## A Review of the Octocorallia (Cnidaria: Anthozoa) from Hawai'i and Adjacent Seamounts: The Genus *Narella* Gray, 1870<sup>1</sup>

Stephen D. Cairns<sup>2,3</sup> and Frederick M. Bayer<sup>3</sup>

**Abstract:** The nine Hawaiian species of *Narella* are revised, including the description of six new species. All species but one (*N. ornata*) are described and illustrated using SEM; all species are keyed and included in a detailed table of comparison. A brief history of octocoral taxonomic research in the Hawaiian Islands is presented, resulting in a total of 90 named species for this region, only five of which occur in shallow water. Specimens were collected from throughout the archipelago and adjacent seamounts, including Cross, Pensacola, Bishop, and Bushnell, from depths of 326 to 1,977 m.

Most of the Northwestern Hawaiian Islands are closed to trawling and dredging activities, as a result of being either a national marine sanctuary or a national marine monument. Nonetheless, it is important to know what animals, especially corals, are being protected in this region. Hawaiian deep octocorals are diverse, and many species, such as those reported herein from the genus Narella, are structure-forming species, providing habitat for many associated invertebrates. Remotely operated vehicles and manned submersibles give an overview of the deep Hawaiian fauna, but it is imperative that some specimens be collected, studied, and serve as material vouchers for this exotic fauna. This is hoped to be the first of a series of papers that will document the deep octocoral fauna of the Hawaiian Islands.

The first octocoral to be reported from the Hawaiian Islands was the precious coral *Co-rallium secundum* Dana, 1846, collected by the U.S. Exploring Expedition. Nutting (1908),

however, published the first and only comprehensive report of Hawaiian octocorals, based on the collections of the USFWS *Albatross* in 1902, in which he reported 68 species including 39 new species. Three shallowwater species reported by Verrill (1928) reputedly from Hawai'i probably did not originate from these waters (Grigg and Bayer 1976, Muzik 1979).

Bayer is responsible for most subsequent reports of species from this archipelago. Following a single species description in 1951, Bayer began a series of revisions of the work of Nutting, also based primarily on the 1902 Albatross collection. His part 1 (Bayer 1952) included a revision of the Alcyonacea, Stolonifera, and Telestacea, whereas part 2 (Bayer 1956) revised the Scleraxonia, together adding 10 new species to the fauna. Although he did not continue this series, over the next 40 vr he added many new species to the fauna in the following publications: Bayer (1982, 1990, 1995, 1996, 1997) and Bayer and Stefani (1988, 1989). Also, as a result of the Sango expeditions of the early 1970s, Grigg and Bayer (1976) published a list of the 59 gorgonaceans collected by that program, only 21 of which were identified to the species level. Nonetheless many taxonomic decisions were made in that paper and a brief history of the Hawaiian octocorals was presented. They also discussed the zoogeography of Hawaiian gorgonians, remarking that only one species, Acabaria bicolor (Nutting, 1908), was known from shallower than 75 m.

Just a year later, Devaney (1977) and

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<sup>&</sup>lt;sup>2</sup> Corresponding author (e-mail: cairnss@si.edu).

<sup>&</sup>lt;sup>3</sup> Department of Invertebrate Zoology, MRC 163, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012.

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Verseveldt (1977) reported four species from shallow water: Acabaria bicolor, Sinularia abrupta [later reidentified as S. densa (Whitelegge, 1897) by Ofwegen and Vennam (1991)], Anthelia edmondsoni (Verrill, 1928) (later transferred back to the genus Sarcothelia by Fenner [2005]), and Telesto riisei (Duchassaing & Michelotti, 1860), the latter species introduced from the western Atlantic and now placed in the genus Carijoa. Verseveldt (1983) described a fifth shallow-water species, Sinularia molokaiensis, and Fenner reviewed and illustrated the five shallow-water species in 2005. Muzik (1978) described the bioluminescent Lepidisis olapa. A year later she (Muzik 1979) produced a beautifully illustrated Ph.D. dissertation on the Hawaiian Paramuriceidae and Plexauridae, in which she described 24 species, 18 of them new, but that work was never officially published. Her manuscript types are deposited at the NMNH. Chave and Malahoff (1998) published a list of 90 octocoral taxa that had been observed in the Hawaiian Islands from Hawai'i Undersea Research Laboratory submersibles, 23 of which were published as in situ color photographs but only 23 of the 90 identified to the species level. The reliability of the identifications is not high. Finally, Berntson et al. (2001) published the 18S rRNA sequences of 11 deepwater Hawaiian species.

#### MATERIALS AND METHODS

The specimens examined resulted from 36 stations of eight vessels (those of six vessels listed in the station list), including two submersibles: *Star II* and *Pisces V* (Appendix). Specimens were collected from Pioneer Seamount to the seamounts south of Hawai'i at depths of 326–1,977 m. Most specimens are deposited at the NMNH, but a set of paratypes is also deposited at the ZMA and BPBM, and types of one species are at the MCZ. Of the 32 previously described species of *Narella*, the types of 23 were examined, five more species were studied based on nontype voucher specimens at the NMNH, and five were based on literature.

Designation of polyp sclerites follows the terminology of Versluys (1906) as modified by Bayer et al. (1983). Synonymies for all species are purported to be complete. The scanning electron microscope (SEM) photomicrographs were taken by both authors on a variety of SEM microscopes located at the Smithsonian. SEM stub numbers prefaced with a C pertain to the series taken by Cairns; those prefaced with a B, to the series of Bayer. In Material Examined sections, specimens are presumed to be preserved in alcohol unless otherwise stated. A "confirmed" depth interval extends from the shallowest deep to the deepest shallow ranges of individual stations, thus being an accurate if conservative estimate of the true depth range of the species.

Abbreviations: *Alb*, USFWS *Albatross*; BPBM, Bernice P. Bishop Museum; H:W, ratio of height to width of a sclerite; LAD, Lāna'i Deep; MCZ, Museum of Comparative Zoology, Harvard, Cambridge; NMNH, National Museum of Natural History (cataloged specimens prefaced with USNM [United States National Museum]); *OES*, R/V *Oscar Elton Sette*; ZMA, Zoölogisch Museum Amsterdam.

#### RESULTS

## SYSTEMATIC ACCOUNT

Subclass Octocorallia Order Gorgonacea Suborder Calcaxonia Family Primnoidae Gray, 1858 Genus Narella Gray, 1870

- Narella Gray, 1870:49 [type species: Primnoa regularis Duchassaing & Michelotti, 1860, by monotypy].—Cairns and Bayer, 2003:618–619.—Cairns and Baco, 2007: (more complete synonymy and discussion).
- Stachyodes Wright & Studer in Studer, 1887:49 [type species: S. regularis Wright & Studer, 1889, by subsequent monotypy].
- Calypterinus Wright & Studer in Studer, 1887:49 [type species: C. allmani Wright & Studer, 1889, by subsequent monotypy].

DIAGNOSIS: Colonies of moderate to large size (up to 80 cm in height), dichotomously or pinnately branched in 1 or more planes, or unbranched. Calyces face downward, arranged in discrete whorls. Each polyp protected by 3 or 4 pairs of large body wall scales (basals, medials, buccals), 1–3 pairs of smaller adaxial buccal scales, and sometimes additional smaller scales scattered on the adaxial body surface. Adaxial side of basals may or may not meet to form a closed but unfused ring. All sclerites tuberculate on inner surface, at least where they come in contact with another sclerite or branch surface; outer surface usually granular. Operculum consists of 8 triangular scales, usually with a medial keel on their inner surface. Coenenchymal scales elongate, elliptical, or irregular in shape, often with tall longitudinal keels. Lower branch axis heavily calcified.

REMARKS: Narella, consisting of 38 valid species (Table 1), has by far the most species among the 32 primnoid genera; the next most diverse genera are *Callogorgia* (28 species) and *Thouarella* (27 species). Additional discussion of the genus and its characteristics are found in Cairns and Bayer (2003) and Cairns and Baco (2007).

DISTRIBUTION: Known from all ocean basins (Table 1) from 55 (undescribed species from New Caledonia) to 4,594 m.

