Calcaxonian Octocorals (Cnidaria; Anthozoa) from Eastern Pacific Seamounts

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Eleven calcaxonian gorgonians are reported from seamounts in the Northeast Pacific, including eight new records for this region, six of which are described as new species. Twenty-one calcaxonians are now known from the Northeast Pacific (exclusive of Alaska). A table of comparisons is given for all six species of *Parastenella* and the three eastern Pacific species of *Calyptrophora*. A neotype is designated for *Chrysogorgia fruticosa*.

Calcaxonian octocorals (those species belonging to the five families Chrysogorgiidae, Primnoidae, Isididae, Ifalukellidae, and Ellisellidae) appear to be one of the few monophyletic groups within the octocorals, supported by both morphological (Grasshoff 1999) and molecular (McFadden et al. 2006) characters. Five hundred fifty-two of the approximately 3100 known octocoral species (17%) are calcaxonians, most of those occurring in deep water. However, surprisingly few have been reported from the Northeast Pacific, a review of the literature revealing only 13 species. Over half of those species were reported by Studer (1894) from tropical East Pacific localities, such as the Galápagos and the Gulf of Panama; those and the reminder are listed in Table 1. In this paper eight new records (including six new species) and three additional records of previously reported species are reported, raising the number of Northeast Pacific calcaxonians to 21 species. Judging from additional unidentifiable fragmentary material, there would appear to be more deep-water species from these East Pacific seamounts.

**MATERIALS AND METHODS**

Most of the specimens reported herein resulted from collections made in 2006 on seamounts off Washington, Oregon, and California by MBARI staff using the ROV *Tiburon*. Additional specimens were donated by James Boutillier (Pacific Biological Station, Nanaimo) from seamounts off British Columbia, and by Amy Baco (WHOI) from Alaskan seamounts.

TABLE 1. Calcaxonian octocorals known from the eastern Pacific north of the Equator (exclusive of Alaska).

<table>
<thead>
<tr>
<th>Name</th>
<th>Reported by</th>
<th>East Pacific Distribution</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Family Chrysogorgiidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chrysogorgia fruticosa</td>
<td>Studer (1894), herein</td>
<td>Gulf of Panama, off Pacific Mexico</td>
</tr>
<tr>
<td>C. pinnata, sp. nov.</td>
<td>herein</td>
<td>Davidson Seamount</td>
</tr>
<tr>
<td>C. monticola, sp. nov.</td>
<td>herein</td>
<td>off California and Washington</td>
</tr>
<tr>
<td>Iridogorgia sp.</td>
<td>herein</td>
<td>Davidson Seamount</td>
</tr>
<tr>
<td><strong>Family Primnoidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphilaphis abietina</td>
<td>Studer (1894)</td>
<td>off Ecuador</td>
</tr>
<tr>
<td>Callogorgia flabellum</td>
<td>Studer (1894)</td>
<td>Gulf of Panama, off Pacific Mexico</td>
</tr>
<tr>
<td>C. kinoshitae Kükenthal, 1913</td>
<td>Studer (1913)</td>
<td>off California</td>
</tr>
<tr>
<td>C. sertosa (Wright &amp; Studer, 1889)</td>
<td>Nutting (1909)</td>
<td>off California</td>
</tr>
<tr>
<td>Calyptrophora agassizii</td>
<td>Studer (1894)</td>
<td>Galápagos</td>
</tr>
<tr>
<td>C. sp. cf. C. antilla</td>
<td>herein</td>
<td>Davidson Seamount</td>
</tr>
<tr>
<td>C. bayeri, sp. nov.</td>
<td>herein</td>
<td>Davidson Seamount</td>
</tr>
<tr>
<td>C. laevispinosa, sp. nov.</td>
<td>herein</td>
<td>off Washington</td>
</tr>
<tr>
<td>Narella ambigua (Studer, 1894)</td>
<td>Studer (1894)</td>
<td>Galápagos</td>
</tr>
<tr>
<td>N. bowersi (Nutting, 1908)</td>
<td>Cairns &amp; Bayer (2007), herein</td>
<td>off British Columbia and Washington</td>
</tr>
<tr>
<td>Parastaenella gymnogaster, sp. nov.</td>
<td>herein</td>
<td>Oregon to Alaska</td>
</tr>
<tr>
<td>P. pacifica, sp. nov.</td>
<td>herein</td>
<td>Oregon to British Columbia</td>
</tr>
<tr>
<td>P. ramosa (Studer, 1894)</td>
<td>Studer (1894), herein</td>
<td>Panama to Alaska</td>
</tr>
<tr>
<td>Plumarella longispina</td>
<td>Nutting (1909)</td>
<td>off California</td>
</tr>
<tr>
<td>Primnoa pacifica Kinoshita, 1907</td>
<td>Cairns &amp; Bayer (2005)</td>
<td>California to Alaska</td>
</tr>
<tr>
<td>P. pacifica willey Hickson, 1915</td>
<td>Hickson (1915)</td>
<td>off British Columbia</td>
</tr>
<tr>
<td><strong>Family Isididae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepidisis evalinae</td>
<td>Bayer (1989)</td>
<td>Galápagos</td>
</tr>
<tr>
<td>L. inermis Studer, 1894</td>
<td>Studer (1894)</td>
<td>off Pacific Colombia</td>
</tr>
</tbody>
</table>

**SYSTEMATIC TREATMENT**

**Subclass Octocorallia**

**Order Gorgonacea**

**Suborder Calcaxonia Grasshoff, 1999**

**Family Chrysogorgiidae Verrill, 1883**

**Chrysogorgia Duchassaing and Michelotti, 1864**

**Type Species.** — *Chrysogorgia desbonni* Duchassaing and Michelotti, 1864, by monotypy.

**Diagnosis.** — Branching from main branch sympodial in an ascending spiral (clockwise or counterclockwise) producing a bottlebrush colony, or dichotomous in one or more planes. Branchlets repeatedly and dichotomously branched; terminal branchlets short. Polyps large in relation to branch and well separated. Sclerites consist of spindles, rods, and scales. Axis with a brilliant metallic luster, usually golden or yellow in color.

**Remarks.** — The 59 valid species of *Chrysogorgia* are listed by group in Cairns (2001); only one species has been described subsequently (Cairns 2002).

In addition to the two species reported below, additional fragments of three *Chrysogorgia* species from San Juan Seamount (1972 m), Gorda Seamount (3169 m), and Vance F Seamount (2280 m) were collected but could not be identified due to their fragmentary nature, but each may well represent an undescribed species. The chrysogorgiid *Iridogorgia* was also common on Davidson Seamount; these specimens are being examined by Les Watling.

**Distribution.** — Known from all ocean basins at depths of 100–3375 m.
Chrysogorgia pinnata Cairns, sp. nov.

Figures 1D, 2.

**Material Examined.**—Types.

**Types and Type Locality.**—Holotype: T947-A5, 35°37.6′N, 122°50.1′W (Davidson Seamount, California), 3114 m, 1.64°C, 1 February 2006, 1 colony in a dozen fragments, SEM stubs 1274–1275, USNM 1102450, and one fragment (CAS 175303). Paratype: T1012-A16, 45.633°N, 130.664°W (Vance B Seamount off Oregon), 1969 m, 3 August 2006, 1.91°C, 1 branch, USNM 1102451.

