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Stephen D. Cairns[1]* & Amy Baco[2]
[1]Department of Invertebrate Zoology, Smithsonian Institution, P. O. Box 37012, MRC 163, Washington, DC 20013-7012, USA
[2]Biology Department, MS#33, Woods Hole, MA 02543, USA

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Review and five new Alaskan species of the deep-water octocoral *Narella* (Octocorallia: Primnoidae)

Abstract Five new species of the octocorallian primnoid genus *Narella* are described from seven seamounts in the Gulf of Alaska, the first records of this genus from the region between Japan and the Galápagos, and including the deepest record of the genus at 4594 m. All species are illustrated with SEM of their sclerites, often with stereo pairs of the polyps. A list of the 32 valid species of *Narella* is given. DNA sequence analysis using the mitochondrial genes ND6 and msh1 was determined for all five species and outgroups, but little to no variation was found among the five morphospecies, consistent with the known slow rate of evolution of the mitochondrial genes in Octocorallia.

Key words *Narella*, Octocorallia, Primnoidae, Alaska, ND6, msh1, seamounts, new species

Introduction

The Primnoidae is a diverse family of deep-water octocorals consisting of 32 genera and approximately 207 species. Although species occur as shallow as 141 m, most live at slope and abyssal depths, the deepest known primnoid being *Convexella krampi* (Madsen, 1956), which was collected from the Kermadec Trench at 5850 m. The second deepest primnoid genus is *Narella*, the deepest of which occurs in the Gulf of Alaska as reported herein for *N. abyssalis* from 4594 m. Although widespread and diverse, this is the first account of this genus from the rather large region of the North Pacific north of a line linking Japan, the Hawaiian Islands, and the Galápagos Islands.

Materials and methods

All specimens reported herein resulted from three NOAA-sponsored exploratory submersible cruises (see Acknowledgements) made on seamounts in the northern Gulf of Alaska. The first was in June–July 2002 using the *Alvin*, the second in July 2004 using the *Jason II*, and the third in August 2004 using the *Alvin*. The second author was present on all three cruises. Station data are given in Table 1.

Designation of polyp scales follows that of Versluys (1906) as amplified by Bayer *et al*. (1983). Also, following the terminology of Bayer (1951), the region or line that separates the lateral face of the basal and medial scales from its dorsal (or abaxial) face is referred to as the basolateral angle or edge. This edge is often, but not always, curved at a 90° angle and often bears a ridge or crest.

* Corresponding author. Email: cairnss@si.edu

The opercular scales of *Narella* have previously been described (Bayer, 1995, 1997) as occurring as four pairs: an abaxial pair, two lateral pairs, and the small adaxial pair; however, close examination of the Alaskan species demonstrates a different symmetry arrangement. Invariably there is one large, symmetrical abaxial opercular scale, opposite which is a pair of small, also symmetrically developed adaxial scales. The remaining five lateral scales are asymmetrical in shape, each having a wider adaxial edge, and being an odd number, three occur on one side of the polyp and only two on the other, giving the polyp a slightly asymmetrical aspect. This arrangement is well illustrated by Fig. 9E and by Versluys (1906: fig. 102).

The SEM photomicrographs were taken by the first author using an AMRAY 1810 scanning electron microscope. Representatives of 24 of the 32 *Narella* species were available at the NMNH for comparison, 14 as type specimens.

DNA sequence analyses were also used as an independent source of characters to classify and compare the five new species. Mitochondrial cytochrome oxidase I (COI) and 16S are typically used for these comparisons in invertebrates, but both of these genes have low variability in octocorals (France *et al*., 1996; France & Hoover, 2001, 2002). Instead the mitochondrial genes for NADH subunit 6 (ND6) and msh1 homologue (msh1) were used. msh1 has been shown to be more variable in octocorals than are COI and 16S (France & Hoover, 2002) and both msh1 and NADH subunits are currently used in octocoral phylogenetics (e.g. France & Hoover 2001; Sanchez *et al*., 2003; McFadden *et al*., 2006, Wirshing *et al*., 2005).

