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Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 6: The genera *Primnoella* Gray, 1858; *Thouarella* Gray, 1870; *Dasystenella* Versluys, 1906

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Abstract.—The seven western Atlantic species belonging to three genera, *Primnoella*, *Thouarella*, and *Dasystenella*, are described and illustrated. Three new species of *Thouarella* are described, which constitute the first records of this genus for the northwestern Atlantic. An annotated and revised list of the 26 species of *Thouarella* is given. Most of the species included occur primarily in the southwestern Atlantic at depths of 50–5000 m; however, one species, *Thouarella grasshoffi*, is amphi-North Atlantic in distribution. Whereas most of the species included herein are small and inconspicuous, *T. grasshoffi* is fairly large and occurs abundantly on seamounts of the New England Seamount Chain as well as on eastern Atlantic seamounts. Specimens of all three genera are still relatively rare in museum collections.

This is the sixth in a series (see Cairns & Bayer 2004) of revisions of the western Atlantic deep-water octocorals, and the fifth and final dealing with the family Primnoidae. Thirty-four primnoid species are now known to occur in the western Atlantic. Most of the species in the three genera investigated in this part have flagelliform colonies or a main stem from which numerous small branchlets occur (bottlebrush colonies) and a reduction in the size and number of adaxial body wall sclerites, which allows for a bending of the polyps toward the branch axis. Specimens from these three genera have been rarely reported, most known only from their type specimens, and those primarily from southern hemisphere locations. Nonetheless, three new species of *Thouarella* are described from the northwestern Atlantic, which is a new record of this genus from this region, a genus that is otherwise very abundant in the Subantarctic and Antarctic regions.

Material and Methods

Although relatively few (26) new lots of specimens are reported herein, they derive from a variety of sources, including 12 research vessels and one private collector. Most are deposited at the NMNH, but some of the examined specimens are also deposited at the BM, MCZ, MNRJ, and the YPM.

Designation of polyp scales follows the terminology used by Versluys (1906) as amplified by Bayer et al. (1983). Synonymies are purported to be complete. The SEM photomicrographs were taken by the author and F. M. Bayer on a variety of instruments in the SEM Lab at the NMNH.

The following abbreviations are used in the text: BM, The Natural History Museum (British Museum), London; *G*, R/V *Gerda*; H:W, height to maximum width of a sclerite; MCZ, Museum of Comparative Zoology, Harvard, Cambridge, Massachusetts; MNRJ, Museu Nacional Departamento de Invertebrados, Rio de Janeiro; NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D. C.; MOM, Musée Océanographique, Monaco; *P*—R/V *Pillsbury*; SEM, scanning electron microscope (B, Bayer series; C, Cairns series of stubs); USNM, United States National Museum (now the NMNH); YPM, Yale Peabody Museum, New Haven, Connecticut.

Subclass Octocorallia
Order Gorgonacea
Suborder Calcaxonia
Family Primnoidae Gray, 1858
Primnoella Gray, 1858

Primnoella Gray, 1858 (not 1857): 286.—Studer, 1878: 644 (in part).—Wright & Studer, 1889: 80–83 (group *Convexae* in part and group *Carinatae*).—Versluys, 1906: 48–51, 52 (group *Carinatae*).—Kükenthal, 1919: 384–387 (in part; key); 1924: 279–281 (in part; key).—Bayer, 1956: F220 (in part); Broch, 1965: 20–21 (in part). —Bayer, 1981: 936, 938 (key).—Bayer & Stefani, 1989: 455 (key).–Bayer, 1996: 165–167 (discussion).

Type species.—*Primnoa australasiae* Gray, 1850 (not 1849), by monotypy.

Diagnosis.—Body wall scales arranged in 6 or 8 longitudinal rows, the two abaxial rows being by far the largest and only scales seen in abaxial view, occurring in alternating rows of 6–32 scales. Outer-lateral, inner-lateral, and adaxial scales smaller, the latter sometimes absent, resulting in a naked adaxial polyp wall. Marginal scales fold over the smaller, inconspicuous opercular scales, the latter of which are not keeled on their inner surface. Polyps compressed in cross section and appressed to branch axis; polyps arranged in whorls of 4–17, usually directed upward. Most colonies unbranched (flagelliform), but two species have sparse branching. Surface coenenchymal scales flat and polygonal, whereas those in lower layer bordering stem canals consist of tuberculate spindles.

Distribution.—Lesser Antilles, entire eastern and southwestern coasts of South America, southeastern Australia, New Zealand, Tasmania (see Kükenthal 1919: pl. 66, map 22, in part); 13–1249 m.

Remarks.—As early as 1889 Wright & Studer implied that there were two groups of species within the genus *Primnoella*, which they called the *Convexae* and *Carinatae*. Kükenthal (1908, 1919, 1924) continued to apply this distinction but called the species groups the *Convexae* and *Compressae*. Species of the former group had polyps round in cross section and four longitudinal rows of body wall scales visible in abaxial view, whereas species of the latter group had flattened polyps (appressed to the branch axis) and only two rows of large abaxial body wall scales visible in abaxial view. It was not until 1996 that Bayer formally recognized the generic distinction of these, including most of the species from the *Convexae* group in the new genus *Convexella*, and the species of the *Compressae* group as *Primnoella* sensu stricto. In addition to the criteria used by Kükenthal to distinguish the two taxa, Bayer (1996) also emphasized that the adaxial body wall scales of *Convexella* were similar in size to all others and thus cover the adaxial body polyp wall, whereas the adaxial body wall scales of *Primnoella* were either lacking or much smaller than the abaxial ones, leaving the adaxial polyp side largely bare. This also explains why the genus *Primnoella* occurs twice in the key of Bayer (1981), the first time (couplet 359–360) keying to the anticipated *Convexella*, and the second time (couplet 384–385) to *Primnoella* sensu stricto. Some of the most comprehensive descriptions of any octocoral are those of several species of *Primnoella* by Aurivillius (1931).

There are eleven species in the restricted sense of the genus: *P. australasiae* (Gray, 1850) Australia, New Zealand; *P. distans* Studer, 1879 (Australia); *P. divaricata* (Studer, 1878) off Argentina; *P. biserialis* Wright & Studer, 1889 (Argentina); *P. grandisquamis* Wright & Studer, 1889 (Australia); *P. scotiae* Thomson & Richie, 1906 (Burdwood Bank); *P. compressa* Kükenthal, 1908 (Chile); *P. delicatissima* Kükenthal, 1909 (Brazil); *P. laevis* (Thomson & Mackinnon, 1911) Australia; *P. philippii* Aurivillius, 1931 (Chile); and *P. polita* Deichmann, 1936 (western Atlantic). Four other Atlantic species originally described in *Primnoella* (*P. magelhaenica* Studer, 1878; *P. flabellum* Studer, 1878; *P. murrayi* Wright & Studer, 1889, from the Falkland Islands; and *P. jungerseni* Madsen, 1952, from Iceland) were transferred to the genus *Convexella* by Bayer (1996). Characters that Kükenthal (1919) used to distinguish species of *Primnoella* included: branched or unbranched nature of the colony; number of polyps per whorl (varies from 4–17); development of adaxial body wall scales (absent, short rows, linear vs. random); and whether the polyp had a longitudinal mid-abaxial ridge. To these species-level characters may be added: number of abaxial body wall scales per row (varies from 6–32), nature of basal attachment (discoidal or dendritic), size and shape of marginal scales (pointed vs. straight distal margin); spacing of whorls on a branch (well-spaced or directly adjacent or overlapping); and size of polyps (varies from 1 to 3 mm in length). The Subantarctic species are in need of revision.

Primnoella polita Deichmann, 1936
Figs. 1D, 2, 3

Primnoella distans.—Wright & Studer, 1889: 85, pl. 17, figs. 1, 1a.

Primnoella polita Deichmann, 1936: 162–163, pl. 26, fig. 12.—Bayer, 1956: F220, figs. 158-5, 159-1; 1959: 30 (listed).—Bayer & Cairns, 2004: pl. 13, fig. 6, pl. 25, fig. 9, ?pl. 83, fig. 5, pl. 94, fig. 2.

Material examined.—*Atlantis II* 32– or 60–159, locality and depth uncertain but presumed to be from the Argentine Basin, 1 complete colony, SEM C1165–1167, USNM 1078185; *Albatross* 2117, 15°24′40″N, 63°31′30″W, 1249 m, 27 Jan. 1884, 1 poorly preserved colony, SEM B382, C1168–1169, USNM 44127; *P*-754, 11°36′N, 68°42′W, 684–1574 m, 26 July 1969, 1 colony, USNM 57063; *P*-847, 11°37′18″N, 59°24′00″W, 733–1281 m, 2 July 1969, 3 colonies, USNM 55921 and 59492; *P*-850, 11°45.4′N, 61°29.5′W, 896–923 m, 3 July 1969, 1 complete colony, USNM 55920; *P*-861, 12°42′N, 61°05′W, 357–658 m, 4 July 1969, 1 complete colony, USNM 56617; specimens reported as *P. distans* by Wright & Studer (1889): *Challenger*-23 (2 colonies, BM 1889.5.27.58) and *Challenger*-122 (4 colonies with bases, BM uncataloged); syntypes of *P. polita* (see below).

Types and type locality.—MCZ 4799 (original Verrill number 5791): the original three syntype branches of *P. polita* are now fragmented into six branches, the longest 10 cm in length; all specimens are dry and are quite fragile. Type locality: *Blake*-136: 17°43′10″N, 64°55′50″W (off St. Croix, Virgin Islands), 921 m.

Description.—Colonies are flagelliform (unbranched), up to 25 cm in length, the axis diameter, even basally, rarely exceeding 0.4 mm (not 2.5 mm as cited by Deichmann, 1936). Several specimens were collected intact, showing that each colony possesses a dendritic calcareous holdfast that is covered with scales, the holdfast undoubtedly an adaptation to a soft substrate.

Polyps are arranged in whorls of 2–5 (usually 3 or 4), but are missing from the basal 6–8 cm of the colony. Distally, polyp whorls are closely spaced, 0.4–0.8 mm apart, whereas proximally the spacing is wider, up to 2.5 mm; however,

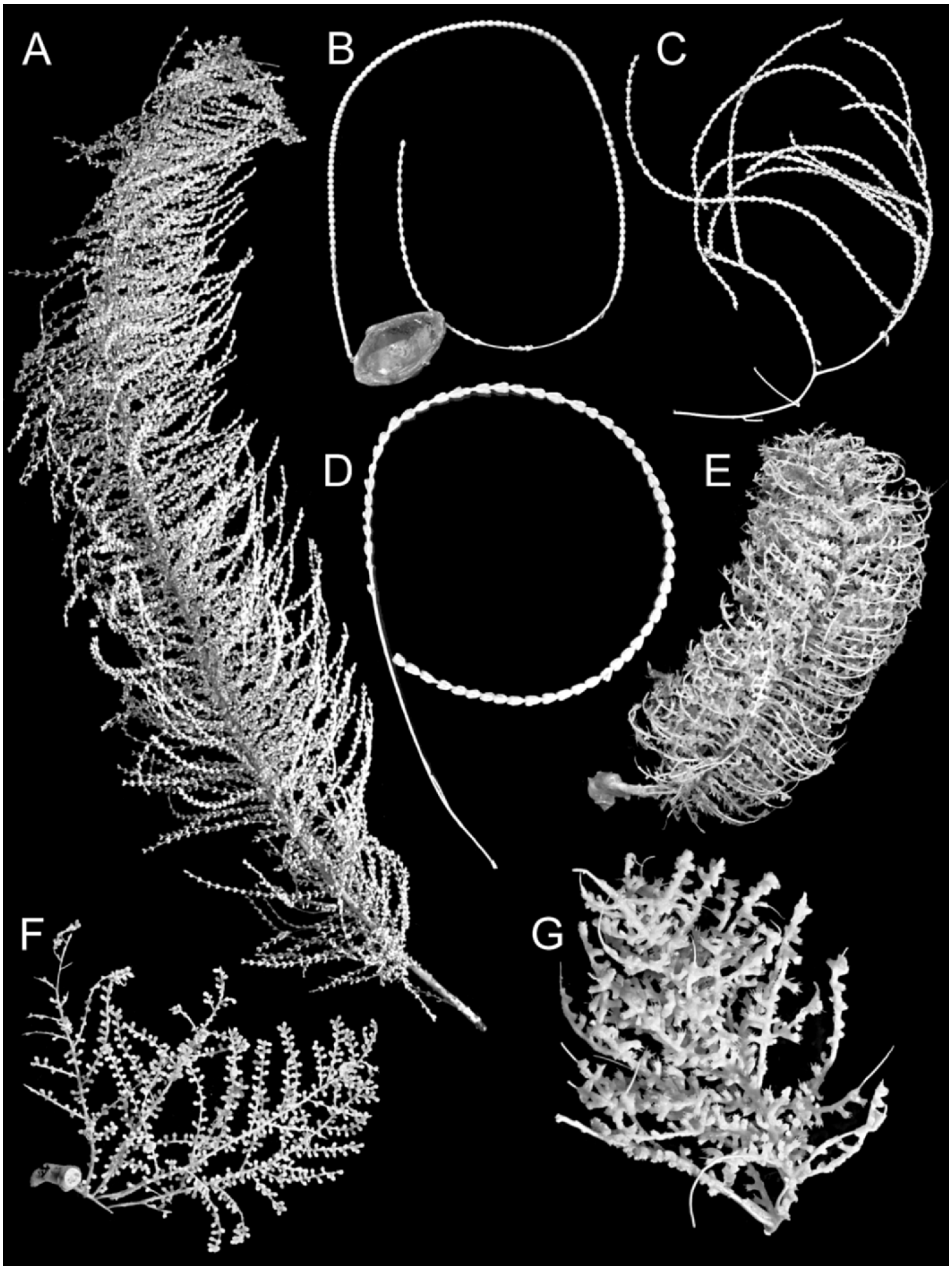

Fig. 1. Whole colony images: A, *Thouarella grasshoffi*, holotype, USNM 1078188, ×0.43; B, *Primnoella delicatissima*, *Saldanha* 1773, ×0.65; C, *Primnoella divaricata*, *Albatross* 2768, USNM 43035, ×0.39; D, *Primnoella polita*, *Atlantis*, USNM 1078185, ×0.56; E, *Dasystenella acanthina*, *Eltanin* 993, USNM 98119, ×0.65; F, *Thouarella bipinnata*, holotype, USNM 53015, ×0.61; G, *Thouarella diadema*, holotype, USNM 1078187, ×1.0.