**Description.**—The holotype was badly damaged in collection, now consisting of over a dozen fragments, the largest 13 cm wide and 6 cm tall (Fig. 1D); the complete colony is estimated to have been about 20 cm tall and equally broad; the base of attachment was not collected. The in situ photograph (Fig. 1G) taken prior to collection shows the colony to have consisted of about 13–15 main branches, all united near the base, the branches roughly aligned in one plane. The main branches of the colony are regularly (every 3.0–3.5 mm) and pinnately branched, the main branches bending in a slightly sympodial manner. The branchlets diverge in an alternating opposite fashion and are straight for about 3–4 cm and bear 4 or 5 polyps, after which they terminate or continue to branch in a dichotomous fashion. On either side of a main branch the branchlets are uniformly parallel to one another. The largest branch axis is 1.4 mm in diameter, branchlet axes being only 0.15 mm in diameter, which produces relatively firm colony support and yet flexible branchlets. The main axis has a metallic dull golden luster.

The polyps are elongate, up to 2.8 mm in length and 0.8 mm in diameter, and well spaced on the branchlets, separated from one another by 4–5 mm. They attach perpendicular to the branchlets (rarely on main branches) and often are oriented downward. Some polyps bear 1–3 globular masses, each up to 1 mm in diameter (Figs. 2D–E), at the base of the polyp and extending to the far side of the branchlet, these assumed to be reproductive pouches. The body wall of the polyp is covered with longitudinally oriented, elongate rods that have flattened tips (Fig. 2A), these rods being 0.27–0.56 mm in length and 0.018–0.036 mm in width (L:W = 10.7–16.7). They are grouped into 8 longitudinal cords along the body wall, which continue apically to support the 8 tentacles, the rods diminishing only slightly in length in the tentacles (about 0.21 mm). These flattened rods are sparsely covered with small (2–3 µm tall), irregularly-shaped granules (Fig. 2C). No specialized tentacular or pinnular sclerites were noted. Toward the base of the polyp and covering the reproductive pouches, as well as the coenenchyme, the sclerites consist of scales (Fig. 2B) 0.135–0.23 mm in length and 0.030–0.046 mm in width (L:W = 3.2–5.4) that are arranged in a random order. The faces of these scales are relatively smooth (i.e., only crystal structure visible), their edges finely serrate. Most sclerites are translucent.

**Comparisons.**—The 59 valid species of Chrysogorgia are divided into three groups depending on whether a species has spindles/rods or scales in their body wall and tentacles (see Cairns 2001). Whereas C. pinnata has well-defined scales in the coenenchyme, the sclerites in the body wall and tentacles are elongate flattened rods with even more flattened tips — a blend of rod and scale characteristics, but perhaps closer to being a rod. This would place it in Group A (“Spiculosae” sensu Wright and Studer 1889), which includes species having rods/spindles in both body wall and tentacles. The unique nature of the sclerites in C. bipinnata distinguishes it from all other species in that group. Another way to compare this species with others is that it has a flabellate colony. Only six other Chrysogorgia species have a flabellate colony: C. curvata Versluys, 1902; C. chryseis Bayer and Stefani, 1988; C. stellata Nutting, 1908; C. electra Bayer and Stefani, 1988; C. scintillans Bayer and Stefani, 1988; and C. desbonni Duchassaing and Michelotti, 1864. Chrysogorgia pinnata differs from these species in having pinnate branching; the others are dichotomously branched.
FIGURE 2. Sclerites from holotype of *Chrysogorgia pinnata*: A. Seven flattened body wall rods. B. Five coenenchymal scales. C. Enlargement of the mid-section of a body wall rod. D. Lateral view of a polyp with a basal brood chamber. E. Stereo lateral view of a polyp with a brood chamber. Scale bars as indicated on figure.
ETYMOLOGY.— The species was named (Latin *pinnatus* = feathered, pinnate) for the pinnate arrangement of its branches.

DISTRIBUTION.— Davidson and Vance Seamounts off California and Oregon; 1968–3114 m. Based on 70 observations, Lonny Lundsten (pers. comm.) has recorded this species from Davidson Seamount from depths of 1968–3275 m (most between 2600–3100 m) and at temperatures of 1.64–1.91°C (most between 1.65–1.75°C).

*Chrysogorgia monticola* Cairns, sp. nov.

Figures 1A, 3.

MATERIAL EXAMINED.— Types.

TYPES AND TYPE LOCALITY.— HOLETYPE: T945-A8, 35°49.4′ N, 122°36.5′ W (Davidson Seamount, California), 2662 m, 1.76°C, 30 January 2006, 1 colony now in 4 pieces and SEM stubs 1204–1208, 1276, USNM 1102452, and 1 piece at CAS 175304.

DESCRIPTION.— The colony is bottlebrush-shaped, the holotype colony being 19 cm tall and 10 cm wide, with a basal branch diameter of 1.55 mm; a holdfast was not present. The branching sequence is 1/3R, *i.e.*, there are three longitudinal rows of branchlets that diverge perpendicular to the main branch, every third branch aligned with one above and below, and the branches appear to spiral upward in a counterclockwise manner when viewed from above, thus the R (right) designation. Branchlets originate every 4–5 mm from the main branch, each dichotomously branching up to 5 or 6 times (having 5–6 nodes); the branching axils are about 45°. The first internode of a branchlet is about 12 mm long, but successive internodes are 7–8 mm in length, resulting in a fully developed branchlet length up to 5 cm. Each internode bears only 1 or 2 polyps, the polyps spaced 3.5–4.0 mm apart. The diameter of a distal branchlet is only 0.1 mm. The axis is metallic gold.

The polyps are rather stout (Fig. 3F), about 1.1 mm tall and 1.0 mm in distal diameter, rarely preserved with their tentacles expanded; a basal swelling was not observed. The body wall and axis of the tentacles are protected by longitudinally oriented flattened rods that have blunt, pleated, and even more compressed tips (Figs. 3A, E). Most of the body wall sclerites are 0.27–0.37 mm in length and 0.050–0.080 in width (L:W=5.5–10.5) but some may be as long as 0.65 mm; their surfaces are smooth or sparsely granular. The base of each tentacle appears to have 1 or 2 large rotund rods that are often irregular in shape, having multiple tips and side projections (Fig. 3B); they measure 0.45–0.65 mm in length and 0.10–0.16 mm in diameter (L:W=3.3–5.0). The tips of the tentacles are covered by small, crescent-shaped pinnular scales (Fig. 3D), which, like the body wall sclerites, have blunt, pleated tips. These scales are 0.072–0.25 mm in length and 0.035–0.050 in width (L:W=4.0–5.5), their size decreasing distally. The coenenchymal sclerites (Fig. 3C) are thin elongate scales 0.170–0.375 mm in length and 0.032–0.080 mm in width (L:W=5–7), having blunt tips, a coarsely irregular margin, a sparsely granular outer surface, and a smooth crystalline inner surface.

COMPARISONS.— Like *C. pinnata*, the body wall sclerites of *C. monticola* are flattened rods (not scales), and some of the tentaculars are rotund rods, which places this species in Group A of *Chrysogorgia*. One of the unique characteristics of the species of *Chrysogorgia* is its variety of formulaic branching sequence (see Versluys 1902, Cairns 2002), some of the most common being 2/5R (16 species), 1/4L (13 species), and 1/3L (9 species), although other sequences include: 2/5L, 1/4R, 1/5R, 1/6R, 1/7R, and several species are flabellate with purely dichotomous branching. Thus, the 1/3R branching sequence of *C. monticola* is unique in the genus.