DNA was extracted from corals using Qiagen DNeasy kits from alcohol-preserved specimens. For PCR amplification, primers were used from Sanchez *et al*. (2003). ND6-1487F and ND3-2126R were used for ND6 and ND42599F and Mut3458R were used to amplify the 5' end of msh1. PCR

Station	°N	°W	depth (m)	Date	Seamount
		Alvin			
3797	53°53.47′	148°30.66′	2680	26 Jun 2002	Murray
3803–4–5	54°49.51′	152°55.73′	3075	2 Jul 2002	Chirikof
4027–10	53°56.97′	137°23.85′	2377	3 Aug 2004	Denson
4029–16	54°37.18′	136°42.54′	2736	5 Aug 2004	Dickins
4033–23	54°59.24′	140°23.99′	2634	9 Aug 2004	Welker
4033–28	54°59.24′	140°23.99′	2634	9 Aug 2004	Welker
4041–3	56°21.03′	146°22.82′	2818	17 Aug 2004	Giacomini
4041–7	56°21.03′	146°22.82′	2818	17 Aug 2004	Giacomini
4041–9	56°21.03′	146°22.82′	2810	17 Aug 2004	Giacomini
		Jason II			
91–bb	53°30.752′	163°26.886′	3277 m	18 Jul 2004	Derickson
93–4	53°02.446′	161°11.018′	4594	21 Jul 2003	Derickson
93–11	53°01.811′	161°12.845′	4091	21 Jul 2003	Derickson
93–14	53°01.229′	161°13.451′	3292	21 Jul 2003	Derickson
93–20	53°0.8′	161°14.421′	3465	22 Jul 2003	Derickson
93–29	52°59.032′	161°14.941′	2775	22 Jul 2003	Derickson
93–32	52°0.586′	161°14.406′	3385	22 Jul 2003	Derickson

Table 1 Station data.

conditions for msh1 were 96 °C for 2 min, and 35 cycles of 94 °C for 1 min 30 s, 57 °C for 30 s, 72 °C for 1 min, followed by an extension at 72 °C for 5 min. PCR conditions for ND6 were 96 °C for 2 min, and 40 cycles of 94 °C for 1 min 30 s, 45 °C for 1 min, 72 °C for 1 min, followed by an extension at 72 °C for 5 min. An Eppendorf MasterCycler epgradient (Eppendorf) thermocycler was used to carry out PCR amplifications of 50 μl final volume with approximately 50 ng of DNA, 1X PCR Buffer (Promega), 2.5 mM $MgCl_2$, 1 mM dNTPs, 1 μM of each primer and 1.5 U Taq polymerase (Promega).

PCR products were purified using QIAquick PCR Purification Kit (Qiagen). Sequences were run on an ABI 3730. Sequences were edited and aligned using Sequencher 4.2.2. Pairwise distances are uncorrected 'p' distances and were calculated in PAUP 4.0b10.

Abbreviations: NMNH = National Museum of Natural History, Smithsonian Institution, Washington, DC; PCR = polymerase chain reaction; SEM = scanning electron microscope; USNM = United States National Museum (now the NMNH); H:W = height to width ratio of a sclerite.

Systematics

Subclass Octocorallia

Order Gorgonacea

Family Primnoidae Gray, 1858

Genus *Narella* Gray, 1870

Narella Gray, 1870: 49 [type species: *Primnoa regularis* Duchassaing & Michelotti, 1860, by monotypy].–Bayer, 1951: 41–43; 1995: 147–148; 1997: 511.–Cairns & Bayer, 2003: 618–619; 2004: 7–10 (proposed neotype for *P. regularis*).

Stachyodes Wright & Studer in Studer, 1887: 49 [type species: *Stachyodes regularis* Wright & Studer, 1889 (not Duchassaing & Michelotti, 1860), = *Stachyodes studeri* Versluys, 1906, by subsequent monotypy (Wright & Studer, 1889: 54)].–Versluys, 1906: 86–88.–Kinoshita, 1908: 45–47.–Kükenthal, 1919: 452–456; 1924: 308–309.

Calypterinus Wright & Studer, in Studer, 1887: 49 [type species *C. allmani* Wright & Studer, 1889, by subsequent monotypy (Wright & Studer, 1889:53)].

Diagnosis

Colonies of moderate size (up to 50 cm), dichotomously or pinnately branched in one or more planes, or unbranched. Polyps face downward in whorls or pairs, only rarely isolated. Polyps protected by three or four pairs of large abaxial body wall scales, the adaxial sclerites reduced to one or two pairs of small buccal scales. Adaxial side of basal scales may meet forming a complete ring, but they do not fuse as in *Calyptrophora*. Operculum consists of eight triangular scales, each with a longitudinal keel on its inner surface. Coenenchymal scales usually elongate, bearing longitudinal keels on their outer surface, but in some species they are polygonal and flat. Branch axis heavily calcified, longitudinally grooved, with a discoidal basal holdfast.

