known are at about 48°N in the northeast Atlantic (Celtic Sea) and at about 37°S in both the southwest Pacific (Three Kings Islands, New Zealand) and the southwest Indian Ocean (Sapmer Seamount southeast of Madagascar). No *Pedicularia* seem to exist at higher northern and southern latitudes whereas stylasterids do occur up to Iceland, Norway, Alaska, and Antarctica. All *Pedicularia* are obligate symbionts on stylasterids (symbiont in its most neutral and etymologic sense of “living together”). The less than centimetric shells may be homochromous with the stylasterid host. *Pedicularia* feeds on its host coral, but how precisely is still unknown. Biology data are scarce. Liltved (1985a, 1985b, 1989) published interesting observations (juveniles still moving freely on the host before becoming sedentary) and speculations on feeding (consuming mucoid secretions of the host).

Adult *Pedicularia* always have their shell edge closely conforming to the configuration of the stylasterid branch at the place where they sit. This is a situation similar to that of a limpet shell adapting to the irregularities of the rock. Under the foot of the snail the branch surface is modified in a somewhat elongate area. It may have the aspect of a slightly prominent flat and smooth “sole”, or even bear distinct crests. In other cases the surface where the foot of the snail adheres is, as a whole, slightly depressed. Whether smooth or with crests, this is presumed to depend on the *Pedicularia* species involved. More distinct “soles” typically correspond to larger specimens (perhaps a matter of time to produce them). It is not intended here to discuss the precise structure of the modified area and how this modification is produced.

Thanks to the modified branch surface at the site where a *Pedicularia* had been sitting, information can be obtained on the occurrence of *Pedicularia* even after the snail and its host coral had become separated (e.g., by handling of the dredge contents), as well as from stylasterid bioclasts collected dead, separated from the sediment.

Given the diversified stylasterid fauna of South Africa and the moderate southern latitude, it is no surprise that *Pedicularia* occurs there. By latitude the South African occurrences fall a few degrees short with respect to the southernmost localities mentioned above for the southwest Indian Ocean and the southwest Pacific. Most data available are from the malacological literature, a supplement that has been obtained from traces left behind on stylasterid branches when the snail had not been preserved together with its host.

Pedicularia had first been mentioned from South Africa by Sowerby (1903), who mistakenly referred his sample to *P. sicula*, the Mediterranean-northeast Atlantic species. Barnard (1963) added three more records (as *P.*

elegantissima). All are (like Sowerby's) from J.D.F. Gilchrist's dredgings on the *Pieter Faure*. All specimens are preserved in the malacological collection of the South African Museum (A 5040, A 8931, A 8932, A 5070, A 8933; seen by HZ in 1980) and correspond to what currently is understood as *P. elegantissima* (not *P. sicula*). Barnard (1963) mentioned that one sample had been taken from "*Stylaster* or *Allopora*" (i.e., the host species is not precisely known) whereas the others had been picked out of "bottom samples". These records range along the coast from off Kwazulu-Natal south of Durban to off Western Cape Province approximately south of Mossel Bay, in the areas of Umkomaas (73m), Cape Morgan (86m, 173m), Hood Point (89m), and Cape St. Blaize (212m). The southwesternmost station is close to 35°S.

Liltved (1985a, 1985b, 1989) reported new records of *P. elegantissima* from the East London and the Nqabara Point areas (both Eastern Cape Province), mentioning as hosts *Errina capensis*, *Errina* sp., and *Stylaster* sp. He illustrated a trace ("scar") of *Pedicularia* on a pink *Stylaster* (herein identified as *Stylaster lonchitis*). Small pieces of two host species sent by Liltved to HZ in 1986 (now deposited at NMNH) are identified herein as the pink *Errinopsis fenestrata* (in 1989 mentioned as *Errina* sp.; off Nqabara Point, northern Eastern Cape Province, 32°27.2'S, 28°55.9'E, 250 m, 12.7.1984), and the pink *Stylaster lonchitis* (off Gonubie, Eastern Cape Province, 33°01.8'S, 28°04.4'E, 85 m, 17.7.1984).