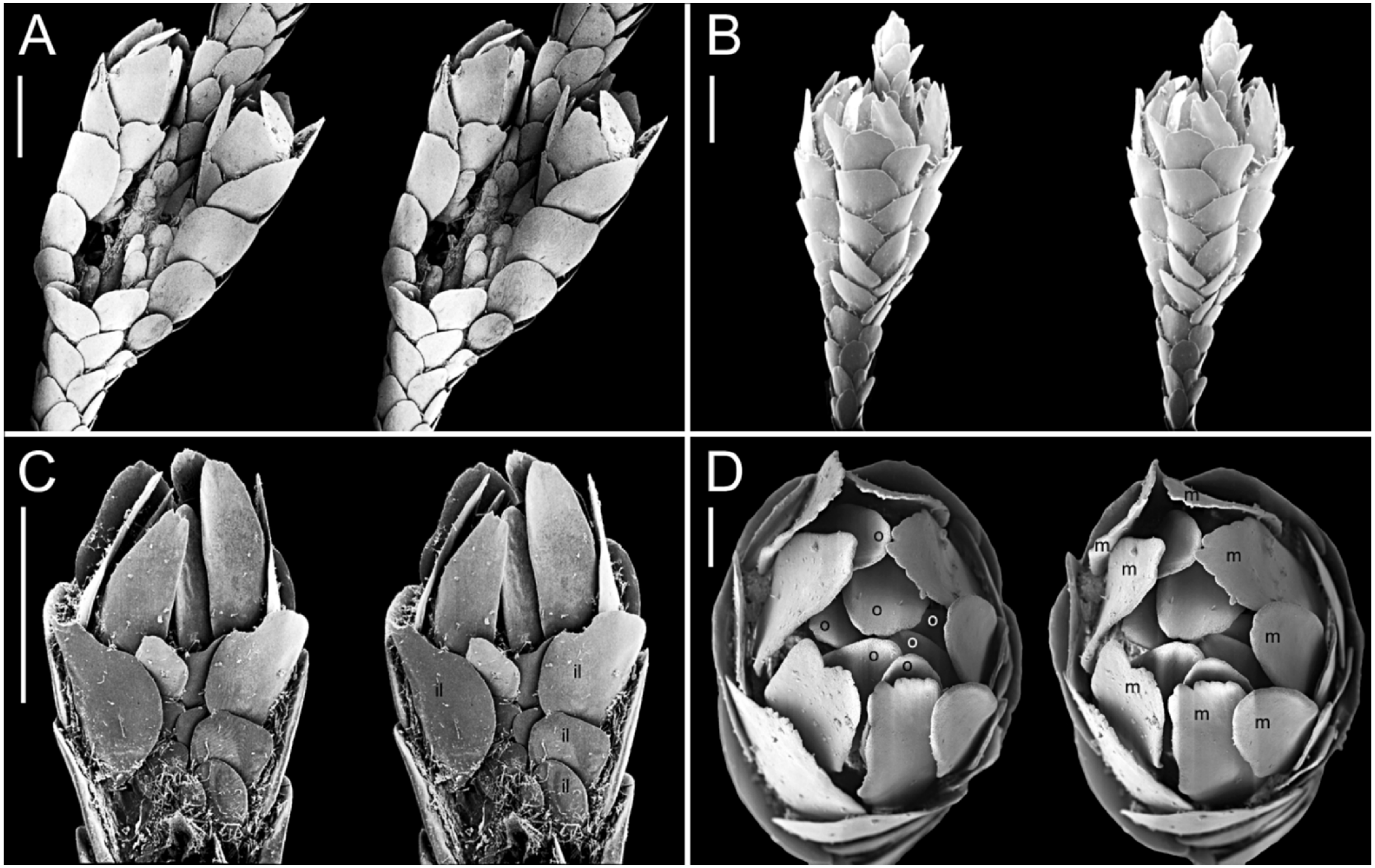

Fig. 2. *Primnoella polita* , stereo views of polyps (A–C, *Albatross* 2117, USNM 44127; D, *Atlantis*, USNM 1078185): A, a whorl missing one polyp; B, a whorl of three polyps; C, adaxial side of a polyp showing 2 short rows of small adaxial scales, 2 rows of larger inner-lateral scales (il), and the projecting crown of distal marginal scales; D, opercular view of a polyp showing 7 opercular (o) and all 8 marginal (m) scales. Scale bars: A–C = 0.5 mm; D = 0.1 mm.

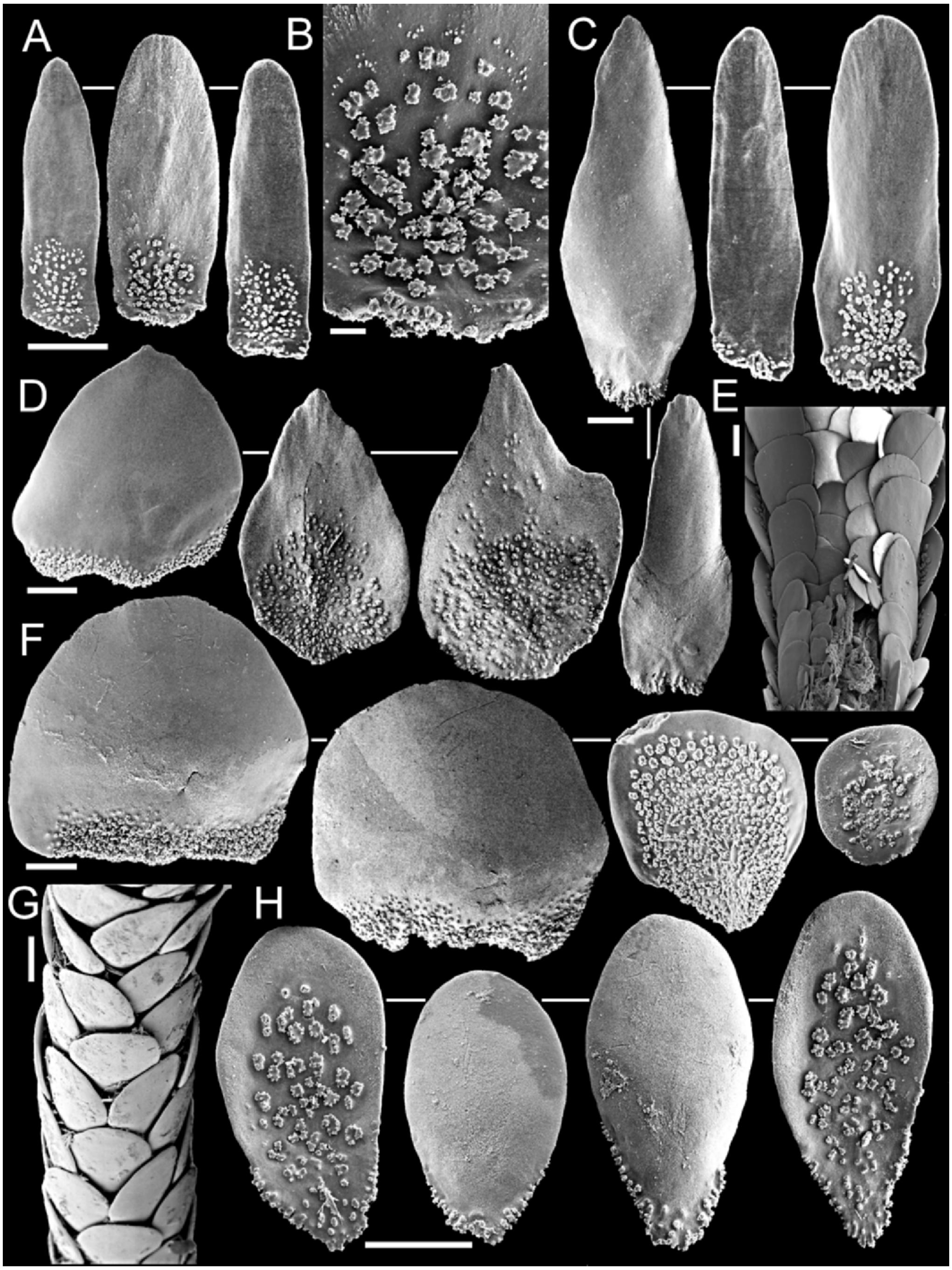

Fig. 3. Sclerites of *Primnoella polita* (A–D, F–H, *Albatross* 2117, USNM 44127; E, *Atlantis*, USNM 1078185): A, inner sides of 3 opercular scales; B, tubercles on inner side of an opercular scale; C, four marginal scales; D, three submarginal scales; E, adaxial side of a polyp showing 2 rows of small adaxial scales flanked by 2 rows of 6–7 larger inner-lateral body wall scales, note naked area toward base not covered by adaxials; F, four body wall scales; G, coenenchymal scales in place; H, four coenenchymal scales. Scale bars: A, C–H = 0.1 mm; B = 0.01 mm.

on at least two colonies (*P*-754 and the syntypes) several consecutive polyp whorls overlap each other, producing a very crowded arrangement of polyps with no space between whorls. Polyps are closely appressed to the branch, directed upward, and somewhat flattened or semicircular in cross-section, the flat edge facing the branch. Polyps are 2.1–2.4 mm in length and 0.8–0.9 mm in diameter.

Each polyp is protected by 4 types of scales: 8 opercular, 8 marginal, 2 submarginal, and a variable number of body wall scales. The opercular scales are elongate with rounded tips: 0.35–0.40 mm in length and 0.10–0.15 mm in width (H:W = 2.5–3.6). They are usually tightly folded over each other in the preserved state. The 8 marginals are similar in shape to the operculars but are larger and sometimes have a pointed tip: 0.45–0.67 mm in length and 0.14–0.24 mm in width (H:W = 2.7–3.3). In the preserved state, the marginal scales fold over the operculars, hiding them from lateral view and often even from opercular view (Fig. 2C). Initially one might perceive the marginal scales to be the opercular crown, but closer inspection reveals the smaller operculars hidden beneath the larger marginals (Fig. 2D). Both operculars and marginal scales have smooth outer and inner surfaces, except for the basal third of the inner surface, which is tuberculate; there is no inner keel. The remaining body wall scales are arranged in 6 rows: 2 rows of large abaxial scales, 2 rows of smaller inner-lateral scales, and 2 rows of even smaller adaxial scales; there are no outer-lateral scales. The 2 distal-most abaxial scales often have a short distal point and a H:W ratio of 1.3–1.7; these are considered to be the submarginal scales. The remaining abaxial body wall scales are thick, slightly convex, wider than tall (H:W = 0.76–0.89), with a rounded distal margin. They are arranged in 2 rows in alternating order and completely cover the abaxial portion of the polyp, decreasing in size toward the proximal end of the polyp such that they imperceptibly grade into the coenenchymal scales. Counting the marginal and submarginal scales there are 6 or 7 scales in each abaxial row. Each inner-lateral row of scales (Figs. 2C, 3E) consists of a line of 7 or 8 elongate scales that also decrease in size proximally; they are up to 0.20 mm wide near the operculum but only 0.10 mm wide proximally. Each adaxial row of scales also consist of 3–9 elongate scales that decrease in size proximally to as small as 0.07 mm width, leaving the most proximal part of the adaxial side of the polyp unprotected. As with the opercular scales, the outer surfaces of the body wall scales are quite smooth (as though polished, and thus the name *polita*), the inner surfaces being covered with tubercles except for the distal and lateral margins, which do not contact the underlying scale and thus are smooth.

The coenenchymal scales are often quite regularly arranged in imbricated rows along the branch (Fig. 3G). They are elliptical to tear-drop shaped, 0.28–0.42 mm in length and 0.16–0.20 in width (H:W = 1.4–2.0), with a tuberculate inner side and smooth outer side, and usually a coarse (tuberculate) proximal margin.

Comparisons.—*Primnoella polita* differs from the other two western Atlantic congeners in almost every character listed in Table 1. It is most easily recognized by its: large, flattened polyps; shiny (polished) body wall scales; elongate marginal scales; and dendritic base. Also, it is by far the deepest-dwelling and most northerly species among the three. It is not similar to any of the other eight species known in the genus.

Remarks.—The specimens reported by Wright & Studer (1889) as *P. distans* from two *Challenger* stations are all typical *P. polita*, as suggested by Deichmann (1936) but having unusually small polyps, none

Table 1.—Distinguishing characteristics of the western Atlantic *Primnoella*.

	Primnoella polita Deichmann, 1936	*Primnoella divaricata* (Studer, 1878)	*Primnoella delicatissima* Kükenthal, 1909
Colony form	Flagelliform (unbranched)	Sparsely branched	Flagelliform (unbranched)
Base	Dendritic	Unknown	Disk-like
Polyps: Shape; Length; Number/whorl; Spacing	Flattened, slightly flared distally; 2.1–2.4 mm; 2–5; well-spaced	Round in cross-section, cylindrical; 1.0–1.3 mm; 4–7; well-spaced	Slightly flattened; 1.0–1.3 mm; 5–7; fairly closely spaced
Abaxial Scales: Number per row; Shape	6–7; slightly broader than tall (H:W = 0.76–0.89)	10–11; broader than tall (H:W = 0.53–0.67)	11–13; much broader than tall (H:W = 0.48–0.60); arranged in chevrons proximally
Marginal scales	Elongate, blunt-tipped, H:W = 2.7–3.3	Squarish, straight margin (similar to other body wall scales)	Similar in shape to other body wall scales
Outer-lateral scales	Missing	7–8 well developed scales per row, partially seen in abaxial view	5–9 well developed scales per row, not visible in abaxial view
Coenenchymal scales	Elliptical to tear-drop shaped, up to 0.42 mm long	Irregular in shape, up to 0.33 mm	Polygonal, up to 0.3 mm, tuberculate spindles also common
Distribution	Lesser Antilles to Recife; 658–1249 m	Uruguay, Argentina; 55–80 m	Off Rio de Janeiro and Amapa Brazil; 55–103 m

more than 1.9 mm in length. The specimen illustrated in pl. 17, fig. 1 is from *Challenger* station 122 and is not reproduced at "natural size" but at a magnification of about 2.5. The polyps figured in pl. 17, fig. 1a may be from *Challenger*-23 and are magnified about ×16. Discounting Wright & Studer's (1889) misidentification as *P. distans*, the records reported herein are the first reports of this species subsequent to its original description.

Distribution.—Lesser Antilles from Virgin Islands to east of Tobago, off Curaçao, south of Recife, Brazil; 658–1249 m.

Primnoella divaricata (Studer, 1878)
Figs. 1C, 4, 5

Narella divaricata Studer, 1878: 643–644, pl. 1, figs. 8a–c.

Calligorgia divaricata.—Studer, 1887: 52 (listed).

Caligorgia divaricata.—Wright & Studer, 1889: L (listed).

Primnoella divaricata.—Versluys, 1906: 54, text-figs. 61–63 (type redescribed).—Kükenthal, 1908: 13 (specimen from Patagonia); 1915: 148 (keyed); 1919: 394–396, pl. 41, figs. 57–58; 1924: 284, text-fig. 160.—Bayer, 1959: 29; 1996: 179.

Primnoella "nitida" (nom. nud.) Bayer & Cairns, 2004: pl. 25, fig. 8, ?pl. 83, fig. 4, pl. 94, fig. 1.

Material examined.—*Albatross* 2768, 42°24′S, 61°38′30″W, 79 m, 1 colony, SEM stubs B383–384, C1170–1172, USNM 43035 (mentioned by Bayer 1959); off Cape Santa Maria, Uruguay, depth unknown, coll. F. Felippone, 3 partial colonies, USNM 49480 (mentioned by Bayer 1959); off Montevideo, Uruguay, depth unknown, coll. F. Felippone, 6 June 1932, 2 dry branches, USNM 43021.

Type and type locality.—Holotype deposited at the Berlin Museum (not examined); Type locality: *Gazelle*-57: 38°10.1′S, 56°26.2′W (off Mar del Plata, Argentina), 55 m.