Remarks

Narella is a species-rich genus, currently with 32 known species (see list below), and judging from the large number of species described herein from a relatively small collection, it is predicted that many more species will be discovered. The most significant observations on this genus were published by

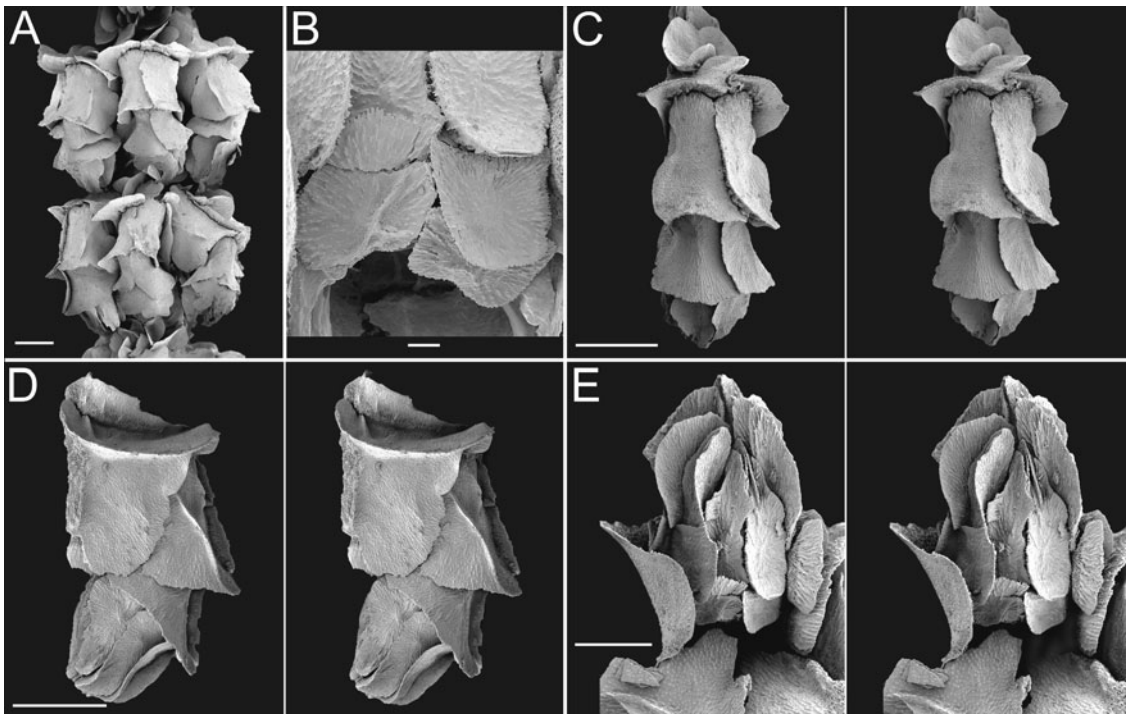

Figure 1 *Narella bayeri*, paratype from *Jason II* 93-14: A, lateral view of two whorls; B, two pairs of adaxial scales; C, stereo abaxial view of a polyp; D, stereo lateral view of a polyp; E, stereo adaxial view of a polyp. Scale bars for A, C-D = 1.0 mm; B = 0.1 mm; E = 0.5 mm.

Versluys (1906), Kinoshita (1908), Kükenthal (1919, 1924), Deichmann (1936), Bayer (1951, 1995, 1997), and Cairns and Bayer (2003, 2004). In particular, Versluys (1906) provided excellent descriptions and illustrations of the Indonesian species he described from the *Siboga* expedition. The genus is in need of revision worldwide, not least of which is because almost every species is known only from its type material, which in most cases consists of just a few specimens. That is no exception in this paper. Nonetheless, the morphological characters used by previous authors to distinguish species appear to be quite distinctive, including the following: branching mode, polyp size, number of polyps per whorl, number of whorls per cm, presence or absence of adaxial buccal scales, ring-like nature of the basal scales, shape of body wall scales (e.g. presence or absence of a basolateral ridge, spines distal edge), shape of opercular scales (e.g. H:W of the abaxial opercular), and shape of coenenchymal scales (elongate and keeled or polygonal and flat). To this we add molecular sequence data. Some of these characters may not be consistent at the species level, as discussed by Cairns and Bayer (2003), but it does seem that each species has a diagnostic shape of its body wall sclerites, usually expressed in shape, size and presence or absence of basolateral ridges. These characters are emphasised in Table 2.

