Review of Octocorallia (Cnidaria: Anthozoa) from Hawai‘i and Adjacent Seamounts. Part 2: Genera *Paracalyptrophora* Kinoshita, 1908; *Candidella* Bayer, 1954; and *Calyptrophora* Gray, 1866[1]

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Abstract: Nine deep-water primnoid octocoral species are described from Hawaiian waters, four of them as new species, bringing the total number of octocoral species known from Hawai‘i to 94. *Candidella gigantea* is reported for the first time subsequent to its original description from Fiji in 1889. To place the two new species of *Calyptrophora* in context, all 16 species in the genus are keyed and analyzed in a morphology-based phylogenetic analysis. Although the analysis did not support the species complexes and species groups established by Bayer, it did suggest two distinct clades based on characters such as the opercular cowl, inclination of the polyps, and cross section and sculpture of the basal scale spines.

Deep-water corals, especially those belonging to the family Primnoidae, form a substantial percentage of the bathyal benthic biomass throughout the Hawaiian Islands, providing habitats for many smaller invertebrates and fish. The images published by Chave and Jones (1991) and Chave and Malahoff (1998), and those unpublished observations made from the *Pisces 5* in 2003, attest to the abundance and size of the Hawaiian primnoid fauna. But, despite their abundance, many species remain undescribed. Thus, it is the objective of this series of papers to document the taxonomy and distribution of these structure-forming primnoid species. This is the second in a series of papers that describes the deep-water octocoral fauna of the Hawaiian Islands. This paper addresses three of the nine primnoid genera known to occur in Hawaiian waters and completes the genera belonging to subfamily Calyptrophorinae. The rationale for the series and a history of the Hawaiian octocoral fauna were given by Cairns and Bayer (2007 [2008]), which constitutes part 1 of the series. The remaining primnoid genera to be revised include *Callogorgia*, *Parastenella*, *Plumarella*, *Thouarella*, and *Fanellia*, altogether consisting of about another 10 species.

Materials and Methods

Specimens were examined from 56 stations of eight vessels, including four research submersibles, and were made from the entire length of the Hawaiian Islands at depths of 249–1,816 m (see Appendix). All of these specimens are deposited at the NMNH. The scanning electron microscope (SEM) images were taken by me (numbers prefaced by C) and by F. M. Bayer (numbers prefaced by B). Specimens should be presumed to be preserved in alcohol unless otherwise stated in the Material Examined sections. A “confirmed” depth range is reported for each species (i.e., the depths of the shallowest deep to the deepest shallow ranges of individual stations).

Abbreviations: *Alb*, USFWS *Albatross;* BM, British Museum of Natural History, London; CI, consistency index; HURL, Hawai‘i Undersea Research Laboratory; L : W, length to maximum width of a sclerite; MCZ, Museum of Comparative Zoology, Harvard; NMNH,

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National Museum of Natural History, Smithsonian Institution (cataloged specimens prefaced with USNM [U.S. National Museum]); NWHI, Northwestern Hawaiian Islands; *P5*, *Pisces 5;* RI, retention index; SUI, State University of Iowa; *TC*, *Townsend Cromwell.*

RESULTS AND DISCUSSION

SYSTEMATIC ACCOUNT

Subclass OCTOCORALLIA
Order ALCYONACEA
Suborder CALCAXONIA
Family PRIMNOIDAE Milne Edwards, 1857
Genus *Paracalyptrophora* Kinoshita, 1908

DIAGNOSIS: Colonies uniplanar or biplanar, branched in a dichotomous or lyrate fashion. Polyps arranged in whorls, the polyps always directed downward. Polyps composed of two pairs of unfused annular sclerites (basal and buccal), the buccal ring of some species having 2–5 additional smaller adaxial scales; a pair of crescent-shaped infrabasal scales also present. Buccal scales have a smooth or often spinose or lobed distal margin. Opercular scales prominently keeled on inner surface. Coenenchymal scales elongate, irregular in shape, granular, and sometimes ridged.

TYPE SPECIES: *Calyptrophora kerberti* Versluys, 1906, by subsequent designation (Cairns and Bayer 2004*a*).

REMARKS: This genus was recently revised by Cairns and Bayer (2004*a*, 2009).

DISTRIBUTION: Southwestern Pacific, Japan, Hawai'i, and North Atlantic, 150–1,480 m.

Paracalyptrophora echinata Cairns, n. sp.
Figures 1*C*, 2–3

TYPES AND TYPE LOCALITY: Holotype: *Pisces 5*-695, 1 dry colony, SEM stubs C1333–1335, USNM 1115283. Paratypes: *Pisces 5*-696, 1 dry branch, USNM 1115282; *Pisces 5*-703, 1 large dry colony, USNM 1115284. Type locality: 24° 16.369′ N, 166° 02.132′ W (Brooks Bank, NWHI), 708 m.

DESCRIPTION: Colonies uniplanar, branching occurring in an even dichotomous fashion (Figure 1*C*) from a main stem up to 3 cm long and 10 mm in diameter. Holotype 24 cm in height and 27 cm wide, but largest specimen (*P5*-703) is 39 cm in height. Branching occurs every 2–3 cm, branching axils in base of colony 20–25°, in distal part of colony decreasing to 15–20°; terminal branches rarely longer than 3 cm. Axis dense and rather inflexible, black to bronze in color. Polyps point downward and arranged in whorls of 6–8 (Figure 2*A*) on terminal branches, but up to 11 on larger-diameter basal branches, and up to 20 on main stem. There are about 12 whorls per 3 cm; whorl diameter 3.5–4.0 mm. Polyps 1.7–2.1 mm in length.

The two basal scales stand up to 1.2 mm in height, distal 0.33–0.42 mm extending as a flat rounded spine or lobe, usually having a blunt tip (Figures 2*A*, 3*C*). Outer surface of basal spine bears hispid ridges, but inner surface bears only small spines (not arranged on ridges). No dorsolateral ridge on basal scales. The two buccal scales are up to 1.3 mm in length, their distal and outer lateral edges finely serrate (Figure 3*B*), serrations only about 20 μm in height; operculars project well beyond buccal scales. Buccals meet along sagittal line in an irregular, raised junction (Figure 2*B*); no accessory adaxial buccal scales. Each of pair of infrabasals about 0.6 mm in height, their outer surface bearing vertical, radiating ridges. Outer surface of body wall scales, as well as operculars, covered with small (up to 25 μm tall) sharp spines, which are aligned sometimes as parallel ridges (Figure 3*A*).

Abaxial opercular 0.85–0.95 mm in length (L : W = 1.5), symmetrical, and longitudinally creased above corresponding to a prominent keel on inner surface; keel bears spinose lateral ridges as well. Lateral operculars 0.85–1.0 mm in length (L : W = 1.6–2.1), asymmetrical, creased above, and often bear multiple keels on their inner surface. Adaxial operculars 0.6–0.7 mm in length (L : W = 1.7–1.9), symmetrical, flat, and bear an inner keel (Figure 3*A*, lower right). Distal margins of operculars serrate like buccal scales. Instead of a pair of ab- and adaxial operculars, it appears (Figure 3*E*) that there is only one

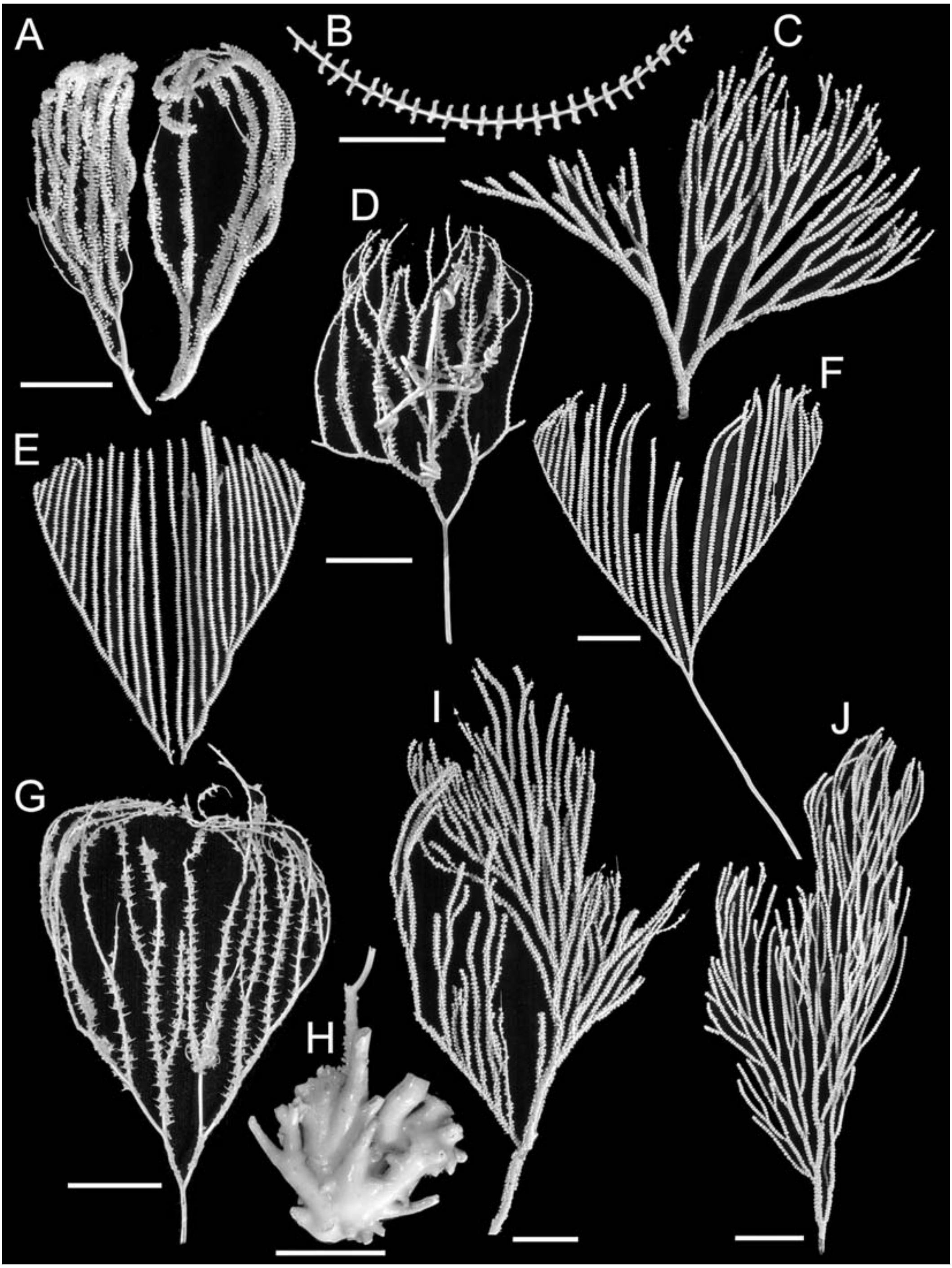

Figure 1. Colony shapes of the species. *A*, *Candidella helminthophora*, USNM 1115296; *B*, *Candidella gigantea*, USNM 1072121; *C*, *Paracalyptrophora echinata*, holotype, USNM 1115283; *D*, *Calyptrophora wyvillei*, USNM 100825; *E*, *Calyptrophora pileata*, holotype, USNM 1010743; *F*, *Calyptrophora angularis*, USNM 56822; *G*, *Calyptrophora clarki*, USNM 91892; *H*, *Candidella helminthophora*, fused calcified basal axes, USNM 56774; *I*, *Calyptrophora alpha*, holotype, USNM 1072134; *J*, *Paracalyptrophora hawaiinensis*, holotype, USNM 1071425. Scale bars: *A–F*, *I–J*, 5 cm; *G–H*, 2.5 cm.

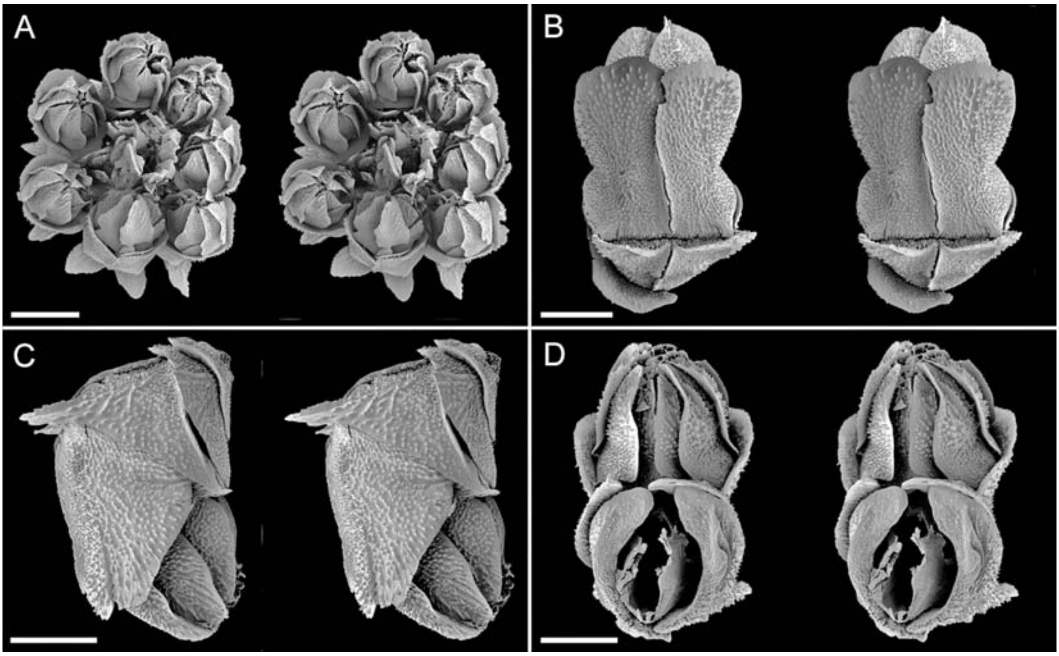

FIGURE 2. Polyps of *Paracalyptrophora echinata* from the holotype (USNM 1115283), stereo views: *A*, opercular view of a whorl having seven polyps; *B*, abaxial view of a polyp showing medial suture; *C*, lateral view of a polyp; *D*, adaxial view of a polyp. Scale bars: *A*, 1.0 mm; *B–D*, 0.5 mm.

abaxial placed opposite one adaxial, which are arranged on sagittal plane, and thus three pairs of lateral scales.

Coenenchymal scales (Figure 3*F*) elongate but irregular in shape, up to 1.3 mm in length (L : W = 3.5–4.0) and granular on their outer surface; outer surface also covered with a reticulate series of low ridges. No pinnular scales noted.

ETYMOLOGY: The species name is from the Latin *echinatus*, meaning spiny, an allusion to the spiny outer surface of body wall and opercular scales.

COMPARISONS: *Paracalyptrophora echinata* is quite similar to *P. mariae* (Versluys, 1906) (the latter known only from Timor Sea and Norfolk Ridge at 418–520 m) and may be the sister species to that taxon. It differs in branching mode: that of *P. echinata* is uniplanar dichotomous and terminating in an uneven upper margin to the colony, whereas that of *P. mariae* is biplanar, beginning in a lyrate fashion, but at the second and/or third branching points producing four branches, two of which go on to form a plane and the other two to form a parallel plane, both through successive dichotomous branching. The top of the colonies of *P. mariae* are fairly level. Thus, *P. echinata* is uniplanar, *P. mariae* biplanar. Furthermore, the outer surface of the basal spines of *P. echinata* is not ridged, and the outer surface ornamentation of the body wall and opercular scales is hispid, not granular, as in *P. mariae*. Comparisons with *P. hawaiinensis* Cairns, n. sp., are made in the following species treatment.

DISTRIBUTION: NWHI: Brooks Bank and Twin Banks east of Nīhoa, 708–1,475 m.

Paracalyptrophora hawaiinensis Cairns, n. sp.
Figures 1*J*, 4–5

Paracalyptrophora n. sp. Parrish and Baco, 2007:192 (listed).

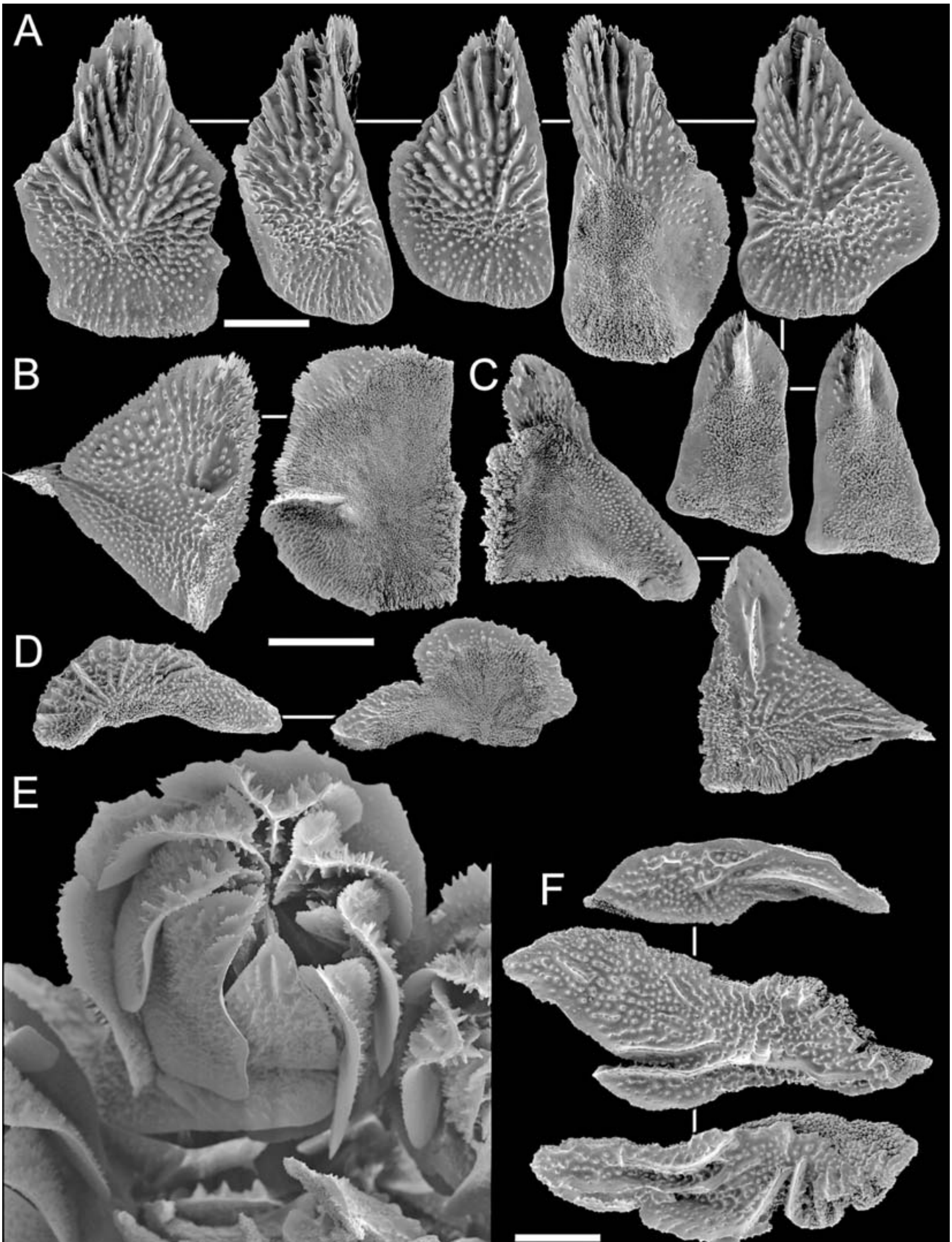

Figure 3. Sclerites of *Paracalyptrophora echinata* from the holotype (usnm 1115283): *A*, opercular sclerites; *B*, buccal sclerites; *C*, basal sclerites; *D*, infrabasal sclerites; *E*, apical view of the operculum; *F*, outer surfaces of three coenenchymal scales. Scale bars: *A*, *E–F*, 0.25 mm; *B–D*, 0.50 mm.