# Key to the nine species of *Narella* that are known to occur in the hawaiian islands (N. *macrocalyx* keyed twice)

1. 1′.	Dorsolateral edge of basal scale curved (not ridged)
2. 2′.	Whorl diameter over 8 mm3Whorl diameter less than 6 mm4
3. 3′.	Colony sparsely branched; calyces up to 5.5 mm in length; polychaete commensal pres- ent; 2–3 pairs of adaxial buccals; coenenchymal scales convex platesN. macrocalyx Colony densely branched; calyces up to 3.0 mm in length; no polychaete commensal; 1 pair of adaxial buccals; coenenchymal scales elongate and keeledN. gigas
4. 4′.	Distal edge of basal scale extends far beyond junction with medial scale; coenenchymal sclerites ridged
5. 5′.	Calyces over 2.5 mm in length; polychaete worm tube not present; tip of operculum touches branch; no additional scales on adaxial body wall
6. 6′.	<ul> <li>Whorl diameter over 8 mm; calyces up to 5.5 mm in length; polychaete worm tube present; often 2–3 pairs of adaxial buccal scales</li></ul>
7. 7'.	All body wall scales and even outer surface of the opercular scales highly sculptured with ridges radiating from center of scale
8. 8′.	Distal edges of all body wall scales serrate to spinose
9.	Calyces small (1.6–2.2 mm in length); whorls closely spaced; medial scales shorter than

Narella Species	Location	Depth
N. gilchristi (Thomson, 1911) = S. capensis Thomson, 1917 = Stachyodes "gilberti" Kükenthal, 1919:316 nom. nud. (misspelling of gilchristi)	Southwest Indian Ocean	90–340 m (Williams 1992) 141–173 m
N. megalepis (Kinoshita, 1908)	Japan	Depth unknown (probably 300–400 m)
N. irregularis (Kinoshita, 1907)	Japan	137 m
N. compressa (Kinoshita, 1908)	Japan	Depth unknown
N. biannulata (Kinoshita, 1907)	Japan	Depth unknown
N. japonensis (Aurivillius, 1931)	Japan	731 m
N. bayeri Cairns & Baco, 2007	Gulf of Alaska	3,291–4,091 m
N. arbuscula Cairns & Baco, 2007	Gulf of Alaska	2,775–3,465 m
N. cristata Cairns & Baco, 2007	Gulf of Alaska	3,385 m
N. abyssalis Cairns & Baco, 2007	Gulf of Alaska	4,594 m
N. alaskensis Cairns & Baco, 2007	Gulf of Alaska	2,377-3,075 m
N. leilae Bayer, 1951	Indonesia	740 m
N. clavata (Versluys, 1906)	Indonesia	204 m
N. horrida (Versluys, 1906)	Indonesia	204 m
N. obscura (Versluys, 1906)	Indonesia	984 m
N. orientalis (Versluys, 1906)	Indonesia	520 m
N. parva (Versluys, 1906)	Indonesia	1,300–1,633 m
N. grandiflora (Kükenthal, 1907)	Sumatra	805 m
N. studeri (Versluys, 1906) (nom. nov. for S. regularis Wright & Studer, 1889)	Kermadec and Indonesia	1,080–1,264 m
N. allmani (Wright & Studer, 1889)	Fiji	"deep"
N. dichotoma (Versluys, 1906)	Indonesia	204–1,264 m
= N. nuttingi Bayer, 1997	Hawaiian Islands	743–1,448 m
N. gigas, n. sp.	Hawaiian Islands	302–399 m
N. alata, n. sp.	Hawaiian Islands	477–750 m
N. vermifera, n. sp.	Hawaiian Islands	275–527 m
N. macrocalyx, n. sp.	Hawaiian Islands	1,206–1,807 m
N. ornata Bayer, 1995	Hawaiian Islands	748–1,007 m
N. bowersi (Nutting, 1908)	Hawaiian Islands	1,218–1,758 m
N. muzikae, n. sp.	Hawaiian Islands	326–381 m
N. hawaiinensis, n. sp.	Hawaiian Islands	1,492–1,921 m
N. ambigua (Studer, 1894)	Galápagos	691 m
N. gaussi (Kükenthal, 1912)	Antarctic	2,450 m
N. bellissima (Kükenthal, 1915)	Amphi-Atlantic	225–1,968 m
N. versluysi (Hickson, 1909) = ?N. elegans Tixier-Durivault & Lafargue 1968	Amphi-Atlantic	550–3,100 m
N regularis (Duch, & Mich., 1860)	Lesser Antilles	159–792 m
N. laxa Deichmann, 1936	New England seamounts	3.186 m
N. pauciflora Deichmann, 1936	Lesser Antilles	738–1.446 m
N. spectabilis Cairns & Baver, 2003	Bahamas	1.485 m
N. alvinae Cairns & Bayer, 2003	Bermuda	3.419 m

 TABLE 1

 List of All Described Species of Narella, Arranged by Ocean Basin (with Depth)



FIGURE 1. Colony shape of Narella species: A, N. gigas, holotype; B, N. hawaiinensis, holotypic branch fragments; C, N. macrocalyx, holotype; D, N. alata, holotype; E, N. vermifera, holotype; F, N. bowersi, holotype; G, N. dichotoma, USNM 98828; H, N. muzikae, holotype. Scale bar: A-D, G-H = 10 cm; E-F = 5 cm.

- Narella gigas Cairns & Bayer, n. sp. Figures 1A, 2A–D, 3A–G
- "Narella sp., probably new" Grigg and Bayer, 1976:170.
- *Narella megalepis.*—Chave and Malahoff, 1998: table 1, figs. 66, 98.

## MATERIAL EXAMINED: Types.

TYPES AND TYPE LOCALITY: Holotype: Star II-2, 1 large dry colony, 3 branches in alcohol, SEM stubs B2350–2351 and C1233– 1235, 1251, USNM 56820. Paratypes: R/V Pele, off Makapu'u Point, O'ahu, 329–421 m, 27 August 1967, 1 dry colony, USNM 1093298; SANGO 10-1, 1 dry colony, USNM 1093299; SANGO 13-1c, several dry branches without calyces, USNM 1093300; SANGO 13-11, several dry branches without calyces, USNM 1093301; SANGO 14-1, 1 dry colony and 1 branch in alcohol, USNM 93213; Star II (station number unknown), Makapu'u Point, O'ahu, 367 m, March 1978, 1 large dry colony in pieces, USNM 56929; and 1 branch fragment, BPBM-D 1130; and 1 branch fragment, ZMA Coel. 09251; and 2 large dry colonies, Mcz 43643, 43644.

Type Locality: 21° 18′ N, 157° 32′ W (off Makapu'u Point, Oʻahu), 367 m.

DESCRIPTION: Colonies large, uniplanar, and flabellate, holotype 78 cm tall and 58 cm broad, but no colony examined contained an intact holdfast. Branching dichotomous and at wide intervals (2–10 cm), some distal undivided branches up to 40 cm in length. Branching from outermost branches of flabellum often secund, leading to a quasi-lyrate branching pattern. Branches thick (up to 14 mm in diameter), straight, and quite rigid, axis longitudinally striate and gray to bronze in color.

Calyces arranged in whorls of 10-14, whorls usually discrete but so closely spaced that operculum of one polyp touches abaxial face of basal scales of preceding polyp (Figure 2B-C), not allowing a view of the branch;



FIGURE 2. Calyces of *Narella gigas* from the holotype (USNM 56820), stereo views: *A*, opercular view of a whorl having 12 calyces; *B*–*C*, lateral views of calyces; *D*, lateral and abaxial views of calyces. All scale bars are 1 mm.

occasionally the whorl structure is irregular, calyces appearing to be arranged longitudinally instead of in whorls. Eleven to 12 whorls occur per 3 cm and, along with their compact placement, leads to a very high density of calyces. Whorl diameter is 9-12 mm. Calyces are 2.5-3.0 mm in length.

Each polyp encased in 3 pairs of large abaxial body wall scales, 1 pair of adaxial buccal scales, and approximately a dozen small adaxial scales placed randomly on adaxial body wall. Basal scales extremely tall (up to 3.3 mm) and narrow, having a straight, vertical lateral edge and an abaxial face that stands perpendicular or tilting slightly distad; its dorsolateral edge not crested but angled; its distal edge straight and projects only about 0.35 mm beyond its junction with medial scales. Although not ridged on outer surface, distal inner surface of all body wall scales coarsely ridged (Figure 3B,D). Basals do not meet adaxially to form a ring, rather they extend parallel to one another aligned with branch axis, separated by about 0.7 mm (Figure 2A). Medial scales tilted upward, 1.3-1.5 in length (about same length as buccals), and have a curved dorsolateral margin. Abaxial buccal scales much wider than medials, also having a curved dorsolateral edge and a straight distal edge. Adaxial buccal pair flat, fairly large (0.45-0.65 mm in width), and rectangular to square. Additional adaxial body wall scales elliptical in shape, flat, and up to 0.80 mm in greater diameter but usually smaller than adaxial buccals. Outer surfaces of larger body wall scales coarsely granular, granules radiating from a central point.

Opercular scales triangular and fairly flat, bearing a rather low, blunt keel on inner distal one-half to one-third; outer surface granular, granules radiating from a central point; sometimes a low medial ridge present (Figure 3A). Large symmetrical abaxial operculars up to 1.1 mm in height and squat (H:W = 1.1-1.2). Asymmetrical laterals only slightly shorter, with a H:W of about 1.6. Small adaxials 0.8–0.9 mm in height, with a H:W of 2.1–2.3. Because of the relatively squat operculars operculum short, obscured from lateral view by a buccal cowl of 0.4–0.5 mm extension. Because of the tall basal scales, upward-tilted medials, and short operculum, operculum usually held at least 1 mm above branch axis.

Coenenchymal sclerites best seen in large basal branches, because they are few and difficult to see on terminal branches. They are thick and irregular in shape, often elongate (up to 2.3 mm) and sometimes bifurcate with coarsely serrate edges. Outer surfaces granular and often bear 1-5 tall (up to 0.5 mm) crests or pinnacles.

ETYMOLOGY: The species name *gigas* (Latin, meaning giant) refers to the large size of the colony and its thick branches.