Only one previously described species of *Chrysogorgia* is known from the eastern Pacific, *C. fruticosa* (Studer, 1894), previously reported only from the Bay of Panama at 837 m (*Albatross*
FIGURE 3. Sclerites from holotype of *Chrysogorgia monticola*: A. Five flattened body wall rods. B. Three massive rods in base of calyx. C. Smooth coenenchymal scales. D. Curved pinnular scales. E. Flattened and pleated tip of a body wall rod. F. Stereo view of a polyp. Scale bar for A–C, 0.1 mm; D, 50 µm; E, 20 µm; F, 0.5 mm.
station 3384, not “7,907” as indicated by Studer). It also has a 1/3 branching sequence but whether sinistral (L) or dextral (R) is unknown, as the original description is inadequate and unillustrated, and the type, which should be deposited at the MCZ (the types of 6 of 19 new species from this paper are at the MCZ), was not present in 2006. Nor is the type deposited at the YPM (Lazo-Wasem, pers. comm), where parts of many of verrill’s octocoral types are deposited. Thus, in order to define *C. fruticosa* and to distinguish it from other species, a neotype was chosen (USNM 98799), collected off Pacific Mexico (*Atlantis II*, AD3016: 12°43′12″N, 102°36′W, “Seamount 6”, 500 km off Acapulco, Mexico) at 1900–1950 m. This specimen, although somewhat larger than the type (30 cm in height) and collected farther to the north and at a greater depth than the type, agrees with all the characteristic mentioned by Studer in his original description. It differs from *C. monticola* in having a branching formula of 1/3L and in having exclusively irregularly-shaped scales (0.25–0.35 mm in length) in its polyps, tentacles, and coenenchyme, which places it in Group C, not Group A, as for *C. monticola*.

**ETYMOLOGY.**—The species name (Latin mont = mountain + -cola = dweller), literally mountain dweller, is an allusion to its habitat on seamounts.

**DISTRIBUTION.**—Davidson Seamount off California. Based on 110 observations, Lonny Lundsten (pers. comm.) has recorded this species from Davidson Seamount from depths of 1711–3015 m (most between 2400–2500 m) and at temperatures of 1.66–2.38°C (most between 1.74–1.84°C). Thus, *C. monticola* is generally found in slightly shallower and warmer water than *C. pinnata*.

**Family Primnoidae Gray, 1858**

*Parastenella* Versluys, 1906

**TYPE SPECIES.**—*Stenella doederleini* Wright and Studer, 1889.

**DIAGNOSIS.**—Colonies flabellate, slightly bushy, or irregularly branched. Calyces occur in whorls, pairs, or individually, oriented perpendicular to branch. Body wall scales arranged in 5–8 longitudinal rows, the 8 marginal scales elongate and usually fluted, offset in alignment from opercular scales. Opercular scales roughly equal in size, with a highly keeled inner surface.

**REMARKS.**—The six species of *Parastenella* are compared in Table 2.

**DISTRIBUTION.**—Known from all ocean basins except the eastern Atlantic (Cairns 2007) at depths of 567–3470 m.

*Parastenella ramosa* (Studer, 1894)

Figures 1E, 4, 5.


*?Stenella doederleini*—Studer, 1894:64 (Pacific Panama, 1429 m).


**MATERIAL EXAMINED.**—*Gilliss-21, 7°11′N, 79°16′W, 1463 m, 18 January 1972, 1 colony, USNM 57554; T628-A12, 34°03′06″N, 121°03′00″W (Davidson Seamount, California), 665 m, 5.1°C, 13 October 2003, 2 colonies, USNM 1027058; T631-A4, 34.04°N, 121.04° W (Davidson Seamount, California), 735 m, 4.94°C, 16 October 2003, 1 colony, USNM 1102453; T941-A4, 35.72°N, 122.72°W (Davidson Seamount, California), 1310 m, 2.96°C, 27 June 2006, 1 branch, USNM 1102454; T833-R56, 36.84°N, 122.51°W (Monterey Bay, California), 1717 m, 2.28°C, 15 March 2005, 1 bushy colony, USNM 1102455; T874-A6, 45.87°N, 129.99°W (Axial 1998 South Flow, Washington), 1702 m, 2.17°C, 8 August 2005, 1 colony and SEM stubs 1277–1280, USNM 1102456, and 1 colony, CAS 175305; *WE Ricker*, Tow 25 (#137), 52°01′39″N, 131°35′37″W (off British Columbia), 1563–1776 m, 5 September 2004, 1 colony, USNM 1094072; *WE Ricker*, Tow 31, 52°42′09″N, 132°26′00″W (off British Columbia), 819–936 m, 7 September 2004, 1 colony,
<table>
<thead>
<tr>
<th>Characteristics</th>
<th>$P. \textit{ramosa}$ (Wright &amp; Studer, 1889)</th>
<th>$P. \textit{doederleini}$ (Wright &amp; Studer, 1889)</th>
<th>$P. \textit{gymnogaster}$, sp. nov.</th>
<th>$P. \textit{pacific}$, sp. nov.</th>
<th>$P. \textit{atlantica}$ Cairns, 2007</th>
<th>$P. \textit{spinosa}$ (Studer, 1894)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony shape</td>
<td>Usually uniplanar, rarely bushy</td>
<td>Uniplanar to slightly bushy</td>
<td>Uniplanar</td>
<td>Uniplanar to slightly bushy</td>
<td>Uniplanar to slightly bushy</td>
<td>Singles and occasional pairs; perpendicular to branch</td>
</tr>
<tr>
<td>Arrangement of calyces</td>
<td>Singles, pairs, and whorls of 3; directed downward</td>
<td>Whorls of 3 or 4; perpendicular to branch</td>
<td>Singles, pairs, and whorls of 3; strongly curved downward</td>
<td>Singles, pairs, and whorls of 3; perpendicular to branch</td>
<td>Singles, pairs, and whorls of 3 or 4; perpendicular to branch</td>
<td></td>
</tr>
<tr>
<td>Symmetry of marginal scales</td>
<td>Adaxial scales smaller and w/o flutes</td>
<td>1-3 adaxial marginals smaller and w/o flutes</td>
<td>Adaxial scales smaller and w/o flutes</td>
<td>Uniform</td>
<td>Uniform</td>
<td>Uniform</td>
</tr>
<tr>
<td>Marginal flutes: shape; % of length</td>
<td>Narrow, tubular; 38-46%</td>
<td>Very narrow, tubular; up to 55%</td>
<td>Broad; 20-25%</td>
<td>Broad, shallow; 30-40%</td>
<td>Broad, shallow; 20-30%</td>
<td>Short and narrow; 22%</td>
</tr>
<tr>
<td>Submarginal body wall scales: number of rows; scales per row</td>
<td>5 rows; 2-3/ row, alternating</td>
<td>5 rows; 3-4/row, alternating</td>
<td>6 rows; 4-6/abaxial row, linearly arranged</td>
<td>8 rows; 3-4/abaxial row, alternating</td>
<td>8 rows; 3-5/row, alternating</td>
<td>5 rows (2 wide abaxial, 3 smaller adaxial); 3-4/row</td>
</tr>
<tr>
<td>Submarginal abaxial body wall scale flutes</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
<td>Absent</td>
<td>Occasionally present</td>
<td>Present</td>
</tr>
<tr>
<td>Adaxial side of body wall</td>
<td>Covered</td>
<td>Covered</td>
<td>Naked basally</td>
<td>Covered</td>
<td>Covered</td>
<td>Covered</td>
</tr>
<tr>
<td>Coenenchymal scales: shape; outer surface</td>
<td>Irregular, flat; granular</td>
<td>Irregular, flat, granular, rounded knobs centrally and peripherally</td>
<td>Elliptical, concave, omatally ridged</td>
<td>Elliptical, concave, ridged</td>
<td>Elliptical, highly concave, granular</td>
<td>Unknown</td>
</tr>
<tr>
<td>Pinnular scales</td>
<td>Up to 0.14 mm; L:D = 10-11</td>
<td>Up to 77 µm; L:D = 5</td>
<td>Up to 97 µm; L:D = 6-8</td>
<td>Up to 0.105 mm; L:D = 5-7</td>
<td>Rare: up to 82 µm; L:D = 7-10</td>
<td>Up to 0.10 mm; L:D = 7-10</td>
</tr>
<tr>
<td>Distribution and depth</td>
<td>Panama to Gulf of Alaska, 665-1750 m</td>
<td>Japan, Indonesia, 732-3427 m</td>
<td>Oregon to Aleutian Islands, 1962-2773 m</td>
<td>Oregon to British Columbia, 1527-1986 m</td>
<td>New England Seamounts, 1984 m</td>
<td>Prince Edward Islands, 567 m</td>
</tr>
</tbody>
</table>
USNM 1094071; WE Ricker, Tow 32 (#209), 52°41′35″N, 132°32′35″W (off British Columbia), 1750–1860 m, 7 September 2004, 1 colony, USNM 1094057; WE Ricker, Tow 28 (#7), 48°19.947′N, 126°23′28″W (off Vancouver Island, British Columbia), 850 m, 7 August 2004, 4 colonies, USNM 1075364; Alvin 4032-2, 55°03′10″N, 140°18′32″W (Welker Seamount, Gulf of Alaska), 1119 m, 15 August 2004, 1 dry colony, USNM 1075376; Alvin 4039-24, 56°10′09″N, 142°42′02″W (Pratt Seamount, Gulf of Alaska), 914 m, 15 August 2004, 2 colonies, USNM 1075378; Alvin 4042-4, 56°22′42″N, 146°21′57″W (Giacomini Seamount, Gulf of Alaska), 1689–1937 m, 18 August 2004, USNM 1075396 and 1075394.