Additional *Pedicularia* occurrences have been inferred during this study from what seem to be traces on *Errina capensis* from the Cape Morgan area, Eastern Cape Province (PF 13394, 123m; SAM H 1233) and on *Conopora sola* from Western Cape Province (UCTES AFR 950, 20.3.1949, 34°44'S, 21°18'E, 201m).

Considering experience from other stylasterid faunas (e.g., northeast Atlantic, New Caledonia) it is probable that *Pedicularia* occurs on even more species of South African Stylasteridae than those presently recognized as host corals.

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References

Appeltans, W., Bouchet, P., Boxshall, G.A., Fauchald, K., Gordon, D.P., Hoeksema, B.W., Poore,G.C.B., Soest, R.W.M van, Stöhr, S., Walter, T.C. & Costello, M.J. (2012) World Register of Marine Species. Available from: http://www.marinespecies.org (Accessed 20 January 2013)

Barnard, K.H. (1963) Contribution to the knowledge of South African marine Mollusca. Part 3. Gastropoda: Prosobranchia: Taenioglossa. *Annals of the South African Museum*, 47 (1), 1–119.

Bauer, M. (1896) *Edelsteinkunde.* Leipzig C.H. Tauchnitz, 858 pp.

Boonstra, H.G. van D. (Ed.) (1994) *South African Commercial Fisheries Review 1992*, 2, Sea Fisheries, Rogge Bay, Cape Town, 1–45.

Best, M.W., FAURE, G. & Pichon, M. (1980) Contributions to the knowledge of the stony corals from the Seychelles and eastern Africa. *Revue de Zoologie Africaine*, 94 (3), 600–627.

Boschma, H. (1956a) Milleporina and Stylasterina. *In:* Moore, R.C. (Ed.) *Treatise on Invertebrate Paleontology*, Geological Society of America Lawrence, Kansas, pp. F90–106.

Boschma, H. (1956b) Notes on the stylasterine coral *Allopora nobilis* Kent. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen*, (C) 59, 154–164.

Boschma, H. (1957) List of the described species of the order Stylasterina. *Zoologische Verhandelingen*, 33, 1–72.

Boschma, H. (1960a) *Gyropora africana*, a new stylasterine coral. *Proceedings Koninklijke Nederlanse Akademie,* 63, 423–434.

Boschma, H. (1960b) The stylasterine coral *Allopora bithalamus* (Broch). *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 63, 435–446.

Boschma, H. (1961) Stylasterina. *Annales de l'Institut Océanographique,* nouvelle série, 39, 193–225.

Boschma, H. (1962) Notes on *Stylaster lonchitis* Broch. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 65, 287–293.

Boschma, H. (1963a) On the stylasterine genus *Errina*, with the description of a new species. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 66, 331–344.

Boschma, H. (1963b) *Errina (Lepidopora) diffusa*, a new stylasterine coral from South Africa. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 66, 391–396.

Boschma, H. (1964) *Errina (Lepidopora) decipiens*, a new stylasterine coral from the West Indies. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 67, 55–63.

Boschma, H. (1965) On stylasterine corals of the genus *Errina* from the island of Mauritius. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 68, 1–7.

Boschma, H. (1966a) Notes on the stylasterine coral *Allopora subviolacea* Kent. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C)69, 267–272.

Boschma, H. (1966b) Stylasterina. *B.A.N.Z.A.R.E. Reports,* (B) 9, 109–120.

Boschma, H. (1967) Comments upon Hickson's notes on Stylasterina in the collection of the Paris Museum. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 70, 324–337.

Boschma, H. (1968) *Errina sarmentosa*, a new stylasterine coral from deep water in the New Zealand region. *Proceedings Koninklijke Nederlanse Akademie van Wetenschappen,* (C) 71, 203–208.