COMPARISONS: *Narella gigas* is distinctive within the genus in having such a high number of calyces per whorl and by its large whorl diameter, both contributing to very thick branches. It is compared with other Hawaiian species in Table 2.

REMARKS: Commensal polychaetes were never found on this species, but the holotype harbored a small white ophiuroid, and one colony (USNM 56929) was overgrown by a zoanthid.

DISTRIBUTION: Kaiwi Channel southeast of O'ahu and a seamount between Brooks Banks and French Frigate Shoals, Hawaiian Islands, 362–399 m (confirmed).

## Narella alata Cairns & Bayer, n. sp. Figures 1D, 4A–D, 5A–G

MATERIAL EXAMINED: Types.

TYPES AND TYPE LOCALITY: Holotype: Pisces 5-595, 1 large dry colony, SEM stubs C1246–1250, USNM 1071418. Paratypes: Pisces 5-593, specimen 9, 1 dry colony, USNM 1071421; Pisces 5-593, specimen 12, 2 dry branches, USNM 1071420, and 1 dry branch, BPBM-D 1133, and 1 dry branch, ZMA Coel. 09254; Pisces 5-593, specimen 13, 1 dry colony, USNM 1071419; OES 03-01-4, 1 colony, USNM 1014744.

Type Locality: 19° 47′ 54″ N, 156° 07′ 47″ W (off Keāhole Point, Hawaiʻi), 679 m.

DESCRIPTION: Colonies uniplanar and flabellate, sometimes wider than tall, holotype measuring 29 cm in height and 31 cm in



FIGURE 3. Sclerites of *Narella gigas* from the holotype (USNM 56820): A, opercular sclerites; B, abaxial buccal sclerites; C, a medial sclerite; D, basal sclerites showing ridges on inner surface; E, outer surface of adaxial buccal sclerites; F, adaxial body wall sclerites; G, coenenchymal sclerites. Scale bars: A, E, F, 0.25 mm; B-D, 0.50 mm; G, 0.50 mm.

width and having a calcified basal stem diameter of 10.8 mm. Branching dichotomous and fairly regular in lower half of colony, upper half consisting of long, straight ascending branches up to 36 cm in length; branching axils  $15-20^{\circ}$ , leading to closely spaced, almost parallel branches. Branches flexible and easily broken; axis is straw colored and longitudinally striate.

Calyces arranged in whorls of 4 or 5 (usually 4), each whorl closed appressed to adjacent ones, the operculum of one often touching abaxial face of basal scale of the more proximal whorl. Nine to 10 whorls per 3 cm branch length; whorl diameter 4.5–5.0 mm. Calyces 2.5–3.1 mm in length, bending at a sharp right angle at junction of basals and medial scales.

Each polyp encased in 3 pairs of large abaxial body wall scales and a pair of rather large adaxial buccal scales. Basals stand perpendicular to branch axis and are up to 2.5 mm in height, delicate distal margin extending up to 1.2 mm above junction with medial scale, this large projection often bearing thin ridges on its inner side, especially when basal scales are enlarged to form a calcareous polychaete worm tube. Dorsolateral edge of a basal curved (not ridged), and lower adaxial edges of these scales form a complete (but unfused) ring (Figure 4C) around polyp. Medial scales short (0.9–1.2 mm, 55–70% length of a buccal), have curved dorsolateral edges, and distally flared upward; their inner distal surfaces ridged (Figure 5C) as for basals. Abaxial buccals large (1.6–1.8 mm long) and wide, having a curved dorsolateral edge and a smooth, undulating distal margin that projects well beyond (0.5 mm) junction with operculars, forming a cowl (Figure 4B) around operculum and shielding the relatively short operculum from lateral view; their inner distal surfaces sometimes ridged as well. Abaxial buccals do not form a ring around polyp, being interrupted by a pair of relatively large (0.6-0.80 mm), thin, rectangular adaxial buccals, which are somewhat concave above and often have a thin transverse ridge (Figure 4F) on their proximal margin.

Opercular scales triangular to somewhat

irregular in shape, highly concave above, and have a low keel on distal two-thirds of their inner surface; outer surface is finely granular. The large, symmetrical abaxial scales broader than tall (H:W = 0.70–0.85), have alate lateral projections on each side, and are about 1.1 mm in height; their inner keel often has additional lateral ridges, which makes keel appear to be swollen (Figure 5*B*). The asymmetrical lateral operculars approximately the same height but bear only 1 adaxially positioned lateral projection, and thus the H:W is greater (1.3–1.6). The small adaxial opercular about 1.0 mm in height with a H:W of about 2.5.

Coenenchymal sclerites elongate (up to 1.5 mm long and 0.25 mm in width), most bearing 1 or more longitudinal crests, some of these crests being quite tall (up to 0.7 mm).

ETYMOLOGY: The species name *alata* (Latin, meaning winged) refers to the prominent distal winglike projections of the basal scales (and abaxial opercular scales), which are characteristic of the species.

COMPARISONS: Narella alata is morphologically similar to N. allmani (Wright & Studer, 1889), originally described from Fiji, both species even having similarly modified arcade calvces that host commensal polychaetes. Narella allmani differs in having thick, polygonal, granular (not ridged) coenenchymal scales; adaxially open basal scales (those of *N. alata* are closed or touching); and occasionally the distal edges of the medial scales are shaped into a small spine (see Kükenthal 1919, 1924, keys to species). Narella alata is also similar to N. leilae Bayer, 1951 (Philippines, 732 m), both species having a commensal worm and adaxially close basal scales, but N. leilae differs in having flat, nonridged coenenchymal scales and much shorter buccal scales, virtually the same length as its medial scales. Narella alata is compared with other Hawaiian species in Table 2.

**REMARKS:** All colonies have arcade calyces with strongly modified basal scales that form continuous worm tubes, which are about 4 mm in diameter.

DISTRIBUTION: Off Keāhole Point, Hawaiʻi, and Cross Seamount, 477–750 m (confirmed).

Characteristic	N. gigas	N. alata	N. dichotoma	N. vermifera
Branching	Uniplanar, flabellate, moderately branched	Uniplanar, flabellate, densely branched	Bushy (verticillate branching in lower half)	Uniplanar, flabellate, densely branched
Calyces/whorl; whorls/3 cm; whorl diameter	10–14; 11–12; 9–12 mm	4–5; 9–10; 4.5–5.0 mm	3–5; 8–11; 4.5–5.0 mm	3–5; 13–15; 3.9 mm
Calyx length Basal body wall scale: height; dorsolateral edge; distal edge; closed adavial ring	2.5–3.0 mm 3.3 mm; right-angled (not ridged); lobed; no	2.5–3.1 mm 2.5 mm; curved; rounded; yes	2.8–3.1 mm 2.4 mm; curved; rounded; yes	1.8–2.0 mm 2.0 mm; curved; rounded; yes
Basals modified to	No	Yes (arcade calyces)	No	Yes (arcade calyces)
Medial body wall scale: % length of the buccal; dorsolateral edge; distal edge	100%; curved; straight	55–70%; curved; rounded	65–75%; curved; rounded	50%; curved; straight
Abaxial buccal body wall scale: length; dorsolateral edge; distal edge; closed adaxial ring	0.45–0.65 mm; curved; rounded; no	1.6–1.8 mm; curved; smooth and undulate; no	1.2–1.4 mm; curved; rounded to straight; no	1.3 mm; curved; smooth and undulate; yes
Adaxial buccal scale: shape; additional adaxial bw scales	1 pair: rectangular, flat; yes	1 pair: rectangular, ridged; no	1 pair: square to rectangular, flat;	1 pair: elliptical, flat; yes
Opercular scales: H:W of abaxials; inner keel	1.1–1.2; blunt keel	0.70–0.85; keel sharp and may have lateral ridges	1.2–1.3; not keeled but medially convex	1.2; blunt keel
Coenenchymal scales	Thick, elongate to irregular in shape, with multiple	Elongate with medial crest	Elongate, having flat to low ridges	Polygonal, thick, mosaiclike, low ridges
Other distinctive characteristics	Inner distal surfaces of all body wall	Inner distal surfaces of body wall sclerites ridged		Inner distal side of adaxial opercular scales culindrical
Depth range	362–399 m	477–750 m	743–1,448 m	275–527 m

 TABLE 2

 Distinguishing Characteristics of the Hawaiian Narella

Narella dichotoma (Versluys, 1906) Figures 1G, 6A–D, 7A–F

- Stachyodes dichotoma Versluys, 1906:88–90, text figs. 98–101, pl. 8, fig. 23.—Nutting, 1908:577 (all four lots: 22561, 91864, 25376, 25375, 1017436 [*Alb*-3889 numbered twice]).
- Stachyodes bowersi Nutting, 1908: in part (pl. 43, fig. 5 = USNM 91864).
- ?"Narella sp., probably N. megalepis" Grigg and Bayer, 1976:170.

Narella sp. Grigg and Bayer, 1976:172.

Narella nuttingi Bayer, 1997:511–518, figs. 1– 5.—France and Hoover, 2001:112 (USNM 94424, Pisces 5-236).—Berntson et al., 2001:239 (USNM 94452, Pisces 5-238). New synonymy.