**Types and type locality.**—The original description is inadequate and unillustrated, and the holotype, which should be deposited at the MCZ, was not present in 2006. Nor is the type deposited at the YPM (Lazo-Wasem, pers. comm), ZMA, BM, or USNM, and thus is assumed to be lost. The specimen reported from Gilliss-21 is topotypic, collected only several km from the type locality, but is not sufficiently well preserved to be deemed a neotype. Type Locality: Albatross-3384: 7°31′30″N, 79°14′W (Gulf of Panama), 837 m.

**Description.**—The holotype was stated to be 17.5 cm in height, whereas the largest specimen reported herein is 33 cm in height and 16 cm in width, with a basal branch diameter of 4.5 mm (USNM 1075364). All colonies but one (T833-R56) are uniplanar, the odd specimen being a small, three-dimensionally branching bush. The axis is dark bronze in color, easily seen beneath a single layer of white, translucent coenenchymal scales. Branching is dichotomous and somewhat irregular, occurring every 9–11 mm, the axils forming an angle of about 30°; terminal branches are straight and rarely more than 3 cm in length. Calyces occur in approximately equal numbers as singles, pairs, and whorls of 3; calyces are spaced about 1.0–1.5 mm apart on the branch and are usually directed toward the base, often pointing downward at a 45° angle; calyces usually tend to favor one side of the flabellum. Calyces are 2.5–3.3 mm in height and flared apically.

Each calyx bears a distinctive arrangement of body wall sclerites. The 8 marginals are asymmetric in shape and size, the 5 on the abaxial and lateral edges each bearing a tall and narrow apical flute (Figs. 4A, 5B), whereas the 3 on the adaxial edge are not fluted, being much smaller and having rounded distal edges (Figs. 4C, 5C). The abaxial marginals are up to 1 mm in height and 1 mm in width, their basal edge bearing stubby digitate processes. Each adaxial marginal bears a well-developed, elongate, hollow flute, which may be up to 0.4 mm in length and 0.23–0.32 mm in width, its length being about 38–46% the length of the sclerite. The fluted part is relatively narrow and may be almost a closed cylinder (tubular) (Fig. 5B). The body wall scales below the marginals are arranged in 5 longitudinal rows. There are no body wall scales below the sagittal abaxial marginal, but on either side of this marginal there is a longitudinal row of 2 or 3 broad (0.8 mm) scales, each of which also bears apical flutes (Fig. 4A). The marginals to either side of these two rows do not have aligned scales, but the 3 marginals on the adaxial side (Fig. 5C) each precede a row of 2 or 3 small (0.3–0.4 mm wide), non-fluted scales (Figs. 4C, 5D), such that the adaxial side of the polyp is completely covered with scales.

The opercular scales are triangular in shape, with a deeply creased outer surface that corresponds to a prominently keeled inner surface (Fig. 5A). Opercular scales range from 0.9–1.3 mm in length and have a L:W ratio of about 1.9. They have a straight proximal edge and sometimes a bifid apical end. The operculum is well developed and easily visible in lateral view.

The coenenchymal scales occur in one thin layer, often exposing the underlying branch axis. They are elongate (up to 0.6 mm) but irregular in shape, flat to slightly concave above, and have a uniformly granular outer surface, the rounded granules 10–13 µm in diameter (Fig. 5E). Only
FIGURE 4. Stereo views of calyces of Parastenella ramosa (figures A, C–D) from T874-A6 (USNM 1102456) and P. doederleini (figure B) from Japan (USNM 50121):

A. Abaxial view of a calyx. B. Lateral view of a calyx. C. Adaxial and opercular views. D. Oblique view of a calyx. All scale bars 0.5 mm.
FIGURE 5. Sclerites of Parastenella ramosa from T874-A6 (USNM 1102456): A, Six opercular scales. B. Five marginal scales showing the distal flute. C. Two non-fluted abaxial marginal scales. D. Three adaxial body wall scales. E. Coenenchymal scales. F. Two pinnular rods. Scale bar for A–E, 0.25 mm; for F, 50 µm.
rarely will a coenenchymal scale bear a short vertical ridge. Pinnular sclerites are common, shaped as small rods 0.13–0.14 mm in length and about 13 μm in diameter (L:D = 10–11); their outer surface appears to be of a coarse crystalline texture (Fig. 5F).

**Comparisons.**— Parastenella ramosa is most similar to the type species of the genus, *P. doederleini* (Wright and Studer, 1889), originally described from off Sagami Bay, Japan at 3427 m (Table 2). Although the type of *S. doederleini* is no longer present at the BM, a small fragment of the type was borrowed from the ZMA (ZMAPOR3085), and for additional comparison a specimen was studied from Sagami Bay at 732 m (USNM 50121, Fig. 4B), as well as the re-description of the species by Versluys (1906) from specimens from Indonesia (1224 m). The two species have the same distinctive arrangement of body wall and marginal sclerites (i.e., 5 rows, with reduced adaxial marginal flutes [see Versluys, 1906: text-fig. 50]) and only two abaxial rows of fluted body wall scales. *P. doederleini*, however, differs in having more elongate (up to 53% of the length of the marginal) and more slender (up to 0.08–0.10 mm wide) marginal flutes, more delicate calyces (only 2.2 mm tall, with a shaft diameter of 0.5 mm and a distal diameter of about 1.5 mm), and having one or more small (up to 0.08 mm), rounded knobs at the center and/or perimeter of the coenenchymal scales (see Versluys 1906: text-fig. 53–54). Given the similarity of the species, it is likely that Studer’s (1894) identification of *S. doederleini* from off Panama at 1429 m (specimen missing from MCZ), taken quite close to the type locality of *P. ramosa*, is probably also *P. ramosa*.

**Distribution.**— Gulf of Panama, Rodriguez Seamount, Davidson Seamount, Monterey Bay, Axial 1998 South Flow, off British Columbia, Gulf of Alaska (Giacomini, Welker, Dickens, and Welker Seamounts); 665–1750 m.

*Parastenella gymnogaster* Cairns, sp. nov.

Figures 1B, 6, 7.

