Studies on western Atlantic Octocorallia (Gorgonacea: Primnoidae). Part 8: New records of Primnoidae from the New England and Corner Rise Seamounts

Stephen D. Cairns

Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A., e-mail: cairnss@si.edu

Abstract.—New records of nine primnoid species are reported from the New England and Corner Rise Seamounts at depths of 1315–3855 m, making a total of 10 primnoid species known from this region. One new genus, Paranarella, and three new species are described: P. watlingi, Calyptrophora clinata, and Parastenella atlantica, the latter being the first record of Parastenella from the Atlantic. Calyptrophora pillsburyae is synonymized with C. microdentata, and the first subsequent report of Convexella jungerseni is noted. The fauna is hypothesized to have colonized the seamounts from the northward flowing Gulf Stream, the southerly flowing Deep Western Boundary Current, and/or via insular steeping stones from the east.

The New England Seamounts (NES) are the longest seamount chain in the North Atlantic, consisting of 30 major peaks along a ridge 1100 km long, extending from Bear to Nashville Seamounts (Houghton et al. 1977). About 300 km east are the Corner Rise Seamounts (CRS), containing about 50 seamounts. Prior to 2000, very few organisms were known from this region; however, since then there have been a series of expeditions sponsored by NOAA OE and the NMFS to several of these seamounts, especially Bear Seamount (Moore et al. 2003, 2004). Currently, 286 species are known from Bear Seamount alone, the easternmost and thus closest seamount to North America, including eight octocoral species (Moore et al. 2003). One of these eight octocorals was reported as a primnoid, Primnoa sp. (Houghton et al. 1977, Moore et al. 2003, Table 1); however, this genus was not found by Cairns & Bayer (2005) from the NES and is herein considered a dubious record for that region. Nonetheless, two primnoid species had been previously reported from these seamounts: Candidella imbricata by Pasternak (1985) from Rockaway Seamount (CRS), and by Cairns & Bayer (2004) from San Pablo, Kelvin, and Muir Seamounts (NES); and Thouarella grasshoffi by Cairns (2006) from Manning and Bear. Furthermore, Calyptrophora microdentata had been reported from the adjacent Corner Rise Seamounts by Pasternak (1985). In this paper, new material of nine primnoid species are reported from eight of the eighty New England and Corner Rise Seamounts, including one new genus and three new species. A tenth primnoid species is known from this region, T. grasshoffi, but no additional records are reported herein.

Materials and Methods

The specimens reported were collected on the New England and Corner Rise Seamounts by the research submersible Alvin (2003) and the ROV Hercules (2004,

C. antilla Bayer, 2001 C. microdentata C. clinata, C. clinata Pasternak, 1985 Branching Uniplanar, flabellate, Uniplanar, Flagelliform Flagelliform dichotomous flabellate, dichotomous Orientation of polyps Up Up Down Down Calyces/whorl; whorls/ 2-3-5; 11-14; 1.4-3-4; 7-11; 1.6-5-6-7; 16-18; 1.3-6-7; 14-15; 3 cm; calyx length 1.8 mm 2.0 mm 1.4 mm 1.5 mm Basal scale spination Short (0.3–0.6 mm), Medium (to 1.4 mm), Tall (to 2.0 mm), Tall (to 1 mm), unridged, smooth curved, ridged ridged and ridged and to granular and serrate serrate serrate Spination of buccal 4-7 needle-like 4 needle-like None, or two low 2 needle-like scale spines (0.25spines (0.45 mm teeth (0.15 mm spines (to 0.50 mm tall), tall), ridged and tall), or rarely 0.8 mm tall), unridged serrate spined (to ridged and 0.55 mm) serrate Distal margin of Coarsely serrate Straight Straight to undulate Straight buccal scale Orientation of buccal Parallel to branch 45° to branch 45° to branch Parallel to branch scale Infrabasal scales Conspicuous Conspicuous Inconspicuous and Inconspicuous (0.28 mm tall) (0.33 mm tall) short (0.2 mm) and short (0.2 mm)

Small anteriorly

Present

1399-1692 m

directed spines

Table 1.—New England Seamount Calyptrophora.

2005), these specimens now deposited at the NMNH and YPM. The five NES from which specimens were obtained were, from west to east: Bear, Retriever, Kelvin, Manning, and Nashville; the Corner Rise Seamounts include: Kükenthal Peak, Caloosahatchee (Verrill Peak), and Lyman.

Coarsely granular

Present

686-2310 m

Outer surface of body

Apical keel on inner

wall scales

surface of operculars

Depth

The following abbreviations are used in the text: CRS, Corner Rise Seamounts; IL, inner-lateral body wall scale; L:W, ratio of the length to width of a sclerite; NES, New England Seamounts; NMFS – National marine Fisheries Service; OE – Office of Exploration; OL, outer-lateral body wall scale; SEM, scanning electron microscopy; USNM, United States National Museum, now the National Museum of Natural History (NMNH); YPM, Yale Peabody Museum, Yale University, New Haven.

Systematics

Small anteriorly

Absent

1316 m

directed spines

Small anteriorly

directed spines

1315-1842 m

Absent

Subclass Octocorallia Order Gorgonacea Suborder Calcaxonia Family Primnoidae Gray, 1860 Genus *Convexella* Bayer, 1996

Type species.—Primnoella magelhaenica Studer, 1879, by original designation.

Diagnosis.—Colonies flagelliform, unbranched, or very sparsely branched. Calyces arranged in whorls; calyces round in cross-section and directed upward, sometimes closely appressed to branch. Body wall scales arranged in 8 longitudinal rows, sometimes fewer scales in rows on adaxial side due to curvature but not resulting in a naked region. Four rows of body wall scales are seen in abaxial view. Eight subopercular (=marginal) scales are large

and triangular, usually larger than and folding over the 8 opercular scales. Inner surface of opercular scales not keeled.

Remarks.—The genus Convexella was proposed and reviewed by Bayer (1996). This is the only species among four in the genus that occurs in the northern hemisphere.

Distribution.—Southern South America, Antarctic, Kermadec Trench, North Atlantic; 73–5850 m (Bayer 1996).

Convexella jungerseni (Madsen 1944) Figs. 1G, 2A–E

Primnoella jungerseni Madsen, 1944: 39–42, figs. 30–32.

Convexella jungerseni.—Bayer, 1996:179 (new combination).

Material examined.—*RB*05-03, *Hercules* dive 2 (LYM 202-2), 35°11.50′N, 47°40.32′W (Lyman Seamount, CRS), 2359 m, 13 Aug 2005,1 colony and *SEM* stubs 1264–1265, USNM 1096709.

Types and type locality.—The types are deposited at the Zoological Museum of Copenhagen. Type Locality: 61°44′N, 30°29′W (southwest of Iceland off Reykjanes Ridge), 2137 m.