MATERIAL EXAMINED: *Alb*-3889, 1 large colony, USNM 1017436; *Pisces* 5-235, 4 colonies, SEM stubs B2315, 2321, USNM 94417–94419, 1092710; *Pisces* 5-236, 2 branches, USNM 94423–94424; *Pisces* 5-237, 6 branches,

## The Genus Narella Gray · Cairns and Bayer

Continuation	of	Table	2

N. macrocalyx	N. ornata	N. bowersi	N. muzikae	N. hawaiinensis
Uniplanar, sparsely branched	Unknown (?unbranched)	Uniplanar, flabellate, densely branched	Uniplanar, flabellate, numerous branches from a basal bolus	Unknown (unbranched?)
4–6; 5; 8–11 mm	3-4; 7-8; 3.5 mm	3-4; 7-8; 4.5 mm	3–6; 13–15; 3–4 mm	3-5; 5-6; 5-6 mm
4.5–5.5 mm 2.8 mm; usually curved, occasionally ridged; rounded; no	3.0 mm 1.6–1.7 mm; radiating multiple ridges; serrate; no	<ul><li>2.5–3.2 mm</li><li>2.3 mm; ridged; hornlike projections; no</li></ul>	<ul> <li>1.7–2.2 mm</li> <li>1.5 mm; numerous discontinuous ridges; hornlike projections; no</li> </ul>	3.4–4.1 mm 2.0 mm; lower half ridged; rounded; no
Yes (arcade calyces)	No	No	No	No
75–85%; curved; rounded	100%; multiple radiating ridges; serrate	80–90%; distal half veined; serrate	70–80%; slightly ridged; rounded	100–110%; curved; rounded
2.2–2.5 mm; curved; rounded; no	1.0 mm; multiple radiating ridges; serrate; no	1.7–2.0 mm; distal half ridged; serrate; no	0.9–1.1 mm; curved; rounded and undulate; no	1.4–1.8 mm; curved; rounded; no
2–3 pairs: rectangular to alliptical flat: yes	1 pair: rectangular, pocket-shaped ridging: po	1 pair: rectangular, diagonally ridged;	1 pair: trapezoidal, pocket-shaped ridging, po	1 pair: square to elliptical, flat; no
1.05–1.20; not keeled but medially convex	1.7; sharp inner keel (also multiple radiating ridges on	1.1; distal keel	0.9–1.0; distal keel (also often medial ridge on outer	1.45; sharply keeled
Smooth, concave saucer-shaped plates	Elongate, highly keeled	Elongate, keeled	Elongate, with multiple keels	Elongate, with tall medial keel
All body wall sclerites thin and fragile		Basal scales also with medial basolateral ridge	Basal scales also with medial basolateral ridge	
1,206–1,807 m	748–1,007 m	1,218–1,758 m	326–381 m	1,492–1,921 m

USNM 94425–94427, 94454; *Pisces* 5-238, 2 branches, USNM 94421–94422; *Pisces* 5-301, 8 colonies, USNM 98824–98831; *Pisces* 5-303, 5 colonies, USNM 98833–98836; *Pisces* 5-464, 1 branch, USNM 1093302; *Pisces* 5-525, 2 branches, USNM 1072106; *Pisces* 5-527, 3 branches, USNM 1072111–1072112; *Pisces* 5-593, 1 colony, USNM 1071422; types and nontypes of *N. nuttingi* reported by Bayer (1997) and Berntson et al. (2001) (USNM 94452). Syntype fragment of *S. dichotoma*, *Siboga* 122 (see Types).

TYPES AND TYPE LOCALITY: Four syntypes of *S. dichotoma* are deposited at the ZMA (Coel. 3422, 3424) (van Soest, 1979: 103); a fragment of the syntype from *Siboga* 122 (ex. Coel. 3422) is deposited at the NMNH (USNM 1097266).

Type Locality: Indonesian region, 204–1,264 m.

The holotype of *N. nuttingi* (USNM 91864, including SEM stubs B2316–2317, 2319–2320, 2333–2337, and C1227–1228) and three paratype lots are deposited at the NMNH.



FIGURE 4. Calyces of *Narella alata* from the holotype (USNM 1071418), stereo views: A, lateral view of two whorls; B, apical view of a whorl of 4 calyces; C-D, adaxial calicular views showing adaxial buccal scales and notch and internal ridges that articulate with lower edge of basal scales. All scale bars = 1.0 mm.

Type Locality: *Alb*-4013: off Hanamā'ulu warehouse, Kaua'i Island, Hawaiian Islands, 730–767 m.

DESCRIPTION: Basal main stem vertical, 4-8 cm in height, and sometimes highly calcified, attaining a diameter of up to 14 mm. This main stem bifurcates leading to two shorter stems 2-3 cm in length, each of which produces a whorl (verticillate branching) of 3-5 additional branches. These branches also produce a whorl of branches or continue to subdivide in a dichotomous manner. Because of the basal verticillate branching, some branches of which project out of the plane of the flabellum, the resultant colony is somewhat bushy to compressed flabellate, attaining a height of 36 cm (USNM 98826). Branches fairly rigid. Axis dark brown and longitudinally striate, often producing a contrast to overlying white calyces.

Calyces arranged in whorls of 3-5 (usually 4), each whorl discrete, separated from one another by 0.8-3.0 mm; 8-11 whorls occur

per 3 cm; whorl diameter 4.5–5.0 mm. Calyces 2.8–3.1 mm in length, tip of operculum usually appressed against branch when preserved.

Each polyp encased in 3 pairs of large abaxial body wall scales and 1 pair of adaxial buccal scales; only rarely is there an extra pair of basal scales; no additional adaxial scales present. Basal scales massive (Figure 7D), tilted slightly proximally, and up to 2.4mm in height, distal edges projecting about 0.5 mm beyond junction with medial scales. Narrow adaxial basal region of basals often meet each other on adaxial side of polyp, forming a complete but unfused ring. Medial scales relatively short (0.8-0.9 mm long) and narrow, only 65-70% length of a buccal, slightly concave above, and flared upward. Abaxial buccal scales large, 1.2-1.4 mm in length. One pair of large adaxial buccal scales, which are square to rectangular and flat, up to 0.55 mm in greater length. Dorsolateral edges of all body wall scales gently



FIGURE 5. Sclerites of *Narella alata* from the holotype (USNM 1071418): A, opercular sclerites; B, keel with lateral ridges of an abaxial opercular; C, abaxial buccal scales showing ridges on inner surface; D, outer surface of medial scales; E, basal scales; F, an adaxial buccal scale; G, coenenchymal scales with tall crests. Scale bars: A,F,G, 0.5 mm; B, 0.25 mm; C-E, 0.5 mm.



FIGURE 6. Calyces of *Narella dichotoma* (*A*, holotype of *N. nuttingi*, USNM 91864; *B–D*, paratype of *N. nuttingi*, USNM 94452), stereo views: *A*, lateral view of a whorl; *B*, lateral view of a calyx; *C*, apical view of a calyx; *D*, adaxial view of a calyx showing adaxial buccal pair. Scale bars: *A–B*, 1 mm; *C–D*, 0.5 mm.

curved (not ridged or meeting at an angle) and their outer surfaces smooth. Their distal margins straight and entire, not produced as spines or serrations.

Opercular scales roughly triangular, longitudinally concave above but not keeled (Figure 7A) on the inner surface, instead bearing an elongate medial convexity. Usually 1 predominant, symmetrically shaped abaxial opercular (not a pair) that is about 1.2 mm in length (H:W = 1.2–1.3), blunt to evenly rounded apically. Lateral operculars of about the same height but more slender (H:W = 1.7-2.1) and asymmetrical, each having a small adaxial basal shoulder. The symmetrical adaxials the smallest operculars (0.95– 1.0 mm in length), with a H:W = 2.7-3.2. Operculum prominent, easily visible in lateral view.

Coenenchymal sclerites elongate (up to 2.8 mm long and 0.5 mm wide) and flat or with only inconspicuous ridging. They are finely granular above and tuberculate below. Those

in the vicinity of an attached ophiuroid sometimes modified to have several mounds up to 0.3 mm in diameter on their outer surface.

COMPARISONS: *Narella dichotoma* is unique among the Hawaiian species as well as all congeners in having verticillate branching, which leads to a bushy colony. It is compared in Table 2 and in the key.

REMARKS: In his description of *N. nuttingi*, Bayer (1997) noted its resemblance to *N. dichotoma* but differentiated it on three characters: its coenenchymal sclerites were not ridged, it had very reduced adaxial operculars, and it was bushy (not uniplanar). However, examination of a syntype of *N. dichotoma* shows that its coenenchymal sclerites are not ridged. Furthermore, the adaxial operculars of *N. nuttingi* are not particularly small (0.95 mm long compared with 1.2 mm for the abaxial), consistent with many other *Narella* species, and, because complete colonies of *N. dichotoma* were not collected by Versluys, it is entirely possible that his



FIGURE 7. Sclerites of *Narella dichotoma* (holotype of *N. nuttingi*, USNM 91864): *A*, opercular sclerites; *B*, abaxial buccal sclerites; *C*, medial sclerites; *D*, basal sclerites; *E*, inner surface of adaxial buccal sclerites; *F*, coenenchymal sclerites. Scale bars: *A*,*E*, 0.25 mm; *B*–*D*, 0.5 mm; *F*, 0.5 mm.

specimens represented the uniplanar end branches that are found in *N. muttingi*. We can find no substantial differences between the two taxa, and thus synonymize *N. nuttingi* with *N. dichotoma*. Furthermore, Bayer's (1995, 1997) later reidentifications of Nutting's *S. regularis* as *N. dichotoma* are in fact *Narella hawaiinensis* Cairns & Bayer, n. sp. (see description later in this paper).