**Material examined.**— Types.

**Types and type locality.**— Holotype: *Alvin* 4033-23, 54°59′1″N, 140°23′59″W (Welker Seamount off British Columbia), 2634 m, 9 August 2004, 1 colony now in many pieces (dry) and SEM stubs 1281–1285, USNM 1075464 and 1 piece, CAS 175306. Paratypes: *Alvin* 1428, 44°40′N, 125°18′W (Juan de Fuca Ridge, Oregon), 2050 m, 9 August 1984, 1 complete colony, USNM 74691; T1007-A8, 45.327°N, 130.385°W (Vance F Seamount off Oregon), 2064 m, 29 July 2006, 1.90°C, several branches in alcohol, USNM 1102457; T1012-A17, 45.623°N, 130.664°W (Vance B Seamount off Oregon), 1962 m, 3 August 2006, 1.91°C, 1 branch, USNM 1102458; JD-093(30), 52°59′01″N, 161°14′57″W (Derickson Seamount, Gulf of Alaska), 2773 m, 20 Jul 2004, colony in alcohol, USNM 1081171.

**Description.**— The holotype colony is fragmented into many pieces, the largest 28 cm in height, having a basal branch diameter of 6.5 mm. All colonies are strictly uniplanar. The axis is bronze in color and faintly longitudinally striate. Branching is dichotomous and somewhat irregular, occurring every 12–15 mm; terminal branches rarely exceed 4 cm in length. Calyces occur as singles, pairs, and in whorls of 3; calyces are closely spaced on the branch, only about 0.4–0.6 mm apart. The calyces are curved strongly toward the base such that the distal end of each calyx almost touches the branch. Calyces are 2.2–3.0 mm in height and flared apically.

Each calyx bears a distinctive arrangement of body wall scales. Like *P. ramosa*, the 8 marginals are asymmetric in shape and size (Fig 6C), the 5 on the abaxial and lateral edges (Figs. 6A, 7B) bearing a short apical flute, whereas the 3 on the adaxial edge (Figs. 6B, 7C) being much smaller and not fluted, having rounded distal edges. The abaxial marginals are wider than tall, about 0.9 mm wide and 0.75 mm tall, each bearing a short, broad (U-shaped, not tubular) marginal flute, which is up to 0.25 mm in length and 0.25–0.35 mm in width, the length of the flute being only about 20–25% the length of the marginal. The body wall scales below the marginals are arranged
FIGURE 6. Stereo views of the holotype of *Parastenella gymnogaster*: A. Abaxial side of a calyx showing fluted body wall scales. B. Adaxial side of a polyp showing bare midline and six of the eight marginal scales, each labeled as m. C. Opercular view showing offset of marginals and opercular scales. D. Coenenchymal scales with ornate ridging. Scale bar for all figures 0.5 mm.
FIGURE 7. Sclerites from holotype of Parastenella gymnogaster: A. Six opercular scales. B. Four marginal scales showing short, broad flutes. C. Four abaxial body wall scales. D. Five coenenchymal scales showing ridges on outer surface. E. Two pinnular rods. F. Abaxial view of a juvenile calyx showing closely-spaced, imbricate, aligned abaxial scales. Scale bar for A–D, F, 0.25 mm; E, 25 μm.
in 6 longitudinal rows. There are no body wall scales below the sagittal abaxial marginal, but on either side of this marginal there is a longitudinal row of 4–6 broad (up to 0.9 mm wide and 0.5 mm tall) scales, each of which also bears short apical flutes (Fig. 7F). These body wall scales are closely spaced, as though stacked, their flutes in direct alignment, their width covering the entire abaxial side as well as part of the lateral edge of the calyx. Toward the base of the calyx they often bear a low longitudinal ridge on their outer surface (Fig. 7D). On each of the adaxial lateral sides of the calyx is a short row of 2–3 small (0.7 mm tall, 0.45 mm wide), non-fluted scales. On the adaxial side of the calyx, each non-fluted marginal is bordered by only one additional body wall scale, which produces a small bare region of the lower adaxial side of the calyx (Fig. 6B).

The opercular scales are triangular in shape, with a deeply creased outer surface that corresponds to a prominently keeled inner surface (Figs. 6C, 7A). The ab- and adaxial operculars are symmetrical, the former with 2 lateral shoulders, the latter with no shoulders; the lateral operculars are asymmetric, each having only one lateral shoulder on the lower adaxial margin. The abaxial operculars are 1.0–1.1 mm in length, having a L:W of 1.0–1.1; the laterals are 0.9–1.0 mm in length, with a L:W of about 1.4; and the small adaxials are only 0.6–0.7 mm in length, with a L:W of 1.7–2.3.

The coenenchymal scales are elliptical to irregular in shape (up to 0.6 mm wide) and have a highly concave upper surface, each bearing one or more tall (up to 0.6 mm) ridges, the ridges sometime taller than the width of the scale. The ridging may sometimes be quite ornate (Figs. 6D, 7D) and complex. Pinnular sclerites are common, shaped as small rods up to 97 µm in length and 12–16 µm in diameter (L:D = 6–8), their outer surfaces bearing small granules (Fig. 7E).

**COMPARISONS.**— *Parastenella gymnogaster* is one of three species having lesser developed adaxial marginal and submarginal body wall scales (Table 2), but is unique in having such a highly curved calyx that results in a naked lower adaxial region. It is also unique in having six rows of body wall scales, the scales of the two abaxial rows being quite broad, crowded, and linearly arranged. Although it overlaps in distribution with *P. ramosa* and even occurs on some of the same seamounts, it is usually found deeper than *P. ramosa*.

**ETYMOLOGY.**— The name *gymnogaster* (Greek, *gymno* = bare + *gaster* = stomach or belly) refers to the naked adaxial region of the body wall that is not covered with scales.

**DISTRIBUTION.**— Juan de Fuca Ridge off Oregon and eastern Pacific seamounts from off Oregon (Vance Seamount) to the Gulf of Alaska south of the eastern Aleutian Islands (Derickson Seamount, Gulf of Alaska); 1962–2773 m.

*Parastenella pacifica* Cairns, sp. nov.

**Figures 1C, 8, 9.**

**MATERIAL EXAMINED.**— Types.

**TYPES AND TYPE LOCALITY.**— **HOLOTYPE:** 45°25′N, 125°11′W (west of Cape Meares, Oregon), 1498–1527 m, date unknown, 1 dry colony broken into many fragments and SEM stubs 1286–1290, USNM 1071799. **PARATYPES:** *WE Ricker* tow 35 (#256), 52°59′41″N, 133°05′06″W (off Queen Charlotte Islands, British Columbia), 1986–2015 m, 8 September 2004, 1 dry colony, USNM 1094060, and one fragment, CAS 175307; *WE Ricker* tow 40 (#300), 54°06′05″N, 134°04′35″W (off Queen Charlotte Islands, British Columbia), 1915–2014 m, 10 September 2004, 1 branch in alcohol, USNM 1094070.

**DESCRIPTION.**— The largest piece of the holotype is 30 cm in height and 15 cm broad, but the dry colony is now fragmented into over a dozen pieces and several hundred unattached calyces. Nonetheless, it is clear that colonies are uniplanar and flabellate, the holotype having a basal branch diameter of 8.8 x 6.5 mm, the greater diameter oriented perpendicular to the flabellum. The axis is bronze to light brown in color. Branching is dichotomous and somewhat irregular, occurring at
intervals of 10–15 mm; terminal branches are relatively short, rarely more than 10 m in length. Calyces occur in approximately equal numbers as singles, pairs, and whorls of 3; calyces are spaced 0.5–1.5 mm apart and are usually oriented perpendicular to the axis; calyces tend to favor one side of the flabellum. Calyces are 2.1–3.0 mm in height and flared apically, having a slender shaft of about 0.85 mm diameter that broadens to a flared apical end 1.7–2.0 mm in diameter.