List of the 32 species of *Narella*

Species known from Alaska: *N. bayeri*, *N. cristata*, *N. arbuscula*, *N. abyssalis*, *N. alaskensis*.

Species known from Japan: *N. irregularis* (Kinoshita, 1907), *N. biannulata* (Kinoshita, 1907), *N. megalepis* (Kinoshita, 1908), *N. compressa* (Kinoshita, 1908).

Species known from Hawaiian Islands: *N. bowersi* (Nutting, 1908), *N. ornata* Bayer, 1951, *N. nuttingi* Bayer, 1997.

Species known from western Pacific, primarily Indonesian region: *N. allmani* (Wright & Studer, 1889), *N. clavata* (Versluys, 1906), *N. horrida* (Versluys, 1906), *N. obscura* (Versluys, 1906), *N. orientalis* (Versluys, 1906), *N. parva* (Versluys, 1906), *N. dichotoma* (Versluys, 1906) [also known from Hawaii], *N. studeri* (Versluys, 1906) [nom. nov. for *S. regularis* Wright & Studer, 1889], *N. grandiflora* (Kükenthal, 1907), *N. leilae* Bayer, 1951.

Species known from eastern Pacific: *N. ambigua* (Studer, 1894).

Species known from Antarctica: *N. gaussi* (Kükenthal, 1912).

Species known from southwest Indian Ocean: *N. gilchristi* (Thomson, 1911) [= *S. capensis* Thomson, 1917; = *S. gilberti* nom. nud., Kükenthal, 1919].

Species known from Atlantic: *N. regularis* (Duchassaing & Michelotti, 1860), *N. versluysi* (Hickson, 1909), *N. bellissima* (Kükenthal, 1915), *N. pauciflora* Deichmann, 1936, *N. laxa* Deichmann, 1936, *N. spectabilis* Cairns & Bayer, 2003, *N. alvinae* Cairns & Bayer, 2003.

Narella bayeri sp. nov.

Figs 1–2

Material examined/Types

Holotype: *Jason II*-93-11, one large colony, two branches, and several short branch fragments, all dry except for one branch, USNM 1080446, and one branch at the BM (NHM2005.2346). Paratypes: *Jason II*-93-14, one colony and four branches, all dry except for one branch, SEM stubs 1138–1142, USNM

	Narella bayeri	*Narella cristata*	*Narella abyssalis*	*Narella arbuscula*	*Narella alaskensis*
Number of pairs and nature of body wall scales	3 (occasionally 4), slightly flared	3 (occasionally 4), flared	4, not flared (compact)	3 (rarely an unpaired 4th) , highly flared	3, quite flared
Branching	Dichotomous, sparse, uniplanar	Dichotomous, sparse, uniplanar	Dichotomous, sparse uniplanar	Dichotomous, sparse, bushy	Dichotomous, sparse, uniplanar
Number of whorls/ 3 cm; whorl diameter	11–12, crowded; 3.5 mm	8–10, well-spaced; 3.4 mm	9, well-spaced; 2.8 mm	6–8, crowded!; 6.8 mm	10.5–12, crowded; 3–7.5 mm
Number of polyps/ whorl	5–6 –7	2–3 –4, usu. absent from one side	2–3 –4, usu. absent from one side	6 –7	4–8 –9
Polyp length and max. width (mm)	2.2–3.4 × 1.4–1.7	2.1–3.0 × 1.3–1.6	1.9–2.4 × 1.0–1.3	3.4–4.7 × 2.5–3.5	2.7–3.2 × 1.3–2.1
Basal body wall scales; apical margin	Right angle basolateral edge with prominent ridge; lobate	Right angle basolateral edge with prominent ridge; lobate	Right angle basolateral edge with prominent ridges; straight	Gently rounded basolateral edge occas. with tall, but short ridge, concave; lobate	Right angle dorsolateral edge with low ridge; prominent sharp spines
Medial body wall scales; apical margin	Right angle basolateral edge with distal ridge; not spinose	Right angle basolateral edge with ridge basally; not spinose	Low ridge at basolateral edge; not spinose	Gently rounded basolateral edge without ridge; not spinose	Right angle dorsolateral edge with low, continuous ridge; spined
Abaxial buccal body wall scales	Striate, rarely ridged	Usually ridged	Low ridge at basolateral edge	Not ridged	Not ridged
Adaxial buccal body wall scales	1 pair	1 pair	1–2 pair	1 pair and numerous smaller scales on adaxial body wall	1–2 pairs and small scales on adaxial bw
H:W of large abaxial opercular scale; keel	1.4; sharp keel	1.4–1.7; rounded keel	2.4–2.7; rounded keel	0.85–1.0; rounded keel	0.9–1.0; sharp keel
Other distinctive characteristics	occasionally outer surface of opercularS is keeled	coenenchymal blades low	basolateral ridges often bifurcate distally		
Distribution	Derickson SM; 3277–4091 m	Derickson SM; 3385 m	Derickson SM; 4594 m	Derickson and Giacomini; SM; 2775–3465 m	Gulf of Alaska Sea-mounts; 2377–3075 m