Short description.—Colony flagelliform and unbranched: 12 cm in length and 0.45 mm in basal branch diameter, but colony is lacking base. Calyces occur in whorls (Fig. 2A) of 2 or 3, the paired calyces occurring closer to the distal end of the colony; calyces closely appressed to the branch, whorls separated by 1.9-2.8 mm. Calyces round in cross-section and cylindrical: 0.6 mm in distal diameter and about 0.48 mm in proximal diameter; calyces 1.6-1.8 mm in length. Body wall scales arranged in 8 longitudinal rows: 7 or 8 scales in abaxial rows, 6 or 7 in the OL rows, 5 or 6 in the IL rows, and only about 4 scales in each adaxial row (Fig. 2B); however, for the basal 0.30-0.35 mm of each calyx the scales are smaller (0.15 mm width) and seemingly arranged in random order (Fig. 2A). The lesser number of adaxial scales does not produce a naked lower adaxial region because the curvature of the calyces results in a shorter adaxial margin. Eight elongate (up to 0.6 mm), pointed, triangular marginal (circum-operculars of Madsen 1944) scales (Fig. 2D) form a distal crown, below which are 8 smaller, similarly shaped opercular scales, most hidden from view by the marginals (Fig. 2C). Proximal to the marginals are 8 submarginals, which have slightly pointed distal edges; remaining body wall scales have rounded distal edges. Most body wall scales about 0.4 mm in width. Coenenchymal scales elliptical in shape, have flat outer surfaces, and are up to 0.30 in greater diameter; they are arranged in an imbricate fashion (Fig. 2E).

Remarks.—This species was thoroughly described and illustrated by Madsen (1944) in the original description, and thus only an abbreviated description of the newly collected specimen and some SEM illustrations are provided above. The species was transferred to Convexella by Bayer (1996) because its calyces are round in cross-section, four rows of body wall scales can be seen in abaxial view, and the adaxial side of the calyces are fully covered with scales of relatively similar size, all characters that distinguish it from the genus Primnoella (see Cairns Although Madsen's drawing 2006). (Madsen 1944: fig. 31) of the adaxial side of a calyx suggests that there is a naked adaxial region, he explained in the figure caption that this was an artifact of it being cut from the branch. The specimen reported herein is the first since its description, and represents a significant range extension, although the depth of capture is consistent with the types.

Distribution.—New England Seamounts (Lyman Seamount), southwest of Iceland; 2137–2448 m.

Genus Parastenella Versluys, 1906

Stenella.—Wright & Studer, 1889:56 (in part: S. doederleini, S. spinosa).—Kü-

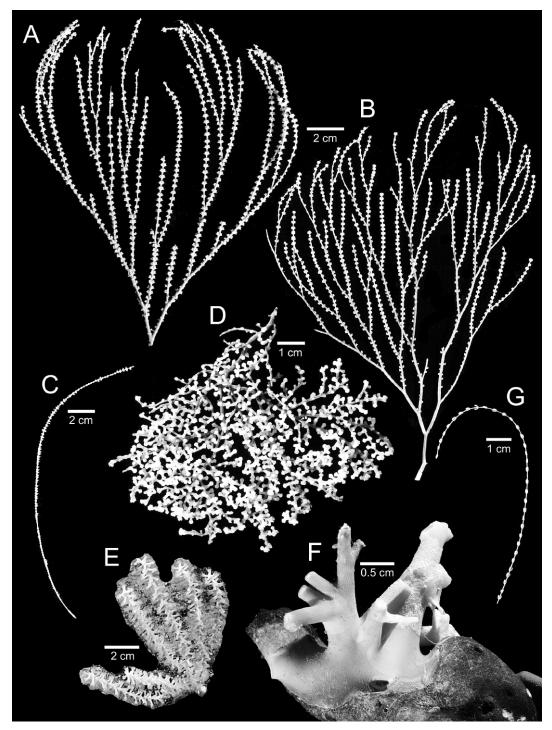


Fig. 1. Whole colony images: A, Calyptrophora antilla, MAN 801-2, USNM 1096713; B, Calyptrophora microdentata, NAS 114-1, USNM 1096712; C, Calyptrophora clinata (typical), holotype, USNM 1096714; D, Parastenella atlantica, holotype, USNM 1096710; E, Paranarella watlingi, holotype in situ, USNM 1096721; F, Narella versluysi, KEL 615-1, USNM 1096709; G, Convexella jungerseni, LYM 202-2, USNM 1096709.

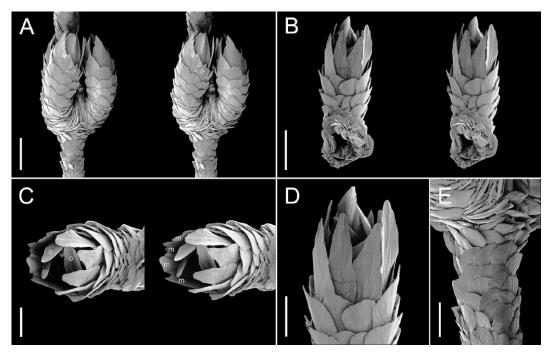


Fig. 2. Convexella jungerseni from LYM 202-2 (USNM 1096709): A, stereo view of a whorl of 3 calyces; B, stereo view of adaxial side of a calyx; C, stereo apical view of a calyx showing eight marginal scales (m) and 3 opercular scales (o); D, apical adaxial view of a calyx showing marginal scales; E, imbricate coenenchymal scales. Scale bars: A, B = 0.5 mm; C-E = 0.25 mm.

kenthal, 1919:443 (in part: *S. doederleini*, *S. spinosa*, *S. ramosa*); 1924:303 (in part).—Aurivillius, 1931:289 (in part).

Stenella (Parastenella) Versluys, 1906:39, 45.

Candidella (Parastenella).—Bayer, 1956: F222, fig. 159, 4a.

Parastenella Bayer, 1981:936 (key to genus).—Bayer & Stefani, 1989:454 (key to genus).

Type species.—Stenella doederleini Wright & Studer, 1889, by subsequent designation (Bayer 1956).

Diagnosis.—Colonies flabellate to slightly bushy, irregularly branched. Calyces arranged in whorls, pairs, or individually, oriented perpendicular to branch. Body wall scales arranged in 8 longitudinal rows, the 8 marginals elongate, highly concave and offset in alignment from the opercular scales. Opercular scales roughly equal in size, with a highly keeled inner surface.

Remarks.—When originally described, Versluys (1906) placed Parastenella as one of four subgenera of Stenella. Subsequently (Bayer 1956, 1981), all four subgenera were raised to genus level based on their differing number of marginal scales. Currently there are four species recognized in the genus: P. doederleini (Wright & Studer, 1889) from Japan, P. spinosa (Wright & Studer, 1889), from the Prince Edward Islands; P. ramosa (Studer, 1894), from Pacific Panama, and P. atlantica (see below), from the New England Seamounts.

Distribution.—Japan, Pacific Panama, Prince Edward Islands, northwest Atlantic; 567–3470 m. Unreported records at the NMNH include: the Aleutian Islands, Pacific Canada, Oregon, California, Hawaii, southern Chile, Macquarie Island, Indonesia, and the Antarctic.

Parastenella atlantica, new species Figs. 1D, 3–5

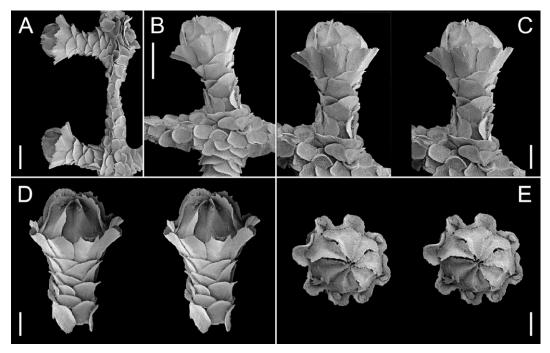


Fig. 3. Parastenella atlantica, holotype, USNM 1096710: A, lateral view of 2 calyces; B, lateral view of a calyx and branch; C, stereo lateral view of a calyx an branch; D, stereo lateral adaxial view of a calyx; E, stereo opercular view of a calyx. Scale bars: A, B = 1 mm; C-E = 0.5 mm.