Boschma, H. & Lowe, T.P. (1969) Distribution of selected groups of marine invertebrates in waters south of 35°S latitude, Stylasterina. *Antarctic Map Folio Series,* 11, 14–15.

Briggs, J.C. (1974) *Marine Zoogeography.* McGraw-Hill, New York, 1–475 pp.

Broch, H. (1914) Stylasteridae. *Danish Ingolf Expedition,* 5, 1–28.

Broch, H. (1936) Untersuchungen an Stylasteriden (Hydrokorallen). Teil 1. *Skrifter utgitt av Norske Videnskaps-Akaddemi I Oslo. 1. Matematisk-Naturvidenskapelig Klasse,* 8, 1–103.

Broch, H. (1942) Investigations of Stylasteridae (Hydrocorals). *Skrifter utgitt av Norske Videnskaps-Akaddemi I Oslo. 1. Matematisk-Naturvidenskapelig Klasse,* 3, 1–113.

Broch, H. (1947) Stylasteridae (Hydrocorals) of the *John Murray* Expedition to the Indian Ocean. *Scientific reports of the John Murray Expedition,* 26, 33–46.

Broch, H. (1951a) Some nomenclatural corrections to the "Investigations on the Stylasteridae (Hydrocorals)" 1942. *Zoologische Mededelingen,* 31, 125–127.

Broch, H. (1951b) Stylasteridae (Hydrocorals) from the Southern Ocean. *Discovery Reports,* 26, 33–46.

Brown, A.C. (1997) John D. F. Gilchrist and the early years of marine science in South Africa. *Transactions of the Royal Society of South Africa,* 52 (1), 2–16.
http://dx.doi.org/10.1080/00359199709520615

Cairns, S.D. (1982) A new subfamily of operculate stylasterine (Coelenterata, Hydrozoa) from the Subantarctic. *Journal of Natural History,* 16, 71–81.
http://dx.doi.org/10.1080/00222938200770051

Cairns, S.D. (1983a) Antarctic and Subantarctic Stylasterina (Coelenterata, Hydrozoa). *Antarctic Research Series,* 38, 61–163.
http://dx.doi.org/10.1029/AR038p0061

Cairns, S.D. (1983b) A generic revision of the Stylasterina (Coelenterata, Hydrozoa). Part 1. Description of the genera. *Bulletin of Marine Science*, 33, 427–508.

Cairns, S.D. (1985) Three new species of Stylasteridae (Coelenterata, Hydrozoa). *Proceedings of the Biological Society of Washington*, 98, 728–739.

Cairns, S.D. (1986a) A revision of the northwest Atlantic Stylasteridae (Coelenterata, Hydrozoa). *Smithsonian Contributions to Zoology,* 418, 1–131.
http://dx.doi.org/10.5479/si.00810282.418

Cairns, S.D. (1986b) Stylasteridae (Hydrozoa, Hydroida) of the Galápagos Islands. *Smithsonian Contributions to Zoology,* 426, 1–42.
http://dx.doi.org/10.5479/si.00810282.426

Cairns, S.D. (1991) The marine fauna of New Zealand, Stylasteridae (Cnidaria, Hydroida). *New Zealand Oceanographic Institute Memoir,* 98, 1–179.

Cairns, S.D. (1992) A generic revision of the Stylasteridae (Coelenterata, Hydrozoa). Part 3. Keys to the genera. *Bulletin of Marine Science*, 49 (1–2), 538–545.

Cairns, S.D. (2011) Global diversity of the Stylasteridae (Cnidaria, Hydrozoa, Athecatae). *PLoS One*, 67, 1–13.

Cairns, S.D & Keller, N.B. (1993) New taxa and distributional records of azooxanthellate Scleractinia (Cnidaria, Anthozoa) from the tropical south-west Indian Ocean, with comments on their zoogeography and ecology. *Annals of the South African Museum,* 103 (5), 213–292.