The 8 fluted marginal scales are all of the same shape and size, producing a symmetrical rosette when viewed from above (Fig. 8C). The marginals are up to 0.8 mm in length and 0.5–0.7 mm in basal width, each bearing a broad and shallow apical flute that constitutes 30–40% the length of the scale (Fig. 9B). The marginal flutes are about 0.30–0.45 mm in length and 0.35–0.40 mm wide, their inner surface covered with small apically directed spines (Fig. 9C). The submarginal body wall scales are roughly arranged in 8 longitudinal rows, each row having 3 or 4 scales that intercalate with those from the adjacent rows (Fig. 8A); however, the alignment is obscured near the calyx base. The polyp is completely covered with body wall scales, there being no naked adaxial region (Fig. 8B). The submarginals are 0.7–0.9 mm in width and length, each having a rounded distal edge; none of them bear flutes (Figs. 8A, 9D). Those near the base of the calyx often bear 1–3 low, longitudinal ridges.

The opercular scales are triangular in shape, with a deeply creased outer surface and longitudinally keeled inner surface (Fig. 9A). There is little difference in the size of the operculars, the symmetrical abaxials being 0.9–1.05 mm in length (H:W = 1.4–1.5), the asymmetric laterals 1.0–1.06 mm in length (H:W = 1.7–2.0), and the symmetric adaxials up to 0.9 mm in length (H:W = 2.2–2.3). The abaxials sometimes have notches on their lateral edges that appear to articulate with a notch on the adjacent lateral, appearing to allow a more efficient closing of the operculum.

The coenenchymal scales form one thin layer over the axis (Fig. 8D) and are elliptical to somewhat irregular in shape, but rarely more than 0.6 mm in width. All coenenchymals have a highly concave outer surface with upturned edges, resembling closely placed water lilies on a pond. Most coenenchymal scales bear at least one if not several tall (up to 0.15 mm) straight ridges on their outer surface, sometimes arranged in a complex pattern (Fig. 9E). Pinnular sclerites are common, shaped as small rods 95–105 µm in length and about 17 µm in diameter, thus having a L:D of about 6; their surface is granular (Fig. 9F).

COMPARISONS.— *Parastenella pacifica* is one of three species having equally developed marginal and submarginal scales (Table 2), and is most similar to *P. atlantica*, the latter known only from the North Atlantic. It differs from that species in having prominently ridged coenenchymal scales, longitudinally ridged body wall scales, and in having numerous pinnular rods of a larger size.

ETYMOLOGY.— Named *pacifica* for its close similarity to *P. atlantica*, perhaps being a geminate pair, but having a range in a different ocean.

DISTRIBUTION.— Continental slope off Oregon to British Columbia (Queen Charlotte Islands), 1527–1986 m.

*Calyptrophora* 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.
FIGURE 8. Stereo views of the holotype of *Parastenella pacifica*: A. Abaxial view of a calyx. B. Adaxial view of a calyx. C. Opercular view. D. Ridged coenenchymal scales. Scale bar for A-B, 0.5 mm; C, 0.5 mm; D, 0.5 mm.
FIGURE 9. Sclerites from holotype of *Parastenella pacifica*: A. Six opercular scales. B. Three marginal scales. C. Spinose and tuberculate inner face of a marginal scale. D. Five abaxial body wall scales. E. Three ridged coenenchymal scales. F. Two pinnular rods. Scale bar for A-B, D–E, 0.25 mm; C, 0.10 mm; F, 25 μm.
REMARKS.— Species of this genus have been discussed by Bayer (2001) and Cairns (2007).

DISTRIBUTION.— Indian, Pacific, and Atlantic Oceans; 229–3701 m.

Calyptrophora sp. cf. C. antilla Bayer, 2001
Figures 1F, 10, 11.


MATERIAL EXAMINED.— T943-A3, 35.739°N, 122.718°W (Davidson Seamount, California), 1683 m, 28 January 2006, 2.54°C, several branches and SEM stubs 1291–1294, 1306–1307, USNM 1102459, and 1 branch, CAS 175308; T943-A6, 35.735°N, 122.719°W (Davidson Seamount, California), 1763 m, 28 January 2006, 2.37°C, several branches, USNM 1102460.

TYPES AND TYPE LOCALITY.— The syntypes of C. antilla are deposited at the USNM (52914). Type Locality: 20°09′N, 73°29′W (Windward Passage between Cuba and Haiti), 1399 m.

DESCRIPTION.— The largest branch fragment is only 11 cm in length and 2.1 mm in basal branch diameter, but in situ photographs taken prior to collection indicate a dichotomously branched, flabellate colony approximately 20 cm in height and width; branch axes 20–25°. The axis is woody in texture and yellow in color; the calyces are white. Calyces are arranged in whorls of 3–5 (Fig. 10A), the larger number corresponding to larger-diameter branches; the calyces face upward. There are 11–13 whorls per 3 cm branch length, the whorls somewhat closely spaced at 0.8–1.0 mm intervals on the branch; the whorl diameter is about 3.6 mm. Calyces are 1.8–2.2 mm in horizontal length.

Each calyx is encased in two pairs of fused, ring-like scales (i.e., the basals and buccals), each pair meeting in a narrow adaxial symphysis (Fig. 10D). The basal scales are 0.8–0.9 mm in height (exclusive of the spines) and have rounded dorsolateral edges. Each basal bears an elongate pointed spine on its anterolateral edge (Fig. 11B). The basal spines are 0.9–1.0 mm in length, 0.16–0.19 mm in basal diameter, round in cross section, and bear finely serrate longitudinal ridges (Fig. 11F); the spines are curved slightly forward. The horizontally oriented buccal scales (Figs. 10D, 11D) are slightly longer, 0.9–1.2 mm in length, and have a rounded dorsolateral edge. Each buccal bears two spines on its distal margin, one spine aligned with each of the abaxial and outer-lateral opercular scales (Fig. 10C). These spines are similar to the basal spines in shape (cylindrical, ridged, serrate) but are smaller, being only 0.5–0.7 mm in length and 0.10–0.13 mm in basal diameter. Two discrete, crescent-shaped infrabasal scales (Fig. 11C), 0.35–0.45 mm in height, form a sleeve into which the calyx articulates with the coenenchymal scales.

The opercular scales (Figs 10C, 11A) are triangular in shape, with a fairly flat outer surface that is uniformly granular, the granules radiating from a point on the midline and near the base of the scale. Apically the outer surfaces of the operculars are slightly longitudinally creased, which corresponds to an elongate, rounded keel on the inner surface, the inner surface otherwise being tuberculate; the tips of the operculars are blunt. The two abaxials are symmetrical in shape, 1.0–1.16 mm in length, and have a L:W of 1.8–2.5. The four lateral operculars are slightly asymmetrical, each having a small shoulder on the basal adaxial edge; they are 0.8–1.0 mm in length, with a L:W of 1.6–1.9. The adaxial operculars are symmetrical, about 0.65 mm in length, and have a L:W of only 1.6. Tentacular sclerites are common, being 0.10–0.15 mm in length, 0.036–0.042 mm in width, and about 0.006 mm in thickness. They are straight or bent as much as 180° in the plane of their lesser axis (Fig. 11G).

The coenenchymal scales (Fig. 11E) are elongate (up to 1.3 mm in length), but often irregular in shape, with a flat, evenly granular outer surface and a tuberculate inner surface.