Description.—Colonies are small and sparsely branched, the specimen from

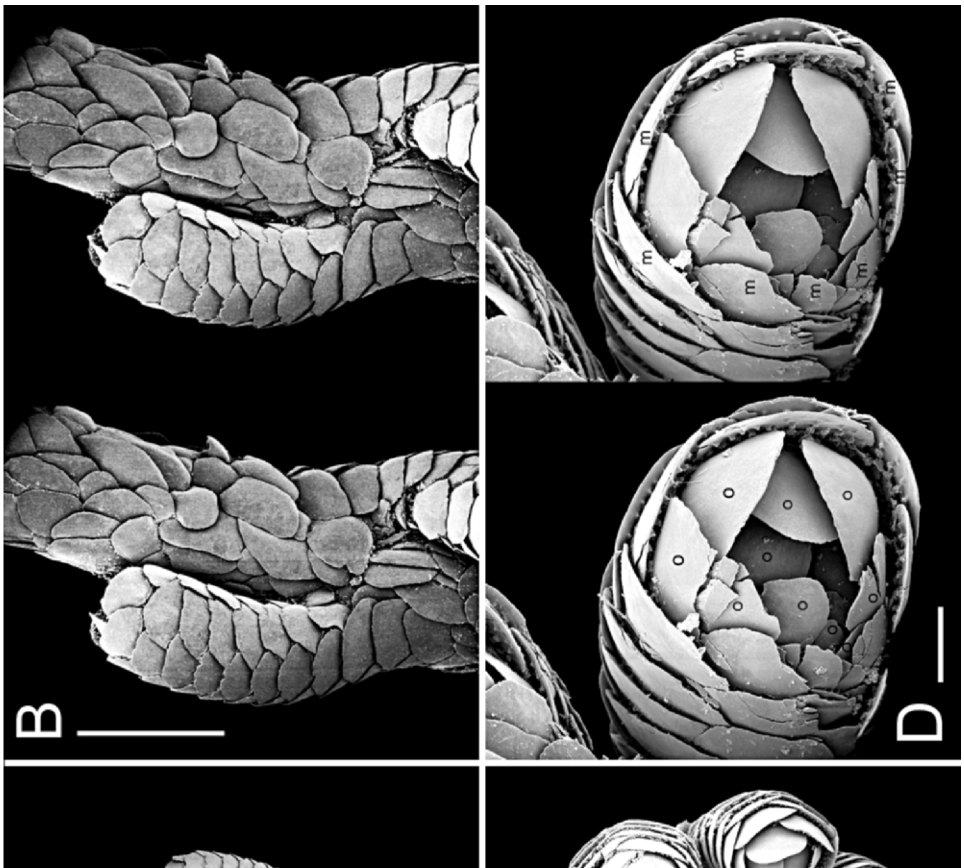

Fig. 4. A–D, *Primnoella divaricata* from *Albatross* 2768, USNM 43035, stereo views of polyps: A, a polyp whorl with a smaller incipient whorl anterior to it; B, lateral view of a polyp and coenenchymal scales; C, opercular view of a whorl of 7 polyps and broken stem; D, opercular view of a polyp showing 8 marginal (m) and 10 opercular (o) scales, the latter number inflated due to breakage? Scale bars: A–C = 0.5 mm; D = 0.1 mm.

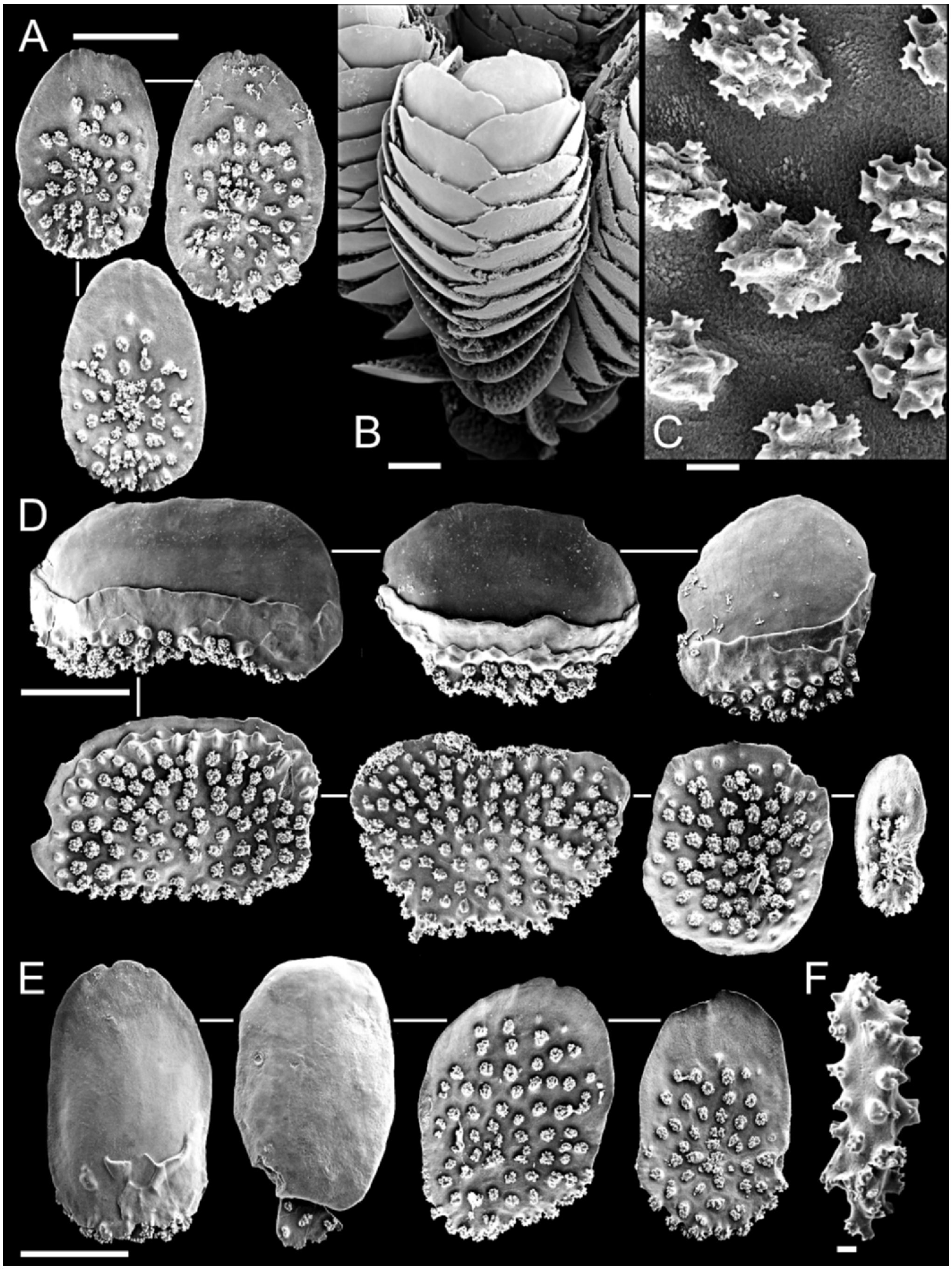

Fig. 5. Sclerites of *Primnoella divaricata* from *Albatross* 2768, USNM 43035: A, inner sides of 3 opercular scales; B, imbrication of abaxial body wall scales; C, tubercles on inner side of an opercular scale; D, seven body wall scales, the smallest being adaxial in position; E, four coenenchymal scales; F, a coenenchymal tuberculate spindle. Scale bars: A–B, D–E = 0.1 mm; C, F = 0.01 mm.

*Alb*atross 2768 being 18 cm in height and having 12 branches from the main stem, none of those being further subdivided and some as long as 11 cm. The holotype is 25 cm in height. The axis is wiry and yellow-golden in color, not over 0.5 mm in diameter even at the base. No colonies with an intact base are known.

Polyps are arranged in whorls of 4–7 (most often 6), the whorls spaced 0.3–1.2 mm apart. Most polyps are directed upward, but in some cases and in no apparent order, they are oriented downward (Fig. 4B); sometimes polyps in the same whorl have an opposite orientation. Polyps lie close but are not appressed to the branch and are cylindrical to only slightly compressed, maintaining a uniform diameter from base to tip. Polyps are 1.0–1.3 mm in length and 0.38–0.45 mm in diameter.

Each polyp is encased in 8 opercular and a variable number of body wall scales; marginals and submarginals are not distinguishable in size or shape from other body wall scales. The abaxial and outer-lateral operculars are squarish in size with a rounded distal margin, a convex outer surface, and are about 0.20–0.23 mm wide. The inner-lateral operculars are smaller (0.13 mm wide), and the adaxial operculars are smaller still (0.08 mm wide) and elongate (Fig. 4D). In the preserved state the operculars are folded over one another and are themselves overshadowed by the marginal body wall scales, often making it quite difficult to distinguish and count the 8 opercular scales. The body wall scales are arranged in 8 rows. The abaxials are arranged in 2 rows in alternating order, each row consisting of 10 or 11 scales (Fig. 5B). These scales are thick, broader than tall (H:W = 0.53–0.67), and up to 0.28 mm in width near the branch. The outer-lateral scales are arranged in rows of 7 or 8, each of which partially overlaps an adjacent abaxial and inner-lateral scale. Outer-lateral scales are roughly square (H:W = 0.9–1.1) and can be partially seen in abaxial view. Inner-lateral scales are similar to the outer-laterals but are less numerous, occurring in rows of 5 or 6. The adaxial scales are quite small (0.07 mm wide, 0.16 mm long, H:W = 2.2), occurring in rows of only 2 or 3, leaving the proximal part of the polyp unprotected. All body wall scales have rounded upper margins. The outer surfaces of all body wall and opercular scales are quite smooth, but in the case of the abaxial and lateral body wall scales there is often a transverse ridge (Fig. 5D) across the scale at about mid-height, corresponding to the level at which the more proximal scales overlaps that scale. The inner surface of all body wall and opercular scales are covered with large (16–18 μm), discrete, rounded, well-separated tubercles, each of which bears 12–20 prominences 2–3 μm in width and height, which themselves bear several smaller projections about 0.7 μm in height (Fig. 5C). These tubercles also occur on the proximal outer edge of the body wall scales.

The coenenchymal scales are irregular in shape and disposition but are invariably longer than wide, up to 0.33 mm in length with a H:W = 1.5–1.7, having a tuberculate inner surface and a smooth outer surface similar to the body wall scales. Tuberculate spindles are uncommon in the coenenchyme (Fig. 5F).

Comparisons.—*Primnoella divaricata* is easily distinguished from other western Atlantic species by having a branching colony (Table 1). It is also distinctive in having a rounded polyp cross section and having outer-lateral body wall sclerites that are clearly visible in abaxial view, allying it to the genus *Convexella* (or the *Convexae* group of *Primnoella* sensu Kükenthal, 1919), but the small size of the adaxial body wall sclerites and their incomplete coverage of the adaxial side of the polyp place it in conventional *Primnoella*. Bayer (1996) chose the latter genus for the species, and I will adopt this placement herein.

The only other branching species of *Primnoella, P. laevis* (Thomson & Mackinnon, 1911), is known from New South Wales, Australia at about 100 m. The Australian species is quite similar in polyp morphology, but differs in having profusely dichotomous branching, only 8 or 9 abaxial scales per row, and fewer inner-lateral scales.

Remarks.—Although not found at the MCZ or YPM (Verrill number 8034), the specimen illustrated by Verrill as *Primnoella ''nitida''* (see Bayer & Cairns 2004) appears to be *P. divaricata*. According to Eric Lazo-Wasem (pers. comm., 2005), that specimen was collected at *Hassler* station 240P (37°42′S, 56°20′W, 80 m, which is extremely close to the type-locality.

Distribution.—Known only from five localities between Cabo Santa María, Uruguay, to off Península Valdés, Argentina, ''Patagonia'' (Kükenthal 1919); 55–80 m.

Primnoella delicatissima Kükenthal, 1909
Figs. 1B, 6, 7

Primnoella delicatissima Kükenthal, 1909: 47; 1919: 402–403, text-figs. 178–179 (redescription of holotype, key); 1924: 286.—Aurivillius, 1931: 276–281, pl. 6, figs. 2a–b, text-figs. 55, 1–8.—Deichmann, 1936: 163.—Bayer, 1959: 30 (listed); 1996: 167 (listed).

Material examined.—*Saldanha* 1773, off Amapa, east of Ilha de Maraca, Brazil; 2°40′05″N 48°03′00″W, 14 Nov. 1967, 103 m, 1 colony, MNRJ; 1 colony and SEM stubs B387, C1175–1176 from same station, USNM 1081592.

Type and type locality.—The holotype was deposited in Munich Museum (Kölliker collection) but is now probably lost. Type locality: 22°47′S, 41°41′W (off Cabo Frio, Brazil), depth unknown.

Description.—Colonies are flagelliform (unbranched), up to 35 cm in length (Aurivillius 1931), the axis diameter rarely exceeding 0.6 mm in diameter. Colonies are firmly attached to hard objects, such as bivalve shells, by a disk-like attachment and thus do not produce dendritic holdfasts adapted to soft substrates.

Polyps are arranged in whorls of 5–7 (usually 6) and are fairly closely spaced every 0.4–1.0 mm. Polyps point upward and are closely appressed to the branch, appearing to bend inward toward the branch such that the adaxial operculars touch the branch. Polyps are elliptical (slightly flattened) in cross-section and uniformly cylindrical, although narrowing slightly at the apex: 1.02–1.29 mm in length and 0.32–0.45 mm in greater diameter.