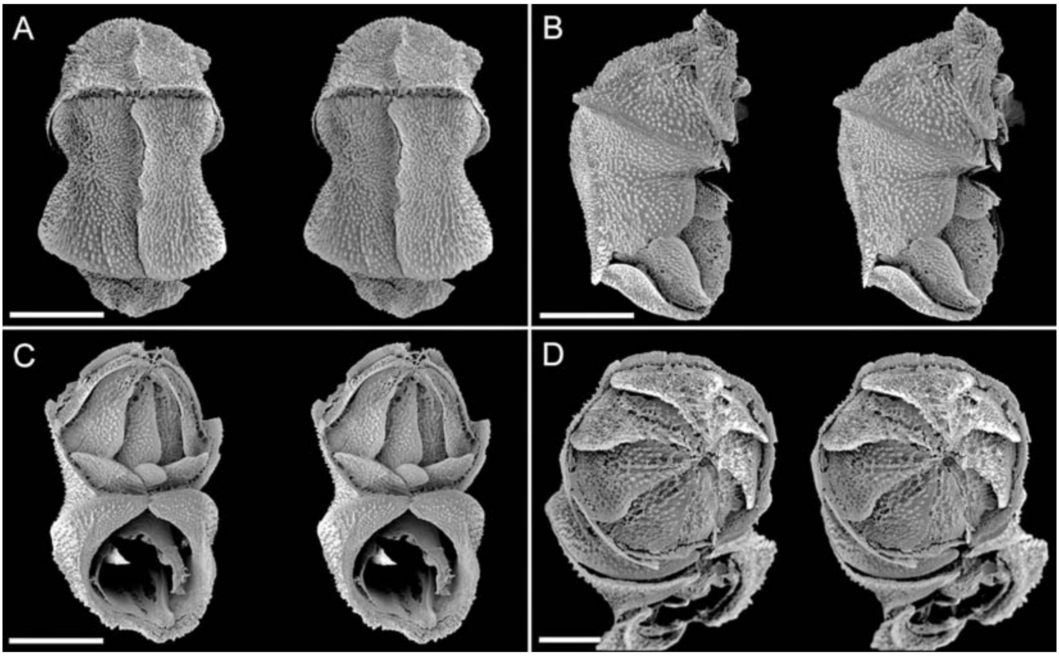

FIGURE 4. Polyps of *Paracalyptrophora hawaiinensis* from the holotype (USNM 1071425), stereo views: *A–B*, abaxial and lateral views, respectively, of polyps; *C*, adaxial view of a polyp showing three small adaxial marginal (= buccal) scales; *D*, opercular view of a polyp. Scale bars: *A–C*, 0.5 mm; *D*, 0.25 mm.

TYPES AND TYPE LOCALITY: Holotype: *Pisces 5*-591, a dry colony and SEM stubs C1359–1361, USNM 1071425. Paratypes: HURL 9-84-213, branches, USNM 1099225; Maui Dive 9, Ka'ena Point, 378 m, 18 Dec. 1973, 1 branch, USNM 93215; *Pisces 5*-141, 1 dry branch, USNM 1092795; *Pisces 5*-300 (PBS111), 1 branch, USNM 98823; *Pisces 5*-545, 1 colony, USNM 1072135; *Pisces 5*-587, branches, USNM 1071245; *Pisces 5*-591, 1 dry colony, USNM 1071426 (topotypic); *Pisces 5*-593, 1 branch, USNM 1071250; *Star II*-2, 3 dry colonies and 1 in alcohol, USNM 56929, 58381, and 1092776; *Sango* 14-2, 1 dry branch, USNM 1115285; unknown vessel, 21° 35′ N, 158° 23′ W, 366 m, 10 Oct. 1974, 1 branch, USNM 93218. Type locality: 18° 42′ 35″ N, 158° 15′ 19″ W (near Cross Seamount, Hawai'i), 367 m.

DESCRIPTION: Colonies uniplanar, branching in an even dichotomous fashion (Figure 1*J*) from a main stem about 2 cm in length and 4–5 mm in diameter. Holotype 39 cm tall and 14 cm wide, with basal axis diameter of 4.2 mm. Branching occurs every 3–4 cm, branching axis 25–30°; terminal branches up to 9 cm in length. Axis fairly inflexible and black. Polyps pointed downward and arranged in whorls of 6–7 on distal branches. There are 14–15 whorls per 3 cm branch length; whorl diameter about 2.7 mm. Polyps 1.5–1.9 mm in length.

The two basal scales 0.75–1.0 mm in height, the distal 0.15–0.19 mm forming rounded lobe or spine that occupies most of abaxial margin of scale. Margin of lobe and anterolateral margin of basal scale finely serrate. Both outer and inner surfaces of basal spine bear parallel, linear rows of spines, as do outer surfaces of all body wall and opercular scales (Figure 5*E–G*). Spines appear to be sharp under dissecting scope, but magnified with SEM are seen to be blunt-tipped (Figure 5*F*), up to 30 μm in height, and usually arranged in lines or even ridges radiating from a point of origin. No dorsolateral ridge on

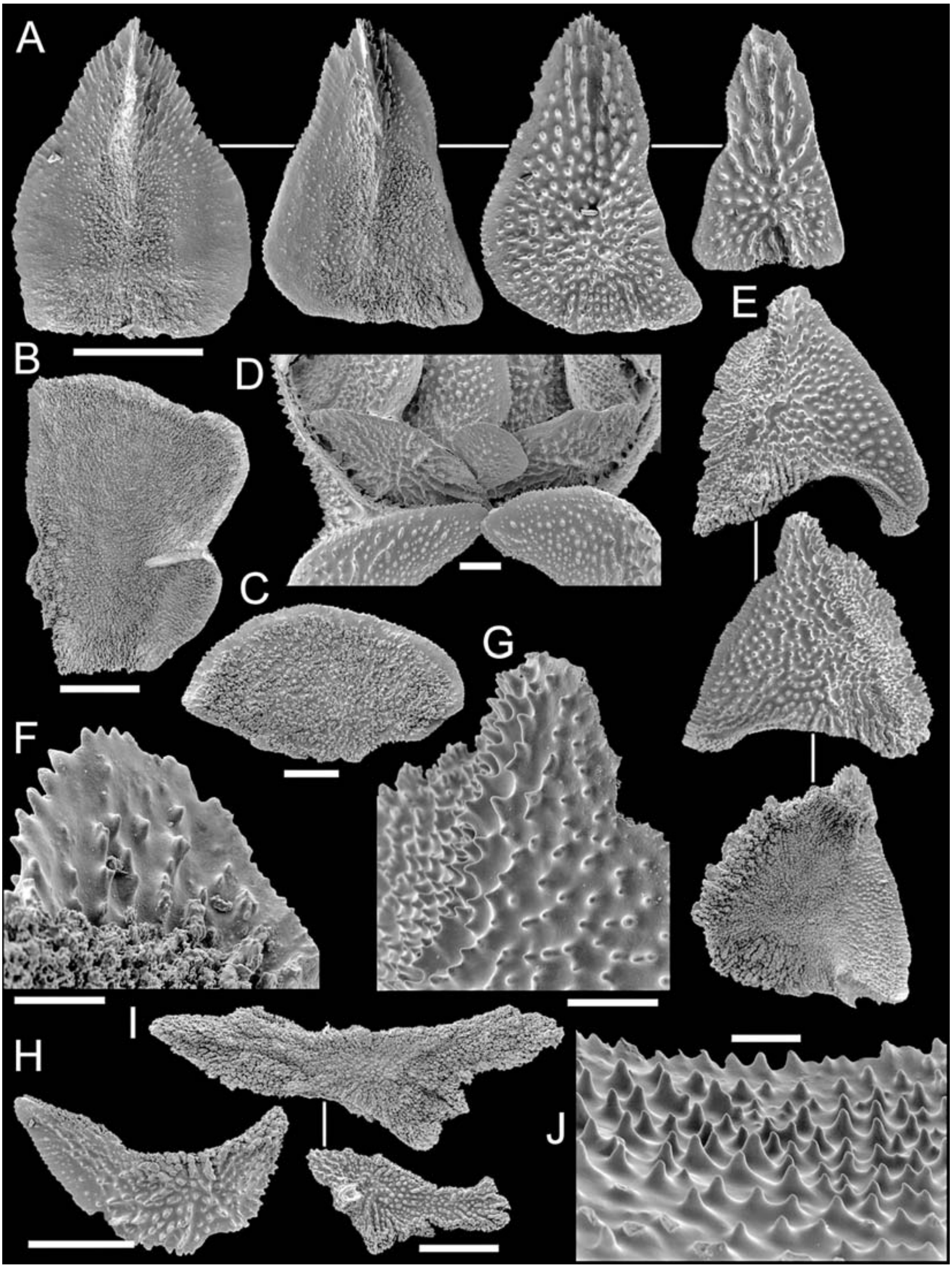

Figure 5. Sclerites of *Paracalyptrophora hawaiinensis* from the holotype (usnm 1071425): *A*, opercular sclerites; *B*, inner surface of an abaxial buccal sclerite; *C*, inner surface of an adaxial buccal sclerite; *D*, three adaxial buccal sclerites in situ; *E*, basal sclerites; *F–G*, inner and outer surfaces, respectively, of a basal sclerite spine; *H*, an infrabasal sclerite; *I*, inner surface of two coenenchymal sclerites; *J*, spines on outer surface of a buccal scale. Scale bars: *A–B*, *H–I*, 0.25 mm; *C–D*, *G*, 0.10 mm; *F*, *J*, 0.05 mm.

basal scales. The two large abaxial buccal scales (Figure 5*B*) up to 1 mm in length, slightly constricted medially, and with very finely serrate distal edges; operculars project well beyond buccal scales. On adaxial side of every polyp are two rather prominent crescent-shaped adaxial buccals, each about 0.45–0.55 mm in width and 0.3 mm in height; they have a serrate distal margin (Figure 5*C*). Between these two adaxial buccals is usually a single rather small (0.18 mm in diameter), elliptical adaxial buccal scale (Figure 5*D*). Also, there may be two intermediate-sized adaxial buccal scales bordering the two large adaxial buccals on their abaxial side. Abaxial buccals and basal scales meet along abaxial sagittal line in a single irregular, raised junction (Figure 4*A*). The two crescent-shaped infrabasals are up to 0.3 mm in height (Figure 5*H*).

Abaxial opercular 0.60–0.65 mm in length (L : W = 1.3), symmetrical, and slightly longitudinally creased above, corresponding to a keel on inner surface. Lateral operculars 0.5–0.65 mm in length (L : W = 1.5–1.6), asymmetrical, and relatively flat above. Adaxial operculars 0.45–0.50 mm in length (L : W = 1.6), symmetrical, and flat (Figure 5*A*).

Coenenchymal scales (Figure 5*I*) elongate but irregular in shape, up to 1.3 mm in length, with a L : W ratio up to 4.5. Their outer surfaces covered with granules but not ridged. No pinnular scales noted.

ETYMOLOGY: Named for the region from which it was first collected.

COMPARISONS: *Paracalyptrophora hawaiinensis* is quite similar to *P. echinata* and was at first thought to be a diminutive form of that species but in fact differs from it in a number of characters, the most important being that it has 3–5 adaxial buccal scales. Also, *P. hawaiinensis* has much smaller basal lobes, and because of its overall smaller polyp size it has correspondingly smaller body wall and opercular scales and whorl diameter. Also, its coenenchymal scales are not ridged. Finally *P. hawaiinensis* occurs at shallower depths and more to the southeast within the Hawaiian Islands. One other species in the genus is known to have adaxial buccal scales, *P. kerberti* (see Cairns and Bayer [2004*a*]), known from Japan, but that species differs in having prominent buccal spines, smooth body wall scales, and a biplanar colony.

DISTRIBUTION: Twin Banks east of Nīhoa, O‘ahu, Moloka‘i, Hawai‘i, Cross Seamount, 320–444 m, with one outlying record at 970 m.

Genus *Calyptrophora* Gray, 1866

DIAGNOSIS: Colonies uniplanar (lyrate, dichotomous, or biplanar in branching) or unbranched (flagelliform). Polyps arranged in whorls, in most species polyps facing upward. Polyps composed of two annular sclerite rings, each composed of two inseparably fused scales; a pair of discrete crescent-shaped infrabasals also present. Distal margin of body wall scales usually spinose, toothed, or lobate, sometimes extended as a protective cowl. Operculum composed of eight triangular scales, each invariably longitudinally creased on its outer surface and usually having a keel on its inner surface. Coenenchymal scales elongate and flat, usually granular. Pinnular rods sometimes present.

TYPE SPECIES: *Calyptrophora japonica* Gray, 1866, by monotypy.

REMARKS: To place the five Hawaiian species in context, representatives of all species of *Calyptrophora* were examined (Table 1), most based on their type specimens, and a key and phylogenetic analysis to the species is provided here. *Calyptrophora* is one of 36 primnoid genera (Cairns and Bayer 2009), its monophyly established by one character (Table 2, character 5): the fact that its basal and buccal body wall scales are inseparably fused into ringlike structures (first suggested by Kinoshita [1908] and later reiterated by Bayer [1956, 1981, 2001] and Cairns and Bayer [2009]). According to a recently published phylogenetic analysis of the primnoid genera (Cairns and Bayer 2009), *Paracalyptrophora* was determined to be the sister group to *Calyptrophora*, and *Arthrogorgia* was purported to be ancestral to those two genera; thus *Paracalyptrophora* and *Arthrogorgia* were used as the outgroups in the analysis. Phylogenetic trees were generated using the principles of

TABLE 1

Listing of the 16 Valid Species of the Genus *Calyptrophora*, Including Their Junior Synonyms, Varieties, and the Attributions of Versluys' (1906) Forms of *C. japonica* (Species Listed Chronologically in Order of Description; Those from the Hawaiian Islands [HI] in **Boldface**)

Taxa	Known General Distribution, Depth Range
C. japonica Gray, 1866 (type species)	Western Pacific, 400–1,300 m
C. trilepis (Pourtalès, 1868)	NW Atlantic, 593–911 m
***C. wyvillei* Wright, 1885**	Kermadecs, HI, 764–1,278 m
= *C. versluysi* Nutting, 1908	
C. agassizii Studer, 1894	Galápagos, 691–1,545 m
[*C. japonica* form A sensu Versluys (1906)]	
***C. angularis* (Nutting, 1908)**	HI, 366–1,723 m
***C. clarki* Bayer, 1951**	HI, 808–1,105 m
= *C. japonica* of Nutting (1908)	
C. juliae Bayer, 1952	Philippines, 729 m
C. spinosa Pasternak, 1984	Kapingamarangi, 910–1,575 m
C. microdentata Pasternak, 1985	W Atlantic, 686–2,310 m
= *C. pillsburyae* Bayer, 2001	
C. gerdae Bayer, 2001	NW Atlantic, 229–556 m
C. antilla Bayer, 2001	NW Atlantic, 1,399–1,642 m
C. cf. *antilla* sensu Cairns (2007)	Davidson Seamount, 1,683–1,763 m
= *C. japonica* form B (in part, specimen #3) sensu Versluys (1906)	
C. bayeri Cairns, 2007	NE Pacific, 1,683 m
C. laevispinosa Cairns, 2007	NE Pacific, 3,107 m
C. clinata Cairns, 2007	NW Atlantic, 1,315–1,842 m
C. clinata var. sensu Cairns (2007)	
C. *pileata*, n. sp.	HI, W Pacific, 227–520 m
= *C. japonica* form C sensu Versluys (1906)	
***C. alpha*, n. sp.**	HI, 1,078–1,220 m

parsimony implemented in PAUP* (Beta version 4b10) (Swofford 1998). Characters were coded as unordered binary variables or as unordered multistate characters as indicated in Tables 2, 3. The taxon *C.* cf. *antilla* sensu Cairns (2007*a*) was not included in the analysis because it had the same set of character states as *C. antilla* Bayer, 2001. A heuristic search was performed using 1,000 random addition sequences followed by branch swapping using the tree bisection-reconnection (TBR) algorithm. Characters were optimized using the Actran algorithm. Fifteen characters, consisting of 41 character states, were employed in the analysis. The characters used included all those morphological attributes that have traditionally been used to distinguish species. Furthermore, characters were presumed to be independent of each other, and their states were presumed to be homologous. Two characters (5 and 15) were included to help distinguish the outgroup taxa. The character states of character 1 (branching pattern) are further illustrated in Figure 8.