Cairns, S.D & Lindner, A. (2011) A revision of the Stylasteridae (Hydrozoa, Filifera) from Alaska. *Zookeys*, 158, 1–88.
http://dx.doi.org/10.3897/zookeys.158.1910

Cairns, S.D, Hoeksema, B.W. & Land, J. van der (1999) Appendix, list of extant stony corals. *Atoll Research Bulletin*, 459, 13–46.

Cairns, S.D & Macintrye, I.G. (1992) Phylogenetic implications of the calcium carbonate mineralogy in the Stylasteridae (Cnidaria, Hydrozoa). *Palaios*, 7, 96–107.
http://dx.doi.org/10.2307/3514799

Cairns, S.D, et al. (2009) Chapter 4, Phylum Cnidaria, Corals, Medusae, Hydroids, Myxozoans. *In:* Gordon, D.P. (Ed.) *New Zealand Inventory of Biodiversity. Vol. 1.* Canterbury University Press. Christchurch, pp. 59–101.

Eguchi, M. (1941) Stylasterinae from Japanese Seas. *Jubilee Publication Committee Prof. H. Yabe's 60th Birthday*, 2, 1171–1194.

Eguchi, M. (1964) A study of Stylasterina from the Antarctic Sea. *JARE Scientific Reports, Biology*, (E) 20, 1–10.

Ehrenberg, C.G. (1834) Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des Rothen Meeres, nebst einem Versuch zur physiologischen Systematik derselben. *Physikalische-Mathematische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* (1832), 1, 225–380.

England, H.M. (1926) Development of gonophores of the Stylasteridae. *Proceedings of the Zoological Society of London*, 1926, 265–283.
http://dx.doi.org/10.1111/j.1096-3642.1926.tb01548.x

Gilchrist, J.D.F. (1921) List of fishes, etc. procured, 1920, Annexure A. *Report of the Fisheries and Marine Biological Survey of the Union of South Africa*, 1, 27–81.

Gray, J.E. (1831) Description of a new genus (*Stylaster*) of star-bearing corals. *Zoological Miscellany*, pp. 36–37.

Gray, J.E. (1835) Characters of two new genera of corals, *Errina* and *Anthopora*. *Proceedings of the Zoological Society of London*, 1835, 85–86.

Greeff, R. (1886) Ueber westafrikanische Stylasteriden. Sitzungsber. *Sitzungsberichte der Gesellschaft zur Beförderung der gesammten Naturwissenschaften zu Marburg*, 1, 11–21.

Griffiths, C.L, Robinson, T.B., Lange, L. & Mead, A. (2010) Marine biodiversity in South Africa, an evaluation of current states on knowledge. *PLoS One*, 5, 1–13.
http://dx.doi.org/10.1371/journal.pone.0012008

Hickson, S.J. (1900) The Alcyonaria & Hydrocorallinae of the Cape of Good Hope. *Marine Investigations of South Africa*, 1, 67–96.

Hickson, S.J. (1912) On the hydrocoralline genus *Errina*. *Proceedings of the Zoological Society of London*, 1912, 876–898.

Hickson, S.J. & England, H.M. (1905) The Stylasterina of the *Siboga* Expedition. Siboga Expedition Monographs, 8, 1–26.

Hickson, S.J. & England, H.M. (1909) The Stylasterina of the Indian Ocean. *Transactions of the Linnaean Society of London*, 12, 345–354.
http://dx.doi.org/10.1111/j.1096-3642.1909.tb00146.x

Kent, W.S. (1870) On a new genus of the Madreporaria or stony corals (*Stenohelia*). *The Annals and Magazine of Natural History*, (4) 5, 120–123.
http://dx.doi.org/10.1080/00222937008696119

Kent, W.S. (1871) On some new and little-known species of Madrepores, or Stony Corals, in the British Museum collection. *Proceedings of the Zoological Society of London*, 1871, 275–286.