Material examined.—Types.

Types and type locality.—Holotype: a colony in alcohol and SEM stubs 1266–1270, RB04-04, Hercules dive 13 (RET 108-2), USNM 1096710. Paratypes: 1 colony from the same station (USNM 1096711) and another colony from the same station (YPM 38951). Type Locality: RET 108-2: 39°48.5454′N, 66°14.9883′W (Retriever Seamount, NES), 1984 m, 23 May 2004.

Description.—The holotype (Fig. 1D) is 10 cm in height, 10 cm broad, and is roughly planar, but some branching occurs out of the plane, resulting in a slightly bushy colony; the base is missing, the basal branch diameter being 1.6 mm. The axis is brown to bronze in color, easily seen through the single layer of white, translucent branch coenenchymal scales. Branching is dichotomous and somewhat irregular; distal branches are straight or sometimes curved, rarely longer than 24 mm. Calyces are arranged irregularly on all sides of all branches,

occasionally paired (Fig. 3A) but never in whorls. Calyces are well spaced and project perpendicular to the branch (Fig. 3B, C), up to 2.6 mm in height, and usually have a flared (Fig. 3C) apical diameter (up to 2 mm) twice that of the basal diameter.

Each calyx is protected by 8 marginal, 8 opercular, and 8 rows of body wall scales. The marginal scales have broad bases and elongate, hollowed, fluted tips (Fig. 4B). The marginals are up to 0.85 mm wide at their base and up to 0.85 mm in length, including the apical projection (flute), which is only 0.12-0.25 mm in length and about 0.45 mm wide, these flared apical projections forming a rosette when viewed from above (Fig. 3E). The base of the marginals bear a series of stubby digitate processes, each about 0.12 × 0.12 mm in size. The marginals alternate in position with the operculars, the midline of each marginal bowed outward and covering the junction of a pair of adjacent

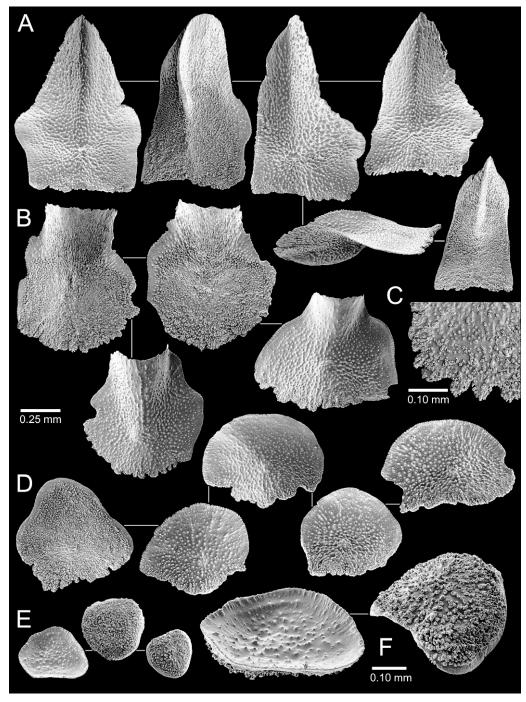


Fig. 4. Sclerites from the holotype of *Parastenella atlantica*, USNM 1096710: A, six opercular scales; B, four marginal body wall scales showing the broad distal flutes; C, enlargement of digitate processes on basal edge of marginal scales; D, five body wall scales; E, three coenenchymal scales; F, greater magnification and oblique views of two coenenchymal scales showing outer concavity of scales. Scale bars: A, B, D, E = 0.25 mm; C, F = 0.1 mm.

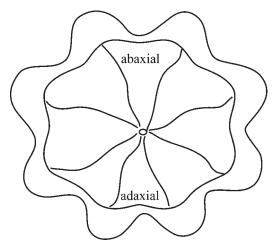


Fig. 5. Parastenella atlantica, holotype, USNM 1096710: Diagram of the opercular view of a calyx showing the offset relation of the marginals to the operculars, and the alignment of the ab- and adaxial operculars on the sagittal axis. Magnification about ×32.

operculars (Figs. 3E, 5). The lateral margins of the marginals are slightly serrate. The remaining body wall scales are broad (0.55–0.85 mm) and semi-circular (0.55-0.70 mm)long), a smooth, curved distal margin but also having digitate processes on their proximal margin; however, occasionally those on the abaxial side have a short apical projection but less developed than that of the marginals. The body wall scales are arranged in 8 longitudinal rows of 3-5 scales but also in alternating transverse rings, each ring having 4 scales, such that successive scales in a longitudinal row are separated by an offset intercalated scale of the adjacent ring. When dried, the body wall scales flare outward.

The opercular scales are triangular, with a longitudinally creased outer surface corresponding to a keeled inner surface (Fig. 4A). The ab- and adaxial operculars are unique (not paired), lying directly on the sagittal axis (Fig. 5). The remaining 6 operculars are termed laterals and are asymmetrical, each having a small shoulder on its lower adaxial margin. Abaxial operculars are up to 1.1 mm in

length, having a L:W of about 1.4. The lateral operculars are 1.0–1.1 mm in length, with a L:W of 1.5–1.6; the adaxial opercular is about 0.8 mm in length, with a L:W of 1.7. The operculum is well developed and easily visible in lateral view.

Coenenchymal scales occur in one thin layer, are elliptical in shape, and highly concave above (Fig. 4F), ranging in size from 0.30–0.55 mm in greater diameter. They are sparsely granular above and tuberculate on their inner surface. Pinnular scales are rare, shaped as rods 60–80 m in length and having a L:W = 5–7.

Comparisons.—Parastenella atlantica differs from the other three species in the genus by having randomly arranged calyces (not in whorls), relatively short calyces, and in having relatively short flutes on the marginal scales. It is the only species of this genus known from the Atlantic Ocean.

Etymology.—Named for the first occurrence of this genus in the Atlantic Ocean.

Distribution.—Known only from the type locality.

Genus Candidella Bayer, 1954

Type species.—*Primnoa imbricata* Johnson, 1862, by monotypy.

Diagnosis.—Colonies uniplanar or flagelliform. Calyces arranged in whorls, each calyx standing perpendicular to the branch. Body wall scales arranged in 2–4 longitudinal rows; only 4 marginal scales. Inner surface of opercular scales keeled.

Distribution.—North Atlantic, Ascension, central and western Pacific; 183–2165 m.

Candidella imbricata (Johnson 1862)

Primnoa imbricata Johnson, 1862:245, pl. 31, figs. 2, 2a.

Candidella imbricata.—Bayer, 1954:296.—Pasternak, 1985: 29 (Rockaway Seamount).—Cairns & Bayer, 2004: 477–

482, figs. 10D, 12D, 13A–G, 14A–D (full synonymy, description).

Material examined.—R/V Ronald Brown 04-04, Hercules dive 11 (KEL5XX), 38°51.1730′N, 63°45.8583′W (Kelvin Seamount, NES), 1959–2004 m, 20 May 2004, several branches, YPM 35396; R/V Ronald Brown 04-04, Hercules dive 6 (MAN 708-3), 38°08.09′N, 61°06.965′W (Manning Seamount, NES), 1718 m, 15 May 2004, 1 colony, YPM 35369.

Types and type locality.—The holotype is deposited at the Natural History Museum, London (1863.1.31.1). A fragment is also at the Zoologische Museum Amsterdam Coel. 3085 (van Soest 1979: 120). Type Locality: Madeira, depth unknown.