The unweighted analysis of the data matrix (Table 3) yielded 286 equally most-parsimonious trees, for which the 50% majority rule consensus tree is presented as Figure 6, showing the percentage of most parsimonious trees containing each node. This tree has a length of 46 steps, a CI = 0.50 and an RI = 0.60. Figure 6 also shows the two clades referred to in the next paragraph.

The 50% majority rule consensus tree (Figure 7), which shows all inferred character state changes, is not phylogenetically robust, in that it contains many polychotomies and demonstrates low support for most branches.

TABLE 2

Characters and Character States Used in the Phylogenetic Analysis of *Calyptrophora*

Colony

1. Branching pattern: 0. Unequal dichotomous (Figure 1*I*); 1. Equal dichotomous (Figures 1*C*, *G*, 8*B*); 2. Lyrate (Figures 1*E*–*F*, 8*C*–*D*); 3. Biplanar dichotomous; 4. Opposite bipectinate, biplanar (Figure 8*E*); 5. Alternate pinnate; 6. Unbranched (Figures 1*B*, 8*A*) (CI = 0.5).

Polyps

2. Orientation of polyps: 0. Proximally (down, Figure 11*A*); 1. Distally (up, Figure 15*A*) (CI = 0.5).
3. Number of whorls/3 cm: 0. More than 10; 1. Less than 10 (CI = 0.5).
4. Horizontal length of polyps: 0. More than 2 mm; 1. Less than 2 mm (CI = 0.25).
5. *Body Wall Scales:* 0. Not fused (independent, Figures 2*B*, 3*B*–*C*); 1. Inseparably fused into a ring (Figures 9*D*–*E*, 10*B*) (CI = 1.0).

Spine on Basal Scale

6. Basal scale spine: 0. Absent or negligible (0–0.2 mm, Figure 10*B*–*D*); 1. Large (over 0.4 mm, Figures 13*A*–*C*, 14*C*–*D*); 2. Small (0.20–0.40 mm) (CI = 0.67).
7. Distal cross section: 0. Flattened (Figure 14*C*); 1. Round (Figures 11*C*, 12*D*) (CI = 0.25).
8. Sculpture on inner side: 0. Serrate ridges (Figures 14*E*, 16*E*); 1. Granular; 2. Smooth (Figure 10*C*–*D*) (CI = 1.0).
9. Curvature: 0. Straight (Figure 13*B*–*C*); 1. Curved forward (Figure 17*B*–*D*) (CI = 0.5).

Buccal Scale

10. Orientation: 0. Horizontal (Figure 17*D*); 1. Inclined (Figure 15*A*–*B*) (CI = 0.5).
11. Distal edge of buccal scale: 0. Smooth: straight to slightly lobate (Figure 12*B*, *left*); 1. Jagged, flattened teeth (Figure 16*C*); 2. Needlelike, cylindrical spines (Figures 13*C*–*D*, 14*B*) (CI = 0.67).

Opercular Region

12. Cowl: 0. Absent (Figure 9*B*); 1. Present (Figure 15*D*) (CI = 0.5).
13. Operculars keeled: 0. Present (Figure 18*A*); 1. Absent (Figure 12*A*) (CI = 0.5).
14. Pinnular sclerites: 0. Common (Figure 18*H*); 1. Rare/absent (CI = 0.2).
15. *Infrabasal Scales:* 0. More than 1 pair; 1. One pair (Figure 11*D*) (CI = 1.0).
16. *Symbionts*: 0. Polychaetes; 1. Ophiuroids (Figure 1*D*); 2. None (CI = 0.67).

Note: Values in parentheses are the consistency indices for each character per the 50% majority rule tree.

TABLE 3

Character State Matrix Used in Phylogenetic Analysis of *Calyptrophora*, as Defined in Table 2 (*C.* cf. *antilla* not included)

	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Arthrogorgia (OG)	0	0	0	0	0	0, 1	0	0	0	0, 1	0, 2	0, 1	0	0	0	0
Paracalyptrophora (OG)	x[a]	0	0	0, 1	0	1	0	0	0	0	0, 1, 2	0, 1	0	1	1	2
C. wyvillei	2	0	1	0	1	1	0	0	0	0	1, 0	1	1	1	1	1
C. agassizii	1	0	0	0	1	1	1	0	0	0	0	1	0	1	1	2
C. clinata	6	0	0	1	1	1	1	0	0	1	0, 1, 2	0	1	1	1	2
C. trilepis	1	0	0	1	1	0	0	2	0	0	0	0	0	0	1	2
C. angularis	2	1	0	0	1	0	0	1	0	1	0, 1	0	0	0	1	2
C. juliae	6	1	0	1	1	1	1	0	0	1	1	0	0	0	1	2
C. japonica	4	1	0	1	1	2	1	0	0	1	1	0	0	1	1	2
C. spinosa	2	1	0	0	1	1	1	0	0	1	1	1	0	0	1	2
C. clarki	1	1	0	0	1	1	1	0	0	0	2	0	0	1	1	1
C. gerdae	1	1	0	1	1	1	0	0	0	1	1	1	0	0	1	2
C. antilla	2	1	1	1	1	1	1	0	1	0	2	0	0	0	1	2
C. microdentata	1	1	0	1	1	1, 2	1	1, 2	0	0	2	0	0	0	1	2
C. bayeri	0	1	0	0	1	1	0	0	0	0	1	1	0	0	1	2
C. laevispinosa	0	1	0	1	1	1	1	2	0	0	2	0	0	0	1	2
C. pileata	2	1	0	1	1	1	0, 1	0, 2	0	1	1	1	0	1	1	2
C. alpha	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	2

[a] Character states 0, 1, 2, and 3.

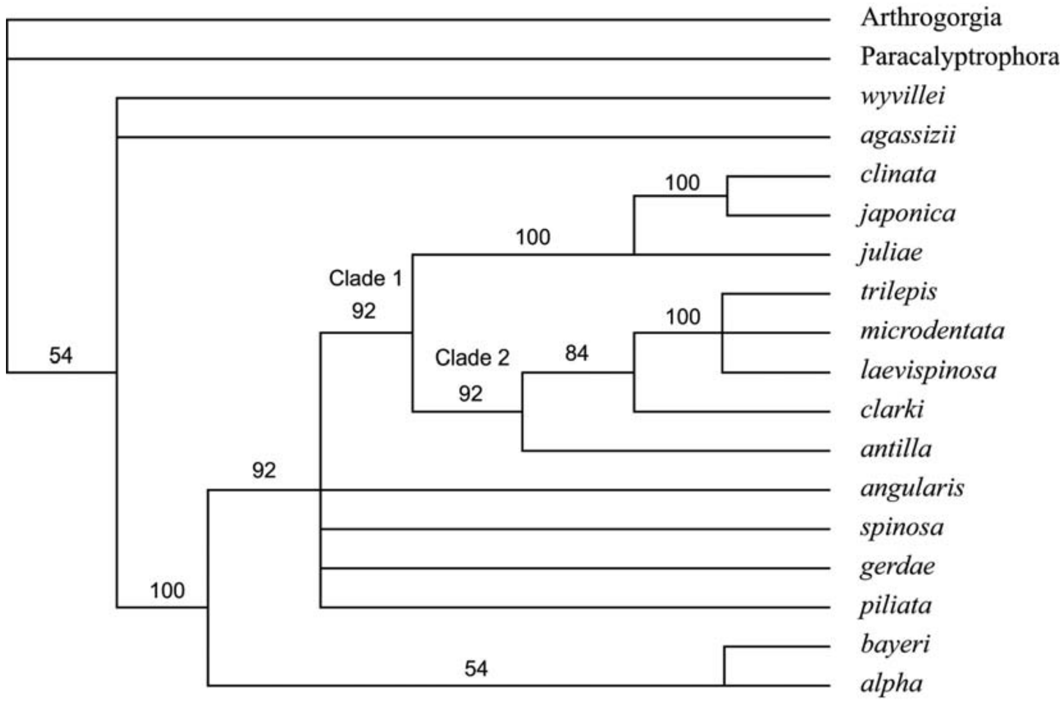

FIGURE 6. Fifty percent majority rule cladogram of the *Calyptrophora* species, showing two clades discussed in text. Percentage of the most parsimonious trees that contain that node listed above line.

Nonetheless, it does not lend support to the species complexes and species groups suggested by Bayer (2001), which were based on the orientation of the polyps (character 2) and the presence of spines on the basal scales (character 6), respectively, and thus these groups, however convenient, are abandoned in this treatment. Only two clades are even nominally supported on the tree. Clade 1 (Figures 6, 7) contains eight species that share having basal spines round in cross section (character 7, state 1) and lacking an opercular cowl (character 12, state 0). And within clade 1 is clade 2, consisting of five species, sharing inclined polyps (character 10, state 0) and needlelike basal spines (character 11, state 2).

DISTRIBUTION: Tropical and temperate latitudes of Atlantic, Pacific, and Indian oceans, 227–3,107 m.

KEY TO THE SPECIES OF *Calyptrophora* (**boldface** = species known from Hawai'i)

1. Polyps in whorls directed downward toward base of main stem 2
1′. Polyps in whorls directed upward toward branch tip 4

2. Colonies unbranched (Figure 8*A*).. *C. clinata*
2′. Colonies branched (Figure 8*B–E*) 3

3. Branching tetrachotomous in basal parts (robust) (Figure 1*D*); operculars not keeled (Figure 12*A*); spines on basals broad-based (spatulate) (Figure 12*D*)....... ***C. wyvillei***
3′. Branching equal dichotomous (delicate); operculars keeled; spines on basals slender, round in cross section .... *C. agassizii*

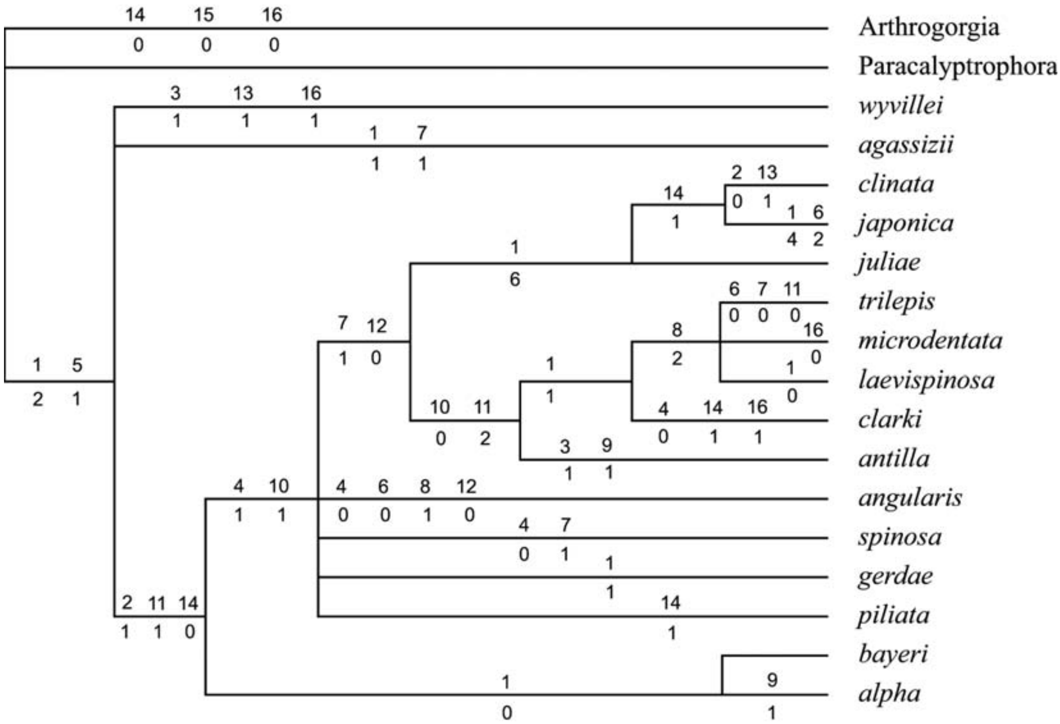

FIGURE 7. Fifty percent majority rule cladogram showing all character state changes (see Tables 2, 3). Number of character above line, and character state below line.

4. Spines on basal scales small (0–0.3 mm tall) 5
4′. Spines on basal scales tall (0.4–2.2 mm tall) 6

5. Branching equal dichotomous (Figure 8*B*); basal spines absent or inconspicuous (<0.1 mm), flat .... *C. trilepis*
5′. Branching lyrate (Figure 1*F*); basal spines missing or very small (<0.20 mm), flat (Figure 10*B–D*) .... ***C. angularis***
5″. Branching biplanar, bipectinate (Figure 8*E*); basal spines up to 0.25 mm, circular in cross section .... *C. japonica*

6. Colonies unbranched .... *C. juliae*
6′. Colonies branched 7

7. Margin of buccal scales bear several broad-based, triangular, flat teeth 8
7′. Margin of buccal scales bear elongate spines 12

8. Colonies lyrate (Figure 8*C*) in branching; buccal scale highly inclined toward branch 9
8′. Colonies dichotomous (Figure 8*B*) in branching; buccal scale horizontal to branch ... 10

9. Coenenchymal scales thick (Figure 16*G*); polyps less than 1.6 mm in length; 15–17 whorls/3 cm (Figure 15*A*) .... ***C. pileata***
9′. Coenenchymal scales not thick; polyps 2.5–2.7 mm in length; 10–12 whorls/3 cm .... *C. spinosa*

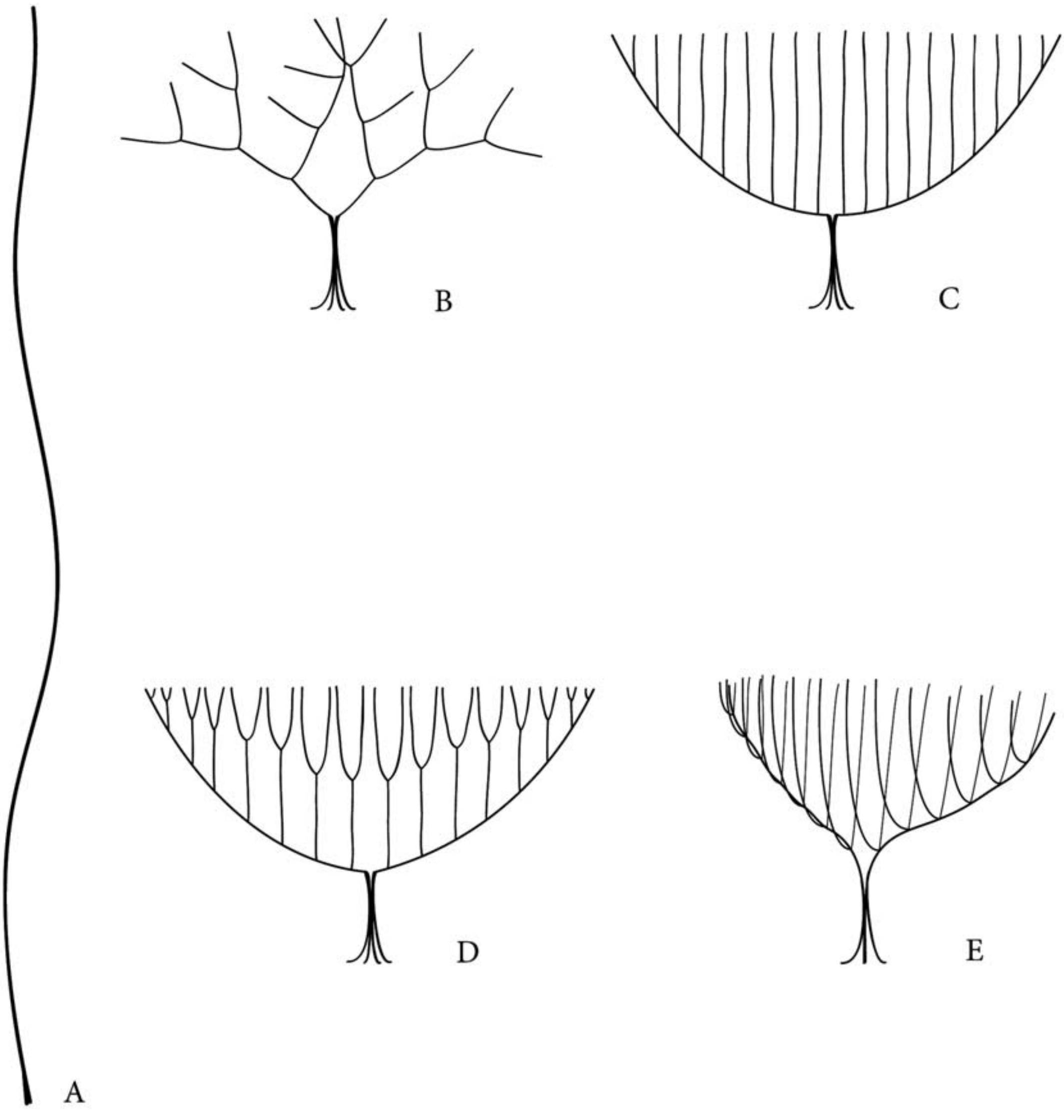

Figure 8. Drawings of the branching patterns of the various species of *Calyptrophora: A*, unbranched; *B*, equal, dichotomous branching; *C*, lyrate branching; *D*, lyrate followed by dichotomous branching; *E*, opposite bipectinate resulting in biplanar flabella.