The nontype specimen of *N. nuttingi* reported by Bayer (1997) as from USNM 25375 is from *Albatross* 4182, not 3989.

Commensal polychaetes or ophiuroids were not found with this species.

DISTRIBUTION: Pioneer Bank, off French Frigate Shoals, continental slopes of Kaua'i, Lāna'i, Maui, and Hawai'i; Bishop, Cross, and Pensacola Seamounts, 743–1,448 m (confirmed).

## Narella vermifera Cairns & Bayer, n. sp. Figures 1E, 8A–D, 9A–H

"Narella sp., new" Grigg and Bayer, 1976:171.

MATERIAL EXAMINED: Types.

TYPES AND TYPE LOCALITY: Holotype: SANGO 13-1b, 1 colony now in 3 pieces, and SEM stubs B2346–2349, C1238–1240, USNM 93216, and 1 branch, BPBM-D 1132, and 1 branch, ZMA Coel 09253. Paratypes: SANGO 13-1b (topotypic), 1 small colony and 2 branches in alcohol, USNM 93220; SANGO 13-1a, 2 dry branches, USNM 1093303.

Type Locality: 23° 02′ N, 162° 05′ W (off Ka'ula Rock, near Ni'ihau), 275–527 m.

DESCRIPTION: Largest piece of holotype colony 13 cm tall and 9 cm in width, having a basal stem diameter of 2.4 mm; it may be complete except for holdfast. Colonies apparently uniplanar and flabellate, having regular, dichotomous branching. Axis golden in color and longitudinally striate.

Calyces arranged in whorls of 3–5 (occasionally in pairs near branch tips), separated from one another by 0.9–1.2 mm; 13–15 whorls occur per 3 cm; whorl diameter about 3.9 mm. Calyces 1.8–2.0 mm in length. Because operculum and medial scales are short, and basal scales are relatively tall, tip of operculum does not rest against branch axis in the preserved state (Figure 8*A*).

Each polyp encased in 3 pairs of large abaxial body wall scales, 1 pair of smaller adaxial buccal scales, and approximately a dozen smaller adaxial scales that cover adaxial body wall. Basals stand perpendicular to branch axis and are about 2.0 mm in height, having rounded distal edges that rise about 0.4 mm above their junction with medials; they have curved dorsolateral edges, a homogeneously granular outer surface (no ridges), and basal adaxial portions usually meet or even overlap on adaxial side, forming an unfused ring (Figure 8B). Those basals modified to form arcade calvces that house polychaetes substantially larger (up to 4 mm in width), having wide, recurved edges that meet with those of adjacent calyces, both laterally within its own whorl and those from adjacent whorls, to form a continuous worm tube (Figure 8D). When this happens medial and buccal scales are greatly reduced in size. Medial scales quite short (0.5–0.7 mm), usually less than half length of the buccal scales, sometimes not even visible in lateral view. Abaxial buccals up to 1.3 mm in length, have a straight undulating distal margin and a gently curved dorsolateral edge. Like basals, their narrow adaxial portions meet each other or overlap to form an unfused ring (Figure 8C) and, together with basals, form a cylindrical body wall. Because buccals reach entirely around body wall, the small adaxial buccals are partially covered by abaxial buccals, being tucked between abaxial buccals and adaxial operculars (Figure 8B-C). Adaxial buccals nonetheless large (up to 0.5 mm in diameter), elliptical, and granular above like body wall scales. Additional smaller, semicircular scales (0.25-0.50 mm in diameter) cover adaxial body wall below adaxial buccal scales, these scales having finely serrate edges and radially ridged outer surfaces (Figure 9G).

Opercular scales triangular, with a slightly concave outer surface and a rather thick, blunt keel on distal half of inner surface. Large abaxial opercular is up to 0.9 mm in height, having a H:W of about 1.2. Asymmetrical lateral operculars about the same



FIGURE 8. Calyces of *Narella vermifera* from the holotype (USNM 93216), stereo views: A, lateral and abaxial view of some calyces; B, apical view of a calyx showing closed rings of buccal and basal pairs; C, adaxial view of a calyx showing ringlike nature of buccal scales, which slightly obscures the adaxial buccal scales; D, arcade calyces with greatly enlarged basal scales forming a worm tube. Scale bars: A, D, 1 mm; B–C, 0.5 mm.

length but narrower (H: W = 1.7-1.9). Small adaxial operculars only 0.6–0.7 mm in length with a H: W of 1.7–2.1, highly concave above, and bearing a rounded, almost cylindrical keel that is strongly bent downward (Figure 9*B*).

Coenenchymal scales large (up to 2 mm in width), thick (up to 0.2 mm), and flat; polygonal and placed in a mosaic pattern. They bear low granules and/or very low ridges on their outer surface.

ETYMOLOGY: The species name *vermifera* (Latin, meaning worm bearer) is an allusion to the commensal polychaete that is found with this species.

COMPARISONS: Narella vermifera most closely resembles N. biannulata (Kinoshita, 1907), in that both the basal and buccal body wall sclerites form complete (but unfused) body wall rings. Kinoshita (1908) placed this single species in his "group 3" (group 1 contains species that have nonringed body wall scales, and group 2 with species having only the basals forming a ring). Narella biannulata is known only from off Japan at 146 m and was most recently redescribed and figured by Utinomi (1979). Although *N. vermifera* is similar to *N. biannulata* in this and most other characters, it differs in having a pair of prominent adaxial buccal scales, additional adaxial body wall scales, and in having a commensal relationship with polychaetes (also see Table 2).

**REMARKS:** All colonies have arcade calyces with strongly modified basal scales that form continuous worm tubes; the polychaetes are thought to be an undescribed species of the genus *Gorgoniapolynoe* (Polynoidae).

DISTRIBUTION: Off Ni'ihau and Nīhoa, 271–527 m.

Narella macrocalyx Cairns & Bayer, n. sp. Figures 1C, 10A–D, 11A–H

MATERIAL EXAMINED: Types.

TYPES AND TYPE LOCALITY: Holotype: *Pisces 5-544*, 1 large dry colony and 1 branch



FIGURE 9. Sclerites of *Narella vermifera* from the holotype (USNM 93216): *A*, abaxial and lateral opercular sclerites; *B*, adaxial opercular sclerites; *C*, abaxial buccal sclerites; *D*, outer surface of a medial sclerite; *E*, basal sclerites; *F*, adaxial buccal sclerites; *G*, adaxial body wall sclerites with serrate edges; *H*, thick coenenchymal sclerites. Scale bars: *A*,*H*, 0.25 mm; *B*, 0.10 mm; *C*–*E*, 0.5 mm; *F*,*G*, 0.25 mm.



FIGURE 10. Calyces of *Narella macrocalyx* from the holotype (USNM 93216), stereo views: A, lateral view of a calyx; B, lateral view of an arcade calyx with enlarged basal scales that form the worm tube; C, adaxial calyx view showing multiple pairs of adaxial buccal scales and additional adaxial body wall scales; D, opercular view of a calyx. All scale bars = 1 mm.

in alcohol, SEM stubs C1241–1242, 1252– 1253, USNM 1072133. Paratypes: Pisces 5-301 (LAD 104), 1 colony, USNM 98820; Pisces 5-525, 3 branches (USNM 1072105); Pisces 5-532, 1 colony and 1 branch, USNM 1072117; Pisces 5-534, specimen 12, 2 dry branches, USNM 1072118, and 1 dry branch, BPBM-D 1134, and 1 dry branch fragment, ZMA Coel. 09255; Pisces 5-542, 1 dry colony and 1 branch in alcohol, USNM 1072122.

Type Locality:  $23^{\circ}$  19' 00" N, 163° 41' 00" W (seamount east of Necker Island), 1,443 m.

DESCRIPTION: Colonies are uniplanar and very sparsely branched, small colonies often unbranched and larger colonies with only 3-5 distal branches. Holotype is 38 cm tall, 25 cm in width, and 4.2 mm in basal branch diameter, having only 4 distal branches, 3 of them branching within 3-4 cm of the base; one distal branch is 34 cm in length. Branching axils wide ( $45-90^{\circ}$ ). Axis is golden in color and longitudinally striate. Colony purple when alive.

Calyces are arranged in whorls of 4–6 (usually 5), each whorl discrete and widely separated from one another by up to 2 mm; only about 5 whorls occur per 3 cm; whorl diameter 8–11 mm. Calyces long (4.5–5.5 mm) but relatively narrow.