Remarks.—This species is well described and illustrated by Cairns & Bayer (2004) and thus will not be redescribed. They also reported it from several New England Seamounts as well as a larger range extending from northern Florida to the Lesser Antilles (including the northern Gulf of Mexico) at depths as shallow as 514 m, and the from northeast Atlantic (815–2165 m). The seamount localities are the deepest of the western Atlantic depths for this species. The specimens reported herein extend its known distribution to Manning Seamount.

Distribution.—New England Seamounts (San Pablo, Muir, Kelvin, Manning), Corner Rise Seamounts (Rockaway); 1718–2063 m.

Genus Calytrophora Gray, 1866

Type species.—Calyptrophora japonica Gray, 1866, by monotypy.

Diagnosis.—Colonies uniplanar or flagelliform. Calyces arranged in whorls, in most species the calyces facing upward. Calyces composed of two annular sclerite rings, each composed of two inseparably fused scales; a pair of crescent-shaped infrabasals is usually present. Distal margin of body wall scales often spinose. Operculum composed of 8 triangular

scales each usually having a longitudinal keel on inner surface. Coenenchymal scales elongate and flat.

Remarks.—Bayer (2001) divided the 13 species in this genus into two species complexes: the "japonica-complex" consisting of 10 species with calyces facing upward, and the "wyvillei-complex" consisting of the remaining three species with calyces facing down. He further divided the japonica-complex into two species groups: one having marginal spines on the basal scales (8 species) and the other lacking marginal spines (2 species). Two of the three species from the New England Seamounts belong to the species having marginal spines in the japonicacomplex; the new species belongs to the wyvillei-complex. C. microdentata, collected at 2310 m, represents the deepest record of this genus to date.

Distribution.—Indian, Pacific and Atlantic Oceans; 229–2310 m.

Calyptrophora microdentata Pasternak, 1985 Figs. 1B, 6A–E

Calyptrophora microdentata Pasternak, 1985:30–32, figs. 3–4.—Bayer, 2001:374 (mention).

Calytrophora pillsburyae Bayer, 2001: 370–374, fig. 3.

Material examined.—RB05-03, Hercules dive 10 (NAS 114-1), 34°34.75′N, 56°50.47′W (Nashville Seamount, NES), 2119 m, 24–25 Aug 2005, 1 complete colony, SEM 1254, USNM 1096712; R/V Ronald Brown 04-04, Hercules dive 10 (KEL 402-1), 38°46.7305′N, 63°57.7797′W (Kelvin Seamount, NES), 2310 m, 18 May 2004, 3 branches, YPM 35400; part of holotype of C. microdentata (Fig. 6A, D); holotype of C. pillsburvae.

Types and type locality.—The holotype of *C. microdentata* is deposited at the Institute of Oceanology, Moscow, and a fragment of the type and SEM stub

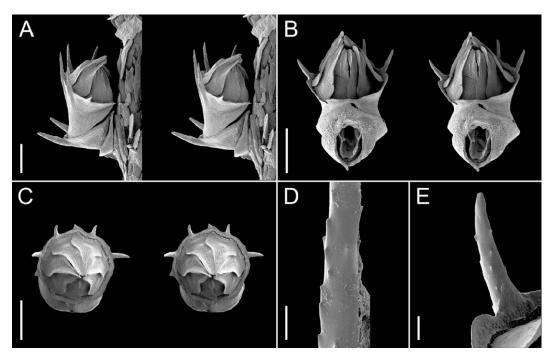


Fig. 6. Calyptrophora microdentata (A, D, holotype, USNM 1097263; B–C, E, NAS 114-1, USNM 1096712): A, stereo lateral view of a calyx; B, stereo adaxial view of a calyx; C, stereo opercular view of a calyx; D–E, portion of spines on basal scale, showing them to be unridged. Scale bars: A–C = 0.5 mm; D, E = 50 m.

1263 are deposited at the USNM 1097263. Type Locality: *Vityaz* 80B (not 80b, pers. comm., Tina Molodtsova): 35°38.8′N, 52°03.2′W (Rockaway Seamount, CRS), 1940–2040 m.

The holotype of *C. pillsburyae* is deposited at the USNM (52743). Type Locality: 16°55′N, 62°43′W (west of Montserrat, Lesser Antilles), 686–1125 m.

Remarks.—After describing Calyptrophora pillsburyae from a similar locality and depth to that of C. microdentata, Bayer (2001) suggested that his species might be a junior synonym, but differentiated it as having calyces in whorls of 4 or 5, whereas those of C. microdentata were paired. He did not have access to the type of C. microdentata at that time. Examination of the type of C. microdentata shows that the calyces are often arranged in whorls of three, the third calyx often missing and thus appearing as two. Also, the buccal spines (Fig. 6A),

stated by Pasternak to be only 0.1 mm in length and probably the basis for the name of the species, are often as long as 0.5 mm, which may have also misled Bayer. The basal spines of the holotype of *C. microdentata* are sometimes even longer (up to 0.6 mm). Direct comparison of the types of the two species shows them to be synonymous.

Because this species was recently described and well figured as *C. pillsburyae*, it will not be redescribed. Its diagnostic characters are listed in Table 1 and illustrated in Fig. 6. The complete colony from NAS 114-1 is 21 cm tall and 15 cm wide, larger than the type of *C. microdentata* but not as tall as the holotype of *C. pillsburyae*, but wider and a more complete specimen. It differs from the type of *C. microdentata* only in having shorter body wall spines.

Distribution.—Lesser Antilles, New England Seamounts (Nashville and Kel-

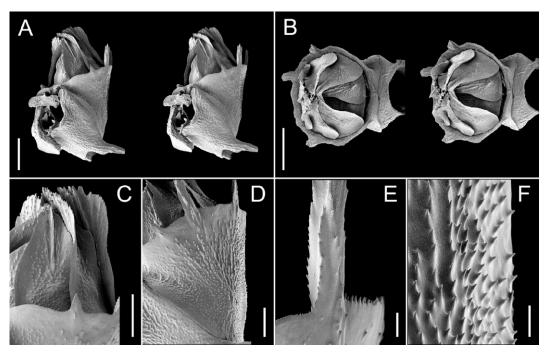


Fig. 7. Calyptrophora antilla from MAN 801-2, USNM 1096713: A, stereo lateral view of a calyx; B, stereo opercular view of a calyx; C, lateral view of the operculum of a calyx; D, lateral view of a buccal scale; E, serrate, ridged apical spine of a buccal scale; F, spination on outer surface of a buccal scale. Scale bars: A, B = 0.5 mm; C, D = 0.25 mm; E, F = 50 m.

vin), Corner Rise Seamounts (Rockaway), 686–2310 m.

Calyptrophora antilla Bayer, 2001 Figs. 1A, 7A–F

Calyptrophora antilla Bayer, 2001:374–375, fig. 4.

Material examined.—RB04-04, Hercules dive 7 (MAN 801-2), 38°08.843'N, 61°05.869'W (Manning Seamount, NES), 1692 m, 16 May 2004, 1 large colony and SEM stub 1255, USNM 1096713; Alvin 3905 (BEA110-1), 39°53'42"N, 67°23'07"W (Bear Seamount, NES), 1684 m, 17 Jul 2003, 1 branch, USNM 1083871; syntypes.

Types and type locality.—Several badly damaged syntype branches (most calyces detached), presumably of the same colony are deposited at the USNM (52914). Type Locality: 20°09′N, 73°29′W (Windward

Passage between Cuba and Haiti), 1399 m.