COMPARISONS.— Bayer (2001) divided the species of Calyptrophora into two species com-
FIGURE 10. Stereo views of Calyptrophora sp. cf. C. antilla from T943-A3 (USNM 1102459): A. Two whorls of calyces. B. Lateral view of a calyx. C. Opercular view of a calyx. D. Inner view of a pair of fused buccal scales, showing ridged spines. Scale bar for A, 1 mm; B, 0.5 mm; C-D, 0.5 mm.
FIGURE 11. Sclerites of *Calyptrophora* sp. cf. *C. antilla* from T943-A3 (USNM 1102459): A. Six opercular scales. B. Adaxial view of a pair of fused basal scales. C. Two infrabasal scales. D. Adaxial view of a pair of fused buccal scales. E. Three coenenchymal scales. F. Enlargement of basal spine showing serrate ridges. G. Five curved pinnular scales. Scale bar for A, 0.25 mm; B–E, 0.5 mm; F–G, 25 µm.
plexes, the *japonica*-complex, having polyps that are directed upward, and the *wyvillei*-complex, having polyps directed downward. The *japonica*-complex was further divided into two species groups, the first having marginal spines on the buccal scales, the second lacking buccal marginal spines. This species clearly falls into the first species group of the *japonica*-complex, which contains seven of the 12 species: four occurring in the western Pacific and three in the western Atlantic. It has been compared to the types of seven of these species and topotypic specimens of *C. japonica*, and surprisingly, this taxon is most similar, if not the same, to the western Atlantic *C. antilla*, which has a known range of the Greater Antilles and the New England Seamounts at 1399–1692 m (Cairns 2007). It differs from *C. antilla* only in having slightly longer buccal spines (those of *C. antilla* are rarely more than 0.45 mm long), which is probably within the range of variation for the species.

This taxon is also quite similar, and may be the same, as *Calyptrophora japonica* form B (specimen 3) of Versluys (1906), a specimen collected from Indonesia at 1301 m. As Bayer (2001:372) suggested, this species is very similar to *C. clarki* Bayer, 1951, except that the latter has broader plate-like basal spines. Although not examined, Versluys’ specimen appears to differ only in having longer basal spines (up to 1.0 mm). According to Bayer (2001:372), Versluys’ variant forms are undescribed species different from *C. japonica*.

**DISTRIBUTION.**— Davidson Seamount, 1683–1763 m; ?Western Atlantic (Cairns 2007) and ?Indonesia (Versluys 1906), 1301–1692 m.

*Calyptrophora bayeri* Cairns, sp. nov.
Figures 1H, 12, 13.


**MATERIAL EXAMINED.**— Types.

**TYPES AND TYPE LOCALITY.**— **HOLOTYPE:** T943-A3’, 35.739°N, 122.718°W (Davidson Seamount, California), 1683 m, 28 January 2006, 2.54°C, one branch and SEM stubs 1295–1297, 1302–1303, USNM 1102461, and 1 branch, CAS 175309.

**DESCRIPTION.**— The largest branch fragment is only 11 cm in length and 2.6 mm in basal branch diameter, clearly part of a larger colony that was loosely dichotomously branched and having branch axils of 40–50° divergence. The axis is woody in texture and a dark golden brown in color, easily seen through the thin, single layer of translucent coenenchymal scales. Calyces are white and arranged in whorls of 3 or 4 (usually 4); calyces face upward (Fig. 12A). There are 10–11 whorls per 3 cm branch length, the whorls spaced 1.0–1.2 mm apart; the whorl diameter is about 3.8–4.2 mm. Calyces are 2.2–2.7 mm in horizontal length.

The basal scales are 1.0–1.2 mm in height (exclusive of the spines) and have dorsolateral edges that met at a 90° angle, but not associated with an external ridge. Each basal scale bears a massive spine on its anterolateral edge (Fig. 13C). These spines are up to 1.0 mm in length and round in cross section only distally, for the most part being quite flattened, up to 0.5 mm wide at their base and only 0.1 mm in thickness. Their inner faces bear parallel rows as small granules and spines (Fig. 13F), whereas their outer surface bears low, rounded granules. The buccal scales are 1.8–2.2 mm in length and have rounded dorsolateral edges. They too bear flattened distal spines or teeth, each calyx having 4, 6 or 8 (usually 6) triangular protuberances, each of which is rarely over 0.2 mm in length (Figs. 13B, H). The infrabasal scales (Fig. 13D) are of the typical crescent shape and are up to 0.6 mm in height.

The opercular scales (Fig 13A) are triangular in shape, but with a somewhat blunted distal point. Apically the outer surface is longitudinally creased, which corresponds to a sharp keel on the
FIGURE 12. Stereo views of the holotype of Calyptrophora bayeri: A. Two whorls of calyces. B-C. Lateral views of calyces. D. Adaxial view of a calyx. Scale bar for A, 1 mm; B–D, 0.5 mm.
FIGURE 13. Sclerites from holotype of Calyptrophora bayeri: A. Five opercular scales. B. Adaxial view of a pair of fused buccal scales showing the dentate distal margin. C. Ab- and adaxial views of two pairs of fused basal scales. D. Two infrabasal scales. E. Two coenenchymal scales. F. Inner side of a basal scale spine showing parallel rows of spines. G. Four curves pinnular scales. H. Enlargement of buccal spines. I. Coenenchymal scales in place. Scale bar for A, E, 0.25 mm; B–D, 0.5 mm; F, 0.1 mm; G, 50 µm; H, 0.1 mm; I, 0.25 mm.
inner surface; the tuberculate region on the inner surface seems to be somewhat raised. The abaxial operculars are symmetrical in shape, 0.96–1.07 in length, and have a L:W of 1.4–1.55. The four lateral operculars are slightly asymmetrical, 0.79–0.91 mm in length, and have a similar L:W ratio. The adaxial operculars are 0.75–0.8 mm in length, symmetrical with a pointed tip, and have a L:W of about 1.5–1.7. Tentacular sclerites are common, measuring up to 0.15 mm in length, 0.056 mm in width, and about 0.007 mm in thickness (Fig. 13G). They are usually curved in the plane of their lesser axis.

The coenenchymal scales (Figs. 13E, I) are fusiform (L:W = 3–4), up to 1.15 mm in length, with a flat to slightly concave outer surface and tuberculate inner surface. Occasionally, a coenenchymal is attached on edge (Figs. 12A), these located between infrabasal scales of adjacent calyces.

**Comparisons.**—*Calyptrophora bayeri* was compared to type material of all species in the *japonica*-complex, except for *C. japonica*, for which topotypic specimens from Japan were examined (USNM 30027, 49323). Its flattened basal spines and short triangular buccal spines distinguish it from all other species, except for *C. japonica* form C sensu Versluys (1906), which Bayer (2001) implied was a separate species. Comparisons to other eastern Pacific congeners are made in Table 3.

**Etymology.**—This species is named in honor of Frederick M. Bayer, in acknowledgment of his many papers on the taxonomy of primnoid genera.

**Distribution.**—Known only from type locality off California and questionably form off Timor, 520 m (Versluys 1906).

*Calyptrophora laevispinosa* Cairns, sp. nov.

Figures 1G, 14, 15.

**Material Examined.**—Types.

**Types and Type Locality.**—Holotype: T885-A1, 46.683°N, 126.782°W (Gorda 1996 Flow, off Washington), 3107 m, 24 August 2005, 1.76°C, 9 branches from same colony and SEM stubs 1298–1300, 1304–1305, USNM 1102462, and 1 branch, CAS 175310.

**Description.**—The holotypic colony is now represented only by 10 branch fragments, the largest measuring 10 cm in length, however the *in situ* photograph (Fig. 1G) taken before collection shows a stately, flabellate colony approximately 32 cm in height and 59 cm in width, branches originating from the main branch just 1 cm from the basal attachment and filling approximately 160° of the flabellate plane. Branching is dichotomous and the branching axes are quite narrow, about 10–15°. The axis is straw colored, the calyces white. Calyces are arranged in whorls of 3 or 4 (usually 4) and face upward (Fig. 14A). There are 10–12 whorls per 3 cm branch length, the whorls spaced 1.2–1.3 mm apart, in the case of the types occasionally pushed together by post-collection trauma; the whorl diameter is 2.8–3.9 mm. Calyces are 1.5–2.0 mm in horizontal length.