Each polyp is encased in 8 (or more) opercular scales and 8 longitudinal rows of body wall scales, although there is little difference in shape between the operculars and distalmost body wall scales. The abaxial operculars are large (0.16 mm wide) and rhomboidal in shape, with a rounded distal margin. The lateral and adaxial operculars are progressively smaller, the adaxials being elongate and only about 0.70 mm in width, quite similar in shape and size to the adjacent adaxial body wall scales. Furthermore, sometimes some of the opercular scales are ''duplicated'' (see Aurivillius 1931), resulting in more than 8 opercular scales, which makes it difficult to distinguish the opercular scales from the adjacent body wall scales, especially those on the adaxial side (Fig. 6D). This duplication may be due to breakage. The operculars are tightly folded over one another and eclipsed by the adjacent marginal body wall scales. The abaxial body wall scales are arranged in 2 rows in alternating order, each row consisting of 11–13 scales. These scales are quite thick (0.04 mm, Fig. 7C), broader than tall (H:W = 0.48–0.60), and up to 0.33 mm in width, the widest scales occurring proximally where they are arranged in

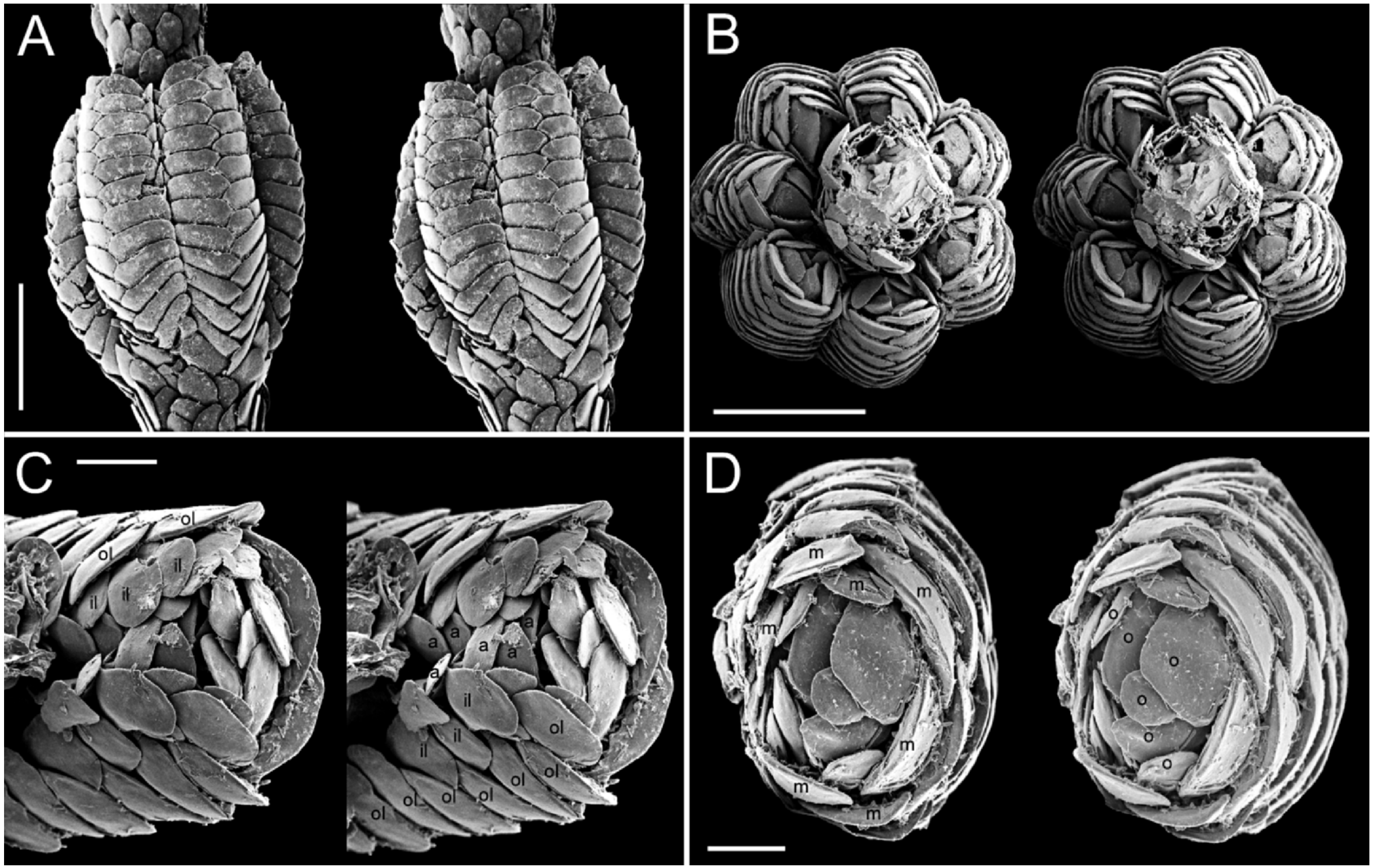

Fig. 6. A–D, *Primnoella delicatissima* from *Saldanha* 1773, USNM 1081592, stereo views of polyps: A, lateral view of a polyp whorl showing chevron-arranged abaxial sclerites; B, opercular view of a whorl of 7 polyps and broken stem; C, adaxial view of polyp showing adaxial (a) and inner- (il) and outer-lateral (ol) rows of scales; D, opercular view of polyp showing 6 opercular (o) and 7 marginal (m) scales, the adaxial scales not labelled. Scale bars: A–B = 0.5 mm; C = 0.12 mm; D = 0.10 mm.

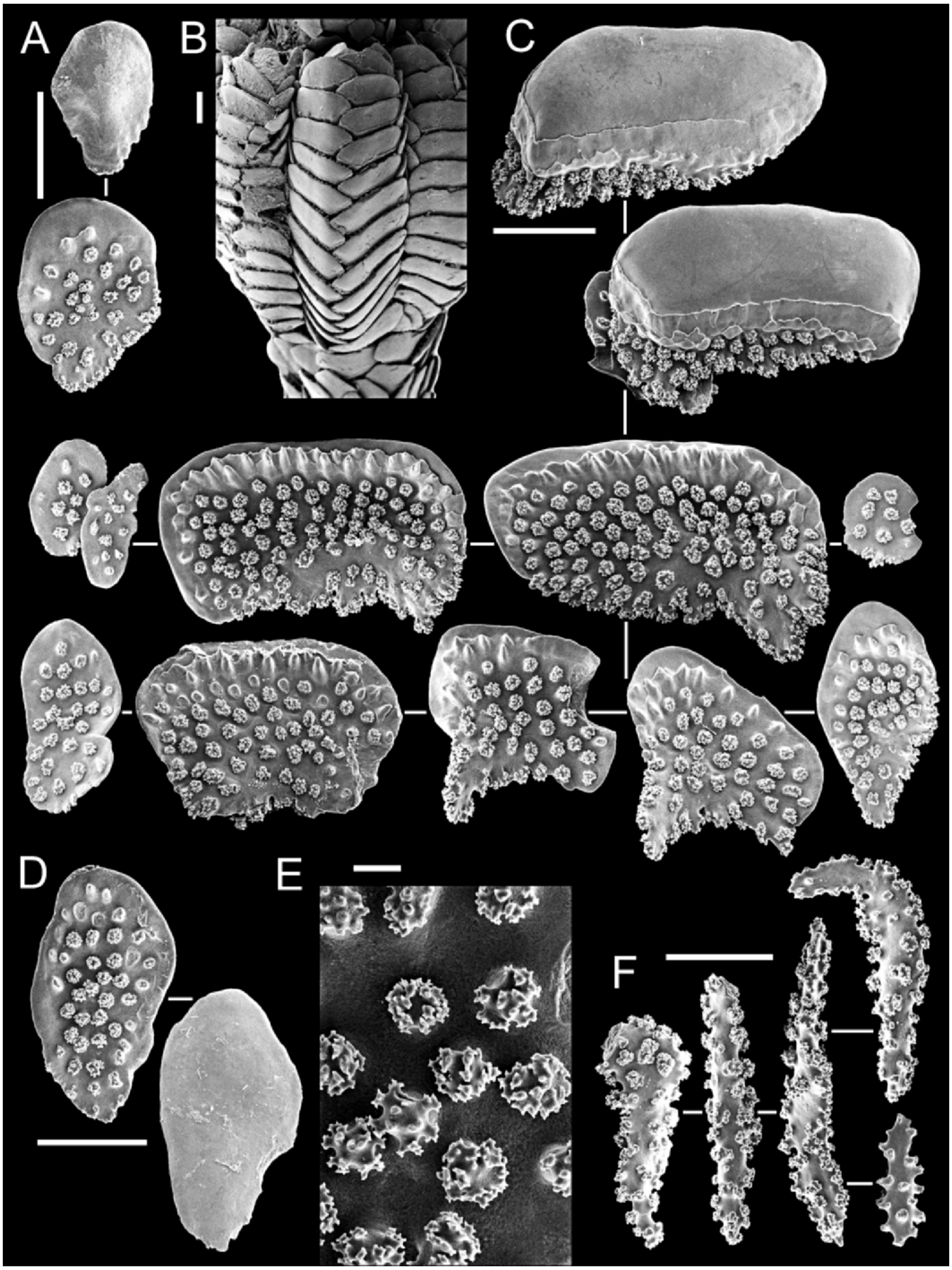

Fig. 7. Sclerites of *Primnoella delicatissima* from *Saldanha* 1773, USNM 1081592: A, two opercular scales; B, chevron-shaped arrangement of abaxial body wall scales; C, twelve body wall scales, the large scales in the abaxial position, the smallest being adaxial, the odd-shaped being laterals; D, two coenenchymal scales; E, tubercles on inner side of a coenenchymal scale; F, five spindles. Scale bars: A–D, F = 0.1 mm; E = 0.01 mm.

a staggered, chevron-shaped arrangement (Fig. 7B). The outer-laterals are arranged in rows of 5–9, and, like the abaxials, are rectangular in shape and increase in size proximally, attaining a maximum width of about 0.17 mm. They are usually not visible in abaxial view. Inner-lateral body wall scales occur in rows of 3–5 and are square in shape, often with a short appendix on the proximal abaxial corner, and are 0.11–0.17 in width. Adaxial body wall scales are quite small and elliptical in shape, rarely over 0.06 mm in length, occurring in rows of 0–2 sclerites, leaving most of the adaxial polyp surface naked. The outer surface of all opercular and body wall scales is smooth, and, in the case of the abaxial body wall scales, there is often a thin transverse ridge that delimits the extent that overlap of the proximal most scale. The inner surface of these scales is covered with large (17–10 µm diameter), discrete, well-separated, rounded tubercles, which also occur on the proximal outer edge of the body wall scales.

The coenenchymal scales are elliptical to polygonal in shape (H:W = 1.5–3.0), occasionally star-shaped (Kükenthal 1919), irregularly arranged, and up to 0.30 mm in greater diameter. These coenenchymal scales are ornamented similar to the body wall scales. Beneath the outer layer of flattened scales is an interior layer of elongate, tuberculate spindles that are up to 0.32 mm in length and rarely more than 0.04 mm in diameter. These spindles may be straight, bent or clavate (Fig. 7F).

Comparisons.—*Primnoella delicatissima* is compared to the other two western Atlantic congeners in Table 1. It is most distinctive in having a chevron-type arrangement of the proximal abaxial body wall scales and an abundance of tuberculate spindles that line the longitudinal coenenchymal canals. It differs from the other Subantarctic South American species in having small polyps, a relatively small number of polyps per whorl, close but non-contiguous polyp whorls, and only 11–13 abaxial body wall scales (some Subantarctic species having as many as 32).

Remarks.—In addition to the type, this species was reported only once again virtually from the type locality by Aurivillius (1931), who provided a remarkably detailed description of the species. His specimens differed from the type and the one reported herein in having slightly longer polyps (1.5 mm) and consequently several more adaxial (14–16) and outer-lateral (10–13) body wall sclerites per row.

Distribution.—Known only from the small region between Rio de Janeiro and Cabo Frio, and off Amapa, Brazil; 55–103 m.

Thouarella Gray, 1870

Thouarella Gray, 1870: 45.—Wright & Studer, 1889: xlix, 59–61.—Versluys, 1906: 22–24.—Kükenthal, 1908: 10–11 (in part).—Nutting, 1912: 66.—Kükenthal, 1919: 405–408, 848, pls. 67, 84 (in part: not *Amphilaphis* or *Dicholaphis*); 1924: 287–288 (in part).—Bayer, 1956: F220; 1981: 936 (keyed).

?*Hookerella* Gray, 1870: 45 (type species: *H. pulchella* Gray, 1870, by monotypy).

Primnodendron Nutting, 1912: 70 (type species: *P. superbum* Nutting, 1912, by monotypy).

Rhopalonella Roule, 1908: 2–3 (type species: *R. pendulina* Roule, 1908, by monotypy).

Euthouarella Kükenthal, 1915: 149 (type species: *Primnoa hilgendorfi* Studer, 1878 by subsequent designation (Bayer, 1956)).

Thouarella (*Euthouarella*).—Kükenthal, 1919: 414; 1924: 292.—Bayer, 1956: F220. —Bayer & Stefani, 1989: 455 (keyed).

Thouarella (*Parathouarella*) Kükenthal, 1915: 150 (type species: *Primnoa antarctica* Valenciennes, 1846); 1919: 425; 1924: 296–297.

Thouarella (*Epithouarella*) Kükenthal, 1919: 435 (type species: *T. crenelata*

Kükenthal, 1907 by subsequent designation (Bayer, 1956)); 1924: 299–300.—Bayer, 1956: F220.

Thouarella (Thouarella).—Bayer, 1956: F220.—Bayer & Stefani, 1989: 455 (keyed).

Type species.—*Primnoa antarctica* Valenciennes, 1846, by monotypy. Type locality: Falkland Islands, depth not given.

Diagnosis.—Body wall scales arranged in 6–8 longitudinal rows: 8 near the calyx, but reducing to 6 near the branch, the inner-lateral scales widening to take the place of the smaller or absent adaxials. Marginal scales occur as 2 circles of 4 that alternate in 2 transverse rows below operculum; marginals fold over the opercular scales. Both marginals and opercular scales prominent and bear a keel on their inner surface. Polyps circular in cross-section and usually stand perpendicular to branch; polyps occur individually, paired, or in whorls. Colonies usually sparsely branched, numerous short branches of uniform length originating from all sides of the main branch (bottle-brush arrangement); some species have pinnately arranged branches.

Distribution.—Widespread in all oceans (Kükenthal 1919: plate 67) at depths of 106–1644 m.

Remarks.—*Thouarella* was named to honor Abel DuPetit-Thouars, the captain of the famous *Venus* (1836–1839) expedition. Following its establishment, several dozen species were described by Wright & Studer (1889), Versluys (1906), Kinoshita (1907), Kükenthal (1907), and Nutting (1912). Early on these species were arranged in parataxonomic species groups: three groups by Versluys (1906) and four groups by Kükenthal (1908). These groups were finally formalized as four subgenera by Kükenthal (1915), who later (Kükenthal 1919) greatly amplified and discussed them, including two keys to all the known species. One of Kükenthal's subgenera, *Amphilaphis* Studer, 1887, was removed from the genus by Bayer (1981) in his key to the octocoral genera as differing from the other three in having polyps with eight rows of body wall scales from calyx to branch. Subgenus *Epithouarella* differs from the remaining two in having marginal scales without a pointed distal margin, the other two having elongate pointed tips. Subgenus *Euthouarella* has polyps arranged in pairs or whorls, whereas subgenus *Parathouarella* has ungrouped polyps. It was unnecessary to assign a new subgeneric name to the *Parathouarella* subgenus as that one included the type species of the genus and was thus the nominate subgenus. Only one species has been described since 1912, *T. abies* Broch, 1965, which is now considered closer to *Fannyella* than *Thouarella*.

Currently 26 species and three subgenera are recognized in the genus (Table 2). Kükenthal (1919) was able to distinguish all species using the following characters: branching mode (bottle-brush, pinnate), number of whorls per cm, number of polyps per whorl, number of body wall sclerites in the abaxial rows, and polyp shape. As with *Primnoella*, this genus is in need of revision.

Thouarella (Thouarella) bipinnata, n. sp.