Kirkpatrick, R. (1887) Description of a new genus of Stylasteridae. *The Annals and Magazine of Natural History*, (5) 19, 212–214.
http://dx.doi.org/10.1080/00222938709460229

Liltved, W. R. (1985a) Notes on *Pedicularia elegantissima* Deshayes, 1863. *Shell and Sea Life*, 16 (11), 195–196.

Liltved, W.R. (1985b) Notes on *Pedicularia elegantissima* Deshayes, 1863. *Bulletin of the Conchological Society of South Africa*, 213, 6–7.

Liltved, W.R. (1989) *Cowries and their relatives of Southern Africa.* Gordon Verhoef, Seacomber Publications, Cape Town, 1–208.

Lindner, A., Cairns, S.D. & Cunningham, C.W. (2008) From offshore to onshore: multiple origins of shallow-water corals from deep-sea ancestors. *PLoS ONE*, 3 (6), e2429.
http://dx.doi.org/10.1371/journal.pone.0002429

Lutjeharms, J.R.E. & Shannon, L.V. (1997) A century of physical oceanography in South Africa, in search of the legacy of John D. F. Gilchrist. *Transactions of the Royal Society of South Africa*, 52 (1), 17–50.

Millard, N.A.H. (1975) Monograph on the Hydroida of southern Africa. *Annals of the South African Museum*, 68, 1–513.

Milne Edwards, H. & HAIME, J. (1849) Mémoire sur les polypiers appartenant à la famile des Oculinides, au groupe intermédiaire des Pseudoastréides at à la famile des Fongides. *Comptes rendus hébdomadaires des Séances de l'Académie des Sciences, Paris*, 29, 67–73.

Milne Edwards, H. & Haime, J. (1850) *A Monograph on the British Fossil Corals. Part 1. Introduction*. Palaeontological Society, London, pp. i–lxxxv.

Monod ,T. (1929) *L'Industrie des Pêches au Cameroun*. Paris, Société d'éditions géographiques, maritimes et coloniales, 504 p., 25 pls., ill., maps. (not seen)

Moseley, H.N. (1879) On the structure of the Stylasteridae, a family of the hydroid stony corals. *Philosophical Transaction s of the Royal Society London***,** 169, 425–503.
http://dx.doi.org/10.1098/rstl.1878.0014

Moseley, H.N. (1881) Report on certain hydroid, alcyonarian, and madreporarian corals procured during the voyage of H. M. S. *Challenger*, in the years 1873–1876. *Report on the Scientific Results of the Voyage of H. M. S. Challenger during the Years 1873–76, Zoology,* 2, 1–248.

Moseley, H.N. (1892) *Notes by a Naturalist, an account of observations made during the voyage of H.M.S. "Challenger" round the world in the years 1872–1876,* T. Werner Laurie, Ltd., London, 1–540.

Pourtalès, L.F. de (1871) Deep-Sea Corals. *Illustrated Catalogue of the Museum of Comparative Zoölogy, Harvard* (also, *Memoirs of the Museum of Comparative Zoölogy*, volume 2), 4, 1–93.

Rudd, S. (1978) *A preliminary investigation of the morphology, some chemical components and calcification rates of* Allopora nobilis, *hydrocoral*. Unpublished MS thesis, University of Cape Town, 36 pp., 13 tables, 30 figures.

Sowerby, G.B. (1903) Mollusca of South Africa. *Marine Investigations South Africa*, 2, 213–232.

Spalding, M.D. et al. (2007) Marine ecoregions of the World, a bioregionalization of coastal and shelf areas. *BioScience,* 57, 573–583.
http://dx.doi.org/10.1641/B570707

Studer, T. (1878) Übersicht der Steinkorallen aus der Familie de *Madreporaria aporosa, Eupsammina* und *Turbinaria*, welche auf der Reise S. M. S. Gazelle um die Erde gesammelt wurden. *Monatsbericht der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1877, 625–654.