10. Marginal teeth on buccal scales small, less than 0.2 mm in height .... *C. bayeri*
10′. Marginal teeth on buccal scales taller: 0.3–0.6 mm in height 11

11. Branching unequal dichotomous to lyrate (Figure 1*I*); polyps 2.2–2.4 mm in length (Figure 17*B*); basal spines up to 1.3 mm and curve forward (Figure 17*B*, *E*) .... ***C. alpha***
11′. Branching equal dichotomous; polyps less than 1.5 mm in length; basal spines up to 0.65 mm and straight .... *C. gerdae*

12. Basal spines smooth or sparsely granular (not ridged or serrate) 13
12′. Basal spines bear serrate longitudinal ridges 14

13. Colonies quasi-pinnate, in multiple fronds; buccal spines up to 0.6 mm long; basal spine often with a smaller shoulder spine on abaxial side . . . . *C. laevispinosa*
13′. Colonies equal dichotomous in branching; buccal spines 0.2–0.4 mm long; basal spines discrete . . . . *C. microdentata*

14. Colonies equal dichotomous in branching (Figure 1*G*); base of basal spines flattened, up to 1.5 mm in length (Figure 14*D*); 2–6 buccal spines per polyp, but usually 2 (Figure 13*C–D*) . . . . ***C. clarki***
14′. Colonies lyrate (branchlets may be secondarily dichotomous); basal spines circular in cross section and only up to 1 mm in length; 4 buccal spines per polyp 15

15. Buccal spines up to 0.45 mm long . . . . *C. antilla*
15′. Buccal spines 0.9–1.2 mm long . . . . *C.* cf. *antilla*

Calyptrophora angularis (Nutting, 1908)
Figures 1*F*, 9–10

Stachyodes angularis Nutting, 1908:576, pl. 43, fig. 7; pl. 48, fig. 1.—Kükenthal, 1919:467; 1924:316.
Paracalyptrophora angularis.—Chave and Malahoff, 1998: table 1.
Calyptrophora clarki.—Chave and Malahoff, 1998:31, table 1, fig. 62 (in situ).
Calyptrophora angularis.—Bayer, 2001:367.—Parrish and Baco, 2007:191 (listed).

material examined: Types; unknown *Alb* station, 2 branches, usnm 49640 (ex usnm 25390, *K. flabellum*); *Alb*-3998, 1 branch, usnm 49638; *Pisces 4*-46, 1 large colony, usnm 1010724; *Pisces 5*-543, 1 branch (robust form), usnm 1072128; *Pisces 5*-696, 1 large dry colony (robust form), usnm 1115290; 21° 12.75′ N, 157° 44.35′ W, 450–550 m, 1 large dry colony, usnm 1115288; *Star II*-2, large colony, usnm 56822.

types and type locality: Holotype: one very badly damaged colony in several pieces, the longest 10.5 cm and SEM stubs C1336–1337, deposited at the usnm (25346). A fragment is also deposited at the bm (1920.02.27.012); exact type locality not given, but certainly from the 1902 *Albatross* expedition to the Hawaiian Islands.

description: Colonies uniplanar and strictly lyrate in branching (Figure 1*F*). Main stem vertical, straight, and up to 25 cm in length (usnm 450–550 m), larger colonies having a basal main stem diameter of 4.0–4.5 mm; axis golden to bronze in color, main stem devoid of polyps. One of the largest colonies (usnm 56822) is 44 cm tall and 31 cm wide, including 21 cm main stem. After initial bifurcation, which forms an axil angle of about 50°, branches originate unilaterally every 1.5–2.0 cm on either side of flabellum; in illustrated specimen (Figure 1*F*) 14 branches occur on one side of colony, 16 on the other. These branches remain unbranched and all reach to about same height in colony, thus forming a horizontal upper margin, resulting in first formed branches being much longer (up to 22 cm) than last formed branches. Polyps point upward and arranged in whorls of 5–8, often depending on branch diameter. There are 12–15 whorls per 3 cm; whorl diameter is about 4.0 mm. Polyps 1.9–2.2 in length.

Basal ring, composed of the two fused basal scales (Figure 10*B*), stands up to 1.3 mm in height, including its distal spines, and has smoothly curved dorsolateral edges. Each basal bears a small, triangular, flat spine up to 0.2 mm in height, which occur at outer edges of articulating ridge (Figure 10*C–D*). Basal spines smooth (not ridged or spinose) but may bear some small granules. The fused buccal scales (Figure 9*D–E*) up to 1.1 mm in length and inclined sharply downward toward branch axis. Their distal margins straight to slightly undulate and only rarely produced into 4 short (0.12 mm), flat teeth (the latter

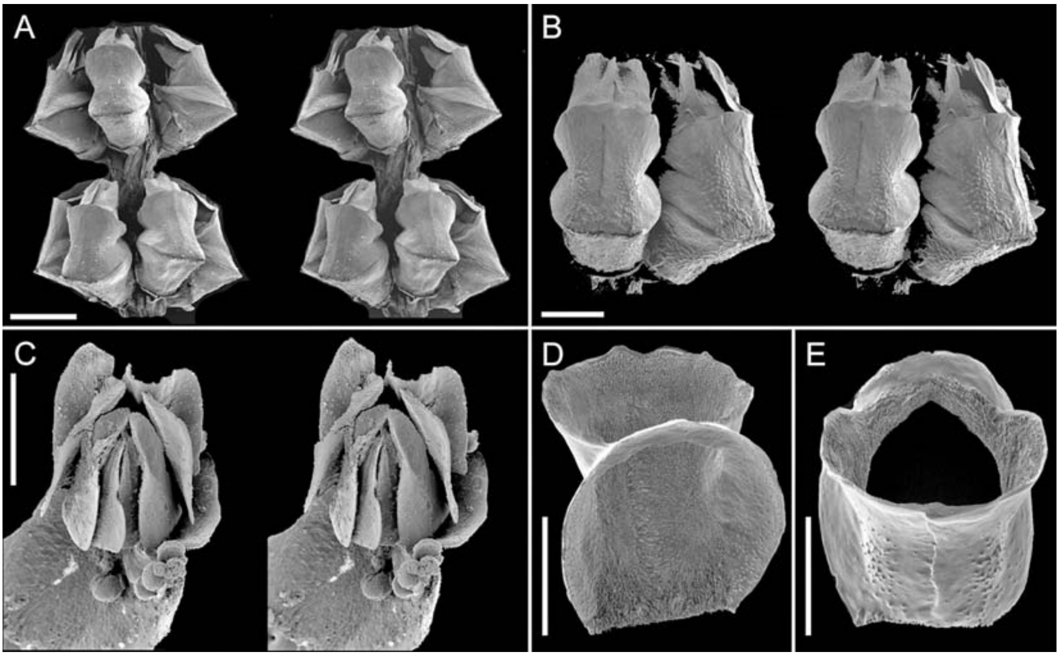

FIGURE 9. Polyps and some individual sclerites of *Calyptrophora angularis* (*A–B*, *Star II*-2, USNM 56822; *C–E*, holotype, USNM 25346); *A–C* are stereo views: *A*, lateral view of two whorls of polyps; *B*, abaxial and lateral views of two polyps; *C*, adaxial view of the opercular crown; *D–E*, adaxial and opercular views, respectively, of buccal sclerites. Scale bars: *A*, 1.0 mm; *B–E*, 0.5 mm.

more common on newly formed polyps on ends of branches) and not formed into a protective cowl; most of length of opercular scales thus easily visible in abaxial view. Infrabasals (Figure 10*E*) well developed, up to 0.45 mm in height.

Abaxial opercular scales about 0.8–0.9 mm in length (L : W = 1.6) and roughly rectangular, with deeply serrate distal edge (Figure 10*A*) and deeply creased outer surface. Lateral operculars triangular, only slightly smaller (0.65–0.80 mm, L : W = 1.7–1.8), and slightly asymmetrical. Adaxial operculars also triangular and rather small (0.50–0.55 mm, L : W = 1.7). All operculars bear a low keel on their inner surface. Pinnular sclerites (Figure 10*F*) common; they are curved and about 65–70 μm in length.

Coenenchymal sclerites elongate (up to 1.5 mm, L : W = 2.5–3.0) and somewhat irregular in shape (Figure 10*G*). Their outer surface covered with rather coarse granules or nodules, each up to 50 μm in diameter.

COMPARISONS: *C. angularis* belongs to a "species group" (sensu Bayer 2001) consisting of only two species that have very reduced or absent buccal and basal spines; the other species is *C. trilepis* (Pourtalès, 1868). *Calyptrophora angularis* is distinguished from *C. trilepis* by having lyrate branching, slightly larger polyps, and basal teeth up to 0.2 mm (see Table 3 and key).

REMARKS: Two colonies, designated as the "robust form" here, differ from the typical form in having larger polyps (3.1–3.2 mm long), a correspondingly larger whorl diameter of about 5.5 mm, and a much more robust colony, the axis diameter attaining up to 7 mm; they are otherwise identical to the typical form. This robust form also occurs in much deeper water and farther to the west in the Hawaiian Islands.

DISTRIBUTION: Hawaiian Islands: off Kaua'i, O'ahu, and Maui, 366–430 m; robust form off Brooks and Blank Banks, NWHI, 1,498–1,723 m.

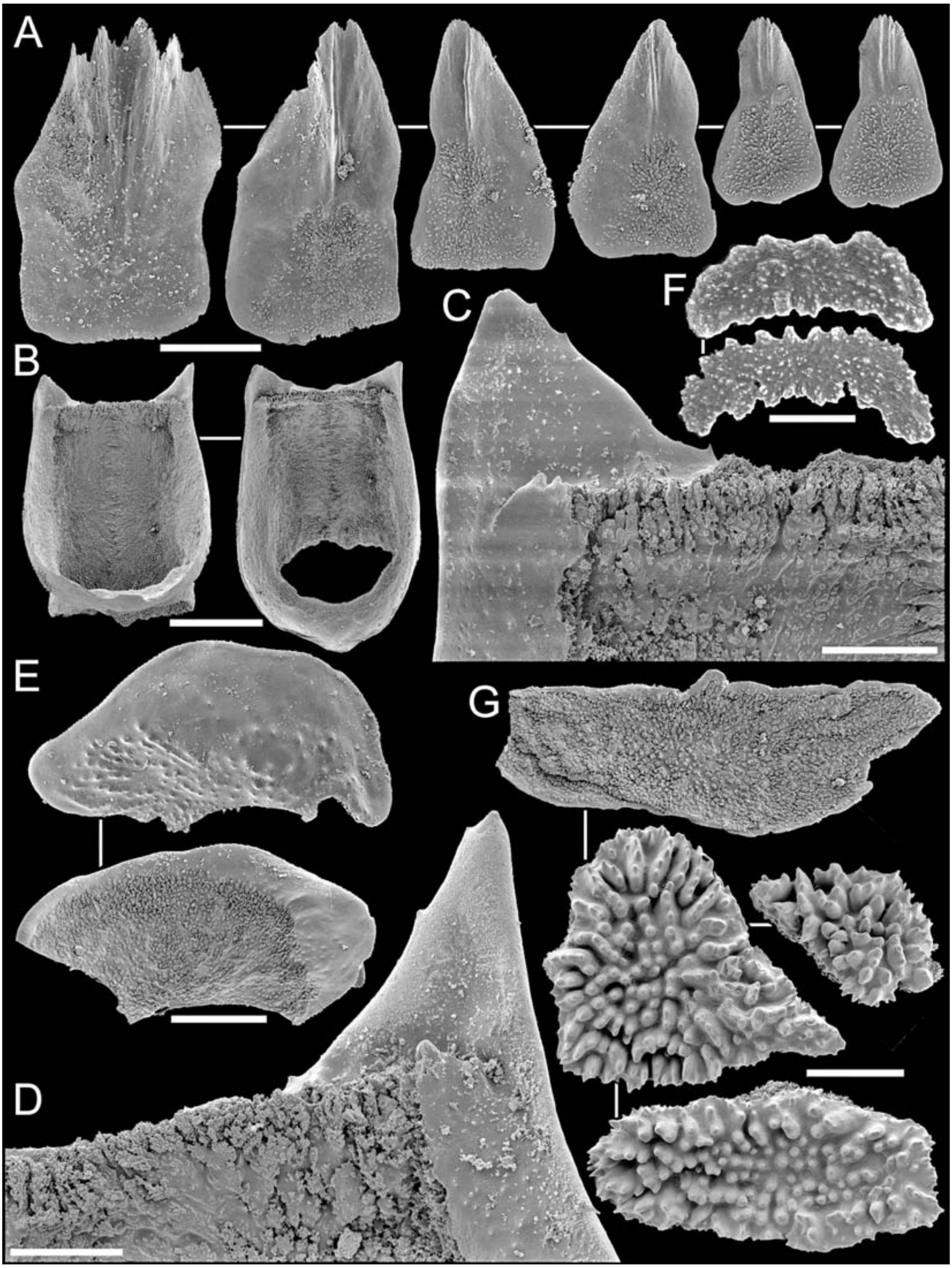

FIGURE 10. Sclerites of *Calyptrophora angularis* (A–E, holotype, USNM 25346; *F*, USNM 56822): *A*, opercular sclerites; *B*, inner view of two basal sclerites; *C–D*, enlargement of the smooth inner surface of two basal spines, showing articulating ridge; *E*, infrabasal scales; *F*, tentacular or pinnular sclerites; *G*, coenenchymal sclerites. Scale bars: *A*, *E*, *G*, 0.25 mm; *B*, 0.5 mm; *C–D*, 0.10 mm; *F*, 0.025 mm.

Calyptrophora wyvillei Wright, 1885
Figures 1*D*, 11–12

Calyptrophora wyvillii Wright, 1885:690.—Nutting, 1908:578.
Calyptrophora wyvillei.—Wright and Studer, 1889:52, pl. 19, figs. 2, 2*a*; pl. 20, fig. 5 (justifiable emendation).—Versluys, 1906:110–112, pl. 7, fig. 22, text figs. 146–150.—Kükenthal, 1919:474 (no new data); 1924:318 (key to species).—Aurivillius, 1931:301 (key to species).—Grigg and Bayer, 1976:171 (listed).—Bayer, 2001:367 (listed).—Parrish and Baco, 2007:192 (listed).
Calyptrophora versluysi Nutting, 1908:579, pl. 43, fig. 8.—Bayer, 2001:367 (listed).
Calyptrophora agassizii.—Grigg and Bayer, 1976:171 (listed).—Parrish and Baco, 2007:191 (listed).
Calyptrophora wyvilli.—Chave and Malahoff, 1998: table 1 (incorrect spelling).
Not *Calyptrophora agassizii*.—Chave and Malahoff, 1998:31, table 1, fig. 60.

MATERIAL EXAMINED: Types of *C. versluysi; Alb*-3997, 1 colony, USNM 100825 (reported by Nutting [1908]); *Alb*-4007, 1 colony, USNM 49608 (topotypic but not part of type series); Midway Survey, 25° 30′ N, 168° 39′ W, 1,154 m, 1 branch, USNM 100763; *Pisces* 5-216, 1 dry branch, USNM 93182; *Pisces* 5-234, 1 dry colony, USNM 1099198; *Pisces* 5-299 (OAD-110), 1 large colony, USNM 98819; *Pisces* 5-301 (LAD 102), 1 large colony, USNM 98115; *Pisces* 5-303 (HAD 9, 11, 15, 107), 2 dry and 2 alcohol-preserved colonies, USNM 98814, 98817, 98818, 98816, respectively; *Pisces* 5-464-12, 1 dry colony, USNM 1092794; *Pisces* 5-524, 1 colony, USNM 1071947; *Pisces* 5-525, 1 dry colony, USNM 1072107; *Pisces* 5-543, 1 branch, USNM 1072130; *Pisces* 5-595, 1 dry colony, USNM 1071423; *Pisces* 5-666, 1 dry colony, USNM 1113909; *Sango* 13-2, 1 colony, USNM 1114583; *Sango* 16-10, 2 branches, USNM 1114609; *TC* 52-122, 1 colony, USNM 1114610.

TYPES AND TYPE LOCALITY: *C. wyvillei*: The holotype, which should be deposited at the BM, cannot be located and is presumed to be lost. Type locality: *Challenger*-171: 28° 33′ S, 177° 50′ W (Kermadec Islands), 1,097 m.

C. versluysi: Holotype (*Alb*-4007, USNM 25382, colony and SEM stubs C1338–1341) and paratype (*Alb*-3997, USNM 43102). Type locality: *Albatross*-4007: 21° 50′ 20″ N, 159° 31′ 40″ W (south of Kaua'i), 929–1,018 m.

DESCRIPTION: Colonies essentially uniplanar and lyrate in branching sequence, but in lower half of colony branching slightly more bushy and irregular. Main stem vertical, straight, and up to 15 cm in length and 3.1 mm in diameter, dark (usually dark brown, black, or bronze) in color and completely covered with whorls of polyps (Figure 1*D*). At first branching point a whorl of four branches originate (i.e., tetrachotomously), two in the eventual plane of colony and two perpendicular to plane of colony, the latter two branchlets curving upward and usually not branching again; these ascending branchlets may be up to 45 cm long. After 1.5–2 cm the two branches in plane of colony both give rise to four more branches, as described for first branching point, but in this case innermost lateral branch curves upward and often bifurcates after about 5 cm, outermost lateral leading to third branching point, which may also produce four branches. The largest colony (USNM 98819), which is 45 cm tall exclusive of main stem and has the same width, consists of eight branching points on each side of main branching point, first four branching points giving rise to four branches, the latter four being only bifurcate. Thus, later branching points restricted to bifurcating only confer uniplanar and lyrate aspect to colony. Polyps point downward and arranged in whorls of 3–5 (usually 4), but on larger diameter main stem may be in whorls of 8. Usually 7–8 whorls per 3 cm, whorls being fairly closely spaced; whorl diameter about 3.5 mm on distal branches. Polyps 2.5–2.7 mm in horizontal length.