Table 2 Characteristics of the five Alaskan species of *Narella* (SM = seamount).

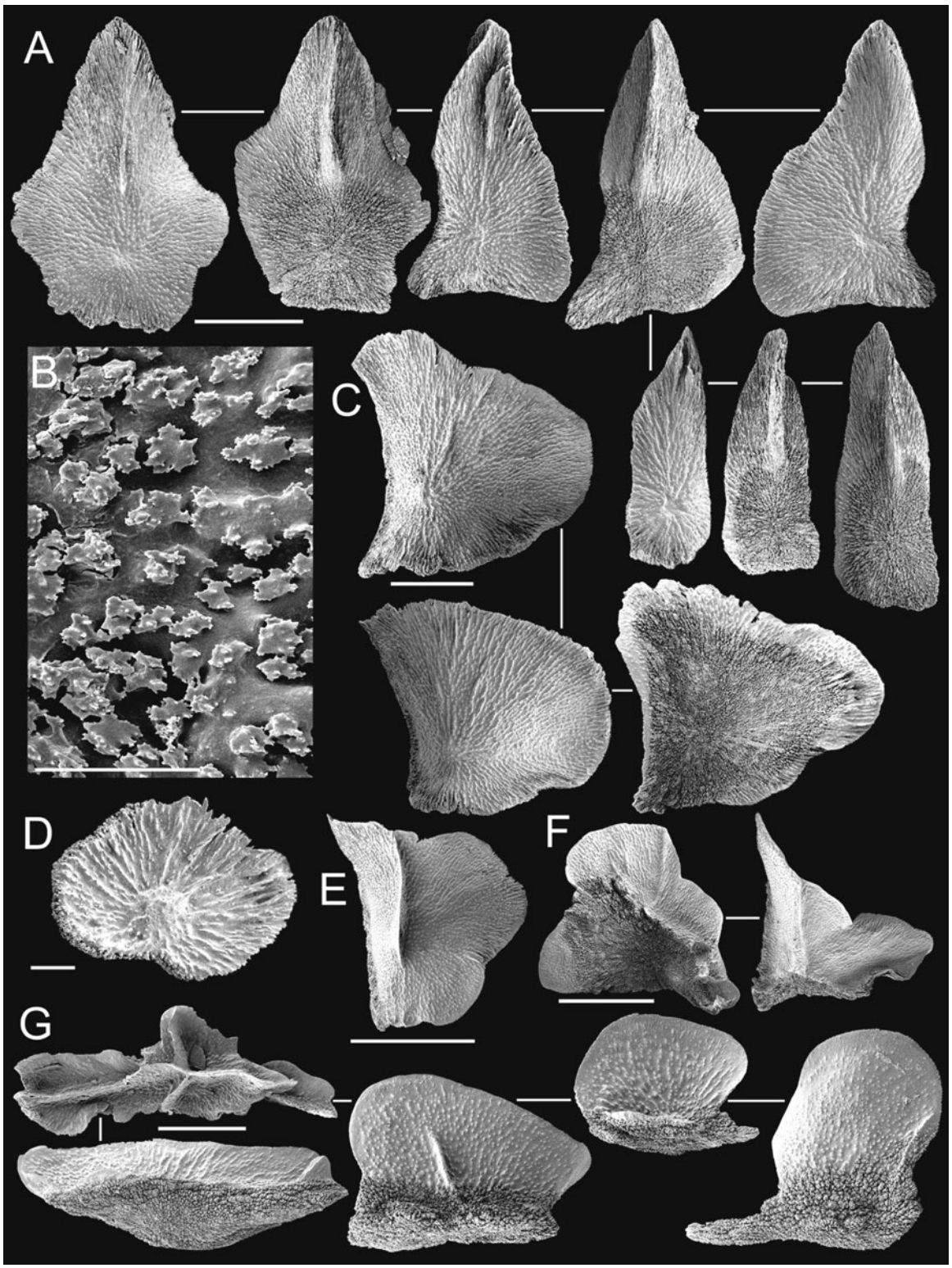

Figure 2 *Narella bayeri*, paratype from *Jason II* 93-14: A, opercular scales; B, tubercles on inner surface of an opercular; C, abaxial buccal scales; D, an adaxial buccal scale; E, a medial scale; F, basal scales; G, coenenchymal scales. Scale bars for A, C = 0.5 mm; B = 50 Φm; D = 0.1 mm; E-F = 1 mm; G = 0.5 mm.

1080447; *Jason II*-91-biobox, two branches in alcohol, USNM 1080448.

Type locality

53°01.811 N, 161°12.845′W (Derickson Seamount, Gulf of Alaska), 4091 m.

Description

Colonies are uniplanar and sparsely dichotomously branched, the largest specimen (the holotype) measuring 29 cm in height and 20 cm in maximum width, with a basal axis diameter of 4.7 mm, although no colonies were collected with their bases intact. Early branching low in the colony occurs at intervals

of every 13–25 mm, but terminal branches are quite long, up to 17 cm in length. The axis is yellow-brown in colour and woody in texture.

Polyps are arranged in whorls of 5 to 7, 6 being the most common number, each whorl separated by a distance of 0.5–1.0 mm; 11–12 whorls occur per 3 cm. Polyps are 2.2–3.4 mm in length (including the projecting opercular scales) and 1.4–1.7 mm in greatest width.

Each polyp is protected by three pairs of large abaxial body wall scales and one pair of small adaxial buccal scales, although about 10% of the polyps have an extra pair or just one extra medial scale. The basal scales are the largest, standing perpendicular to the axis up to 2.1 mm in height, the uppermost region of each basal scale projecting as much as 0.5 mm above its connection to the adjacent medial scales as a vertical, flared rounded lobe. Each basal scale covers a