Each polyp encased in 3 pairs of large abaxial body wall scales, 2 or 3 pairs of smaller adaxial buccals, and a variable number of even smaller adaxial body wall sclerites. Basal scales stand perpendicular to axis up to 2.8 mm in height, the distal 1 mm extending beyond junction with medials as smoothedged lobes. Dorsolateral edge usually curved (Figure 11*B*) but occasionally crested, especially when basal scales are modified to form a calcified worm tube. In the latter case, edges of basals greatly enlarged and recurved, together with others forming a cylindrical tube about 3.2 mm in diameter. Medial scales 75–



FIGURE 11. Sclerites of *Narella macrocalyx* from the holotype (USNM 93216): A, opercular sclerites; B, abaxial buccal sclerites; C, medial sclerites; D, outer surface of basal sclerites; E, outer surface of adaxial buccal sclerites; F, adaxial body wall sclerites; G, coenenchymal sclerites; H, tentacular sclerites. Scale bars: A-D,G, 0.5 mm; E,F, 0.25 mm; H, 50 µm.

85% length of buccals, having smooth distal edges that are strongly flared upward. Distal margins of abaxial buccals also smooth and strongly flared, forming a cowl (Figure 10D) 0.8-1.0 mm long; they are 2.2-2.9 mm in length and have a gently curved dorsolateral edge. All body wall scales extremely thin and fragile (brittle), often resulting in distal edges being broken. Often with 2 or 3 pairs of thin, flat rectangular to elliptical adaxial buccal scales, each about 0.5-0.6 mm in greater diameter, pairs largely overlapping one another. Proximal to these scales are a variable number of smaller (0.25-0.45 mm), elliptical to elongate scales that sparsely cover adaxial side of polyp (Figures 10B, C, 11F).

Opercular scales triangular and undulate, their outer surface being longitudinally furrowed, corresponding to an elongate medial convexity on inner surface but not as a structure that could be termed a keel. Symmetrical, blunt-tipped abaxial operculars are up to 2.2 mm long and almost as wide as long (H:W = 1.05 - 1.20). Asymmetrical lateral operculars almost as long but narrower (H:W = 1.4-2.1). Slender adaxial operculars 1.5-1.6 mm in length, having a H:W of 2.3-3.1. Operculum fairly prominent in lateral view, its tip usually closely adjacent to branch or worm tube. This is the only species for which tentacular scales were noted. They were elongate and flat, with irregular edges, 0.13-0.15 mm in length and 0.038-0.050 mm in width, sometimes slightly curved (Figure 11*H*).

Most coenenchymal scales thin-edged, saucer-shaped (highly concave above), granular (not ridged or crested), and elliptical in shape, reaching up to 2.2 mm in greater length but having a thick middle central portion that is highly tuberculate below. Because they are concave above they do not conform to the opposite curvature of the narrow branch axis, thus they often appear to be crested because the thin, obliquely upwardoriented edges of adjacent scales resemble crests; however, a small number of coenenchymal scales do bear short crests (Figure 11*G*, lower right).

ETYMOLOGY: The species name *macro*calyx (Greek, meaning long cup or calice) is in reference to the large size of the calyces of this species.

COMPARISONS: This species is unique in the genus in having the largest calyces (up to 5.5 mm in length) and in having 2 or 3 pairs of adaxial buccal scales.

REMARKS: Worm tubes are common to all specimens of this species, and thus it appears to be an obligate association. Many polynoid polychaetes may live on the same colony within the continuous tube formed by the arcade calyces. Unlike *Narella vermifera*, the medial and buccal scales are not reduced in size if a polyp is transformed into an arcade polyp.

One specimen, USNM 1072117, has smaller calyces (2.5–3.0 mm in length) and thus more calyces per whorl (about 9), and a whorl diameter of only 8 mm but otherwise is identical to the others. It is a completely unbranched colony 14.5 cm in height and is interpreted herein to be a juvenile or poorly developed colony.

DISTRIBUTION: Pioneer Bank, seamount southeast of Laysan, east of Necker Island, southwest of Lānai; 1,206–1,807 m (confirmed).

#### Narella ornata Bayer, 1995

Narella ornata Bayer, 1995:148-151, figs. 1-3.

MATERIAL EXAMINED: Holotype.

TYPES AND TYPE LOCALITY: Holotype: *Alb*-4019, 1 branch 6.5 cm long, SEM stubs B2352–2354, 2401, USNM 94617.

Type Locality: 13 km off Hanamā'ulu warehouse, Kaua'i, Hawaiian Islands, 748–1,007 m.

DESCRIPTION: This species is not redescribed because it is well characterized and illustrated in the original description, and no additional specimens have been collected to describe variation. However, for ease of comparison, its distinctive characteristics are summarized in Table 2.

COMPARISONS: When Bayer (1995:151) described *N. ornata*, he stated that its characters were "so conspicuously unlike those of any species of *Narella* now known" that it was safe to describe it as a new species based

on only 1 small fragment. However, N. ornata is remarkably similar to the western Atlantic (738–1,473 m) N. pauciflora Deichmann, 1936, both species having prominent, radially ridged body wall scales, as well as prominent ridges on the coenenchymal scales, adaxial buccals (in the form of cuplike pockets), and ridges even on the outer surfaces of the opercular scales (see Cairns and Bayer [2003] for illustrations of N. pauciflora). Most other characters usually reported are also within range of each other, the only differences I (S.D.C.) can find being that N. ornata has more prominent ridges and it is found in a different ocean basin. Although the species are kept separate here, their similarity raises the possibility that some species may have a multiocean distribution or perhaps are geographically separated subspecies.

DISTRIBUTION: Known only from 1 fragmentary specimen from the type locality.

Narella bowersi (Nutting, 1908) Figures 1F, 12A–D, 13A–F

- *Stachyodes bowersi* Nutting, 1908:577–578, pl. 43, fig. 6 (not fig. 5, = *N. dichotoma*), pl. 48, fig. 2.—Kükenthal, 1919:467–468; 1924: 316.
- Narella bowersi Bayer et al., 1983: fig. 77; Bayer, 1995:148 (mention); 1997:511 (mention).—Chave and Malahoff, 1998: table 1, fig. 30.—Berntson et al., 1999: 422; 2001:239.

MATERIAL EXAMINED: *Pisces* 5-301, 1 colony, USNM 98822; *Atlantis II*-AD2969, 3 branches, USNM 98821; type and nontypes cited by Nutting (1908) and Berntson et al. (1999, 2001) (USNM 94450: *Pisces* 5-236).

TYPES AND TYPE LOCALITY: The holotype, consisting of a main colony, several branches, and many detached calyces, 1 permanent slide, and SEM stubs B403 and C1229–1230, is deposited at the NMNH (USNM 25377). The additional dry specimen (USNM 43101) mentioned by Nutting from *Alb*-4174 is considered to be a nontype.

Type Locality: *Alb*-4153: 23° 05′ N, 161° 52′ W (near Bird Island, Nīhoa), 1,758– 1.936 m. DESCRIPTION: Colonies uniplanar and dichotomously branched, branching axils averaging 30°. Branching apparently starts very close to holdfast, most branching occurring in lower half of colony, resulting in distal branches up to 15 cm in length. Largest colony (USNM 98822) 22.5 cm in height, but no colony examined is complete with a holdfast. Axis white to light yellow and longitudinally striate; lower main branch heavily calcified and up to 7 mm in diameter.

Calyces arranged in whorls of 3 or 4 (usually 4), each whorl discrete and separated from one another by 0.6–1.5 mm; 7–8 whorls occur per 3 cm; whorl diameter about 4.5 mm. Calyces 2.5–3.2 mm in length and 2.1– 2.2 mm in width, tip of operculum appressed to branch when preserved.

Each polyp encased in 3 pairs of large body wall scales and 1 pair of smaller adaxial buccals; no additional adaxial scales present. Basal scales large, stand perpendicular to branch, and up to 2.3 mm in height, distal edges projecting up to 0.75 mm beyond junction with medial scales as two apical projections. They bear a well-defined dorsolateral ridge and occasionally a shorter basolateral ridge (Figure 12B); their narrow adaxial portions do not meet or form a ring on adaxial side of polyp. Medial scales 1.3–1.5 mm in length, somewhat concave above, and 80-90% length of the more distal buccal scales. Each medial scale bears a low dorsolateral ridge on its distal half and terminates in 2 or 3 toothlike points. Large abaxial buccal scales 1.7-2.0 mm in length and bear 4-6 low ridges on their lateral and adaxial (dorsal) sides as though veined, each of which terminates in a small distal tooth, producing a serrate margin to these scales (Figures 12A,B,D, 13B). Adaxial buccals relatively large (up to 1 mm in greater length), rectangular, and bear a tall (up to 0.2 mm), narrow ridge oriented diagonally across its lower, outer surface (Figure 13*E*).

Opercular scales triangular and undulate, having a medially furrowed outer surface that corresponds to a keel on distal half of inner surface. Symmetrical abaxials about 1.4 mm in length and about as wide as long (H:W = 1.1), having a blunt distal



FIGURE 12. Calyces of *Narella bowersi* (A,C-D, holotype, USNM 25377; B, *Pisces* 5-236, USNM 94450), stereo views: A, a whorl of calyces including a juvenile; B, lateral view of a calyx and branch showing characteristic ridges on all scales; C, adaxial view of a calyx showing adaxial buccal pair; D, oblique abaxial view of a calyx showing an intercalation of the buccal scales. All scale bars = 1.0 mm.

tip. Asymmetrical lateral operculars slightly shorter and narrower (H:W = 1.3-1.4). Small adaxial operculars only 0.9–1.0 mm in length with a H:W of 1.7–2.2. Both lateral and adaxial operculars have pointed tips. Operculum is easily seen in lateral view but is not prominent.