Vervoort, W. & Zibrowius, H. (1981) Annotations on H. Boschma's work on Hydrocorals (Milleporina, Axoporina, Stylasterina), with additions to his list of the described species of Stylasterina. *Zoologische Verhandelingen,* 181, 1–40.

Williams, G.C. (1986) What are corals? *Sagittarius*, 1 (2), 11–15.

Zibrowius, H. & Cairns, S.D. (1992) Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria, Hydrozoa). *Mémoires du Muséum national d'Histoire Naturelle, (A, Zoologie)*, 153, 1–136.

Station List and Sample Numbers

	Latitude (°S)	Longitude (°E)	Depth (m)	Date
Anton Bruun (International Indian Ocean Expedition)				
8—420A	2°42′	40°53′	140	6 Nov 1964
Danish *Galathea*				
196	29°55’	30°20’	445–460	13 Feb 1951
197	29°57′	31°26′	605	14 Feb 1951
French *Marion Dufresne (MD)*				
*MD*08/7/DC57	36°48.9′	52°07.7′	380	19 Mar 1976
Meiring Naudé (MN)				
SM38	28°21.9′	32°34.6′	775–825	28 May 1975
SM43	28°45.5′	32°24.5′	360–420	29 May 1975
SM85	27°59.5′	32°40.8′	550	22 May 1976
SM86	27°59.5′	32°40.8′	550	22 May 1976
SM90	28°09.8′	32°47.4′	940	23 May 1976
SM92	28°14.5′	32°40.6′	650–720	23 May 1976
SM94	28°16.3′	32°38.8′	670	23 May 1976
SM103	28°31.7′	32°34.0′	680	24 May 1976
SM107	28°37.8′	32°38.4′	1000–1200	25 May 1976
SM123	30°33.4′	30°48.6′	690	10 May 1977
SM129	30°53.4′	30°31.7′	850	11 May 1977
SM131	30°43.2′	30°48.8′	780	11 May 1977
SM134	31°00.0′	30°27.2′	900	12 May 1977
SM162	32°55.0′	28°31.0′	630	25 May 1978
SM163	33°04.6′	28°06.6′	90	25 May 1978
SM165	33°06.0′	28°08.3′	?	26 May 1978
SM179	33°30.3′	27°22.1′	80	29 May 1978
SM180	33°29.4′	27°21.2′	80	29 May 1978
SM184	33°39.4′	27°11.7′	86	31 May 1978
SM185	33°39.3′	27°01.6′	90	31 May 1978
SM226	32°28.6′	28°58.8′	710–775	24 June 1979
SM228	32°29.5′	28°57.1′	650–700	24 June 1979
SM232	32°14.9′	29°10.4′	620–650	25 June 1979
SM234	32°15.0′	29°09.1′	500–520	25 June 1979
SM237	32°15.4′	29°09.7′	600–650	25 June 1979
XX129	27°20.6′	32°47.1′	95–200	5 June 1987
ZF2	29°09.0′	32°05.4′	85	10 June 1987

Pieter Faure (*PF,* sample numbers)