portion of the abaxial and lateral regions of the polyp, producing a right angle basolateral edge that bears a prominent, sharp ridge for its entire length. The basal scales do not meet adaxially and thus do not form a closed ring. The medial scales are roughly rectangular, up to 1.6 mm in length, and also wrap around the abaxial and lateral regions of the polyp, and, like the basals, bear a prominent ridge at the basolateral edge, but this ridge occurs only for the middle third or distal two-thirds of the scale. The abaxial buccals are large and flared, saddle-shaped, up to 1.5 mm in length, their basolateral edges rounded (not at a right angle), rarely bearing a ridge. There is usually one pair of small (0.30–0.50 mm) rectangular adaxial buccal scales. The upper surface of the body wall scales is granular, the granules often aligned as short longitudinal ridges on the buccals, and the inner surfaces are tuberculate.

All opercular scales are elongate-triangular in shape, having a keel on the distal half of their inner surface and a concave upper surface, but occasionally the upper surface will also bear a short, longitudinal distal ridge. The primary abaxial opercular scale is the largest of the operculars, up to 1.40 mm in length and 1.0 mm in greatest width (H:W = 1.4) and is symmetrical, with rather broad shoulders to either side of the keel. The inner- and outer-lateral operculars are smaller (1.2–1.3 mm in length and 0.7–0.8 mm wide, H:W = 1.5–1.9) and are asymmetric, each bearing a shoulder to the adaxial side of the keel. The two adaxial operculars are by far the smallest (1.0–1.1 mm in length and 0.40 mm wide, H:W = 2.7) and are symmetric in shape. Dissolution of several polyps did not reveal any small sclerites that could be attributed to tentacular sclerites.