Fused basal scales (Figure 12*D*) stand perpendicular to stem up to 2.5 mm tall including spines, having smoothly curving dorsolateral edges. Each basal bears a large (up to 1.2 mm long), thin, spatulate or blade-like spine, the bases of which occupy entire length of articulating ridge. Distal basal

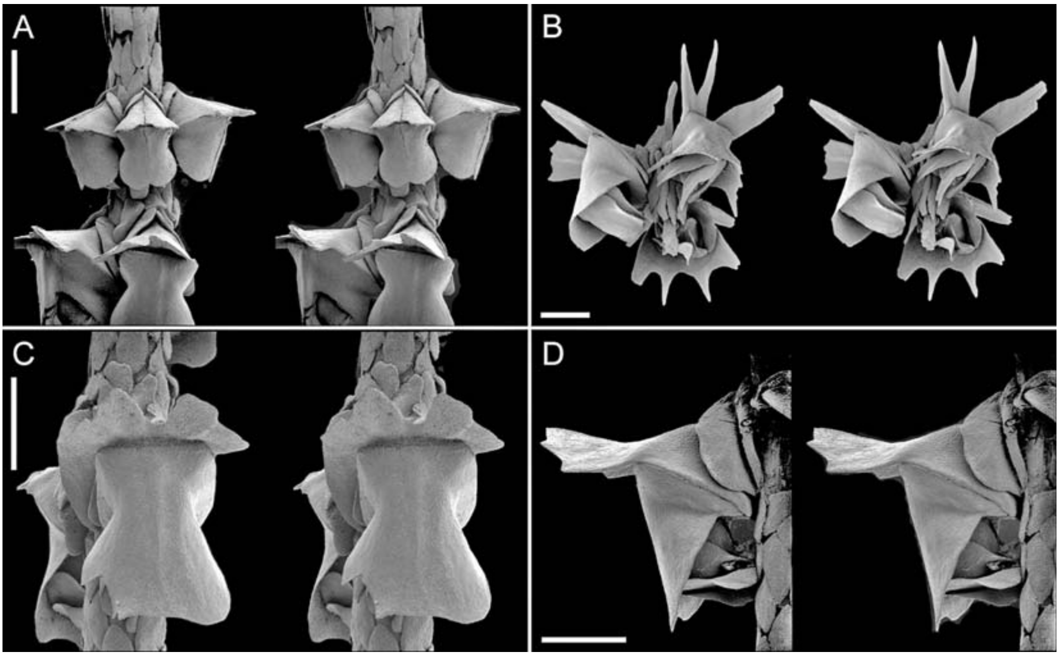

FIGURE 11. Polyps of *Calyptrophora wyvillei* (holotype of *C. versluysi*, USNM 25382), stereo views: *A*, lateral view of two whorls of polyps; *B*, opercular view of a whorl, showing polyps with both spinose and entire buccal scales; *C–D*, abaxial and lateral views, respectively, of polyps. All scale bars 1 mm.

spines variously shaped, but each usually terminates in 2–4 distal tips and often resemble antlers. Inner faces of basal spines covered with very low, inconspicuous, parallel ridges consisting of small aligned spines (Figure 12*E*). Fused buccal scales horizontal and up to 2.0 mm in length, slightly constricted basally but flaring distally into a cowl (up to 0.7 mm wide) that completely envelopes opercular scales, hiding them from an abaxial point of view (Figures 11*C–D*, 12*B*). Its inner surface is covered with inconspicuous serrate ridges. Distal edge of buccal scales usually smooth and continuous, but may be bilobate or occasionally bears up to four prominent teeth; this variation sometimes occurs in polyps of the same whorl (Figure 11*B*). The pair of unfused collarlike infrabasal scales well developed, each up to 0.67 mm in height and usually remaining attached to stem after a polyp has become detached (Figure 12*F*).

Abaxial opercular scales quite large (up to 1.4 mm in length, L : W = 1.65–1.75) and roughly rectangular, with blunt distal end and deeply longitudinally creased outer surface (Figure 12*A*). Lateral operculars somewhat smaller (up to 1.25 mm, L : W = 2.1–2.3), pointed, and asymmetrical in shape. Adaxial operculars small (0.85 mm, L : W = 2.0) and pointed, overshadowed by abaxial operculars. None of operculars keeled. Tentacular sclerites not observed.

Coenenchymal sclerites (Figure 12*G*) elongate (fusiform), up to 1.3 mm in length with L : W = 3.0–3.6, arranged in a mosaic pattern with little overlap. Their outer surface flat and slightly granular, however where an ophiuroid attaches to colony coenenchymal sclerites often bear 1–3 small circular nodules.

COMPARISONS: Only two other species in the genus have their polyps arranged in a downward-pointing direction (i.e., the *wyvillei* species complex sensu Bayer [2001]: *C. agassizii* Studer, 1894, and *C. clinata* Cairns, 2007*a*). *Calyptrophora wyvillei* is distinguished from *C.*

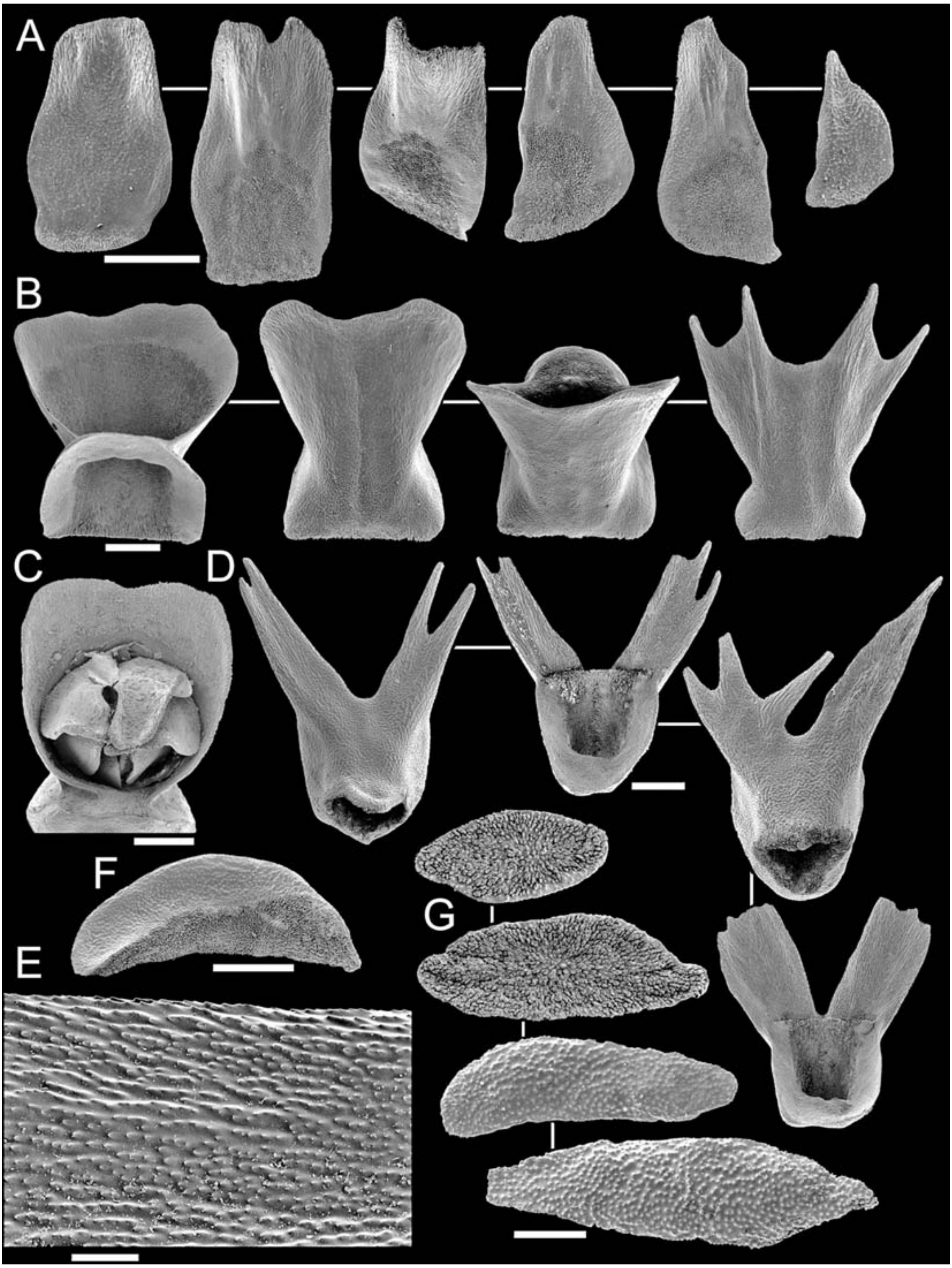

FIGURE 12. Sclerites of *Calyptrophora wyvillei* (holotype of *C. versluysi*, USNM 25382): *A*, opercular sclerites; *B*, buccal sclerites, some with a spinose distal edge, others with smooth edge; *C*, opercular view of a polyp showing cowl; *D*, highly spinose basal sclerites; *E*, spination of basal spine; *F*, an infrabasal scale; *G*, coenenchymal sclerites. Scale bars: *A–D*, *F*, 0.50 mm; *E*, 0.10 mm; *G*, 0.25 mm.

agassizii (Galápagos, 704 m) not in polyp size as implied by Kükenthal (1919, 1924) and Aurivillius (1931), because the polyps of *C. agassizii* are about the same size as those of *C. wyvillei* (2.2 mm, type examined: MCZ 4815), but by its unique branching pattern (that of *C. agassizii* is a delicate equally dichotomous branching) and very broad basal spines (those of *C. agassizii* are narrow, prominently ridged, and circular in cross section at the tips). Furthermore, *C. agassizii* has keeled opercular scales. *Calyptrophora clinata*, known only from the New England Seamounts from 1,315 to 1,842 m, differs in having an unbranched colony, smaller polyps arranged in a greater number per whorl and thus a greater number of whorls per centimeter, a downward sloping buccal scale, and highly ridged, serrate basal spines (see Table 3 and key).

REMARKS: The type of *C. wyvillei* was too small to determine its growth form, but if Versluys' (1906) *Siboga* specimens are accepted as conspecific, the figure of one colony fragment shows the characteristic tetrachotomous branching pattern followed by a secondary lyrate pattern. Thus, Nutting (1908) was probably correct to identify two Hawaiian lots as *C. wyvillei*, but his *C. versluysi* is also the same species, named separately perhaps because of the enormous variation in the distal marginal spination of buccals and basals. (Nutting gave no distinguishing characteristics between the two species.)

It is common for larger specimens to host one or more specimens of a large (disk diameter up to 1 cm) commensal ophiuroid (*Asteroschema edmondsoni* Clark, 1949), which are white in color blending with that of the octocoral (Figure 1*D*). The ophiuroid does not cause colony deformation, as do many commensal polychaetes, only a slight modification of the coenenchymal outer surface granulation.

DISTRIBUTION: Probably widespread in the western Pacific; known thus far from the Kermadec Islands, Celebes Sea, and Hawaiian Islands (from Pioneer Seamount to Cross Seamount and many of the intervening islands), 784–1,278 m.

Calyptrophora clarki Bayer, 1951
Figures 1*G*, 13–14

Calyptrophora clarki Bayer, 1951:40–41, fig. 1*A–F*.—Grigg and Bayer, 1976:171 (listed).—Bayer, 2001:367 (listed).—Parrish and Baco, 2007:191 (listed).

Calyptrophora japonica.—Nutting, 1908:578 (in part: *Alb*-4007, 4108).—Grigg and Bayer, 1976:171 (listed).—Parrish and Baco, 2007:191 (listed).

MATERIAL EXAMINED: Types; *Alb*-4108, 1 colony and SEM stub B2402, USNM 91892 (ex SUI 20969, *C. japonica* of Nutting [1908]); *Pisces* 5-527, 1 dry branch, USNM 1072113; *TC* 52-108, 1 large colony and branch, USNM 93214 and 94573.

TYPES AND TYPE LOCALITY: The holotype is now fragmented into numerous pieces, most of which have lost their polyps (also SEM stubs C1342–1343), USNM 25370. The paratype is a much better preserved, intact specimen 11 cm in height (also SEM stubs B1570, 1571) but from an unknown *Albatross* station in the Hawaiian Islands, USNM 43139. Type locality: 21° 50′ 20″ N, 159° 31′ 40″ W (south of Kaua'i), 929–1,018 m.

DESCRIPTION: Colonies uniplanar and equally dichotomously branching (Figure 1*G*); after the first bifurcation, subsequent branches originate at intervals of 8–9 mm, branching axils relatively small (10–15°). Main stem vertical, but only up to 14 mm in length and with a basal diameter of only 2.4 mm, which contributes to a delicate colony; it does not appear to support polyps. Axis yellow to golden in color. Largest colony (USNM 93214) 25 cm tall and less wide. Polyps point upward and arranged in whorls of 3 or 4; 10–12 whorls per 3 cm; and whorl diameter about 4.0–4.5 mm, including buccal spines. Polyps 2.1–2.5 mm in length, including buccal spines.

Basal ring (fused basal scales) stands up to 2.2 mm in height, but as much as 65% of that height contributed by distal spines, which may be up to 1.5 mm long (Figures 13*A–B*, 14*C*). Two basal spines occur per polyp, their bases flat and occupying most of extent of ar-

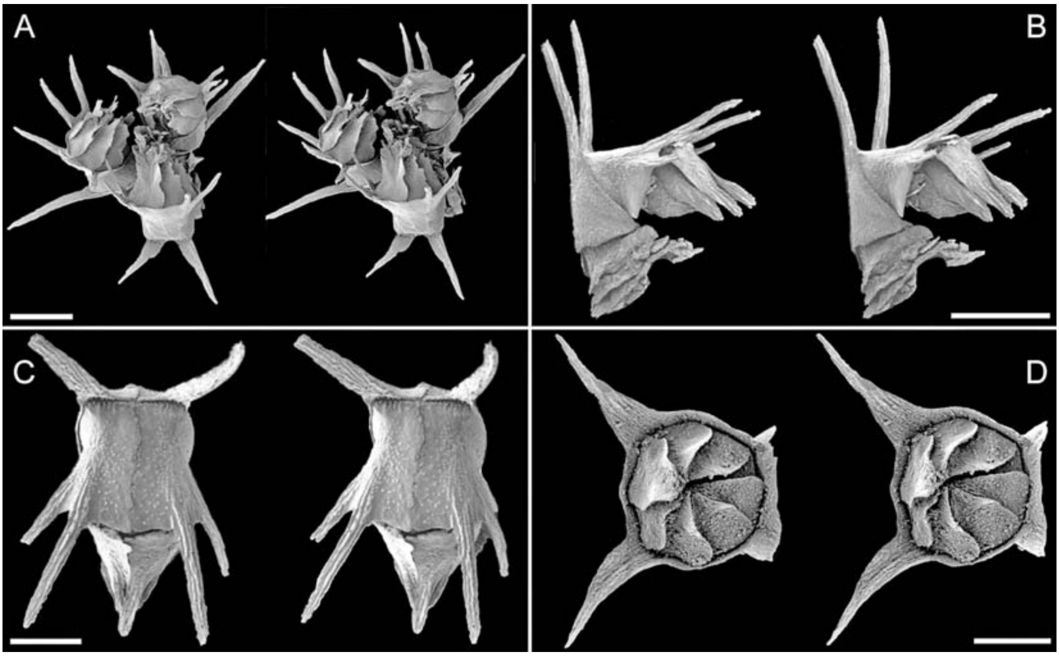

FIGURE 13. Polyps of *Calyptrophora clarki* from the holotype (USNM 25370), stereo views: *A*, apical view of a whorl of three polyps; *B–D*, lateral, abaxial, and opercular calycular views, respectively. Scale bars: *A–B*, 1.0 mm; *C–D*, 0.5 mm.

ticulating ridge, whereas their tips are circular in cross section. These spines, as well as buccal spines, bear prominently serrated (Figure 14*E*) ridges. Fused buccal scales horizontal and up to 1.0 mm in length, each polyp bearing one pair of elongate spines similar to those described for basal scales (Figures 13*D*, 14*B*) but usually slightly smaller (only up to 1.1 mm). Occasionally a second pair (Bayer [1951: fig. 1*A*] and Figure 13*C* herein) of equal-sized buccal spines occur on a polyp, and in rare cases rudiments of a third pair. Buccal scales do not form a cowl around operculars and thus operculars easily visible. Infrabasals (Figure 14*F*) 0.29–0.32 mm in maximum height.

Abaxial opercular scales (Figure 14*A*, *left*) 0.8–1.1 mm in length (L:W = 2.2–2.4), with a finely (laciniate) serrate distal tip and a deeply creased outer surface. Lateral operculars 0.65–0.85 mm in length (L:W = 1.7–2.5) and asymmetrical. Adaxial operculars triangular and almost equilateral in shape, only 0.5–0.6 mm in length (L:W = 1.2–1.5). Symmetry of operculars appears to be one large abaxial opposite a small adaxial scale, with three laterals between the two on either size. All operculars bear a keel on their inner surface. Pinnular scales not noted.

Coenenchymal scales (Figure 14*G*) elongate, up to 1.0 mm in length, having a L:W ratio of 7–8. Their outer surfaces finely granular, not ridged.

COMPARISONS: As mentioned by Cairns (2007*b*), *C. clarki* and *C.* sp. cf. *C. antilla* sensu Cairns, 2007*b*, are quite similar, but *C. clarki* can be distinguished by having longer basal spines that are flat at their base (not circular in cross section) and equal dichotomous branching (not lyrate). Furthermore, although both species may have two pairs of buccal spines, *C. clarki* usually has only one pair (see key).

REMARKS: Colonies often host several small specimens of the white ophiuroid *Ophiomoeris inflata* Clark, 1949.