Figs. 1F, 8, 9

Material examined/Types and type locality.—Holotype: *G*-177, 1 colony, USNM 53015. Paratypes: *G*-177, 2 colonies, SEM stubs B217, C1173–1174, USNM 1078186; *G*-170, 27°06′N, 79°32′W, 659–677 m, 29 June 1963, 20 colonies, USNM 53017; *Albatross* 2672, 31°31′N, 79°05′W, 507 m, 5 May 1886, 1 colony, USNM 14465; *Gosnold* 2452, 27°23′48″N, 79°29′18″W, 695 m, 12 Sept. 1965, 4 colonies, USNM 57296; *P*-689, 8°14′N, 57°38′W, 1000 m, 15 July 1968, 25 colonies, SEM stub B218, USNM 53018 and 53019; *P*-691, 8°25′N, 58°08′W, 32–88 m (?), 15 July 1968, 3

Table 2.—List of the 26 currently recognized species and 3 subgenera of the genus *Thouarella* Gray, 1870, and their general localities. Species described herein in bold face. Type species of subgenera indicated with an asterisk.

T. (Thouarella) Gray, 1870	
**T. antarctica* (Valenciennes, 1846)	Faulkland, 1005 m
T. variabilis typica Wright & Studer, 1889	Prince Edward I., 567 m
—var. *brevispinosa* Wright & Studer, 1889	Prince Edward I, 567 m
—var. *gracilis* Wright & Studer, 1889	Heard I., 278 m
T. koellikeri Wright & Studer, 1889	Patagonia, 320–730 m
T. versluysi Kükenthal, 1907	South Africa, 500 m
T. striata Kükenthal, 1907	Bouvet, 450 m
T. clavata Kükenthal, 1908	South Africa, 500 m
T. pendulina (Roule, 1908)	Antarctic
T. hicksoni Thomson, J.S. 1911	South Africa, 137 m
T. alternata Nutting, 1912	Japan, 934 m
=*T. attenuata* Kükenthal, 1924 (misspelling of *alternata*!)	
T. recta Nutting, 1912	Japan, 869–924 m
T. superba (Nutting, 1912)	Alaska, 60–79 m
***T. bipinnata*, n. sp.**	Northwestern Atlantic, 507–1000 m
***T. diadema*, n. sp.**	Brazil, 1000 m
T. (Euthouarella) Kükenthal, 1915	
**T. hilgendorfi* (Studer, 1878)	Japan & Kei Is., 256 m
T. moseleyi Wright & Studer, 1889	Kermadec & Indonesia, 794–1080 m
T. laxa Versluys, 1906	Indonesia & Japan, 400–1301 m
T. tydemani Versluys, 1906	Indonesia, 520 m
?=*Hookerella pulchella* Gray, 1870	
T. flabellata Kükenthal, 1907	East Africa, 1644 m
T. typica Kinoshita, 1907	Japan, "deep littoral"
T. carinata Kükenthal, 1908	Japan, 732 m
T. tenuisquamis Kükenthal, 1908	Great Nicobar, 752 m
=*T. regularis* Kükenthal, 1907 (jr. homonym)	
T. longispinosa Kükenthal, 1912	Antarctica, 385 m
***T. grasshoffi*, n. sp.**	North Atlantic, 720–1760 m
T. (Epithouarella) Kükenthal, 1915	
T. affinis Wright & Studer, 1889	Tristan da Cunha, 106–128 m
**T. crenelata* Kükenthal, 1907	Bouvet, 457 m
T. chilensis Kükenthal, 1908	Chile

branches, USNM 53020; *Johnson-Sea-Link* I-4683, 30°31.0473′N, 79°39.6208′W, 544–568 m, 10 June 2004, 2 branches, USNM 1078320. Type locality: *Gerda* 177: 27°17′N, 79°34′W (Straits of Florida off northwest corner of Little Bahama Bank), 686 m, 30 June 1963.

Description.—Colonies are uniplanar and delicate, the largest specimen (the holotype) 9 cm in height and 10 cm in width, having a basal axis diameter of 1.6 mm. Branching is irregularly pinnate to bipinnate, the holotype producing 4 larger-diameter branches near the base of the colony, each of which generates a series of branchlets up to 3 cm in length roughly in opposite alternating fashion at intervals of 5–15 mm, although occasionally 2 branches occur contiguously on the same side of the stem, and the spacing between branchlets is quite variable. Sometimes a branchlet increases in diameter and length and produces additional branchlets, thus the term bipinnate. The axis is golden-yellow in color; colonies are firmly attached to a hard substrate (often a dead corallum of the scleractinian coral *Enallopsammia pro-*

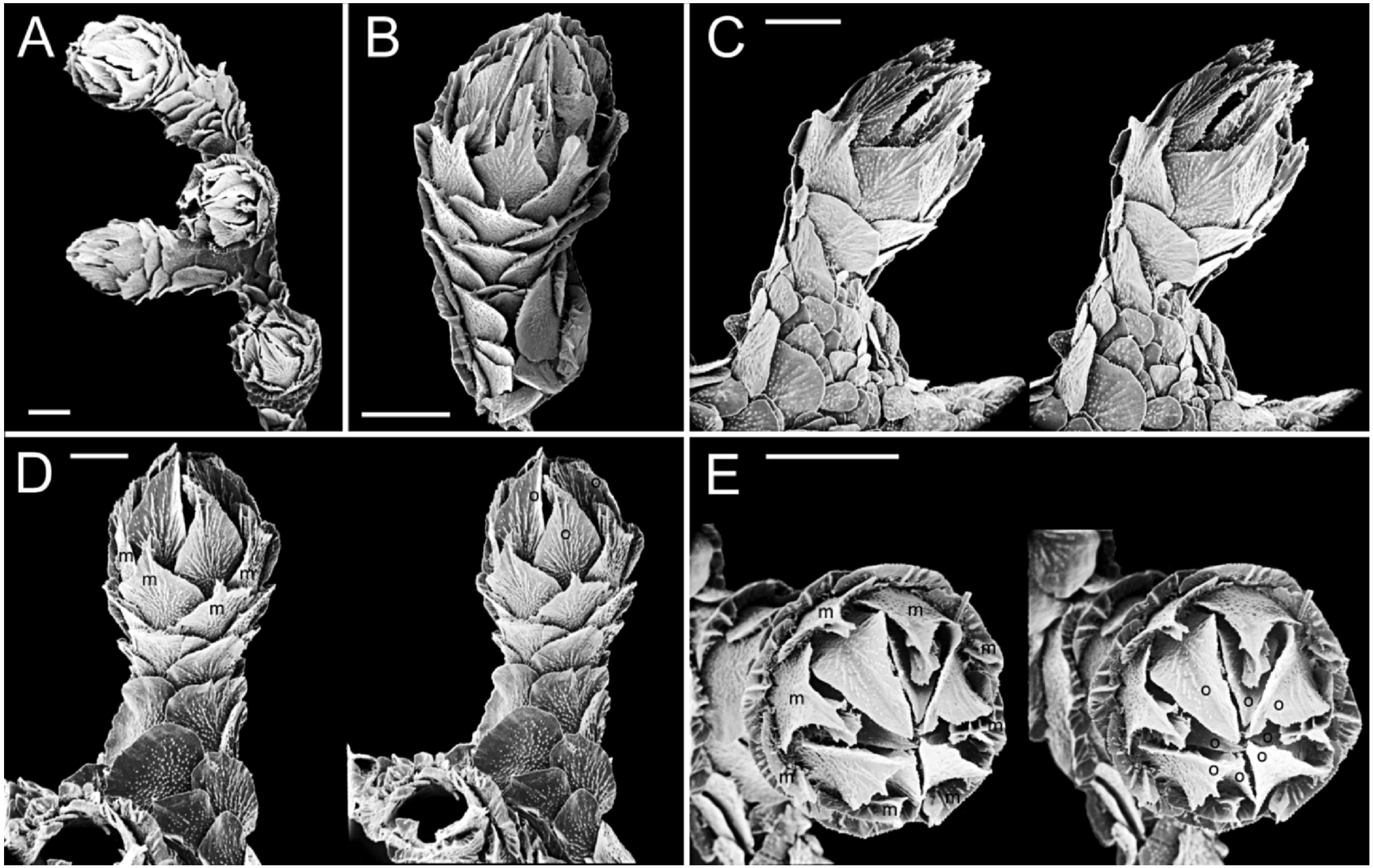

Fig. 8. *Thouarella bipinnata* (A–B, D–E, *Gerda* 177, USNM 53015; C, *P*-689, USNM 53018), polyps: A, terminal branch with 4 polyps; B, abaxial side of polyp showing various scales; C, lateral stereo view of polyp; D, lateral stereo view of a polyp with 4 marginal (m) and 3 opercular (o) scales labelled; E, opercular stereo view of a polyp showing all 8 opercular (o) and 8 marginal (m) scales. Scale bars are all 0.5 mm.

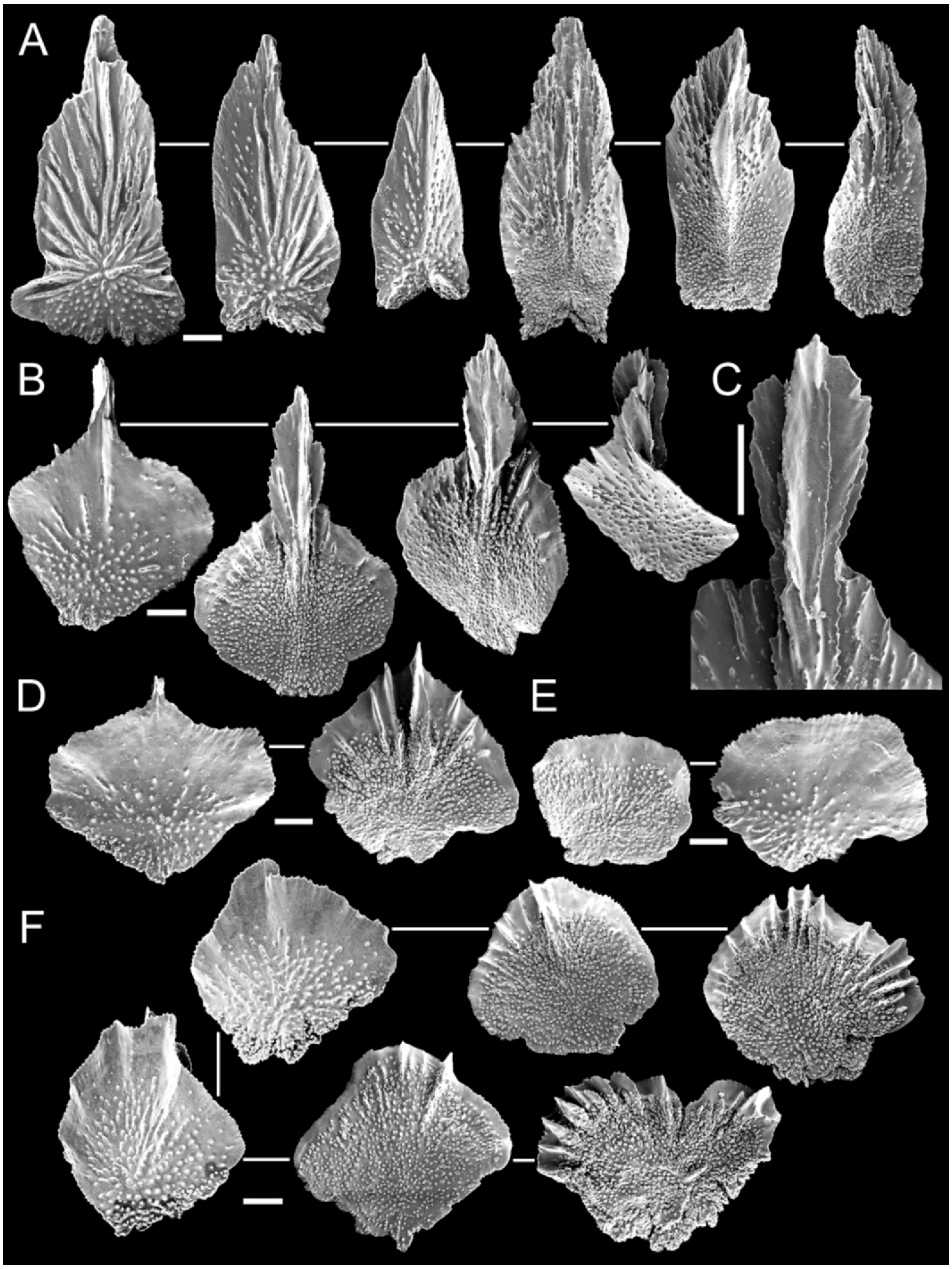

Fig. 9. Sclerites of *Thouarella bipinnata* from *Gerda* 177, USNM 53015: A, six opercular scales; B, four marginal scales; C, enlargement of inner distal tip of a marginal scale showing the multiple ridges; D, two submarginal scales; E, two coenenchymal scales; F, six body wall scales. Scale bars are all 0.1 mm.

funda or *Lophelia pertusa*) by a white, calcareous, discoidal holdfast.

Polyps occur on the main stem (even directly adjacent to the discoidal holdfast) and branchlets in roughly an alternating opposite arrangement, occasionally with 2 polyps arranged opposite each other, but with no tendency toward pairing or arrangement in whorls. In the holotype the polyps are oriented toward one face of the colony. Adjacent polyps are spaced 0.5–1.5 mm apart and stand perpendicular to the branch. Polyps are slightly clavate, up to 2.4 mm in height, and have a H:W of 1.8–2.2.

Each polyp is encased in 4 types of scales: 8 operculars, 8 pointed marginals, 8 submarginals, and a variable number of body wall scales. The opercular scales are shaped as isosceles triangles up to 0.90 mm in height, having a H:W of 2.1–2.9. Their tips all join in an apex of a well-defined operculum (Fig. 8E). The mid-longitudinal region of their outer surface is highly concave, which corresponds to a prominent keel on their inner surface, the keel sometimes having multiple finely serrate ridges. The outer surface also bears several prominent ridges that radiate from the proximal region, and the inner surface is minutely spinose distally and covered with tubercles on its proximal half. The lateral edges of the operculars are also finely serrate. The marginal scales are finely pointed and are about the same height as the operculars but have a much broader base, and thus a lower H:W of 1.3–2.1. Their outer and inner surfaces are similar to those of the operculars, but the inner keel is much more developed, having lateral serrate ridges oriented perpendicular to the main keel (Fig. 9C). Each marginal closely folds over its correspondingly aligned opercular scale, its complex inner keel lying along the concave trough of the outer side of the opercular (Fig. 8E). The marginals are arranged in an inner and outer ring of 4 scales each: the lateral edges of the marginals of the inner ring being overlapped by the lateral edges of those from the outer ring. Submarginal scales often occur just proximal to the marginals, distinguished by having a short but acute medial spine; these scales are only about 0.5–0.6 mm in height, with a H:W of 0.90–0.95. The remaining body wall scales are arranged in 6–8 longitudinal rows, their size increasing proximally as the polyp decreases in diameter, such that at the base of the polyp there are no adaxial scales and the inner-laterals are either decreased in size or also absent. These body wall scales are roughly rectangular and often broader than wide (H:W = 0.85–0.95), those near the branch as wide as 0.8 mm. Their outer surface is granular and sometimes ridged, their inner surfaces tuberculate, but also bearing multiple ridges at their distal margins (Fig. 9F). As with all other scales, their margins are finely serrate. Including the marginals and submarginals, there are only 3–5 scales in each longitudinal row, fewer in the adaxial and inner-lateral rows.

The coenenchymal scales are irregular in shape and have highly concave outer surfaces. They are sculptured as the other scales and up to 0.6 mm in greater length.