Each coenenchymal scale consists of a dense, white, granular, rod-shaped base from which one or more thin translucent, smooth blades originate at a right angle, sometimes several blades originating from one elongate scale. The basal structure of a coenenchymal scale measures up to 2.1 mm in length, but rarely more than 0.5 mm in width, whereas the erect blades are up to 0.90 mm in height. The bases of the coenenchymal sclerites are coarsely tuberculate, the surface of the upper blades granular, as are the upper surfaces of all the scales. Tubercles measure 15–20 Φm in diameter.

Comparisons

Narella bayeri is distinguished from the other Alaskan species in Table 2. Among the 32 species in the genus, *N. bayeri* is most similar to *N. alvinae* Cairns and Bayer, 2003, a species known only from Bermuda, but at a similar depth to *N. bayeri*. These species have similarly shaped and sized polyps, but *Narella bayeri* has more whorls per cm, more polyps per whorl, and bears a ridge on the basolateral edge of the medial scales, which is lacking in *N. alvinae*.

Distribution

Derickson Seamount and a seep west of that seamount, Gulf of Alaska; 3277–4091 m.

Etymology

This species is named in honour of Frederick M. Bayer, who has named five species within this genus and who has devoted much of his career to the study of deep-sea octocorals (Bayer, 2001).

Narella cristata sp. nov.

Figs 3–4

Material examined/Types

Holotype: *Jason II*-93-32, 15 branches and branch fragments (4 dry and 10 in alcohol), SEM stubs 1154–1158, USNM 1080449, and one dry fragment, BM (NHM 2005.2345).

Type locality

52°0.586'N, 16°14.406′W (Derickson Seamount, Gulf of Alaska), 3385 m.

Description

The holotypic type series consists of about nine branches, several short branch segments, and several detached polyps, all presumably from the same colony; the largest branch is 8.5 cm in length with five terminal branches. Branching appears to be sparsely dichotomous and uniplanar, branching axils being 40°–50°. The axis is golden-yellow and stiff, the largest branch having an axis diameter of only 2 mm; the base of attachment was not collected.

Polyps are arranged in whorls of only 2–4, 3 being the most common number, one face of the colony usually devoid of polyps. Whorls are well separated by 1.3–2.2 mm; 8–10 whorls occur per 3 cm branch length. Polyps are 2.1–3.0 mm in length and 1.3–1.6 mm in greatest width, the distal end of each polyp directed obliquely downward toward the branch axis, at least in preserved specimens.

Each polyp is protected by three pairs of large abaxial body wall scales and one pair of smaller adaxial buccals, although rarely a polyp may have an additional medial body wall scale. The basal scales stand perpendicular to the axis up to 1.2 mm in height, their upper region lobate, projecting well above the junction with their adjacent medial scales. The basolateral edge of each basal scale curves at a right angle and bears a prominent ridge that is continuous across the scale. The basal scales do not meet adaxially and thus do not form