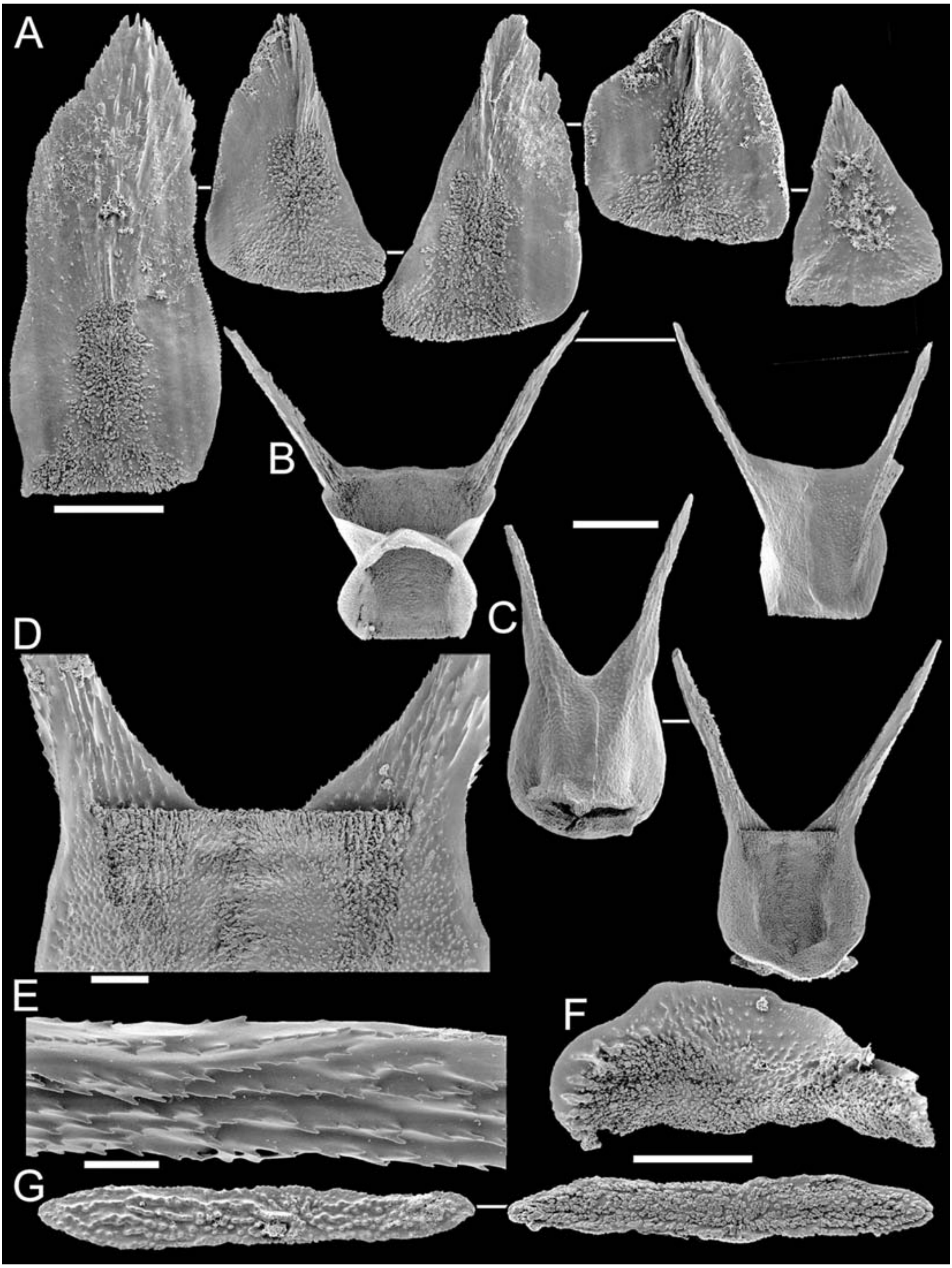

FIGURE 14. Sclerites of *Calyptrophora clarki* from the holotype (USNM 25370): *A*, opercular sclerites; *B*, two buccal scales; *C*, two basal scales; *D*, the articulating ridge of a basal scale; *E*, the serrate ridges of a basal spine; *F*, an infrabasal scale; *G*, two coenenchymal scales. Scale bars: *A*, *F–G*, 0.25 mm; *B–C*, 0.50 mm; *D*, 0.10 mm; *E*, 0.05 mm.

DISTRIBUTION: Off Kaua'i, O'ahu, and Moloka'i, Pioneer Seamount (NWHI), 808–1,105 m.

Calyptrophora pileata Cairns, n. sp.
Figures 1*E*, 15–16

Calyptrophora japonica Form C.—Versluys, 1906:119–122, pl. 10, figs. 28–29, text figs. 170–174 (specimens 8–10).
Calyptrophora japonica.—Nutting, 1908:578 (in part: *Alb*-3882).
Calyptrophora sp. cf. *C. gerdae*.—Bayer, 2001:374 (*Alb*-3882).

TYPES AND TYPE LOCALITY: Holotype: *Pisces 4*-69, 1 large colony and SEM stubs C1344–1345, USNM 1010743. Paratypes: *Alb*-3882, 1 colony and SEM stub B1702, USNM 25369 (*C. japonica* in part of Nutting [1908]); *Sango* 13-13, 1 branch, USNM 93219; *Sango* 13-15, 6 small colonies and 2 branches, USNM 93217 and 100779. Type locality: 20° 55′ 44″ N, 157° 31′ 33″ W (Penguin Bank, off southwestern Moloka'i), 227 m.

DESCRIPTION: Colonies uniplanar and strictly lyrate in branching (Figure 1*E*). Largest colony (holotype) missing its main stem, but upper branching part of colony measures 20 cm in height and 17 cm in width. Main stem and two principal branches (branches from which ascending branchlets diverge) on each side of flabellum dark in color, sometimes tinged with green; polyps occur on main stem. Axis of inner, ascending branchlets yellow. After initial bifurcation, branchlets originate unilaterally every 1.0–1.5 cm on either side of flabellum, these branchlets themselves being unbranched, directed upward, and parallel to one another, all terminating at same height, such that first-formed branchlets much longer than those at tips of colony. In holotype, 12 branchlets diverge from one side of flabellum, 14 from the other. Polyps point upward and arranged in whorls (Figure 15*A–B*) of 5 on ascending branchlets, but whorls of 6–7 on larger diameter main stem and principal branches of flabellum. Whorls very closely spaced, 15–17 per 3 cm; whorl diameter about 3.5 mm. Polyps 1.4–1.6 mm in length.

Fused basal scales (Figure 16*D*) stand up to 1.6 mm in height, usually half of this height consisting of its two distal spines, which are up to 0.9 mm in length. Basal spines broad and flat basally, becoming more attenuate and circular in cross section toward tip. Lower half to two-thirds of inner surface of basal spines covered with 9–12 parallel serrate ridges (Figure 16*E*), but distal portion and entire outer surface smooth. Fused buccal scales (Figures 15*C–D*, 16*B–C*) up to 1.25 mm in length and inclined sharply downward, almost touching branch. Their distal margins extend far (0.3 mm) beyond operculum, thus forming a protective cowl (Figure 15*D*) around opercular scales, this cowl being translucent. Distal margin of cowl consists of 2–7 low (0.10–0.15 mm) equilaterally triangular teeth. Inner surface of cowl bears longitudinally arranged aligned granules but not ridges (Figure 16*C*). Infrabasals uniquely shaped (Figure 16*F*) and about 0.3 mm in maximum height.

There is not a large difference among opercular scales (Figure 16*A*) in size or L:W ratio. Abaxial operculars 0.45–0.48 mm in length (L:W = 1.3–1.4), not creased above but keeled below. Lateral operculars 0.40–0.45 mm in length (L:W = 1.3–1.4) and slightly asymmetrical. Adaxial operculars small and equilaterally triangular in shape, up to 0.33 mm in length, but having an L:W ratio of 0.96–1.02. All opercular scales curved along their longitudinal axis such that when closed they form a squat, hemispherical operculum (Figure 15*D*), which is well covered by buccal cowl. Pinnular scales not observed.

Coenenchymal sclerites (Figure 16*G*) elongate (up to 1.4 mm, L:W ratio up to 5), with rounded edges. Their outer surface covered with sparse low granules. These sclerites are unique among this genus in being quite thick (up to 0.1 mm) and appear to give a distinct rigidity or stiffness to the branches and colony.

ETYMOLOGY: The species name is from the Latin *pileatus*, meaning capped, or cowled, an allusion to the well-developed translucent cowl that encircles the operculum.

COMPARISONS: *Calyptrophora pileata* is unique in having extremely thick coenenchy-

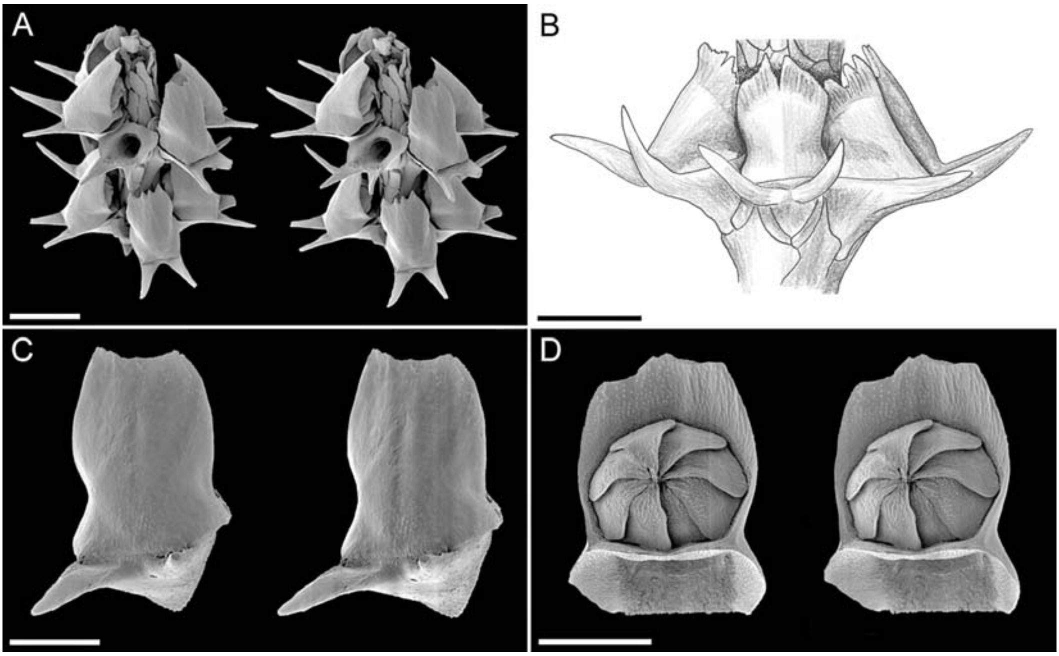

FIGURE 15. Polyps of *Calyptrophora pileata* (*A*, holotype, USNM 1010743; *B–D*, paratype, USNM 25369), *A*, *C–D*, stereo views: *A*, lateral view of two whorls of polyps; *B*, drawing of a lateral view of a whorl by F. M. Bayer; *C*, abaxial view of a polyp; *D*, opercular view of a polyp showing its low operculum and prominent cowl. Scale bars: *A–B*, 1.0 mm; *C–D*, 0.5 mm.

mal scales, which confers a stiff or brittle aspect to the colony. It is most similar to *C. echinata*, as implied in Table 3 and the key.

REMARKS: Bayer (2001:374) referred to the paratype from *Alb*-3882 as being biplanar bipectinate, but there is no evidence from that specimen or any other of this species that it is anything other than uniplanar and unipectinate.

DISTRIBUTION: Hawaiian Islands: French Frigate Shoals, off Moloka'i, 227–244 m. Elsewhere: Indonesia, 120–520 m (Versluys 1906).

Calyptrophora alpha Cairns, n. sp.
Figures 1*I*, 17–18

?Primnoid gorgonian Chave and Jones, 1991: fig. 4.

TYPES AND TYPE LOCALITY: Holotype: *Pisces* 5-544, 1 large dry colony, several hundred individual polyps, and SEM stubs C1346–1349, USNM 1072134. Paratypes: *Pisces* 5-534, 2 branches, USNM 1072119. Type locality: 23° 18′ 43″ N, 163° 40′ 56″ W (southeast of Necker Island), 1,078 m.

DESCRIPTION: Colonies uniplanar but their branching pattern not easily categorized in that within the same colony it is unequal dichotomous followed by quasi-lyrate, distal branches of which may again be dichotomous (Figure 1*I*). Largest colony (holotype) 54 cm in height and 28 cm broad, including a 14 cm main stem that has a basal diameter of 6.7 mm. Branching subsequent to first bifurcation occurs every 1–2 cm, but in an irregular manner as already mentioned, but some distal branchlets reach up to 15 cm in length. Polyps point upward and arranged in whorls of 3 or 4, more polyps per whorl occurring on larger diameter basal branches such as main stem. There are 10–12 whorls per 3 cm; whorl diameter about 5 mm. Polyps 2.2–2.4 mm in length.

Fused basal scales (Figures 17*D–E*, 18*C*–

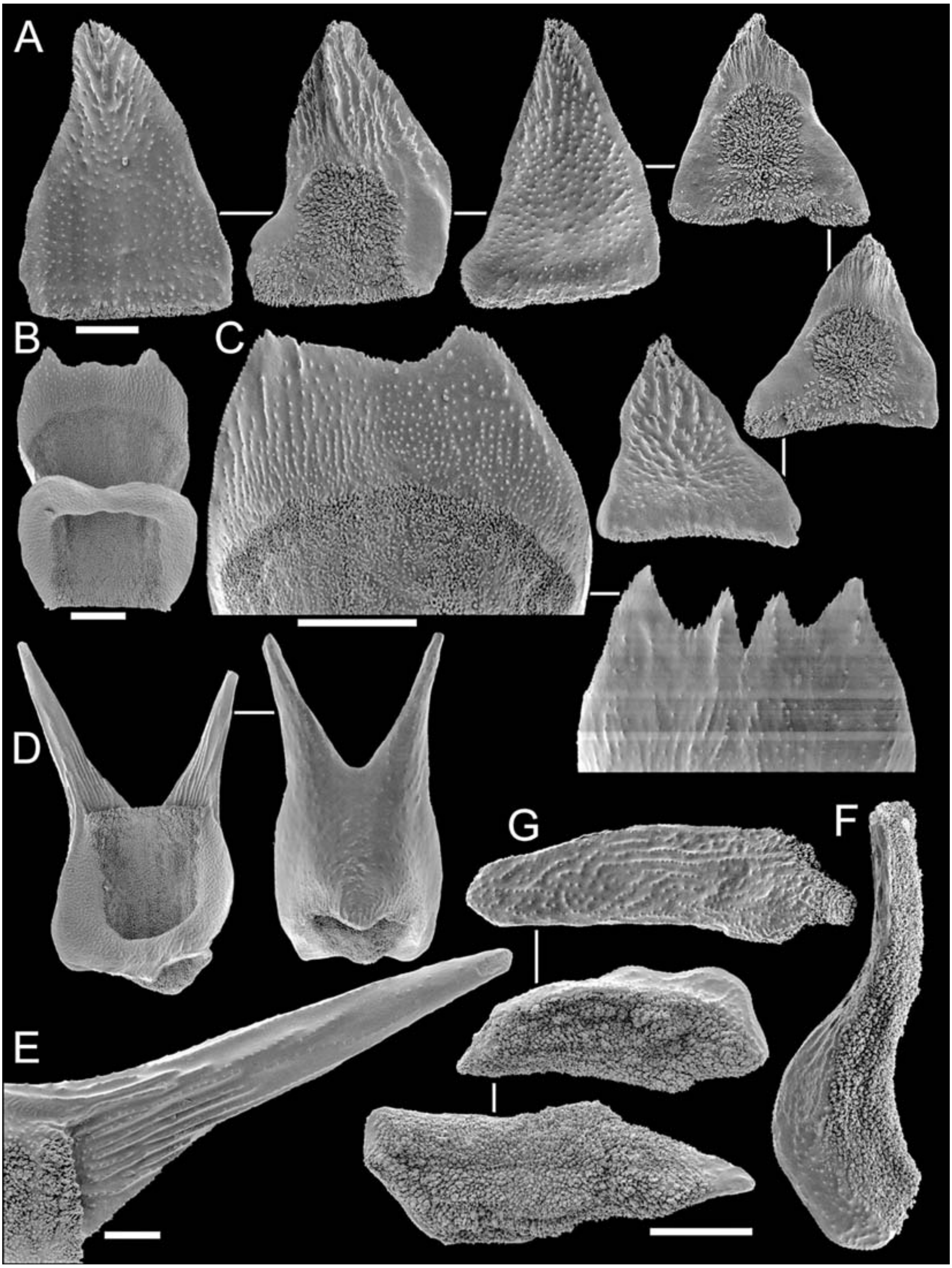

Figure 16. Sclerites of *Calyptrophora pileata* from the holotype (USNM 1010743): *A*, opercular sclerites; *B*, inner surface of a buccal sclerite; *C*, enlargement of the serrate buccal margin of two sclerites; *D*, inner and outer views of basal sclerites; *E*, inner surface of spine on basal sclerite, showing articulating ridge and serrate ridges on spine; *F*, an infraopercular sclerite; *G*, three coenenchymal scales. Scale bars: *A*, *E*, 0.10 mm; *B–D*, *F–G*, 0.25 mm.

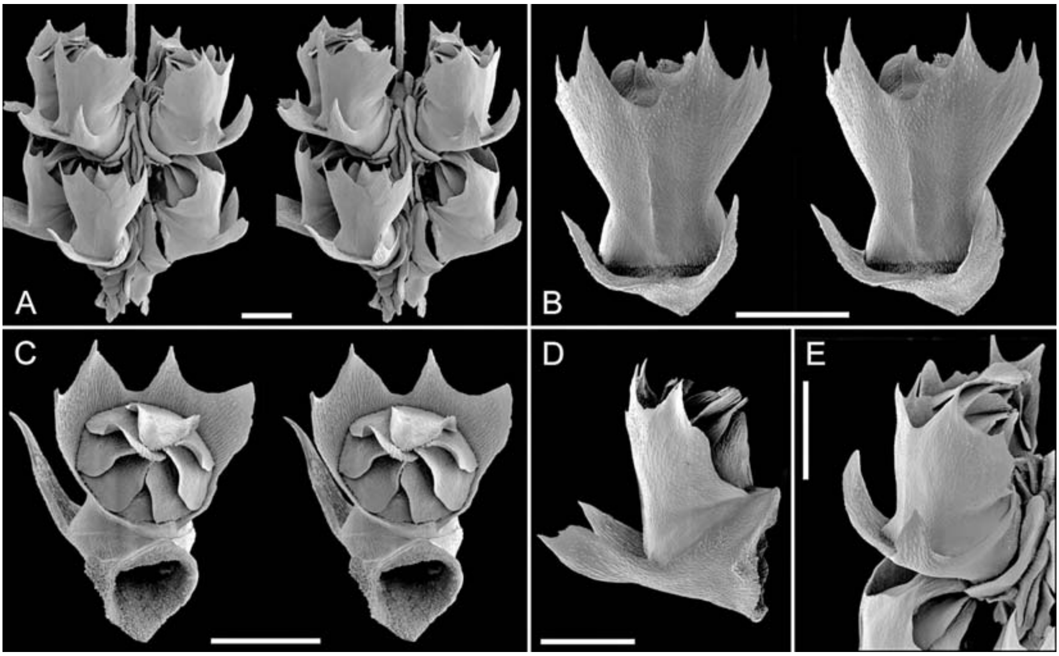

FIGURE 17. Polyps of *Calyptrophora alpha* from the holotype (USNM 1072134), *A–C* are stereo views: *A*, lateral view of two whorls of polyps; *B*, abaxial view of a polyp showing forward curved basal spines; *C*, opercular view of a polyp; *D–E*, lateral and oblique lateral calycular views. All scale bars 1.0 mm.