Comparisons.—This species differs from all other Atlantic species by the combination of characters of being branched and having ridged body wall scale spines (see Table 1).

Remarks.—Because this species was recently described and well figured, it is not redescribed. Its diagnostic characters are listed in Table 1 and illustrated in Fig. 7. The complete colony from MAN 801 (Fig. 1A) is 18 cm tall and 16 cm wide, much larger and in better condition than the type material. As with the New England records of *C. microdentata*, it differs from the type material only in having slightly smaller calyces (1.6–1.8 mm vs 1.8–2.1 mm in length for the syntypes). This represents a substantial geographic range extension for this species.

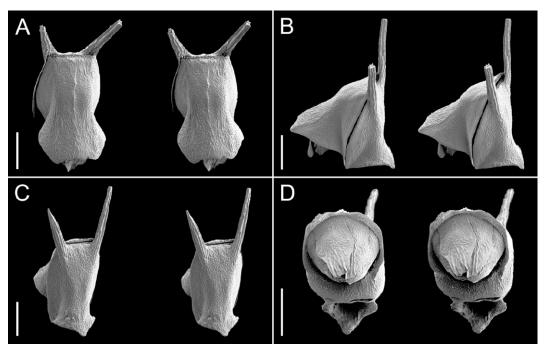


Fig. 8. Calyptrophora clinata, stereo views of calyces from the holotype, USNM 1096714: A, abaxial view of buccal scale showing abaxial fusion of scales, elongate basal spines, and smooth edged buccal scales; B, lateral view of a calyx showing downward slant of buccal scales; C, abaxial view of the basal scale; D, opercular view of a calyx. Scale bars all 0.5 mm.

Distribution.—Greater Antilles (type locality) and New England Seamounts (Bear, Manning); 1399–1692 m.

Calyptrophora clinata, new species Figs. 1C, 8–10

Material examined.—Types.

Types and type locality.—Holotype: RB05-03, Hercules dive 5 (VER 101-2), colony and SEM stubs 1256-1259, 1262, USNM 1096714. Paratypes (variety): *RB*05-03, *Hercules* dive 9 (KUK 207-1), 35°33.41′N, 51°48.88′W (Kükenthal Peak, CRS), 1842 m, 22 Aug 2005, 1 branch and SEM stubs 1260–1261, USNM 1096715 and 1 branch, YPM 38952; RB05-03, Hercules dive 9 (KUK 222-1), 35°33.32′N, 51°49.55′W (Kükenthal Peak, CRS), 1436 m, 23 Aug 2005, 1 branch, USNM 1096716; *RB*05-03, *Hercules* dive 9 (KUK 225-3), 35°33.34′N, 51°49.58′W (Kükenthal Peak, CRS), 1315 m, 23 Aug 2004, 1 short branch, USNM 1096717. Type Locality:

VER 101-2: 34°39.82′N, 49°49.01′W (Verrill Peak of Caloosahatchee Seamount, CRS), 1316 m, 18 Aug 2005.

Description.—The holotype (Fig. 1C) is 24 cm long and has a basal axis diameter of 0.85 mm, but the colony is not complete in that is lacks the holdfast. Based on the personal observation of L. Watling during collection, it would appear to be a flagelliform (unbranched) colony. The axis is golden in color and faintly longitudinally striate. Calyces are arranged in whorls of 5-7 and face downward. There are 16-18 whorls per 3 cm branch length and the whorl diameter is about 4.5 mm. Whereas the basal scales are perpendicular to the branch, the abaxial side of the fused buccal scales slope at a 45° angle toward the branch axis (Fig. 8B), the tips of the opercular scales usually touching the coenenchymal sclerites. This tends to foreshorten the length of the calyces,

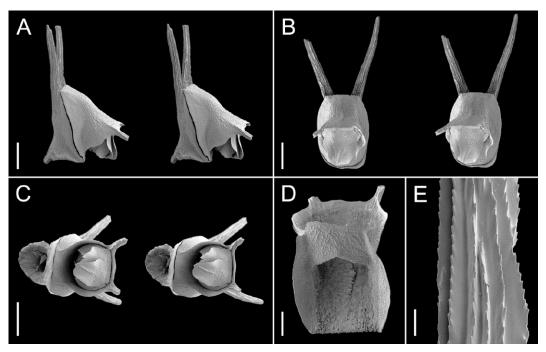


Fig. 9. Calyptrophora clinata var., KUK 207-1, USNM 1096715: A, stereo lateral view of a calyx showing long basal spines; B, stereo abaxial view of a calyx showing well-developed buccal and basal spines; C, stereo adaxial/opercular view; D, adaxial view of a detached buccal showing complete adaxial fusion of sclerites; E, portion of serrate, ridged basal spine. Scale bars: A-C = 0.5 mm; D = 0.25 mm; E = 50 mm.

which are only 1.3–1.4 mm in length, despite a buccal sclerite length of 1.3 mm.

Each calvx is encased in two pairs of solidly fused ring-like scales (i.e., the basals and buccals), the symphyses not detectable on either adaxial or abaxial side. The basal scales (Figs. 8C, 10B) are up to 1.25 mm in height, and bear a pair of thin, elongate, pointed spines on their anterolateral margins. These spines are often broken, but a fully intact spine measures up to 0.9 mm (and rarely up to 1.4 mm) in length, 0.15 mm in basal diameter, and bears finely serrate ridges for its entire length (Figs. 9E, 10D). At the base there are about 10 ridges but toward the tip these reduce to about 5. The base of the abaxial side of the fused basal is produced as a triangular projection (Figs. 8B-D). Its center is a circular hole through which the polyp passes (Fig. 10B). The downward sloping buccal scales are slightly longer (up to 1.3 mm) and also have a curved dorsolateral edge and a flat adaxial platform adjacent to the basal scale (Figs. 9D, 10E). The distal edge of the buccal scales is often straight, or sometimes produced into two blunt, triangular teeth (0.10 mm tall), and in rare cases (<10%) project as two slender, ridged, serrate spines up to 0.55 mm in length (Fig. 10E). The body wall scales are covered on their outer surfaces with a fine anteriorly directed spination. Crescent-shaped infrabasal scales (Fig. 10F) up to 0.2 mm in height join the basals to the coenenchymal scales, although invariably they remain attached to the branch when a calvx is detached, unlike the condition for the branching species of this genus.