Etymology.—Named for the bipinnate form of the colony.

Comparisons.—*Thouarella bipinnata* differs from other species in the subgenus in having a uniplanar, bipinnate colony, all other species having a bottlebrush ("walzenförmig") colony shape. Regarding its uniplanar shape, it is similar to many species in the subgenus *Euthouarella*, but differs in having its polyps arranged individually on the branchlets, not in pairs or whorls. *T. bipinnata* is also similar to some species of *Amphilaphis* in many characteristics, including colony shape, but differs in having less than eight rows of body wall scales near the polyp base and marginal scales that fold over the operculars (Bayer 1981).

Remarks.—Most colonies of this species host small white ophiuroids that cling to the branches and polyps for support. They have tentatively been diagnosed as an undescribed species of the genus *Ophiomitrella* (Family Ophiocanthidae) by Milena Benavides-Serrato (pers. comm., 2005). Several colonies also contain completely covered tunnels that run along the main branches, each probably housing a polychaete worm, although the worm was never recovered. The shape and size of the coenenchymal sclerites forming the tube were not affected.

The two lots from off Guyana (*P*-691, 689) are morphologically identical to those from off Florida but differ in having smaller polyps (only about 1.2 mm in height) and thus a more delicate colony.

Distribution.—Disjunct distribution: Blake Plateau off northern Florida and Straits of Florida off Little Bahama Bank; off Guyana; 507–1000 m.

Thouarella (Thouarella) diadema, n. sp.
Figs. 1G, 10, 11

Material examined/Type and type locality.—Holotype: *Calypso* 1776, 1 colony fragment, SEM stub B219–222, C1177–1179, USNM 1078187. Type locality: 24°54.4′S, 44°26.0′W (off São Sebastião, Brazil), 1000 m.

Description.—The holotype is a colony fragment 6 cm tall and 4.5 cm wide, consisting of a main stem with numerous closely spaced branchlets that originate on all sides of the main stem (bottlebrush type arrangement), most of these branchlets undivided and up to 3 cm in length. The axis is golden in color, 1.3 mm in diameter at the basal break, and fairly stiff in tension.

Polyps are closely spaced on the main stem and branchlets in a roughly alternating arrangement, occasionally opposite one another, but with no tendency toward pairs or whorls. Polyps stand perpendicular to all sides of the branches and branchlets. Polyps are slightly wider at the opercular region; including the marginal spines, which may extend considerable beyond the operculum, polyps reach up to 4.2 mm in height and are about 1.5 mm in maximum diameter.

Each polyp is encased in 3 types of sclerites (scales): 8 operculars, 8 pointed marginals, and a variable number of body wall scales. The opercular scales are shaped as isosceles triangles with somewhat blunt tips, and occur in 2 alternating sets: 4 larger operculars, which are associated with the outer marginal ring, up to 0.7 mm in height and thus greater than the radius in length; and 4 smaller operculars, which are associated with the inner marginal ring, only up to 0.4 mm in length, about the length of the polyp radius. The operculars usually lie horizontally and thus do not form a peaked operculum. The lateral edges of the smaller operculars are usually covered by the adjacent edges of the larger operculars and are often obscured form opercular view (Fig. 10D). The H:W of the operculars ranges from 1.5 to 2.7. Their outer surfaces are covered with low granules arranged in a radiating pattern; their proximal inner surfaces are tuberculate, whereas their distal inner surfaces are quite smooth (not keeled). As in *T. bipinnata*, the marginal scales are arranged in an inner and outer ring of 4 scales each. The marginals have a broad squarish base, often with short digitate processes proximally, and a prominent echinulate spine distally, which is round in cross-section. The length of the spine is somewhat variable, even within the same polyp, but seems to increase in length with time, those on small polyps being quite short. Well-developed spines may constitute 75% of the length of a marginal scale, these scales reaching up to 1.8 mm in length (H:W = 1.4–2.1). The outer

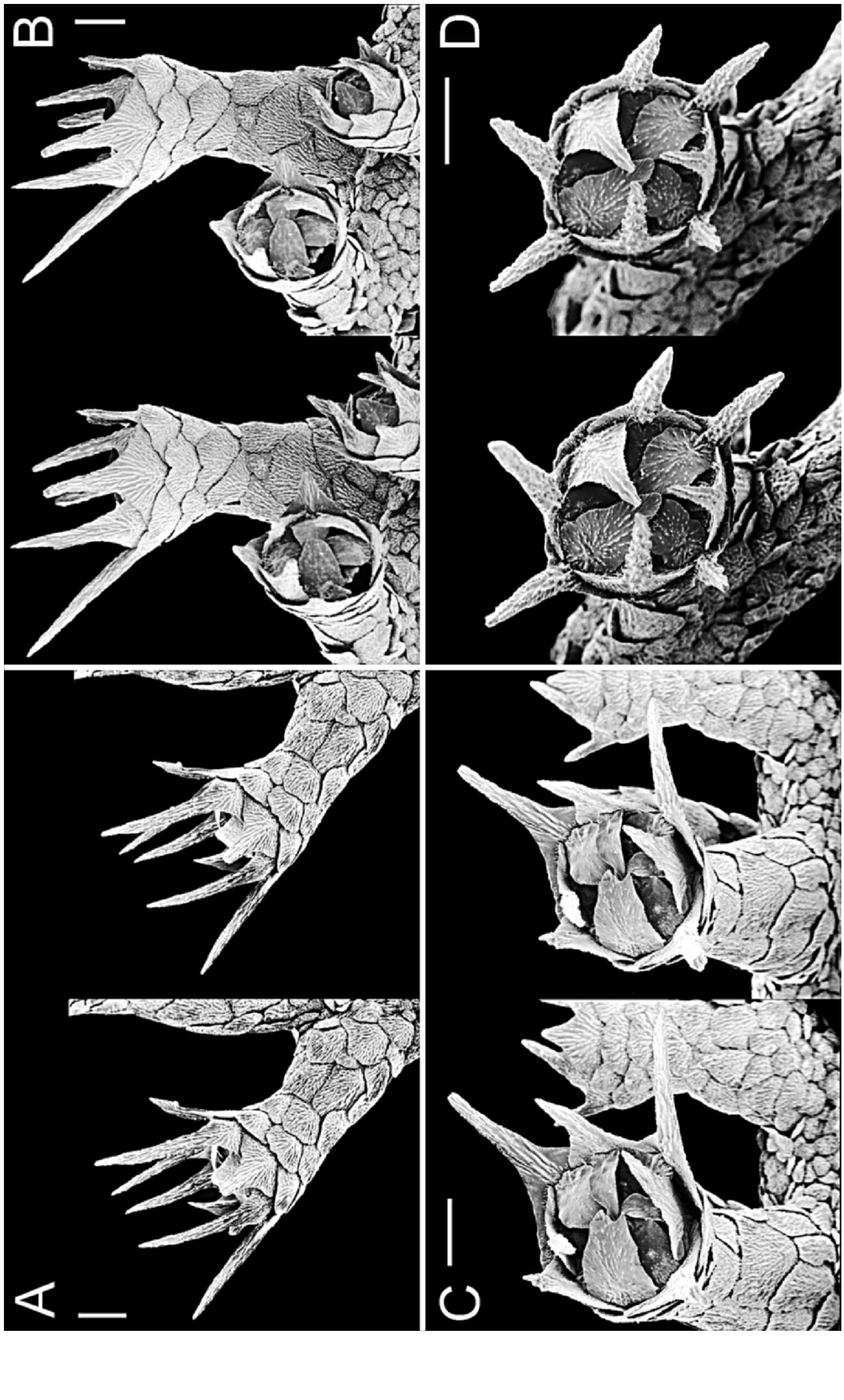

Fig. 10. A–D, *Thouarella diadema*, holotype from *Calypso* 1776, stereo views of polyps: A, lateral view of a polyp; B, lateral view of a polyp and opercular view of two smaller polyps; C, opercular view of a polyp showing all 8 marginals and only 5 opercular scales; D, opercular view of a polyp showing all 8 marginal and 8 opercular scales, the smaller inner ring of 4 operculars partially obscured by the overhanging marginals. Scale bars are all 0.5 mm.

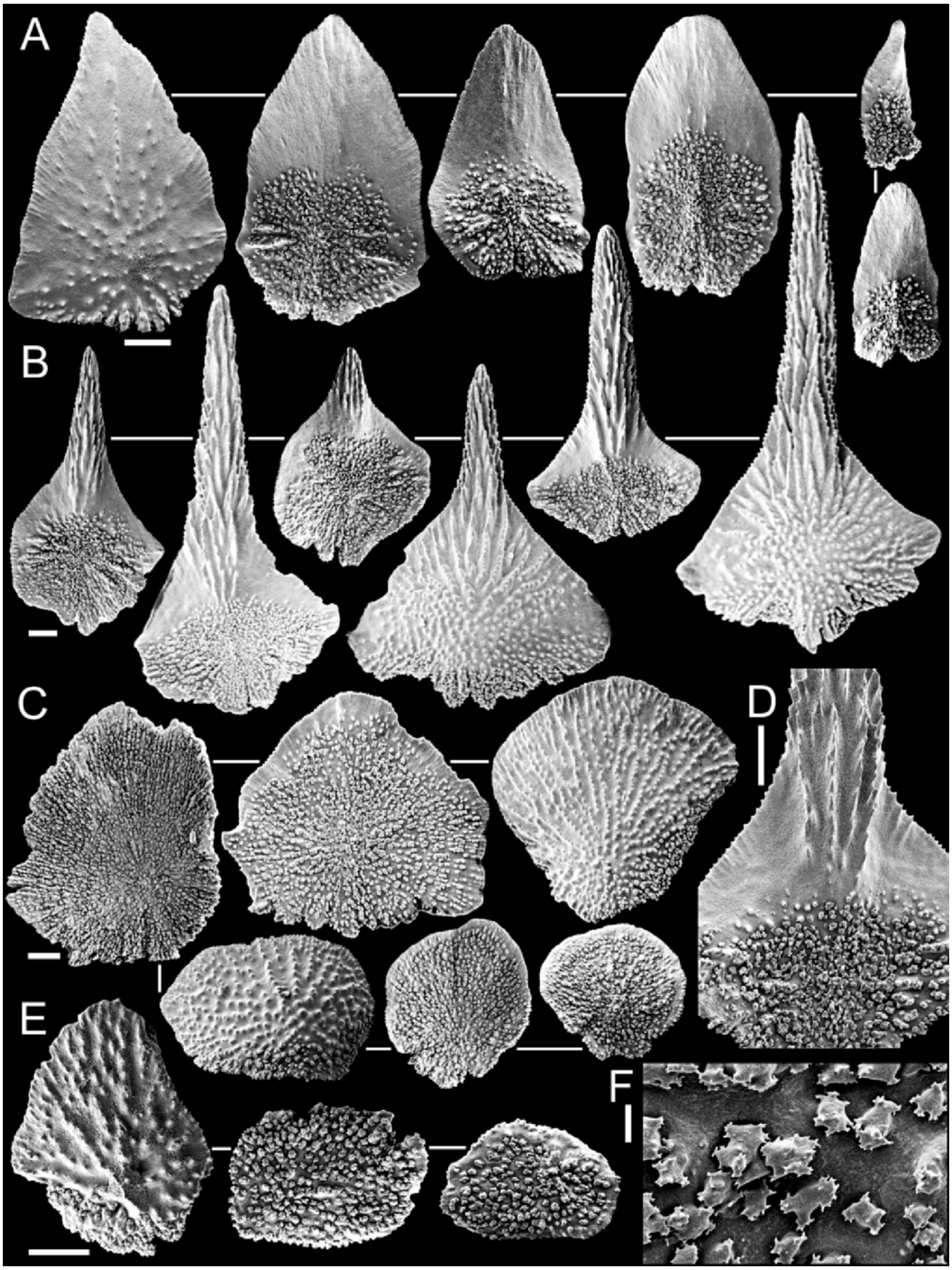

Fig. 11. Sclerites of *Thouarella diadema* from *Calypso* 1776: A, six opercular scales, the 2 smallest being from the inner ring; B, six marginal scales; C, six body wall scales; D, higher magnification of the inner side of a marginal scale; E, three coenenchymal scales; F, tubercles on inner side of a coenenchymal scale. Scale bars: A–E = 0.1 mm; F = 0.01 mm.

surface of the basal portion of the marginals is granular; the inner surface, tuberculate; and their lateral edges finely serrate. The massive distal spine is not keeled but bears several (4–10) finely serrate longitudinal ridges covering all sides (Fig. 11D). The body wall scales are arranged in 6–8 longitudinal rows of 3–5 scales (including the marginals), their size increasing proximally, such that near the branch the scales are arranged in a mosaic (Fig. 10A, B), and adaxial scales are not recognizable. The shape of the body wall scales also changes from wider than long near the marginals (H:W = 0.6) to longer than wide near the base (H:W = 1.4). These scales are tuberculate below and granular above, with finely serrate margins.

The coenenchymal scales are elliptical to irregular in shape, with a tuberculate inner surface and a granular outer surface, rarely exceeding 0.4 mm in length. The tubercles measure up to 15 µm in diameter.

Etymology.—The species name *diadema* (Greek for crown), treated as a noun in apposition, is an allusion to the tall spines of the crown-like marginal sclerites.

Comparisons.—*Thouarella diadema* differs from other consubgenerics in having large polyps (up to 4 mm in length) with extremely long marginal spines (up to 1.8 mm). Also unusual in this species is the lack of keels on the inner side of the opercular scales. It is otherwise similar to *T. versluysi* Kükenthal, 1907 (South Africa) in general colony shape.

Remarks.—Thomson (1927) and Tixier-Durivault & d'Hondt (1974) reported another species of this subgenus from Cape Verde and the Azores at depths of 810–1642 m, *T. variabilis* Wright & Studer, 1889, a species otherwise known from the southern Indian Ocean and Antarctica. It has a bottlebrush colony shape and marginals with relatively short spines. It was not examined in this study.

Distribution.—Known only from the type locality.

***Thouarella (Euthouarella) grasshoffi*, n. sp.**
Figs. 1A, 12, 13

Not *Plumarella Hilgendorfi* Studer, 1878: 648–649, pl. 2, fig. 15a–e.

Thouarella hilgendorfi.–Thomson, 1927: 33–34, pl. 1, fig. 23, pl. 6, figs. 4–5.—Deichmann, 1936:166 (comment).—Tixier-Durivault & d'Hondt, 1974: 1411.—Carpine & Grasshoff, 1985: 32.—Pasternak, 1985: 29.—Watling & Auster, 2005: 295.

Thouarella cf. *hilgendorfi*.—Grasshoff, 1982a: 747, map 3; 1982b: 948, figs. 18–19.

Thouarella n. sp. Watling & Auster, 2005: 284, 295.