D) stand up to 2.3 mm, uppermost 0.8–1.3 mm constituting prominent distal spines. The two basal spines broad and flat basally (occupying most of articulating ridge), becoming more attenuate and pointed toward tip; inner surface of spines bears numerous low, parallel, serrate ridges that extend to tip of spine (Figure 18*D*). These basal spines often bent forward (upward) as much as 90°, as well as sometimes being slightly twisted (Figure 17*A–B*, *E*). Fused buccal scales (Figures 17*B–E*, 18*B*) up to 2.1 mm in length, horizontal to branch axis, their distal margin produced into 3–8 pointed teeth, these teeth often unequal in size and measuring up to 0.6 mm in length. Distal 0.8–0.9 mm of fused buccals, including spines, translucent and forms a cowl (Figure 17*C*) surrounding operculum; inner surface of cowl covered with low parallel serrate ridges. Infrabasal scales (Figure 18*E*) robust, up to 0.55 mm in height. Often coenenchymal scales adjacent to infrabasals (subinfrabasals) modified to curve around polyp base (Figure 18*G*).

Abaxial operculars 1.1–1.2 mm in length (L : W = 1.8), slightly creased above, and with a finely serrate blunt tip. Lateral operculars slightly less long (0.8–1.1 mm, L : W = 1.7–2.0), slightly asymmetrical, and with a pointed tip. Adaxial operculars 0.6–0.7 mm in length (L : W = 1.3–1.4). All operculars (Figure 18*A*) keeled below and granular above. Small elliptical platelets 65–90 μm in length presumed to be pinnular (Figure 18*H*).

Coenenchymal sclerites (Figure 18*F*) elongate (up to 1.8 mm in length, L : W = 4) and somewhat irregular in shape. Their outer surface covered with low granules.

ETYMOLOGY: The Greek letter *alpha*.

COMPARISONS: *Calyptrophora alpha* is unique in having flattened basal spines that curve forward, sometimes as much as 90°. Otherwise, it is most similar to the western Atlantic *C. gerdae* Bayer, 2001, as seen in Table 3 and the key.

DISTRIBUTION: Off Laysan and a seamount southeast of Necker Island, 1,078–1,220 m.

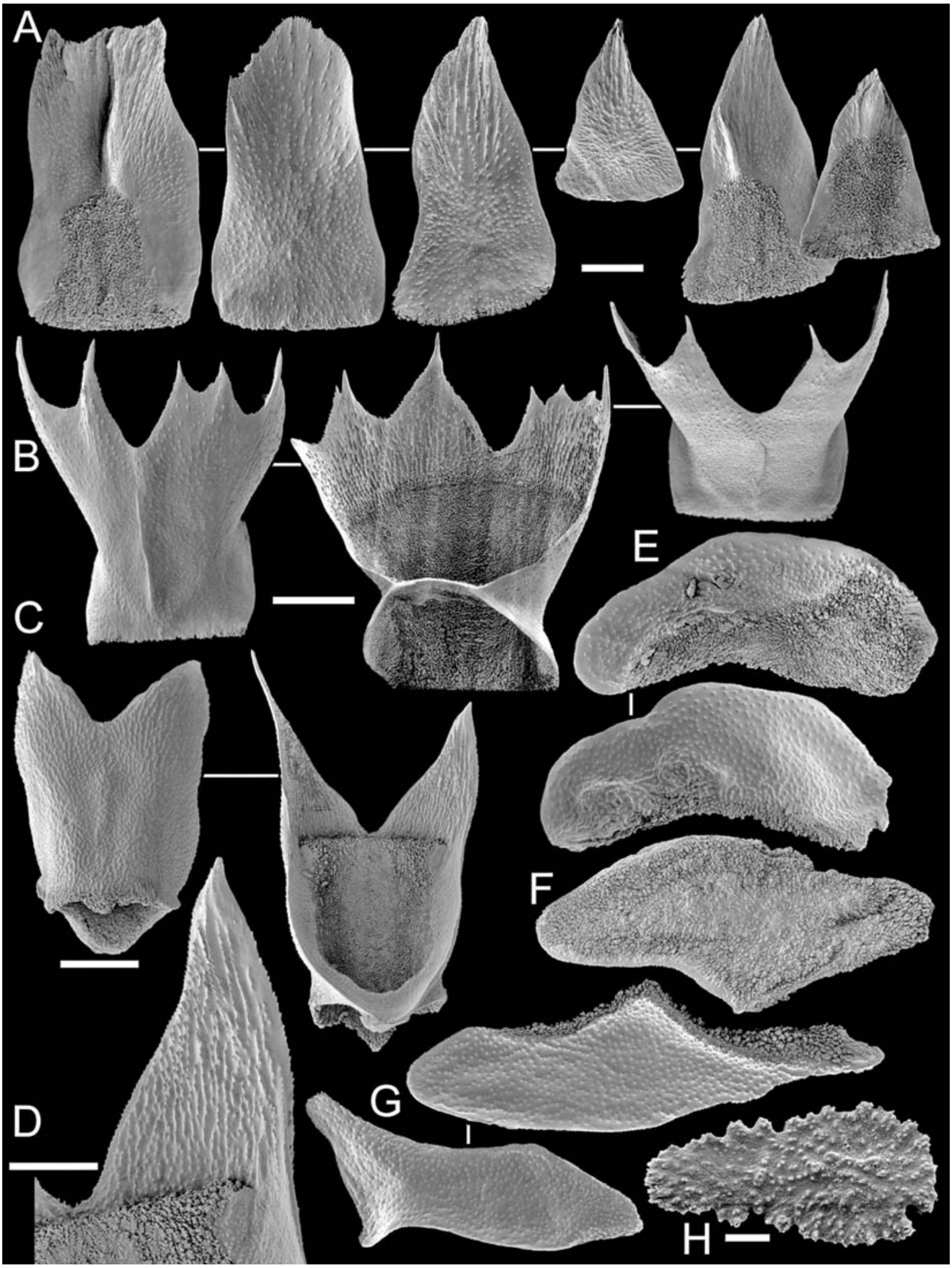

Figure 18. Sclerites of *Calyptrophora alpha* from the holotype (usnm 1072134): *A*, opercular sclerites; *B*, toothed buccal sclerites; *C*, outer and inner views of basal sclerites; *D*, inner surface of spine on basal sclerite, showing articulating ridge and serrate ridges on spine; *E*, infrabasal sclerites; *F*, inner surface of a coenenchymal scale; *G*, two subinfrabasal scales; *H*, a tentacular (pinnular) scale. Scale bars: *A*, *D*–*G*, 0.25 mm; *B*–*C*, 0.50 mm; *H*, 0.01 mm.

Genus *Candidella* Bayer, 1954

DIAGNOSIS: Colonies dichotomously branched in one plane or unbranched. Polyps arranged in whorls that stand perpendicular to branch. Four marginal scales present, corresponding more or less to four longitudinal rows of body wall scales. Opercular scales longitudinally creased above and prominently keeled below. Coenenchymal scales arranged in one layer, elliptical to elongate in shape, often concave above.

TYPE SPECIES: *Primnoa imbricata* Johnson, 1862, by monotypy.

REMARKS: The type species of this genus was recently redescribed by Cairns and Bayer (2004*a*) and the genus revised by Cairns and Bayer (2009). Four species are currently assigned to the genus.

DISTRIBUTION: Amphi-Atlantic, South Pacific, Hawaiian Islands, 384–2,165 m.

Candidella helminthophora (Nutting, 1908)
Figures 1*A*, *H*, 19–20

Stenella helminthophora Nutting, 1908:575–576, pl. 44, figs. 6–9; pl. 47, fig. 5.—Kükenthal, 1919:449; 1924:306.

Candidella helminthophora.—Grigg and Bayer, 1976:171 (listed).—Parrish and Baco, 2007:192 (listed).

Candidella helminthopora [*sic*].—Chave and Jones, 1991:785 (listed).—Chave and Malahoff, 1998: table 1, fig. 64 (in situ).

MATERIAL EXAMINED: (* indicates variant form): Types; *Alb*-3467, 1 colony, USNM 49667; *Alb*-3977, 1 branch, USNM 22589; Midway-13, 1 dry colony, USNM 1115295; *Moore 1718, Bushnell Seamount, 1,645 m, 1 colony, USNM 79394; **Pisces 5*-464, 1 dry colony, USNM 1092798; **Pisces 5*-526, 2 branches, USNM 1072110; **Pisces* 5-542, 2 branches, USNM 1072123; *Sango* 13-1, 4 branches, USNM 1115296; *Sango* 13-4, 1 colony, USNM 56774; *TC* 35-23, 1 colony, USNM 1017253.

TYPES AND TYPE LOCALITY: Holotype: *Alb*-3973, 1 large colony now in many pieces and SEM stubs C1350–1352 and B170, USNM 23385. Paratypes: *Alb*-3868, 1 colony, USNM 25374; *Alb*-3973 (topotypic), 1 branch, USNM 25317; *Alb*-3974, 1 colony and 1 damaged branch, USNM 91863 and 91895; *Alb*-4157, 1 dry colony, USNM 1099827 (ex SUI 21107). Type locality: 23° 47′ 10″ N, 166° 24′ 55″ W (off French Frigate Shoals), 722–726 m.

DESCRIPTION: Colonies uniplanar, branching every 3–5 cm in an even, dichotomous fashion (Figure 1*A*) from a main stem only 2–3 cm long. Base of a colony sometimes a highly calcified fusion of several main stems (Figure 1*H*), one colony (USNM 1099827) having a basal diameter of 15 mm. Largest colony (USNM 91863) 28 cm in height; colonies usually taller than wide due to relatively small branching axils of 15–20°. Axis white to straw yellow in color. Polyps project perpendicular to branch, reaching up to 3.8 mm in height and arranged in whorls of 4–7, but discrete whorl structure often obscured in region of branch modification caused by polychaete symbiont (Figure 19*A*). There are 12–13 whorls per 3 cm; whorl diameter about 8–9 mm. Polyps flared distally, 3.4–3.8 mm in length and about 2.2 mm in distal diameter.

Only four buccal (marginal) scales: two very large convex abaxial scales (Figure 20*B*) that encircle most of polyp, each 1.3–1.5 mm in width, and two much smaller adaxial buccals (Figure 19*C–D*), tucked beneath adaxial edges of larger buccals, each about 0.7–0.9 mm in width. They have smooth distal margins and together project as a short cowl surrounding operculum but not shielding it from lateral view. Proximal to buccal scales are 2 or 3 circles of ab- and adaxial body wall scales (Figure 20*C–D*), those on abaxial side being slightly larger (0.8–1.0 mm wide) than those on adaxial side (0.3–0.6 mm wide); these body wall scales have a rounded distal margin. Base of each polyp consists of two large, concave scales (Figure 20*E*), which constrict base of polyp and usually remain attached to branch after polyps have become detached. Each basal scale up to 1.4 mm in height and about 1 mm wide; however, when a polychaete symbiont is present on that branch segment, these scales widen up to 3.5 mm and meet and fuse with basal scale of adjacent polyp within whorl as well as those distal and proximal to it, forming a hollow tube

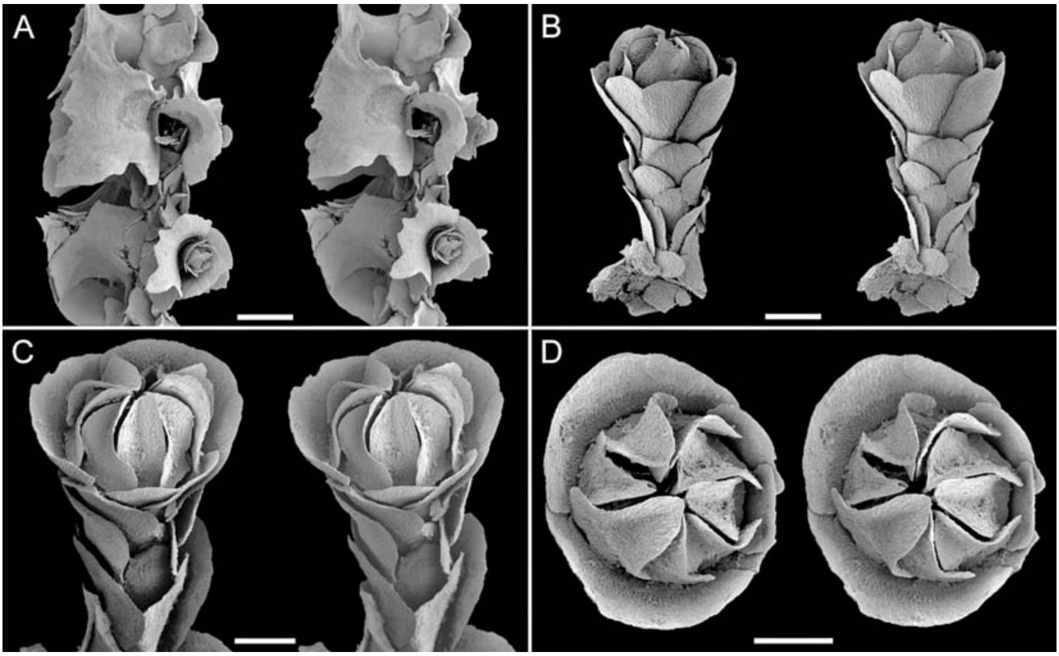

FIGURE 19. Polyps of *Candidella helminthophora* from the holotype (USNM 25385), stereo views: *A*, lateral view of two reduced polyps with highly modified basal scales forming a worm tube; *B*, adaxial view of a polyp; *C*, adaxial-opercular calycular view; *D*, opercular calycular view. Scale bars: *A*, 1.0 mm; *B–D*, 0.5 mm.

(arcade) approximately 2 mm in diameter for the polychaete (Figure 19*A*). All body wall scales covered with low granules.

Abaxial opercular scale about 1 mm in length, symmetrical, having a L:W ratio of about 1.3–1.4. The six lateral operculars asymmetrical, 1.0–1.1 mm in length, and have a L:W ratio of 1.5–1.8. Adaxial opercular 1.0–1.05 mm in length, symmetrical, and has a L:W ratio of 2.1–2.2. All operculars (Figure 20*A*) deeply longitudinally creased above, corresponding to a blunt keel on inner side. Pinnular scales not seen.

Coenenchymal scales (Figure 20*F*) circular to slightly elliptical, up to about 0.5 mm in length and highly concave on their outer surfaces.

COMPARISONS: Three of the four species in the genus are exceedingly similar: *C. imbricata* (Johnson, 1862) (North Atlantic, 514–2,165 m), *C. johnsoni* (Wright & Studer, 1889) (Ascension Island, 768 m), and *C. helminthophora;* the Hawaiian species is most similar to *C. imbricata*, as explained by Cairns and Bayer (2004*a*). *Candidella helminthophora* differs from *C. imbricata* more in degree than in quality, having 4–7 polyps per whorl (versus 3–4), 12–13 whorls per 3 cm (versus 5–6), taller polyps (3.4–4.7 mm versus 2.1–2.5 mm), elliptical highly concave coenenchymal scales (versus polygonal slightly concave scales), and in having in general more body wall scales.

REMARKS: Colonies from four stations (asterisked in Material Examined) collected from throughout the range differ from the typical form in having larger polyps (up to 4.7 mm in length and 2.2 mm in distal diameter) and in having polyps that bend downward, often at a 90° angle. Otherwise they are similar to the type and are thus interpreted as intraspecific variation.

In addition to the commensal polynoid polychaete, dozens of which may occur in one large colony, some colonies (e.g., the holotype) support a large number of small

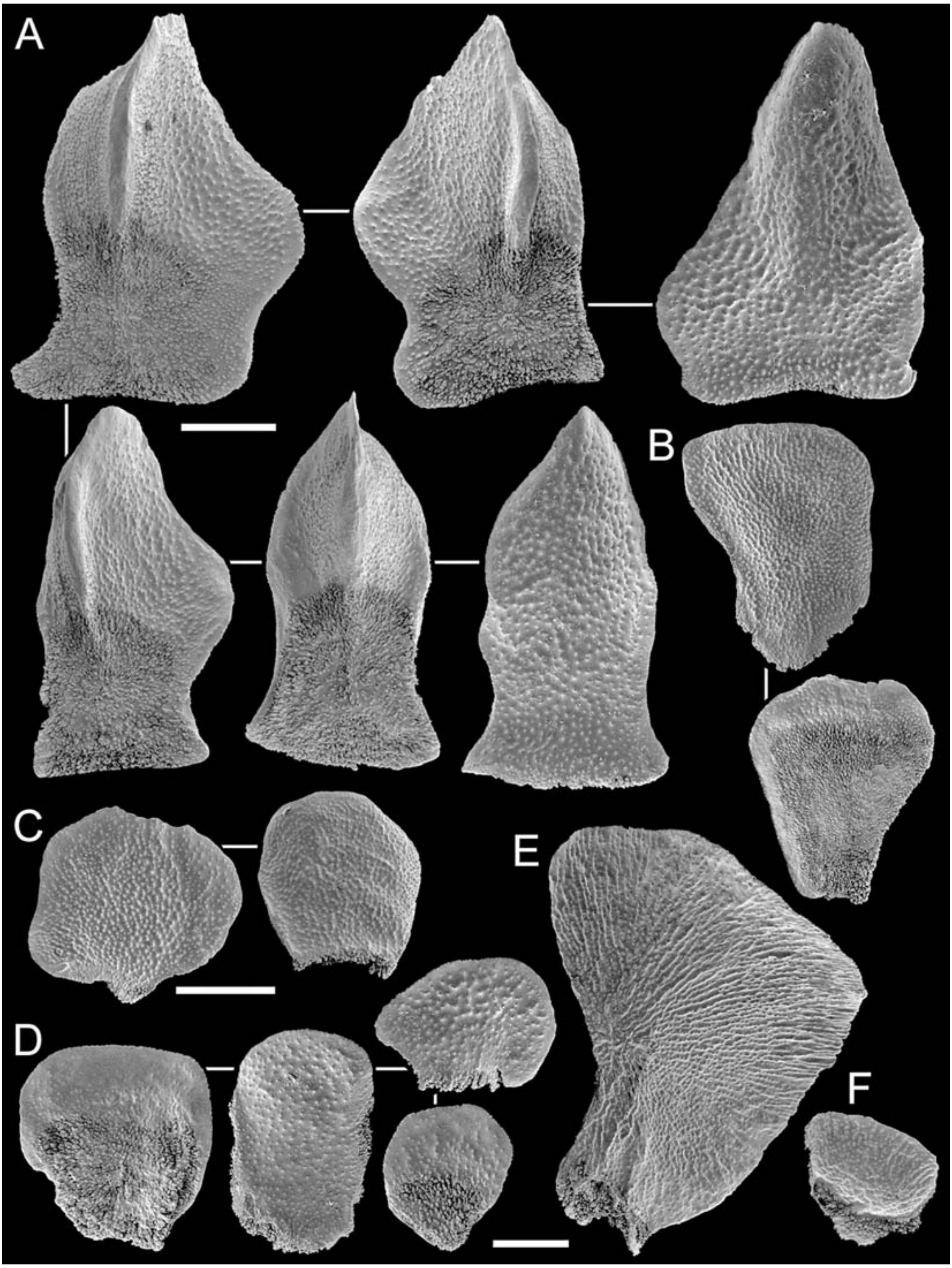

FIGURE 20. Sclerites of *Candidella helminthophora* from the holotype (USNM 25385): *A*, opercular sclerites; *B*, abaxial buccal scales; *C*, abaxial body wall scales; *D*, adaxial body wall scales; *E*, outer surface of a basal scale; *F*, outer surface of a coenenchymal scale. Scale bars: *A*, *D–F*, 0.25 mm; *B–C*, 0.50 mm.