The operculars (Figs. 8D, 10A) are roughly triangular in shape with a blunt apex, and are fairly flat. The distal part of

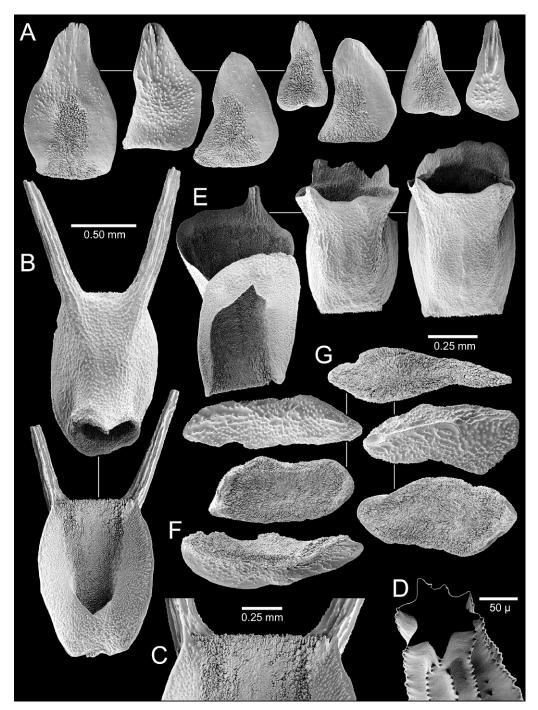


Fig. 10. Sclerites from the holotype of *Calyptrophora clinata*, USNM 1096714: A, seven opercular scales showing a lack of a keel on the inner side; B, ab- and adaxial view of fused basal scales showing ridged spines; C, enlargement of distal inner region of a basal scale; D, broken basal spine showing serrate ridged surface; E, ad- and abaxial views of three buccal scales showing complete fusion of sclerites; F, an infrabasal scale; G, five coenenchymal scales. Scale bars: A, C, F–G, 0.25 mm; B, E, 0.5 mm; D, 50 mm.

their upper surface often bear several parallel ridges, whereas their inner surface is not keeled, but smooth distally and tuberculate proximally. There is one large symmetrical abaxial opercular, 6 asymmetrical adaxial operculars, and one symmetrical adaxial opercular. The abaxial opercular is up to 0.8 mm in length, with a L:W of 1.7; the laterals up to 0.65 mm in length (L:W = 1.7-1.9); and the adaxial opercular 0.45-0.50 mm in length (L:W = 1.5-1.7).

The coenenchymal scales (Fig. 10G) are elongate (up to 1.1 mm long), somewhat irregular in shape, and quite thick. Their outer surface is granular and flat but may bear a very low ridge.

Comparisons.—Because of its downward facing calyces, *C. clinata* belongs to the *wyvillei*-complex of species, which includes only *C. wyvillei* Wright, 1885 and *C. agassizii* Studer, 1894, both of which differ in being branching species and in having significantly different calyx architecture.

Only two species of *Calyptrophora* are known to have unbranched colonies, both in the *japonica*-complex of species: *C. juliae* Bayer, 1951 and an undescribed species from New Caledonia (see Bayer 2001). *Calyptrophora clinata* differs from both species in the morphology of its calyces and slender basal spines; furthermore, the calyces of *C. juliae* face in the upward direction.

Remarks.—The three paratypes from Kükenthal Peak (Fig. 9A–E) consistently differ from the holotype in several minor aspects but are otherwise identical to the type and are thus considered to be a variety of the typical form. The differences are one of degree (Table 1), the variety having longer basal spines (up to 2.0 mm, Fig. 9A, B) and the consistent presence of buccal spines (Fig. 9B), some as long as 0.8 mm but usually much shorter. The typical form has basal spines up to 0.9 mm in length (rarely up to 1.4 mm), and usually lacks buccal spines,

but in a small percentage (<10%) of calyces a pair of buccal spines is present, some as long as 0.55 mm. Because of the similarity of these specimens and the variation found on the holotype, the specimens with longer spines from Kükenthal Peak are considered to be a long-spined variety, not a distinct species or subspecies.

257

Etymology.—The species name is from the Latin *clinatus*, meaning sloped or slanted, and refers to the sloped abaxial margin of the buccal body wall scales.

Distribution.—Corner Rise Seamounts (Verrill and Kükenthal Seamounts), 1315–1842 m.

Genus Narella Gray, 1870

Narella Gray, 1870:49.—Cairns & Bayer, 2003:618–619.—Cairns & Baco, 2007.
—Cairns & Bayer, 2007: (includes a list of all species and a more complete synonymy of the genus).

Type species.—Primnoa regularis Duchassaing & Michelotti, 1860, by monotypy.

Diagnosis.—Colonies dichotomously or pinnately branched in one plane, or slightly bushy, or unbranched. Calyces arranged in whorls or pairs facing downward. Calyces protected by 3 or 4 pairs of large abaxial body wall scales (basal, medial, buccal), and 1 or 2 pairs of adaxial buccal scales. Operculum consists of 8 triangular scales, each with a longitudinal keel on its inner surface. Coenenchymal scales usually elongate, flat and granular or highly crested.

Remarks.—Narella is the most diverse of the primnoid genera, with 38 species (Cairns & Bayer 2007). Faunistic revisions of this genus have recently been published by Cairns & Bayer (2003), the western Atlantic species; Cairns & Baco (in press), the Alaskan species; and Cairns & Bayer (2007), the Hawaiian species.

Distribution.—Known from all ocean basins from 55–4594 m.

Narella versluysi (Hickson 1909) Fig. 1F

Stachyodes versluysi Hickson in Stephens, 1909:10–13.

Narella versluysi.—Deichmann, 1936:171.
—Cairns & Bayer, 2003:635–641,
Figs. 1F, 9A–C, 10A–D, 14 (complete description and full synonymy).

Material examined.—RB05-03, Hercules dive 15 (KEL 615-1), 38°45.95′N, 64°05.43′W (Kelvin Seamount, NES), 2118 m, 31 Aug 2005, 14 branch fragments and 3 basal pieces, USNM 1096718.

Types and type locality.—Five syntypes are deposited at the Natural History Museum, London (1962.07.20.172). Type Locality: off Ireland, 698–914 m.

Comparisons.—The western Atlantic species of Narella are keyed and compared by Cairns & Bayer (2003). N. versluysi differs from N. alvinae by having non-ridged coenenchymal scales and much lower distal basal scale lobes.

Remarks.—This species is well described and illustrated by Cairns & Bayer (2003) and thus is not redescribed. The specimens reported herein consist of 14 branch fragments, some as long as 12 cm, and three basal segments, showing that contrary to previously thought, this species is not exclusively unbranched but within 1 cm of the attachment may produce several branches from about the same level (Fig. 1F). Also, whereas the basal scales were described by Cairns & Bayer (2003) as having no dorsolateral ridge, in about 10% of the calyces examined there is a small, short ridge on the basal scales.

Distribution.—Previously known from the northeast Atlantic and the western Atlantic from the Straits of Florida and Bermuda at depths of 550–3100 m, it was not unexpected to find this species on Kelvin Seamount at 2118 m.

Narella alvinae Cairns & Bayer, 2003

Narella alvinae Cairns & Bayer, 2003:632–635, Figs. 6E–I, 7, 8A–D.

Material examined.—Alvin 3904 (KEL 201-4 and 5), 38°51.60′N, 63°54.847′W (Kelvin Seamount, NES), 2172 m, 16 Jul 2003: 2 branch fragments of 12 and 15 cm length (USNM 1096719–20), and 2 branches of 3.5 and 3.0 cm length (YPM 28603 and 28604).

Types and type locality.—The holotype is deposited at the Royal Ontario Museum (B3521) and some branches from the same colony are at the USNM (100778). Type Locality: 32°35′N, 64°55′W (25 km northwest of Bermuda), 3419 m

Remarks.—This species was well described and illustrated by Cairns & Bayer (2003) and thus is not redescribed. All of the branches reported herein are distal, unbranched segments. These specimens differ from the type only in lacking discrete dorsolateral ridges on the basal scales.

Distribution.—This is the second report of this species, extending its known distribution from Bermuda to Kelvin Seamount and from 3419–2172 m.

Genus Paranarella, new genus

Type species.—*Paranarella watlingi*, here designated. Gender: feminine.