393	Buffels Bay, False Bay, Cape Peninsula		unknown	16 Oct 1898
503	33°58′	25°51′30”	46	1 Nov 1898
559	33°51′30”	26°00′20”	60	8 Nov 1898
622	34°05′20”	25°43′	95	14 Nov 1898
808	33°09′30″	28°03′	86	28 Dec 1898
907	33°06′30″	28°11′	155	28 Jan 1899
1915	Cape St. Blaize, NxE 1/4E, 67 mi.		164–183	22 Dec 1899
2675	Vasco da Gama (Cape Peninsula), NW3/4 N, 8 mi.		75	27 Apr 1900
2819A	Vasco da Gama (Cape Peninsula), N71°E, 18.5 mi.		420	4 May 1900
7014	Sebastian Bluff,WxN3/4N, 6 mi.		51	7 July 1900
7023	Sebastian Bluff,WxN3/4N, 6 mi.		47	7 July 1900
11555	Tugela River mouth, NWxN, 22.5mi.		86	29 Jan 1901
12104	O'Neil Peak, NNW1/4W, 8 mi.		101	28 Feb 1901
12312	Port Shepstone, N 8 mi.		66	14 Mar 1901
12314	Port Shepstone, N 8 mi.		66	14 Mar 1901
12729	Buffalo River, NW1/2W, 19 mi.		548	16 Apr 1901
13061	Hood Pt. Lighthouse, NxW 1/2W, 11.5 mi.		90	15 Jul 1901
13063	Hood Pt. Lighthouse, NxW 1/2W, 11.5 mi.		90	15 Jul 1901
13394	Cape Morgan, NW1/4N, 11.5 mi		159	13 Aug 1901
13395	Cape Morgan, NW1/4N, 11.5 mi.		159	13 Aug 1901
13465	Sandy Point, NExN, 6.5mi. (near Cape Morgan)		93	18 Aug 1901
13476	Sandy Point, N1/4E, 10 mi. (near Cape Morgan)		174	14 Aug 1901
13479	Sandy Point, N1/4E, 10 mi. (near Cape Morgan)		174	14 Aug 1901
13599	Great Fishpoint Lighthouse, WxN, 5 mi.		40	29 Aug 1901
13654	33°31′10″	27°00′34″	93	3 Sept 1901
13959	Bird Island Lighthouse, NxE ¾ E, 3 mi.		66	25 Sept 1901
14306	Cape Seal, NxE 3/4E, 37 mi.		146	20 Feb 1902
14356	Cape St. Blaize, NNE, 73 mi.		192	21 Feb 1902
14364	Cape St. Blaize, NExN 1/4N, 94 mi.		212	21 Feb 1902
14743	Constable Hill, E3/4S, 19.5 mi.		265	15 Mar 1902
15614	Rocky Bank, False Bay		31–49	8 Oct 1902
15618	Rocky Bank, False Bay		31–49	8 Oct 1902
15607	Rocky Bank, False Bay		31–49	8 Oct 1902
15675	Cape Pt. Lighthouse, NxW1/2 W, 8 mi.		73	9 Oct 1902
15745	off Gordons Bay, Cape Peninsula		11–26	20 Oct 1902
17995	Cape Point, NE3/4N, 39 mi.		566–1023	17 Sept 1903
18347	Flesh Point, NWxN ½ W, 4 mi.		55	28 Dec 1903

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AFR801	32°34.4′	17°52′	71	7 Oct 1947
AFR950	36°44′	21°18′	201	20 Mar 1948
FAL303 (*PF* station)	34°25′	18°24′	70	9 Oct 1902
FAL332	34°15′	18°36′	51	31 Jan 1959
FAL573	34°13.1	18°34′	54	30 Oct 1962
FAL582	34°02.9′	18°43′	33	30 Oct 1962
SCD56	33°37′	26°56.6′	46	19 Aug 1958
SCD289	33°04′	27°57′	84	6 Feb 1962
SCD296	33°09′	28°02′	84	6 Feb 1962
SCD301	33°39′	27°15′	88	6 Feb 1962
SCD311	33°59′	25°51′	50	9 Feb 1962
SCD316	34°15’	25°50.5’	108	9 Feb 1962
TRA23	34°49′	20°21′	unknown	9 Nov 1947
TRA120	34°12′	18°44′	37	25 Jan 1957
TRA151	34°51′	19°55′	22	6 Mar 1958
WCD36	33°06.5′	17°56.7′	18–33	2 May 1960

*Valdivia (*Deutsche Tiefsee-Expedition)

93	33°43.6’	18°04.2’	106	26 Oct 1898
95	34°51′	19°37′08”	80	27 Oct 1898
100	34°08.9	24°59.3′	100	29 Oct 1898
103	35°10.5’	23°02.0’	500	2 Nov 1898
104	35°16′	22°26′07”	155	2 Nov 1898

Vema (Cruise 19)

28	35°40’	21°59’	165	1950’s