Coenenchymal scales elongate, up to 1.6 mm in length, and flat but often bear a low medial ridge on their outer surface, the ridge sometimes bifurcate or ramifying.

COMPARISONS: Narella bowersi is distinctive in having serrate distal edges of the medial and buccal body wall scales (see Table 2).

**REMARKS:** Narella bowersi was poorly described and illustrated by Nutting, leading Kükenthal (1919, 1924) to consider it as a doubtful species. Our study here indicates that it is a valid species, distinct from other members in the genus.

Commensal polychaetes or ophiuroids were not found with this species.

DISTRIBUTION: Off Nīhoa, Ni'ihau, Lānai, Pensacola Seamount, and Endeavour Seamount off British Columbia, 1,218– 1,758 m (confirmed for Hawai'i); 2,500 m off Washington.

## Narella muzikae Cairns & Bayer, n. sp. Figures 1H, 14A–D, 15A–F

*Narella* sp. 1 Chave and Malahoff, 1996: table 1, figs. 59, 60.

MATERIAL EXAMINED: Types (see next section). Nontypes: SANGO 3-8, numerous dry branches without calyces, USNM 1093309; SANGO 5-3, 1 dry calcareous base, USNM 1093310; SANGO 13-4, 4 dry bases with no calyces, USNM 1093311.

TYPES AND TYPE LOCALITY: Holotype: *Star II*-1, 1 colony in alcohol, SEM stubs B2342–2344 and C1236–1237, USNM 56814. Paratypes: *Star II*-1, topotypic, 20 branches,



FIGURE 13. Sclerites of *Narella bowersi* from the holotype (USNM 25377): *A*, opercular sclerites; *B*, abaxial buccal sclerites; *C*, outer surface of a medial sclerite; *D*, basal sclerites; *E*, outer surface of adaxial buccal sclerites showing the pocketlike ridging; *F*, crested coenenchymal sclerites. Scale bars: *A*,*E*,*F*, 0.5 mm; *B*,*C*, 0.5 mm; *D*, 0.5 mm.



FIGURE 14. Calyces of Narella muzikae from the holotype (USNM 56814), stereo views: A, lateral view of a whorl; B, apical (basal scale) view of a whorl of 4 calyces; C, opercular view of a calyx showing cowl and ridges on adaxial operculars; D, adaxial view of a polyp showing highly ridged adaxial buccal scales. Scale bars: A-B, 1.0 mm; C-D, 0.5 mm.

USNM 94506; Star II-1, 1 dry colony, USNM 56819; Star II, off Makapu'u Point, O'ahu, 366 m, March 1978, 1 dry colony, SEM stubs B2345-2346, USNM 56933, and 1 dry colony, врвм-D 1131, and 1 dry colony, zмA Coel. 09252; R/V Pele, off Makapu'u Point, O'ahu, 329-421 m, 27 August 1967, 4 dry branches, SEM stub B2340, USNM 1093304; R/V Makalii M43, 91, 6 dry branches, USNM 1093305; SANGO 4-1, 6 dry colonies and several branches, USNM 1093306; SANGO 10-1, 4 dry colonies and branches, most without calyces, USNM 1093307; SANGO 13-1, 1 dry branch, usnм 100238; SANGO 14-1, 20 dry branches most without calyces, USNM 1093308; SANGO 14-2, 1 dry colony with few calyces, USNM 1011541.

Type Locality: 21° 18′ N, 157° 32′ W (off Makapu'u Point, Oʻahu), 366 m.

DESCRIPTION: Basal main stem very short (0-3 mm) and thick (up to 1 cm in diameter), immediately giving rise to 5–8 branches that

radiate in a flabellate manner from a common bolus. Main stem, bolus, and lower part of basal branches transformed into a thick skeleton of white calcium carbonate, this characteristically shaped basal part remaining long after the octocoral has died. Largest colony (holotype) 23 cm in height and 18 cm broad; however, some colonies are equally broad as tall. Branching occurs dichotomously and regularly in upper part of colony, branching axils only 10–15°; straight adjacent branches almost parallel to one another. Axis straw colored and longitudinally striate.

Calyces arranged in whorls of 3–6, each whorl discrete, separated from one another by only 0–0.3 mm; 13–15 whorls occur per 3 cm; whorl diameter 3–4 mm. Calyces small, only 1.7–2.2 mm in length, tip of operculum resting close to branch surface.

Each polyp covered by 3 pairs of large abaxial body wall scales and 1 pair of smaller adaxial buccal scales; there are no additional

adaxial body wall scales. Basal scales tilt slightly proximally and are up to 1.5 mm in height, distal 0.6 mm projecting beyond junction with adjacent medial scales as a prominent horn. Dorsolateral edge of basals and often basolateral edge bear numerous discontinuous ridges; sometimes additional short ridges on abaxial surface (Figure 15D); adaxial portion of basal scales do not meet adaxially to form a ring. Medial scales 0.6-0.8 mm in length, about 70-80% length of buccals, having a rounded distal edge and often a slightly ridged dorsolateral edge. Abaxial buccals large (0.9-1.1 mm) and campanulate, their distal edge smooth (not serrate or toothed) but undulating, extending about 0.4 mm beyond junction with opercular scales in form of a cowl (Figure 14C); these scales have curved dorsolateral edges. Each of pair of adaxial buccal scales large (0.65 mm), trapezoidal, and bears 1 or 2 curved, transverse ridges on their lower outer surface that form 1 or 2 cuplike pockets (Figure 15*E*).

Opercular scales triangular and undulate, having a medially furrowed outer surface that corresponds to a keel on distal half of inner surface. Symmetrical abaxial operculars up to 0.9 mm in length and usually broader than long (H: W = 0.9-1.0). Asymmetric lateral operculars only slightly shorter (0.8–0.9 mm) and more slender, with a H:W of 1.2-1.3. Small adaxial operculars 0.65–0.75 mm in length with a H:W of 1.7-2.1; often proximal outer face of these scales bears a thin ridge. Because operculars are relatively short and cowl formed by distal edges of buccal scales encloses most of operculum, operculum short and usually not visible from lateral view (Figure 14A).

Coenenchymal scales elongate, up to 1.25 mm in length, and have irregular edges. Most scales bear either 1 tall (up to 0.6 mm) longitudinal keel or a complex set of smaller ridges that are often interconnected (Figure 15F).

ETYMOLOGY: This species is named in honor of Katherine (Katy) M. Muzik, as a tribute to the research she has done on Hawaiian octocorals (Muzik 1978, 1979), as well as having collected the holotype.

COMPARISONS: Among the previously de-

scribed species in the genus, *N. muzikae* is most similar to the type species *N. regularis*, the latter known only from the western Atlantic at 366–792 m (see Cairns and Bayer 2003), both species having very similar body wall and coenenchymal sclerites and ridging, as well as similar polyp size and whorl characteristics. However, *N. muzikae* differs in colony shape (branching from a basal bolus versus dichotomous); an operculum hidden from abaxial view by long, campanulate buccals that are much longer than the medials; and adaxial buccals with pocketlike ridging.

Narella muzikae is also similar to N. parva (Versluys, 1906), which is known only from the Indonesian region from 1,300 to 1,633 m. These species are similar in size, colony and polyp morphology, and sclerite shape, but N. muzikae differs in having multiple ridges on the dorsolateral and basolateral edges of the basal scales (N. parva has only one ridge relegated to the lower half of the dorsolateral region), having ridged coenenchymal scales, and occurring in much shallower water. A syntype of Stachyodes parva was examined from Siboga 226 (USNM 1097269, ex ZMA Coel. 3428).

REMARKS: Commensal polychaetes and ophiuroids were not found on this species, but it was not uncommon for living colonies to have several branches encrusted by zoanthids.

DISTRIBUTION: Off Nīhoa; off Makapu'u Point, O'ahu; off western Hawai'i; 326–381 m (confirmed).

Narella hawaiinensis Cairns & Bayer, n. sp. Figures 1B, 16A–E, 17A–F

Stachyodes regularis.—Nutting, 1908:577 (USNM 22546).

Narella studeri.—Grigg and Bayer, 1976:172.

Narella dichotoma.—Bayer, 1995:147; 1997: 511, 518.

MATERIAL EXAMINED: Types.

TYPES AND TYPE LOCALITY: Holotype: Moore #1723C, 3 branches, SEM stubs B2340–2341, USNM 79396. Paratypes: *Alb*-3879, 1 short branch of 8 whorls, USNM 22546; *Pisces 5*-526, 1 colony now in 3 pieces,



FIGURE 15. Sclerites of *Narella muzikae* from the holotype (USNM 56814): *A*, opercular sclerites; *B*, abaxial buccal sclerites; *C*, medial sclerites; *D*, outer surface of basal sclerites; *E*, outer surface of adaxial buccal sclerites showing pocketlike ridging; *F*, highly ridged coenenchymal sclerites. Scale bars: *A*,*E*,*F*, 0.25 mm; *B*–*D*, 0.5 mm.