The basal scales are 0.8–0.9 mm in height (exclusive of spines) and have rounded dorsolateral edges. Each basal scale bears a smooth (non-granular, non-ridged) spine on its dorsolateral margin that extends up to 0.55 mm. These spines are round in cross section, about 0.1 mm in diameter at the base. However, most of these spines also have a lower secondary spine or extension on their sagittal side, these spines only 0.12–0.15 mm in height and flattened in shape (Figs. 15C–D). The buccal scales are 1.0–1.05 mm in length and have rounded dorsolateral edges. Each calyx bears 4 (rarely 6) perfectly smooth, slender buccal spines, intact spines up to 0.6 mm in length and 0.1 mm in basal diameter (Figs. 14B, D, 15B, G). These spines are round in cross section, similar in size and shape to the primary basal spines, and aligned with the abaxial and outer-lateral opercular
scales. The crescent-shaped infrabasal scales (Fig. 15F) are up to 0.45 mm in height; the two adjacent coenenchymal scales are often reflected upward near the calyx, functioning as a second set of infrabasals (Figs. 14B, 15I). These secondary infrabasals are up to 2 mm in length.

The opercular scales (Fig. 15A) are triangular in shape, with a pointed tip, the abaxial operculars sometimes being bifid of trifid. The operculars are longitudinally creased above and keeled on their inner surface; their edges are finely serrate. The abaxial operculars are symmetrical in shape, 0.95–0.97 mm in length, with a L:W of 2.2–2.4. The 4 lateral operculars are only slightly asymmetrical, 0.71–0.90 mm in length, with a L:W of 1.7–2.1. The small adaxial operculars are symmetrical, about 0.7 mm in length, with a L:W of about 2. Tentacular sclerites are common, measuring up to 0.13 mm in length and 0.40 mm in width, curved in the plane of the lesser axis.

The coenenchymal scales (Fig. 15E) are elongate to elliptical in shape, usually with rounded ends, up to 1.3 mm in length. They are sparsely granular above and tuberculate below.

**Comparisons.**— *Calyptrophora laevispinosa* was compared to type material of all species in the *japonica*-complex, except for *C. japonica*, for which toptotypic specimens from Japan were examined. It is perhaps most close to *C. spinosa* Pasternak, 1984 (Kapingamarangi Atoll, 910–1575 m), particularly in the shape of its basal spines, but *C. laevispinosa* differs in having cylindrical buccal spines, and smooth (not ridged) buccal and basal spines. Comparisons to other eastern Pacific congeners are made in Table 3.

**Etymology.**— The species name (Latin *laevis* = smooth + Latin *spinatus* = spined) is an allusion to the smooth buccal and basal spines of this species.

**Distribution.**— Known only from the type locality off Washington. At 3107 m, this is the deepest *Calyptrophora* ever collected.

*Narella Gray, 1870*

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

**Diagnosis.**— Colonies dichotomously or pinnately branched, or unbranched. Calyces arranged in whorls, the calyces always facing downward. Each polyp enclosed by 3 or 4 pairs of unfused body wall scales (1 pair of basals, 1 or 2 pairs of medials, and 1 pair of buccals), 1–3 pairs of small adaxial buccal scales, and occasionally additional small, unpaired scales on the adaxial
FIGURE 14. Stereo views of the holotype of *Calyptrophora laevispinosa*: A. Two whorls of calyces. B. Abaxial view of a calyx showing spines. C. Adaxial view of a calyx showing fusion of basal scales. D. Opercular view of a calyx. Scale bar for A, 1 mm; B–C, 0.5 mm; D, 0.25 mm.
Figure 15. Sclerites from holotype of *Calyptrophora laevispinosa*: A. Six opercular scales. B. Adaxial view of a pair of fused buccal scales. C. Ad- and abaxial views of two pairs of fused basal scales. D. Inner view of broad basal spines. E. Two coenenchymal scales. F. Two infrabasal scales. G. Smooth buccal spines. H. Three curved pinnular scales. I. Articulation of infrabasal scales between basal and coenenchymal scales. Scale bar for A, E, 0.25 mm; B, 0.25 mm; C, F, 0.25 mm; D, 0.1 mm; G, 0.1 mm; H, 50 µm; I, 0.5 mm.
body surface. Distal margin of body wall scales often lobate or spinose; dorsolateral edge of basal scales often ridged. Operculum consists of 8 triangular scales, each with a pronounced medial keel on its inner surface. Coenenchymal scales usually elongate or elliptical in shape, often bearing tall vertical keels or ridges.

**Remarks.**—This is most prolific of the primnoid genera, consisting of 38 valid species (see listing by Cairns and Bayer 2008 [in press]). In addition to *N. bowersi* reported below, three additional branch fragments of *Narella* were collected from San Marcos Seamount, off southern California (2193 m), Rodriguez Seamount, off southern California (664 m), and “North Cleft”, off Washington (2349 m) but these could not be identified due to their fragmentary nature; each one may represent an undescribed species. The genus has recently been studied by Cairns and Bayer (2003, 2008 [in press]) and Cairns and Baco (2007).

**Distribution.**—Known from all ocean basins from 55–4594 m (Cairns and Bayer 2008 [in press]).

*Narella bowersi* (Nutting, 1908)

*Stachyodes bowersi* Nutting, 1908:577–578, pl. 43, fig. 6, pl. 48, fig. 2 (not pl. 43, fig. 5, which is *N. dichotoma*).

*Narella bowersi.*—Cairns and Bayer, 2008 (in press), figs. 1F, 12A–D, 13A–F (synonymy).

**Material examined.**—T1007-A3, 45.327°N, 130.385°W (Vance F Seamount, off Oregon), 2070 m, 29 July 2006, 1.90°C, 3 branch fragments, USNM 1102463.

**Types and type locality.**—The holotype is deposited at the USNM (25377). Type Locality: 23°05′N, 161°52′W (off Nihoa, Hawaiian Islands), 1758–1936 m.

**Discussion.**—Originally described from Hawaii, this species was recently reported from Endeavour Seamount off British Columbia at 2500 m (Cairns and Bayer 2008 [in press]). The specimen reported herein is simply a slight range extension for the species. Because it was described and illustrated so recently it is not re-described herein.

**Distribution.**—Hawaiian Islands and Pensacola Seamount, 1218–1758 m; Northeast Pacific seamounts (Endeavour and Vance) off British Columbia and Washington, 2070–2500 m.

**Acknowledgments**

I am grateful to Lonny Lundsten, Jim Barry, Dave Clague (MBARI), and Andrew DeVogelaere (MBNMS) for permission to examine the specimens collected by their institutions. The MBNMS expedition was funded by NOAA’s Office of Ocean Exploration. Likewise I am grateful to Amy Baco and James Boutillier for their material contributions. The Alaskan specimens were collected on two NOAA Office of Ocean Exploration cruises and a NOAA West Coast and Polar Programs NURP cruise to seamounts in the Gulf of Alaska during 2002 and 2004. I would like to acknowledge the following grant numbers awarded to Amy Baco: UAF 040118 and NA040AR4600051. I thank Ardis Johnston (MCZ) for the loan of Studer (1894) types, and Rob van Soest (ZMA) for the loan of Wright and Studer (1889) *Challenger* specimens. Tim Coffer designed and enhanced the Photoshop plates. I would also like to thank Gary Williams, who reviewed the manuscript and made helpful suggestions.

**Literature Cited**