Diagnosis.—Colonies uniplanar, with long terminal branches all originating from near base. Calyces arranged in whorls, but orientation unknown. Body wall sclerites consist of 5 abaxial pairs, 1 pair of outer- and inner-lateral marginals, and 3 or 4 pairs of small adaxial scales, the lower adaxial body wall naked. Operculum consists of 8 longitudinally creased and keeled scales. Coenenchymal scales prominently keeled. Axis smooth and flattened in cross section.

Remarks.—The arrangement and number of body wall scales (i.e., 5/1/1/3-4, abaxial, OL, IL, adaxial, respectively) and a strict interpretation of the generic key of Bayer (1981) would place this taxon as a Callogorgia. However, other characters, such as its non-pinnate branching, dimorphic abaxial body wall scales, discrete

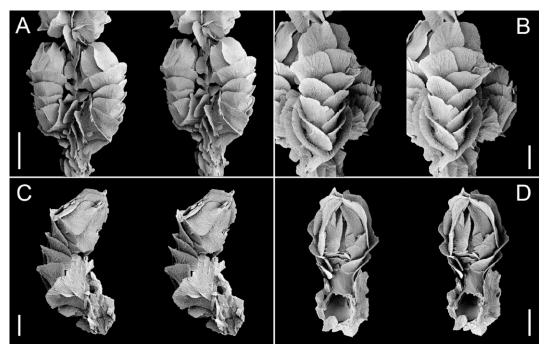


Fig. 11. Paranarella watlingi, stereo views of calyces from the holotype, USNM 1096721: A, lateral view of a whorl of three calyces; B, abaxial view of a calyx; C, lateral view of a calyx; D, adaxial view of a calyx showing bare region. Scale bars: A = 1 mm; B-D = 0.5 mm.

number of body wall scales, keeled coenenchymal scales, dorso-lateral ridging of the basal abaxial scales, and great depth of capture, are outside the definition of *Callogorgia* but favor the closely related genus *Narella*. It differs from all species in *Narella* in having one pair of OL and IL marginal scales (*Narella* has none), five pairs of abaxial body wall scales (*Narella* has 3 or 4 pairs), and a smooth, flattened axis (*Narella* has a striated round axis).

Etymology.—Named Paranarella because of its similarity to the genus Narella.

Distribution.—New England Seamounts; 3855 m.

Paranarella watlingi, new species Figs. 1E, 11–12

Material examined.—Type.

Types and type locality.—Holotype: RB05-03, Hercules dive 13 (RET 102-1), 3 branches from the same colony (7, 3.5,

and 3.5 cm in length) and SEM stubs 1271–1273, USNM 1096721. Type Locality: 39°45.0754′N, 66°14.9408′W (Retriever Seamount, NES), 3855 m, 23 May 2004.

Description.—Judging from an in situ photograph of the holotype taken before collection (Fig. 1E), the colony would appear to have been approximately 9 cm tall, consisting of 6 long branches roughly arranged in a plane, each branch originating within 1 cm of the base. The distal branches are 6–7 cm long; only 3 of these branches where collected, not including the basal branch. The axis is goldenyellow in color and smooth, the calyces white. The axis is flattened in crosssection, e.g., 0.95×0.52 mm in diameter. Calyces are arranged in whorls of 4 or 5, and as evidenced form the in situ photograph, are oriented perpendicular to the axis, but in the preserved state curve close to the branch axis; their orientation is unclear. There are about 9 whorls per

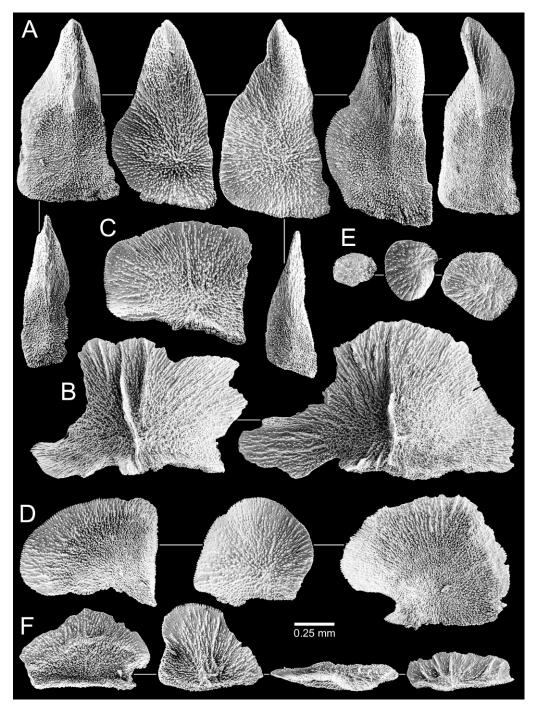


Fig. 12. Sclerites from the holotype of *Paranarella watlingi*, USNM 1096721: A, seven opercular scales; B, two basal scales showing dorsolateral ridges; C, a body wall scale adjacent to basal scale; D, three abaxial body wall scales; E, three adaxial body wall scales; F, four coenenchymal scales. Scale bars all 0.25 mm.

3 cm branch length and the whorls are very closely spaced (0–0.3 mm apart); the whorl diameter is about 3 mm. Individual calyces are 2.9–3.4 mm in length.

Each calyx is encased in 5 pairs of abaxial body wall scales, 1 pair of outerand inner-lateral buccal (=marginal) scales, and 3-4 pairs of small adaxial body wall scales, the lower half of the adaxial body wall being (Fig. 11D). The abaxial body wall scales consist of a large basal pair and 4 pairs of smaller scales, occasionally a sixth unpaired scale being present (Fig. 11B). The basal abaxial scales (Fig. 12B) are tall (up to 0.95 mm) and curve around the base of the calyx but do not meet on the adaxial side; at the dorsolateral margin they bear 1-3 prominent ridges. The abaxial body wall scale directly adjacent to the basal scale (Fig. 12C) may also have a small dorsolateral ridge, but the remaining abaxial scales are shorter (0.6-0.8 mm tall) and are not as wide as the basals. having a gently curved dorsolateral edge (Fig. 12D). The outer- and inner-lateral buccal (marginal) scales are similar in size and shape to the abaxial marginal body wall scales. The 3-4 pairs of adaxial body wall scales are rectangular, flat, and much smaller, those closest to the operculum being 0.45 mm in greater width, those farther away only 0.25 mm in width. The distal edges of the body wall scales, as well as the operculars and coenenchymal scales, are finely serrate, having about 10 small teeth per 0.1 mm.

The opercular scales (Fig. 12A) are triangular, with a longitudinally highly creased outer surface corresponding to an apically keeled inner surface. The symmetrical adaxial operculars are up to 1.2 mm in length and have a L:W of about 1.75. The asymmetrical lateral operculars are 1.1–1.3 mm in length, with a L:W of 1.9–2.0. The small, narrow, sharp adaxial operculars are only 0.8–0.9 mm in length, with a L:W of 2.7–3.1. The operculum is easily visible in lateral view.

The coenenchymal scales (Fig. 12F) are elongate and up to 0.75 mm in length, each bearing a single, medially placed crest that sometimes reaches up to 0.55 mm tall, the crest laterally ridged and distally serrate. Tentacular sclerites were not observed.

261

Etymology.—This species is named in honor of Les Watling, for his pioneering work on the invertebrate fauna of the New England Seamounts (Watling & Auster 2005).

Distribution.—Known only from the type locality.