Material examined/Types and type locality.—Holotype: ROV *Hercules* dive 7, station MAN808, large colony, USNM 1078188, and two fragments of holotype, YPM 35377 and 35378. Paratypes: *Alvin* station OCE 102-6: 40°17.014′N, 68°07.123′W (Oceanographer Canyon), 814 m, 10 Sept. 2001, 1 colony, SEM stubs C1180–1183, USNM 1014915, and 1 colony, YPM 36360; R/V *Delaware II* DE04-08-39, 40°14.49′N, 67°40.95′W (SE of Nantucket I.), 1103–1356 m, 25 May 2004, 1 colony, YPM 35976; R/V *Delaware II* DE04-08-41, 40°16.47′N, 67°42.36′W (slope SE of Nantucket I.), 824–892 m, 25 May 2004, 3 colonies, YPM 36997, 36999, and 37000; R/V *Delaware II* DE04-08-52, 40°13.87′N, 68°01.31′W (slope SE of Nantucket I.), 835–1053 m, 27 May 2004, 2 colonies, YPM 36983, 36984; R/V Delaware II DE04-09-18, 39°55.417′N, 67°25.157′W (Bear Seamount), 1112–1255 m, 7 June 2004, 2 colonies, YPM 35495 and 36719.

Non-Types: MOM 743 (see Thomson 1927), USNM 1078189; MOM 1193 (see Thomson 1927), USNM 1078190; *Tha-*

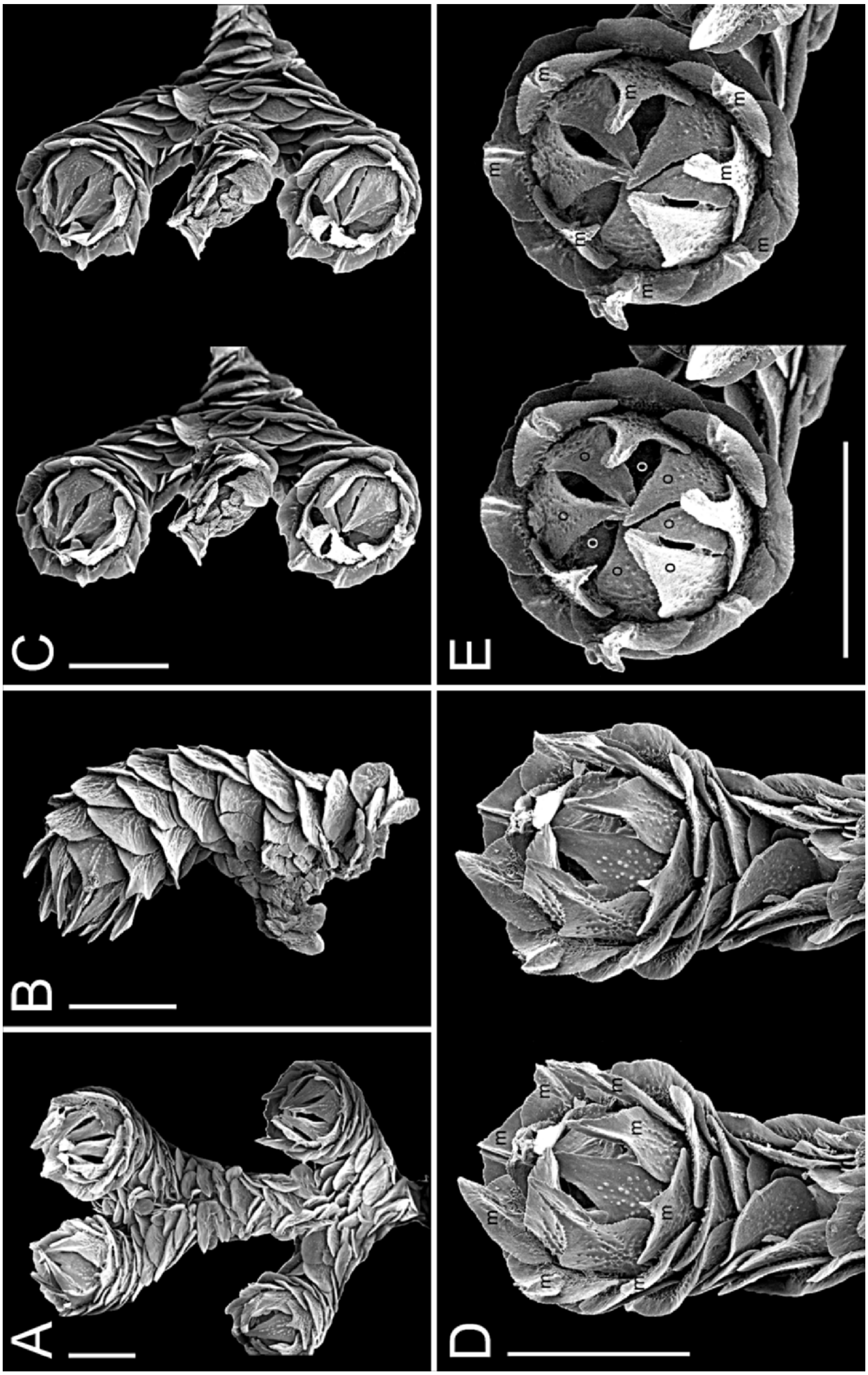

Fig. 12. A–D, *Thouarella grasshoffi*, paratype, USNM 1014915: A, distal twig with 4 polyps; B, lateral view of a polyp; C, opercular stereo view of a pair of polyps; D, oblique opercular stereo view with the 8 marginal (m) scales labelled; E, opercular stereo view illustrating all 8 opercular (o) and 8 marginal (m) scales. Scale bars are all 0.5 mm.

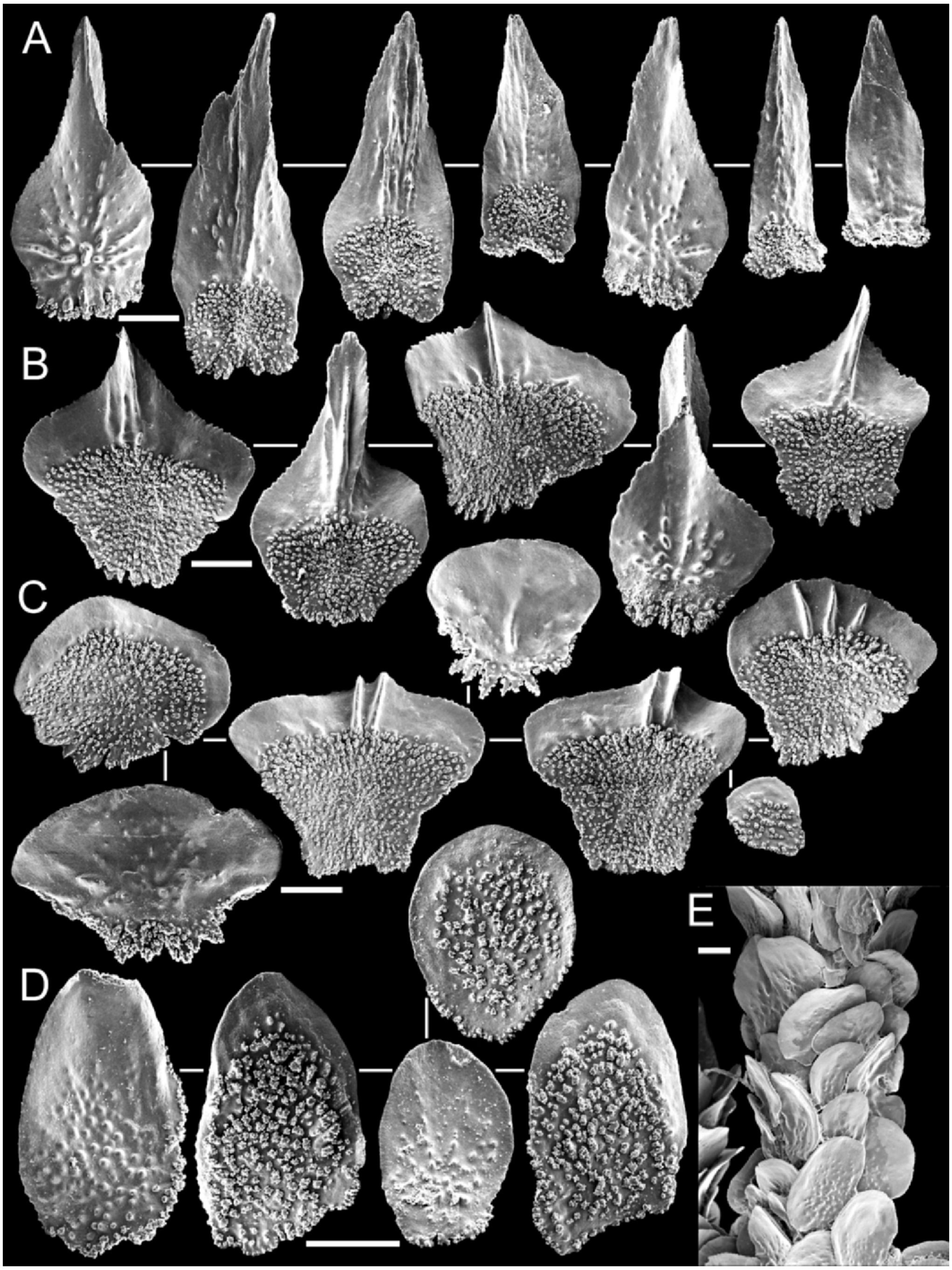

Fig. 13. Sclerites of *Thouarella grasshoffi*, paratype, USNM 1014915: A, seven opercular scales, the 2 smaller ones at right adaxial in position; B, five marginal scales; C, seven body wall scales, the small one adaxial in position; D, five coenenchymal scales; E, coenenchymal scales in place. Scale bars are all 0.1 mm.

lassa Z430 (see Grasshoff 1982b), USNM 1078191.

Type locality: 38°08.74′N, 61°05.473′W (Manning Seamount), 1458 m, 16 May 2004.

Description.—Colonies consist of 1–3 main branches, from which numerous closely-spaced (usually less than 2 mm apart) branchlets originate on all sides of the main branch in a bottlebrush arrangement. The branchlets are undivided, about 4.5 cm in length, and flexible in tension. The holotype is a single main stem 35 cm tall and 8–9 cm in width that has been broken from its base, the axis being 2.4 mm in proximal diameter and brownish in color.

Polyps occur randomly on the main stems and regularly on the branchlets in pairs (or in whorls of three about 10–20% of the time) every 1.5–1.9 mm along the branchlet. The polyps curve upward toward the branch tip and are rarely more than 1.3 mm in length and about 0.7 mm in diameter at the calyx; they are white in color.

Each polyp is encased in 3 types of sclerites: 8 operculars, 8 pointed marginals, and a variable number of body wall scales. The opercular scales are shaped as isosceles triangles with a pointed apex and do not appear to be arranged in a double ring pattern. Although they range in length from 0.26 to 0.62 mm, most operculars are 0.45–0.55 mm in length and have a H:W of 2.1–3.2. The proximal quarter of the inner surface is tuberculate; the distal half bears one to several finely serrate keels. The outer surface bears low granules arranged in a radiating pattern. The lateral edges of the operculars are finely serrate, and the proximal edge is coarsely digitate. Marginal scales are not arranged in two well-defined rings as in most *Thouarella*; instead, both lateral edges of 3 of the marginals overlap those of the adjacent marginals, both lateral edges of 3 other marginals are overlapped by adjacent marginals, and the lateral edges of the 2 remaining marginals have one side above and the other below their adjacent marginal (Fig. 12E). The marginals have an acute, pointed tip but a rather broad base, resulting in a H:W of 0.93–2.1; they are up to 0.54 in length. The proximal half of the inner surface is tuberculate; the distal half bears 1–3 longitudinal keels. The outer surface is granular and the lateral and proximal edges finely serrate and coarsely digitate, respectively, as for the operculars. The remaining body wall scales are arranged in 6–8 longitudinal rows of 5–7 scales each, all scales somewhat flared outward. These scales have a rounded distal margin and are broader than tall (H:W = 0.65–0.89). They are up to 0.34 mm in length, those on the adaxial side rarely more than 0.22 mm in length. Toward the branch axis the inner-lateral scales are quite wide, reaching over and sometimes replacing the smaller adaxial scales, resulting in only 6 rows. The proximal three-quarters of the inner surface is tuberculate, the distal quarter being smooth, those near the branch axis often bearing 1–3 longitudinal ridges at their margin (Fig. 13C). The outer surface is smooth or bears several low granules.

The coenenchymal scales are elliptical to elongate in shape, rarely more than 0.32 mm in length, having a H:W = 1.3–1.8. They are tuberculate below and slightly concave as well as smooth or mildly granular above.

Etymology.—Named in honor of Manfred Grasshoff (1936-), the twentieth century authority on octocorals from the eastern Atlantic, who first recognized the distinction of the species.

Comparisons.—Most species in the subgenus *Euthouarella* have flabellate colonies, the main branches being confined to one plane. However, *T. grasshoffi* and *T. typica* have bottlebrush colonies, more typical of the nominate subgenus. *T. grasshoffi* differs from *T. typica*, the latter known only from Japan in the ''deep littoral", in having larger polyps and branchlets that are longer and less frequently spaced on the main branch.

Remarks.—*Thouarella hilgendorfi* was originally described from "Jeddobay" (=Tokyo Bay), Japan at 548 m as *Plumarella hilgendorfi* (Studer, 1878), and later reported from Indonesia (Wright & Studer 1889; Versluys 1906), again from Japan (Nutting 1912), and Sumatra (Kükenthal 1919), at depths of 188–750 m. Thomson (1927) was the first to report this western Pacific species from the North Atlantic (Azores and Cape Verde), followed by Tixier-Durivault & d'Hondt (1974), Azores; Grasshoff (1982b), Biscay Bay; and Pasternak (1985), Great Meteor Seamount, at depths of 720–1760 m, although Grasshoff expressed doubt that the North Atlantic populations were the same as the western Pacific species. I agree with this reservation based on the original description, a voucher specimen considered to be typical *T. hilgendorfi* (USNM 1011763), and the subsequent western Pacific reports of the species, all of which confirm that *T. hilgendorfi* forms a flabellate colony (broader than tall) having 4–6 main branches in one plane, and with most branchlets originating from the edges of the main branches, not from the dorsal or ventral surfaces. *T. grasshoffi*, on the other hand, has very sparse branching resulting in colonies much taller than high (bottlebrush shape), and branchlets that originate uniformly on all sides of the branchlets. Although the polyp morphology is quite similar, the polyps of *T. grasshoffi* are larger than those of *T. hilgendorfi*.

Representative specimens from Cape Verde (from Thomson 1927) and the Bay of Biscay (Grasshoff 1982b) were examined (see Material Examined) and found to be identical to those from the western Atlantic, confirming Deichmann's (1936) prediction that Thomson's (1927) *T. hilgendorfi* would subsequently be found in the western Atlantic. However, the two western Atlantic species that Deichmann (1936) placed in *Thouarella* have been subsequently reassigned to different genera: *Plumarella* and *Acanthoprimnoa* (see Cairns & Bayer 2004).

Ophiuroids of the genus *Astroschema* are common symbionts on colonies, and one colony was encrusted basally by the octocoral *Anthothela*.

Distribution.—Western Atlantic: Manning and Bear Seamounts of the New England Seamount Chain, and Oceanographer Canyon (probably common on the New England Seamounts, Watling, pers. comm.); 814–1458 m; Eastern Atlantic: Cape Verde, Great Meteor Seamount, Azores, Celtic Sea; 720–1760 m.