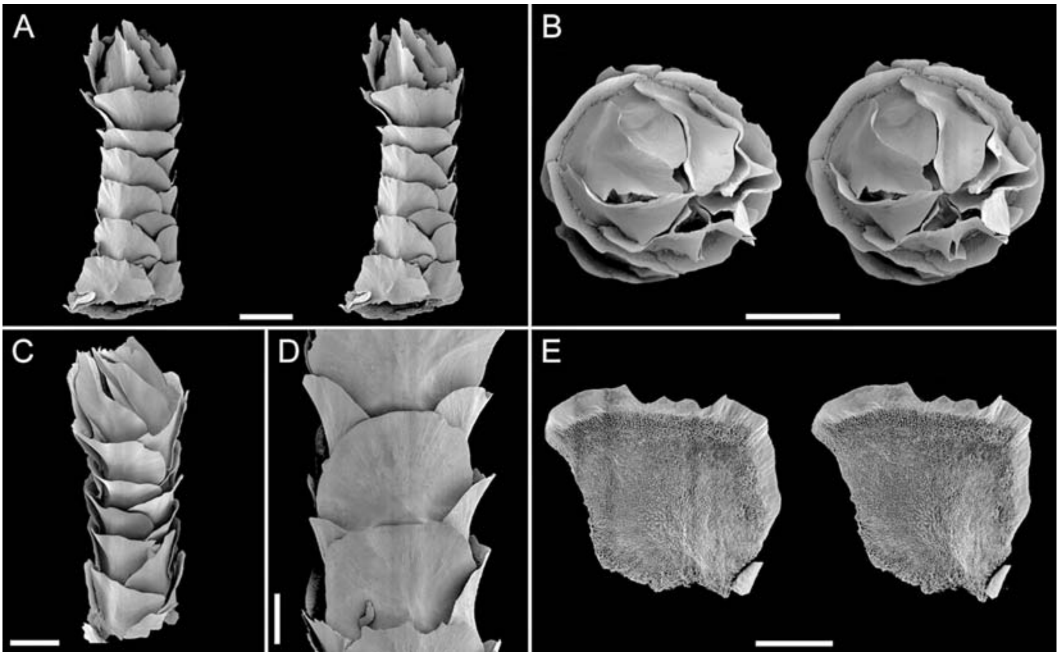

FIGURE 21. Polyps and individual sclerites of *Candidella gigantea* from *Pisces* 5-542 (USNM 1072121), *A–B*, *E* are stereo views: *A*, lateral view of a polyp; *B*, opercular calycular view showing the five marginal scales; *C*, adaxial calycular view; *D*, detail of lateral body wall scales; *E*, inner face of a body wall scale. Scale bars: *A–C*, 1.0 mm; *D–E*, 0.5 mm.

(disk diameter = 3 mm), white ophiuroids identified as *Ophiomoeris inflata* Clark, 1949. Some colonies are also infested with solitary zoanthids, which eventually causes the death of all or part of the colony.

DISTRIBUTION: Throughout the Hawaiian Islands from Pioneer Seamount to Bushnell Seamount south of Hawai'i, 417–1,801 m.

Candidella gigantea (Wright & Studer, 1889)
Figures 1*B*, 21–22

Stenella gigantea Wright & Studer, 1889:57–58, 281, pl. 14, fig. 4; pl. 20, fig. 8.—Versluys, 1906:44.—Kükenthal, 1919:448; 1924:305.

Ellisella sp. Chave and Jones, 1991:785 (listed).—Chave and Malahoff, 1998: table 1, figs. 49, 108.

Candidella gigantea.—Cairns and Bayer, 2004*b*:477 (listed).—Parrish and Baco, 2007:192 (listed).

MATERIAL EXAMINED: *Pisces* 5-525, 1 branch, USNM 1072104; *Pisces* 5-542, 1 dry branch and SEM stubs C1353–1356, USNM 1072121; *Pisces* 5-543, 3 branches, USNM 1072124, 1072125, and 1072127; *Pisces* 5-544, 1 large dry colony, USNM 1072132.

TYPES AND TYPE LOCALITY: The holotype is deposited at the BM (1889.5.27.36). Type locality: *Challenger*-174: 19° 10′ S, 178° 10′ E (Fiji Plateau), 384–1,115 m.

DESCRIPTION: Colonies unbranched (flagelliform) and slightly curved (Figure 1*B*), longest known specimen (holotype) 52 cm in length and 2 mm in axis diameter; largest Hawaiian specimen (USNM 1072132) 35 cm in length and 1.3 mm in axis diameter. Complete specimens including holdfast have not yet been collected. Surface of axis perfectly smooth and pale yellow to white; however, central core of axis of at least one specimen green. Polyps project perpendicular to branch (Figure 1*B*), most 4–7 mm in height and 1.7–1.9 mm in diameter, the

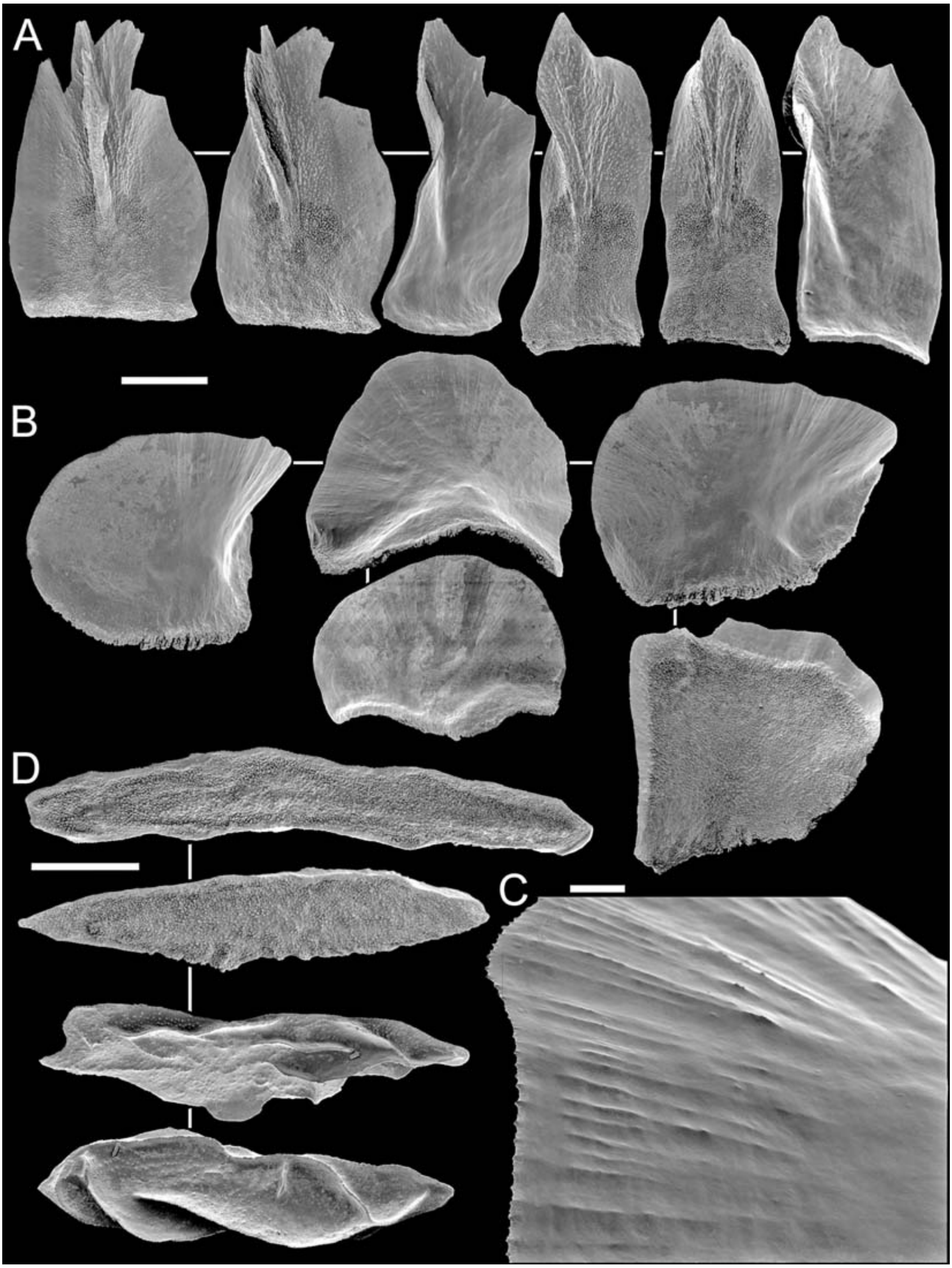

FIGURE 22. Sclerites of *Candidella gigantea* from *Pisces* 5-542 (USNM 1072121): *A*, opercular sclerites; *B*, body wall scales; *C*, outer surface of a finely serrate body wall scale; *D*, elongate coenenchymal scales. Scale bars: *A–B*, *D*, 0.50 mm; *C*, 0.05 mm.

polyps uniformly cylindrical. Height of polyps appears to increase toward distal end of branch. Polyps arranged in discrete whorls of 3–5 (usually 4) and well separated, only 4 whorls occurring in 3 cm; whorl diameter up to 14 mm.

Body wall scales (Figures 21*D–E*, 22*B*) virtually uniform in size and shape, not differentiated into buccal, body wall, and basal scales. At tip of each polyp usually four broad (1.3–1.7 mm wide by 1.2–1.3 mm in height), curved (marginal or buccal) scales that encircle polyp. Each of these four scales preceded by a row of five more similarly shaped scales, these four rows of six scales each constituting body wall scales. These body wall scales thin and rather delicate, each having a semicircular but often broken distal edge; their outer surface virtually smooth, but near margin of each scale surface covered with numerous parallel, very low ridges, each ridge culminating in a very short (4 µm) projection, producing a finely serrate margin (Figure 22*C*). In many polyps a fifth marginal scale sometimes present at or near polyp tip, this scale usually being half to one-third width of a normal body wall scale and having a more acute tip. It rarely has any additional body wall scales aligned with it.

Abaxial opercular scales symmetrical, about 2.1 mm in length, with a L:W ratio of about 2.3. Lateral operculars asymmetrical, 1.8–1.9 mm in length, with a L:W ratio of about 1.5–2.1. Adaxial operculars symmetrical, also about 1.9 mm in length, with a L:W ratio of about 2.6. All operculars (Figure 22*A*) have a highly creased outer surface that corresponds to a prominent keel on inner surface. Operculum extends well beyond distal edges of buccal scales. Pinnular scales not observed.

Coenenchymal scales (Figure 22*D*) elongate (up to 2.8 mm in length) and somewhat irregular in shape, having a L:W ratio of up to 7.5. Their outer surface flat and covered with one or more irregularly shaped longitudinal ridges, ridges up to 0.12 mm in height and sometimes joining one another.

COMPARISONS: By definition (Cairns and Bayer 2004*b*, 2009), *C. gigantea* belongs in the genus *Candidella*, because it has only four marginal scales and polyps that stand perpendicular to the branch; however, in many other respects it is very different from the other three species and probably should be placed in a genus of its own. Points of difference include: nonbranching colonies; uniformly shaped body wall scales; cylindrical polyps; elongate, ridged, flat coenenchymal scales; and lack of a polychaete symbiosis.

REMARKS: This species was previously known from only one specimen, the holotype.

DISTRIBUTION NWHI: Pioneer Seamount and a seamount east of Necker Island, 1,608–1,802 m. Elsewhere: Fiji Plateau, 384–1,115 m.

ACKNOWLEDGMENTS

I thank Amy Baco for donating some of the specimens collected by the *Pisces 5*, and for inviting me on her 2003 cruise. I am also grateful to Les Watling for loaning several Hawaiian specimens and to Alan Baldinger (MCZ) for the loan of the holotype of *Calyptrophora agassizii*. Allen Collins provided assistance with the phylogenetic analyses. Tim Coffer constructed the Photoshop plates, and Molly Ryan drew Figures 6–8. Some of the SEM images were taken from the archive of F. M. Bayer. I would like to dedicate this paper to Cynthia Ahearn (1952–2008), who identified the commensal ophiuroids and who was a good colleague over the last 30 yr.

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Appendix

Station Data

Vessel/Cruise	N Latitude	W Longitude	Depth (m)	Date
USFWS *Albatross*				
3467	21° 13′ 00″	157° 43′ 37″	567	3 Dec. 1891
3868	21° 15′ 45″	156° 29′ 49″	537–1,250	11 Apr. 1902
3882	21° 05′ 20″	156° 40′ 45″	249	16 Apr. 1902
3973	23° 47′ 10″	166° 24′ 55″	722–726	29 May 1902
3974	23° 49′ 30″	166° 25′ 55″	726–757	29 May 1902
3977	23° 05′ 00″	161° 52′ 00″	1,602	2 June 1902
3997	21° 54′ 35″	159° 46′ 00″	764–784	14 June 1902
3998	21° 56′ 25″	159° 48′ 35″	417–430	14 June 1902
4007	21° 50′ 20″	159° 31′ 40″	929–1,018	17 June 1902
4108	21° 20′ 35″	157° 26′ 05″	752–808	24 July 1902
4157	23° 05′	161° 52′	1,394–1,829	6 Aug. 1902
HURL (Hawai‘i Undersea Research Laboratory) *Makali‘i* submersible dive				
9-84-213	21° 17′ 36″	157° 32′ 30″	320	19 Jan. 1984
Midway Cruise				
13	25° 24.88′	168° 38.26′	627–750	Unknown
Pisces 4				
46	20° 29′ 13″	156° 39′ 22″	430	4 Sept. 2002
69	20° 55′ 44″	157° 31′ 33″	227	30 Oct. 2002
Pisces 5				
141	18° 45′ 36″	158° 14′ 06″	970	21 Feb. 1990
216	18° 45′ 01″	158° 14′ 43″	975	4 Sept. 1992
234	18° 44′ 58″	158° 14′ 29″	975	13 Aug. 1993
299	21° 23′ 33″	158° 2′ 42″	876	17 Sept. 1996
300	20° 59′ 23″	157° 19′ 10″	427	19 Sept. 1996
301	20° 46′ 57″	157° 08′ 56″	1,225	20 Sept. 1996
303	19° 36′ 35″	156° 03′ 08″	1,000–1,178	22 Sept. 1996
464	24° 20.672′	166° 01.547′	1,080–1,219	19 Sept. 2001
524	25° 48′ 43″	173° 26′ 13″	1,200	7 Oct. 2003
525	25° 48′ 03″	173° 25′ 56″	1,252–1,807	8 Oct. 2003
526	25° 33′ 55″	173° 30′ 22″	1,801	9 Oct. 2003
527	25° 48′ 43″	173° 24′ 19″	1,105–1,209	10 Oct. 2003
534	25° 39′ 57″	171° 24′ 19″	1,220	20 Oct. 2003
542	23° 20.66′	163° 38.504′	1,449–1,816	31 Oct. 2003
543	23° 13′ 55″	163° 31′ 07″	1,278–1,723	1 Nov. 2003
544	23° 19′ 00″	163° 41′ 00″	1,078–1,608	2 Nov. 2003

Appendix (continued)

Vessel/Cruise	N Latitude	W Longitude	Depth (m)	Date
545	23° 15′ 41″	163° 00′ 04″	444	3 Nov. 2003
587	18° 43′ 59″	158° 15′ 44″	389	8 Oct. 2004
591	18° 42′ 35″	158° 15′ 39″	371	12 Oct. 2004
593	19° 48′ 12″	156° 08′ 02″	398	15 Oct. 2004
595	19° 47′ 54″	156° 07′ 47″	679–865	17 Oct. 2004
666	21° 15′ 03″	156° 47′ 02″	918	31 Aug. 2006
695	24° 16.369′	166° 02.132′	708	7 Nov. 2007
696	24° 23.0′	166° 04′	1,475–1,580	8 Nov. 2007
703	23° 07.261′	163° 07.729′	1,108	17 Nov. 2007
Sango (University of Hawai‘i)				
13-1	23° 02′	162° 05′	353–463	19 Aug. 1971
13-2	21° 41′	160° 30′	1,066–1,222	19 Aug. 1971
13-4	23° 04′	162° 02.6′	374–439	19 Aug. 1971
13-13	23° 57′	166° 41′	244–322	26 Aug. 1971
13-15	23° 58′	166° 40′	216–330	26 Aug. 1971
14-2	21° 18.82′	157° 32.2′	344–454	18 Jan. 1972
16-10	21° 56.38′	159° 56.8′	779–823	9 Mar. 1972
Star II (Maui Divers Jewelry Co., submersible)				
2	21° 18′	157° 32′	367	1 Feb. 1978
Townsend Cromwell (*TC*)				
35-23	21° 15′ 36″	156° 25′ 30″	512	15 Apr. 1968
52-108	21° 25.48′	158° 16.7′	969–1,280	16 Mar. 1971
52-122	21° 46.5′	158° 42.0′	1,188	17 Mar. 1971