Zoogeography

In attempting to explain the disjunct distribution of animals found on Bear Seamount and otherwise distant locations in the North Atlantic, Moore et al. (2004) suggested three dispersal routes that larvae may have followed: 1) coming from the south (e.g., Caribbean and Gulf of Mexico) via eddies of the northward flowing Gulf Stream, 2) coming from the north (e.g., Labrador Sea region) via the Deep Western Boundary Current, and 3) coming from the east on seamount stepping stones, such as the Mid-Atlantic Ride, Corner Rise Seamounts and finally the NES. Although there are very few records of NES primnoids, it is tempting to speculate that two species, Calyptrophora microdentata and C. antilla, may conform to the first option, although the depth of the Gulf Stream does not extend to the tops of the shallowest seamounts of the NES. One species, Convexella jungerseni, is a good candidate for option two, the southward flowing Deep West Boundary Current, and Thouarella grasshoffi, found on both sides of the North Atlantic, may have arrived on stepping stones. Another two species, Candidella imbricata and Narella versluysi occur in the northeast and northwest Atlantic as well as the Caribbean, and thus could fit either mode 1 or 2. Finally, four species are thus far

known only from the NES and CRS and in some cases adjacent Bermuda: *Calyptrophora clinata*, *Parastenella atlantica*, *Paranarella watlingi*, and *Narella alvinae*.

Acknowledgments

I would like to thank Les Watling for making available most of the specimens used in this study, which were collected on two expeditions: "Mountains of the Sea" and "Deep Atlantic Stepping Stones", both funded by the NOAA Ocean Exploration Program. I also thank Eric Lazo-Wasem for loaning additional specimens from the YPM, and Tina Molodtsova for gifting comparative material of Calyptrophora described by Pasternak. I am, as always, grateful to Tim Coffer for his Photoshop arrangement and enhancement of the figures, and to Frederick Bayer, for access to his extensive comparative SEM files.

Literature Cited

- Aurivillius, M. 1931. The Gorgonarians from Dr. Sixten Bock's expedition to Japan and Bonin Islands 1914.—Kungliga Svenska Vetenskaps-Akademiens Handlingar (3)9(4):337 pp., 65 figs., 6 pls.
- Bayer, F. M. 1954. New names for two genera of Octocorallia.—Journal of the Washington Academy of Sciences 44(9):296.
- 1956. Octocorallia. Pp. F166–189, 192–231. in R. C. Moore, ed., Treatise on Invertebrate Paleontology. University of Kansas Press, Lawrence, 498 pp.
- 1981. Key to the genera of Octocorallia exclusive of Pennatulacea (Coelenterata: Anthozoa), with diagnoses of new taxa.—Proceedings of the Biological Society of Washington 94:902–947.
 - —. 1996. The Antarctic genus *Callozostron* and its relationship to *Primnoella* (Octocorallia: Gorgonacea: Primnoidae).—Proceedings of the Biological Society of Washington 109: 150–203.
- 2001. New species of Calyptrophora (Coelenterata: Octocorallia: Primnoidae) from the western part of the Atlantic Ocean.—Proceedings of the Biological Society of Washington 114:367–380.

- —, M. Grasshoff and J. Verseveldt, eds. 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. E. J. Brill, Leiden, 75 pp.
- ———, & J. Stefani. 1989. Primnoidae (Gorgonacea) de Nouvelle-Calédonie.—Bulletin de Muséum national d'Histoire naturelle, Paris (4) 10(3): 449–518, 1 fig., 42 pls.
- Cairns, S. D. 2006. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 6. The genera *Primnoella* Gray, 1858; *Thouarella* Gray, 1870; *Dasystenella* Versluys, 1906.—Proceedings of the Biological Society of Washington 119:161–194.
- ———, & A. Baco. 2007. A review of the Alaskan species of *Narella* (Octocorallia: Primnoidae), with the description of five new species.—

 Systematics and Biodiversity (in press).
- ———, & F. M. Bayer. 2003. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 3: The genus *Narella* Gray, 1870.—

 Proceedings of the Biological Society of Washington 116:617–648.
- ———, &———. 2004. Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 5: The genera *Plumarella* Gray, 1870; *Acanthoprimnoa*, n. gen.; and *Candidella* Bayer, 1954.—Proceedings of the Biological Society of Washington 117:447–487.
- ———, & ———. 2005. A review of the genus *Primnoa* (Octocorallia: Gorgonacea: Primnoidae), with the description of two new species.—Bulletin of Marine Science 77:225–256.
- ———, &———. 2007. A review of the Octocorallia (Cnidaria: Anthozoa) from Hawaii and adjacent seamounts. Part 1. The genus *Narella* Gray, 1870.—Pacific Science (in press).
- Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean.—Memoirs of the Museum of Comparative Zoology at Harvard College 53:317 pp., 37 pls.
- Gray, J. E. 1866. Description of two new forms of gorgonioid corals.—Proceedings of the Zoological Society of London 1866:24–27.
- ——. 1870. Catalogue of the Lithophytes or Stony Corals in the Collection of the British Museum. British Museum, London, 51 pp.
- Hickson, S. J. 1909. Description of a new species of Stachyodes.—Fisheries, Ireland, Scientific Investigations 1907 5:10–13.
- Houghton, R. L., J. R. Heirtzler, R. D. Ballard, & P. T. Taylor. 1977. Submersible observations of the New England Seamounts.—Naturwissenschaften 64:348–355.
- Johnson, J. Y. 1862. Descriptions of two new corals from Madeira, belonging to the genera *Primnoa* and *Mopsea*.—Proceedings of the Zoological Society of London 1862:245–246, pl. 31.

- Kükenthal, W. 1919. Gorgonaria.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898–1899 13(2):946 pp., pls. 30–89.
- 1924. Coelenterata: Gorgonaria. Das Tierreich 47. Walter de Gruyter and Co., Berlin, 478 pp.
- Madsen, F. J. 1944. Octocorallia.—The Danish *Ingolf*-Expedition 5(13):65 pp., 1 pl.
- Moore, J. A., M. Vecchione, B. B. Collette, R. Gibbons, & K. E. Hartel. 2004. Selected fauna of Bear Seamount (New England Seamount Chain), and the presence of "natural invaders" species.—Archive of Fishery and Marine Research 51(1–3):241–250.
- ——, et al. 2003. Biodiversity of Bear Seamount, New England Seamount Chain: results of exploratory trawling.—Journal of Northwest Atlantic Fisheries Science 31:363–372.
- Pasternak, F. A. 1985. Gorgonarians and antipatharians of the seamounts Rockaway, Atlantis, Plato, Great-Meteor and Josephine (Atlantic Ocean).—Trudy Institute Okeanology 120:21–38, 4 figs. (in Russian).

- Soest, R. W. M. von. 1979. A catalogue of the coelenterate type specimens of the Zoological Museum of Amsterdam. 4. Gorgonacea, Actiniaria, Scleractinia.—Beaufortia 29(353): 81–126, 2 pls.
- Versluys, J. 1906. Die Gorgoniden der Siboga-Expedition. II. Die Primnoidae.—Siboga-Expeditie 13a:187 pp., 10 pls., 1 map.
- Watling, L., & P. J. Auster. 2005. Distribution of deep-water Alcyonacea of the northeast coast of the United States. Pp. 279–296 in A. Freiwald and J. M. Roberts, eds., Cold-Water Corals and Ecosytems. Springer-Verlag, Berlin.
- Wright, E. P., & T. Studer. 1889. Report on the Alcyonaria collected by *H.M.S. Challenger* during the years 1873–76.—Report on the Scientific Results of the Voyage of *H.M.S. Challenger* during the years 1873–76, Zoology 31(64):314 pp., 43 pls.

Associate Editor: Stephen L. Gardiner