Dasystenella Versluys, 1906

Stenella Wright & Studer, 1889: 59 (in part).

Stenella (Dasystenella) Versluys, 1906: 39, 48.

Thouarella.—Kükenthal, 1915: 151 (in part); 1919: 441 (in part).

Dasystenella.—Bayer, 1981: 934, 937, 946, fig. 73.—Bayer & Stefani, 1989: 454 (key).

Type species.—*Stenella acanthina* Wright & Studer, 1889, by monotypy.

Diagnosis.—Body wall scales arranged in 5 longitudinal rows (1 abaxial, 2 lateral, and 2 adaxial). Five marginal scales with prominent, finely serrate distal spines. Both opercular and marginal scales bear a prominent keel or keels on their inner surface. Polyps occur in whorls and are curved upward. Colonies consist of a main branch from which numerous branchlets originate from all sides (bottlebrush).

Distribution.—Argentina, Scotia Ridge and South Shetland Islands; 300–5087 m.

Remarks.—Versluys (1906) characterized *Dasystenella*, if only as a subgenus, based on its similarity to several other genera (*Stenella (=Candidella), Parastenella, Pterostenella*) but differing in its colony shape, i.e., bottlebrush. Kükenthal (1919, 1924) ignored the distinction and grouped the type species with *Thouarella*, probably based on its similar gross morphology of the colony, but could not place it in any of his subgenera within *Thouarella*. Bayer (1981), in the context of a key to the octocoral genera and without further discussion, elevated the taxon to the genus level, distinguishing it as having only five marginal scales and bottlebrush-shaped colonies. Only one species is currently assigned to the genus.

Dasystenella acanthina
(Wright & Studer, 1889)
Figs. 1E, 14, 15

Stenella acanthina Wright & Studer, 1889: 59, pl. 14, fig. 3, pl. 20, fig. 10.

Stenella (Dasystenella) acanthina.—Versluys, 1906: 48.

Thouarella acanthina.—Kükenthal, 1915: 151; 1919: 441–442; 1924: 302.—Bayer, 1959: 30 (listed).

Dasystenella acanthina.—Bayer, 1981: 934, fig. 73 (syntype).—Mellado, et al., 2004: 291–299 (steroid chemistry).—Pérez & Zamponi, 2004: 4–6, figs. 1, 2C.

Material examined.—*Eltanin*-992, 61°19′S, 56°28′W, 403 m, 13 March 1964, 3 colonies, USNM 84326; *Eltanin*-993, 61°25′S, 56°30′W, 300 m, 13 March 1964, 4 colonies, SEM stub B1563, USNM 98119; *Eltanin*-1088, 60°49′S, 53°28′W, 587–589 m, 17 April 1964, 2 colonies, USNM 98122; *Eltanin*-1095, 56°06′S, 89°54′W, 5087–5124 m, 20 May 1964, 1 colony, USNM 98097; *Eltanin*-1545, 61°04′S, 39°55′W, 2355–2897 m, 11 Feb. 1966, 2 colonies, USNM 77388; *Islas Orcadas* 876-130, 59°53′06″S, 32°19′30″W, 523–671 m, 1 colony, USNM 82131; syntypes (BM).

Types and type locality.—Syntypes, BM 1889.05.27.48 (alcohol), and SEM stubs B276, C1185–1186, uncataloged at NMNH. Type locality: *Challenger* 320: 37°17′S, 53°52′W (continental slope off Rio de la Plata, Argentina), 1097 m, 2.89°C.

Description.—Colonies consist of a tall main stem up to 391cm in height that gives rise to numerous closely spaced branchlets 2.5–5.0 cm in length standing perpendicular from all sides of the main branch (bottlebrush configuration). The axis is up to 4 mm in diameter at the base. Colonies are attached by a spreading calcareous holdfast.

The polyps occur in discrete whorls of 3–5 polyps (usually 4), the whorls spaced about 1.5 mm apart. Polyps are gently curved upwards and, including the elongate marginal spines, are up to 3.2 mm in length and about 1.0–1.25 mm in maximum diameter at the operculum. The polyps are white.

Each polyp is protected by 3 types of scales: 8 operculars, 5 marginals, and a variable number of body wall scales arranged in 5 longitudinal rows. The operculars are isosceles triangular in shape with a gradually attenuated tip, the adaxial operculars being considerably smaller than the other 6 (Figs. 14D, 15A), i.e., only about 0.5 mm in length compared to 0.9 mm for the abaxial operculars (H:W = 2.1–2.5). The distal portion of the outer surface of each opercular bears a deep longitudinal crease whereas the proximal portion is flat and bears low granules. The distal portion of the inner surface of each opercular bears several finely serrate ridges (keels), whereas the proximal portion is tuberculate. The lateral edges are also finely serrate. The marginal scales are also roughly triangular in shape but with an abrupt change in width leading to a thin elongate distal spine. The abaxial and two lateral marginals are quite large (up to 1.9 mm in length (H:W = 1.8–2.1), each bearing prominent distal spines that may constitute over half its length. The rectangular lower portion is granular above and

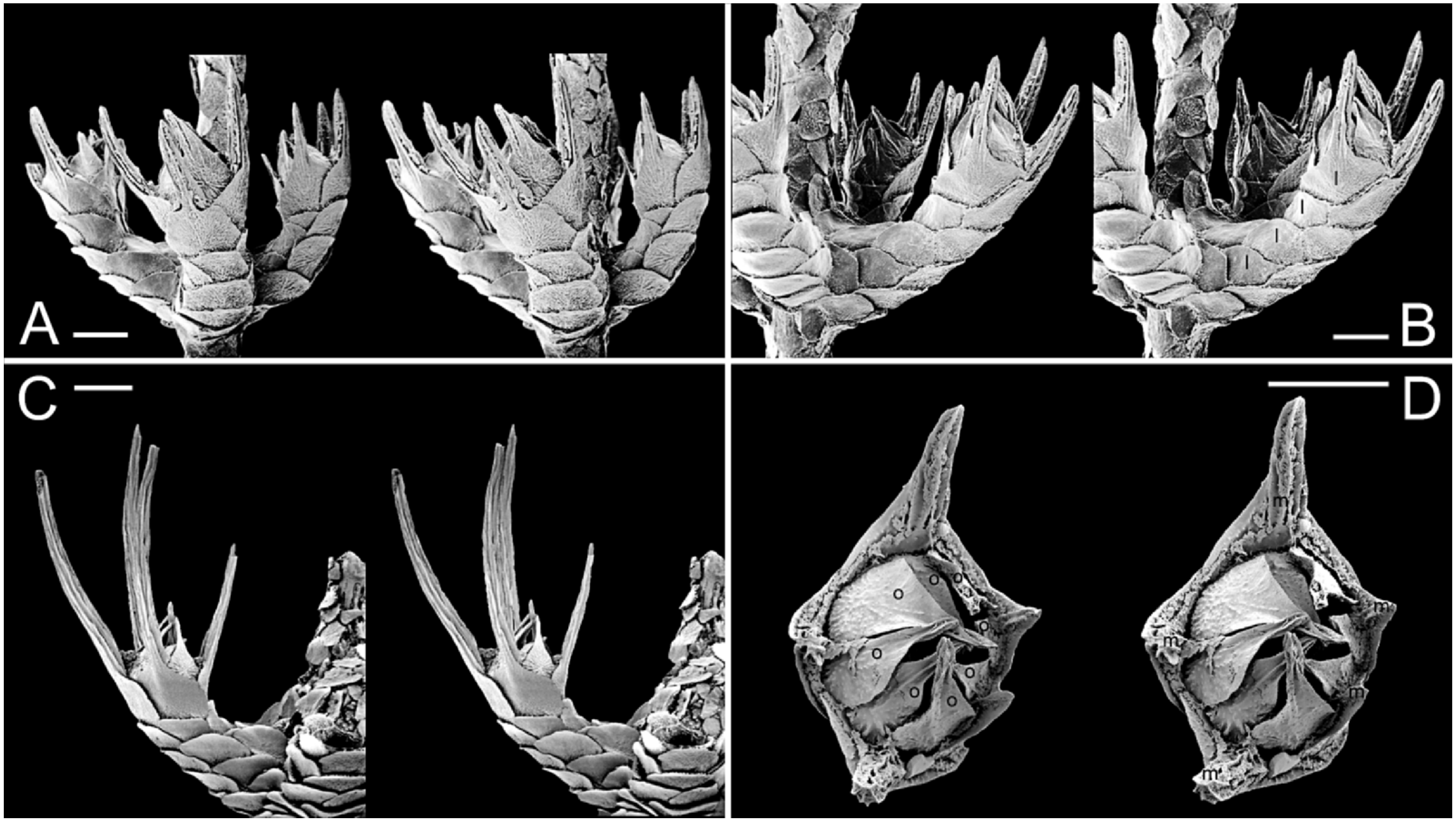

Fig. 14. *Dasystenella acanthina* (A–B, D, syntype, BM 1889.05.27.48; C, *Eltanin* 993, USNM 98119), stereo views of polyps: A, a whorl of 4 polyps; B, lateral view of a whorl showing lateral body wall and marginal scales (l) and some adaxial sclerites on polyp in background; C, a long-spined polyp; D, opercular view showing tall 5 marginal (m) and 8 opercular (o) scales. Scale bars are all 0.5 mm.

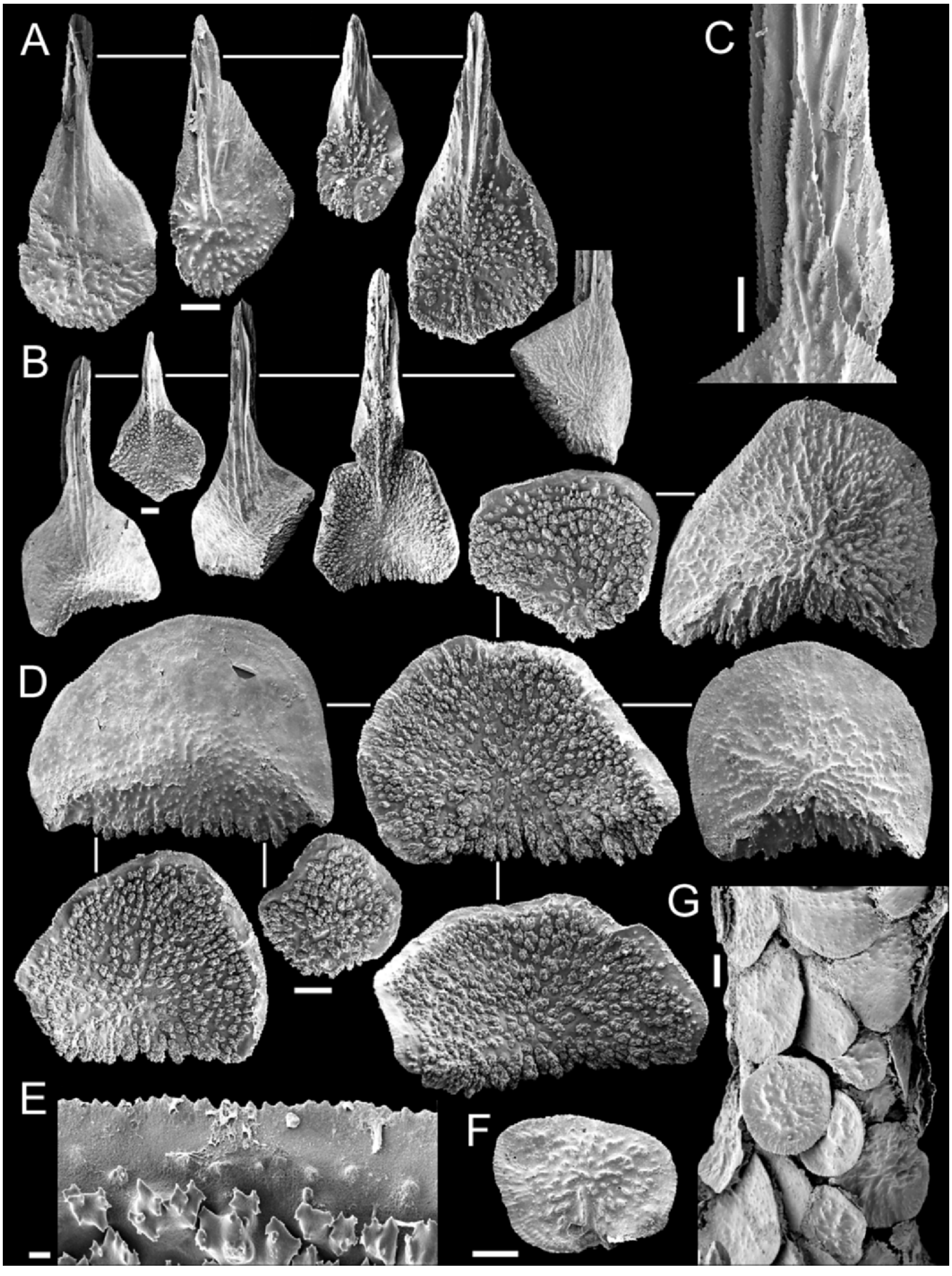

Fig. 15. Sclerites of syntype of *Dasystenella acanthina*: A, four opercular scales, the smallest being from the adaxial position; B, five marginal scales; C, higher magnification of outer surface of tip of a marginal scale showing ridges; D, eight body wall scales; E, finely serrate inner edge of a body wall scale; F, outer surface of a coenenchymal scale; G, coenenchymal scales in place. Scale bars: A–D, F–G = 0.1 mm; E = 0.01 mm.

tuberculate below, but the distal elongate spine is covered on all sides with 6 or 7 prominent longitudinal finely serrate ridges (Fig. 15C); the edges of the marginals also finely serrate. The 2 adaxial marginals are shorter (rarely more than 1 mm in height) and closely fold over the adaxial opercular scales; the other 3 marginals also fold over their adjacent operculars but not as closely as those near the smaller adaxial ones. The base of the lateral marginal is asymmetrical, the side adjacent to the adaxial region seemingly cut off in a straight line (Fig. 15B, 1st–3rd images). Below the abaxial marginal scale the abaxial side of the polyp is covered with one row of 4 or 5 large crescent-shaped to semi-circular scales, each of which may be up to 0.9 mm in width. Both lateral polyp surfaces are also covered with a row of 4 or 5 large body wall scales (Fig. 14B). The adaxial side of the polyp, however, is covered with 2 rows of 3 or 4 much smaller scales, each of which is about 0.4 mm in width. All body wall scales have a prominently tuberculate inner surface and finely serrate margins.

The coenenchymal scales are circular to slightly elliptical, flat and rarely more than 0.35 mm in greater diameter. As with most other scales, they are granular above and tuberculate below.

Remarks.—The non-type specimens reported above are the first records subsequent to the original description. Those more southerly specimens differ slightly in having somewhat smaller polyps and marginal spines that are longer (up to 2.4 mm), especially in relation to their basal width (H:W up to 3.5) and that are slightly curved inward toward the operculum (Fig. 14C).

Distribution.—Off Argentina (type locality and Péres & Zamponi, 2004), South Shetland Islands to Scotia Ridge between South Orkney Islands and South Sandwich Islands; abyssal plain west of Tierra del Fuego; 150–5087 m.

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