FIGURE 16. Calyces and branch coenenchyme of *Narella bawaiinensis* from the holotype (USNM 79396), A-C are stereo views: A, lateral view of a whorl; B, lateral view of a calyx; C, adaxial view of calyx showing the pair of adaxial buccal scales; D, lateral view of a whorl showing a calyx with two apical ends; E, ridged coenenchymal scales. Scale bars: A-B, D, 1.0 mm; C, 0.5 mm; E, 0.25 mm.

originally about 23 cm in length, USNM 1072109; *Pisces 5-594*, 1 branch of 16 whorls, SEM C1231, 1232, USNM 1071215.

Type Locality: 18° 33′ 06″ N, 155° 26′ 06″ W (Bushnell Seamount), 1,921 m.

DESCRIPTION: Largest colony (holotype) 19 cm in length, but no specimens were collected complete with a holdfast or intact enough to ascertain branching mode, if any. Based on the type series, this species is assumed to be unbranched. Axis of holotype straw yellow and 1.25 mm in diameter toward base; calyces white.

Calyces arranged in discrete whorls of 3-5, separated from one another by 0.5-1.5 mm; 5-6 whorls occur per 3 cm; whorl diameter 5-6 mm. Calyces 3.4-4.1 mm in length, tip of operculum touching branch when preserved. In one aberrant case (Figure 16D) two calyces emerge from a common body wall, culminating in two sets of buccal scales and two opercula.

Each calvx encased in 3 pairs of large abaxial body wall scales and 1 pair of adaxial buccal scales. Basal scales large, tilted slightly proximally, and up to 2.0 mm in height, their distal edges projecting only about 0.1 mm beyond junction with medial scales. Lower half of dorsolateral edge of basals usually bears a low ridge (Figures 16B, 17D); their adaxial portions do not meet to form a ring. Medials narrow but equal to or slightly longer than buccals, with a concave outer surface and no ridges. Abaxial buccals 1.4-1.8 mm in length also with a concave outer surface and also with a gently curved dorsolateral region. All body wall scales have a straight, smooth distal margin, without serration, lobulation, or spination. One pair of square to elliptical, thin, flat (nonridged) adaxial buccals, each about 0.80 mm in diameter.

Opercular scales triangular and undulate, having a medially furrowed outer surface that corresponds to a sharp keel on distal



FIGURE 17. Sclerites of *Narella hawaiinensis* from a paratype (USNM 1071215): A, opercular sclerites; B, outer surface of abaxial buccal sclerites; C, outer surface of medial sclerites; D, outer surface of ridged basal sclerites; E, outer surface of adaxial buccal sclerites; F, coenenchymal sclerites. Scale bar: A-F, 0.5 mm.

half of inner surface. Abaxial operculars up to 1.75 mm in length, having a H:W of about 1.45. Lateral operculars 1.6-1.7 mm in length, with a H:W of 1.7-2.1. Small adaxial operculars up to 1.3 mm in length, having a H:W of 2.6-2.8. All operculars have a sharp distal tip. Operculum prominent, easily visible in lateral view.

Coenenchymal sclerites elongate, up to 2.5 mm in length, flat, and granular; however, most of them bear a prominent longitudinal ridge or crest often 0.4 mm in height or as much as 0.7 mm. Those with tallest crests occur in pairs, one located along abaxial side of each basal scale, such that it braces both abaxial side of calyx and dorsolateral ridge on basal scales (Figure 16*B*). A more elongate but lower coenenchymal ridge braces basolateral edge of basals (Figure 16*B*), the ridges of these specialized coenenchymal scales probably helping to secure calyx base onto branch.

ETYMOLOGY: Named for the region in which it was collected.

COMPARISONS: This species is remarkably similar to *N. bayeri* Cairns & Baco, 2007 (Gulf of Alaska, 3,291–4,091 m) but differs in having an unbranched colony, unridged medial scales, and a less prominent dorsolateral ridge on the basal scales.

REMARKS: Although similar to *N. dichotoma*, as suggested by Bayer (1995, 1997), *N. hawaiinensis* differs in having ridged basal scales, relatively long medial body wall scales, and coenenchymal scales with tall keels (see Remarks for *N. dichotoma* and Table 2).

Commensal polychaetes or ophiuroids were not found with this species.

DISTRIBUTION: Pioneer Bank, south of Lāna'i, off northwestern Hawai'i, Bushnell Seamount; 1,492–1,921 m (confirmed).

#### DISCUSSION

Altogether, 84 valid octocoral species in 42 genera have been reported from the Hawaiian Islands (15 pennatulids, 69 nonpennatulids), of which only five (5.5%) occur in shallow water. To this number, six new species of *Narella* are added in this paper, resulting in a total of 90 species. The ratio of shallow to deep gorgonians in other parts of the world is 41–56% (Grigg and Bayer 1976). Judging from the provocative list of Grigg and Bayer (1976), the dissertation of Muzik (1979), and the many new taxa collected on recent *Pisces* 5 cruises, we predict that at least twice that number of octocorals will eventually be known from this region.

#### ACKNOWLEDGMENTS

We thank Rob van Soest for the gift of syntypes of the six species of *Narella* described by Versluys (1906). We also thank Amy Baco-Taylor for collecting and donating some of the deepwater specimens collected on the *Pisces 5* submersible. S.D.C. also thanks her for inviting me to participate in the Northwestern Hawaiian Islands cruise of 2003. And we thank Lu Eldredge for loaning specimens from the Bernice P. Bishop Museum. Kristian Fauchald (NMNH) identified the commensal polychaetes. We thank research assistant Tim Coffer for constructing the Photoshop plates.

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		Station Data		
Vessel Cruise	N Lat.	W Long.	Depth (m)	Date
USFWS Albatross				
3879	20° 26' 45"	157° 13′ 40″	1,688-1,977	15 Apr. 1902
3889	Hanamā'ulu, Kau	a'i	693-915	17 Apr. 1902
R/V Atlantis II				
AD2969	47° 42′ 42″	127° 47′ 24″	2,600	8 Aug. 1995
R/V Makalii	21. 15/	155- 224	(( 1 400 <b>)</b>	
M43, 91	21° 177	157° 33'	"about 400"	Date unknown
R/V Oscar Elton Sette	100 41 270/	1500 17 005/	477	(F1 2002
03-01-4	18° 41.279′	158° 17.905'	4//	6 Feb. 2003
K/V Pele	Off Malarate Da	int Other	220 421	27 Array 10(7
Diana 5	Off Makapu u Point, O anu		329-421	27 Aug. 1967
225	180 161 26"	1500 11/ 10/	1 2 2 5 1 2 0 5	18 Aug 1002
235	10 70 30	150 14 40	1,333-1,393	21 Aug. 1993
230	10 19 10	15/ 19	1,330-1,770	21 Aug. 1993 25 Aug. 1003
237	10 70 70	159 05 50	1,200-1,380	20 Aug. 1993
301	10 50.7 20° 46′ 57″	150 10.0	862 125	29 Aug. 1993 20 Sept. 1006
303	10° 36′ 35″	156° 03' 08″	901 - 123	20 Sept. 1990 22 Sept. 1006
464	24° 20 672'	166° 01 547′	1 219	10 Sept. 2001
525	21 20.072	173° 25′ 56″	1,217 1,252-1,802	8 Oct 2003
526	25 10 05	173° 30′ 22″	1,252-1,002	9  Oct.  2003
527	25 91 27	173° 30′ 27″	1,711	10  Oct.  2003
532	25 10 15	171° 27′ 14″	1,207	10 Oct. 2003
534	25 12 11	171° 24′ 19″	1,007	20  Oct.  2003
542	23° 20 66'	163° 38 504′	1,200	20 Oct. 2003
544	23° 19′ 00″	163° 41′ 00″	1 443	21 Oct. 2003 2 Nov. 2003
593	19° 48′ 12″	156° 08' 02"	743_750	15 Oct 2004
594	19° 47′ 53″	156° 08′ 51″	400-1 492	16 Oct. 2004
595	19° 47′ 54″	156° 07′ 47″	679	17 Oct. 2004
SANGO (University of	Hawai'i)		017	17 000 2001
3-8	21° 17.9′	157° 32′	355-385	12 Aug. 1970
4-1	21° 17′54″	157° 32′ 18″	326	29 Sept. 1970
5-3	19° 48.3′	156° 07.65′	381	22 Oct. 1970
10-1	21° 18.9′	157° 33.45′	344-463	17 June 1971
13-1a	23° 02′	162° 05′	353-417	17 Aug. 1971
13-1b	Kaʻula Rock. Niʻi	hau	271-527	29 Aug. 1971
13-1c	23° 57′	166° 40.5′	399-412	23 Aug. 1971
13-4	23° 04′	162° 02.6′	374-439	19 Aug. 1971
13-11	23° 59'	166° 40′	345-564	25 Aug. 1971
14-1	21° 18.0'	157° 32.9′	362	18 Jan. 1972
14-2	21° 18.82′	157° 32.2'	344-454	18 Jan. 1972
Star II (Maui Divers Je	welry Co., submersib	le)		•
1	21° 18'	157° 32′	366	27 Jan. 1978
2	21° 18'	157° 32'	367	1 Feb. 1978

Appendix

Station Data