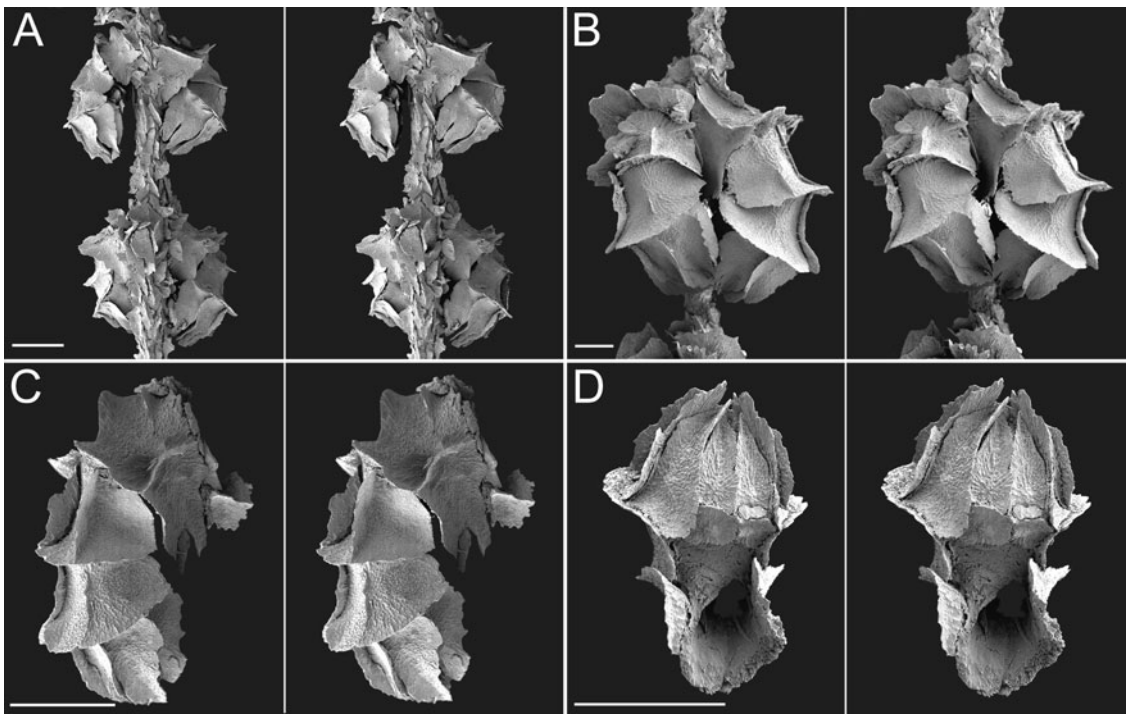

Figure 3 *Narella cristata*, holotype: A, lateral view of two whorls; B, stereo lateral and abaxial view of two polyps; C-D, stereo lateral and adaxial views (respectively) of polyps. Scale bars for A and C = 1.0 mm; B and D = 0.5 mm.

a closed ring. Each medial body wall scale is 0.60–0.85 mm in length, having a curved basolateral edge that bears a low, continuous ridge, as for the basals, their distal edges are flared upwards (away from the polyp). The abaxial buccals are larger (0.9–1.0 mm in length), ridged on their curved basolateral edge, and flared outward. The distal margin of both medials and abaxial buccals are corrugated and irregular in morphology (Figs 4C, E). One pair of adaxial buccal scales is easily seen in adaxial view when a polyp is detached from its whorl, these adaxial buccal scales being elliptical, 0.25–0.35 mm in greater diameter, and bearing a low central boss; they occur directly adjacent to the lower edges of the adaxial opercular scales.

The opercular scales are elongate-triangular in shape, often with an attenuate tip, the larger symmetrical abaxial opercular scale up to 1.1 mm in length and 0.81 in basal width (H:W = 1.4–1.7). The lateral operculars are asymmetrical, of about the same length, but always narrower, as only one side is developed into a shoulder, resulting in a higher H:W of 1.8–2.3. The symmetrical adaxial operculars are the smallest, only 0.65–0.75 mm in length and 0.25–0.30 mm in basal width (H:W = 2.4–2.7). All operculars are highly concave on their outer surfaces, tuberculate below, and bear a poorly developed, rounded keel on the inner distal region.

Coenenchymal scales are fusiform, up to 0.8 mm long and rarely more than 0.15 mm in width, each of which bears a low (usually less than 0.25 mm in height) blade or central boss.

Comparisons

Although similar to *Narella bayeri*, particularly in body scale architecture, *Narella cristata* differs from that species in several significant characters (Table 2): it has smaller polyps, fewer polyps per whorl, and fewer whorls per cm. Furthermore, it has much smaller coenenchymal scales and its abaxial buccal scales are usually ridged and are more flared, as are its medial scales.

Distribution

Known only from the type locality of Derickson Seamount, Gulf of Alaska, 3385 m.

Etymology

The species name *cristata* (Latin: *cristatus*, crested, ridged) is an allusion to the well-developed basolateral ridges present on all three pairs of body wall scales.

***Narella abyssalis* sp. nov.**

Figs 5–6

Material examined/Types

Holotype: *Jason II*-93-4, 20 branches (16 in alcohol, 4 dry), SEM stubs 1150–1153, USNM 1080450 and two dry fragments, BM (NHM 2005.2343).

Type locality

53°02.446′N, 161°11.088′W (Derickson Seamount, Gulf of Alaska); 4594 m.

Description

The holotypic type series consists of about 20 branches and many detached polyps, all presumably from the same colony; the largest branch is 10 cm in length with four terminal branches; the base was not collected. Branching appears to be sparse and uniplanar, branching axils being about 15°. The

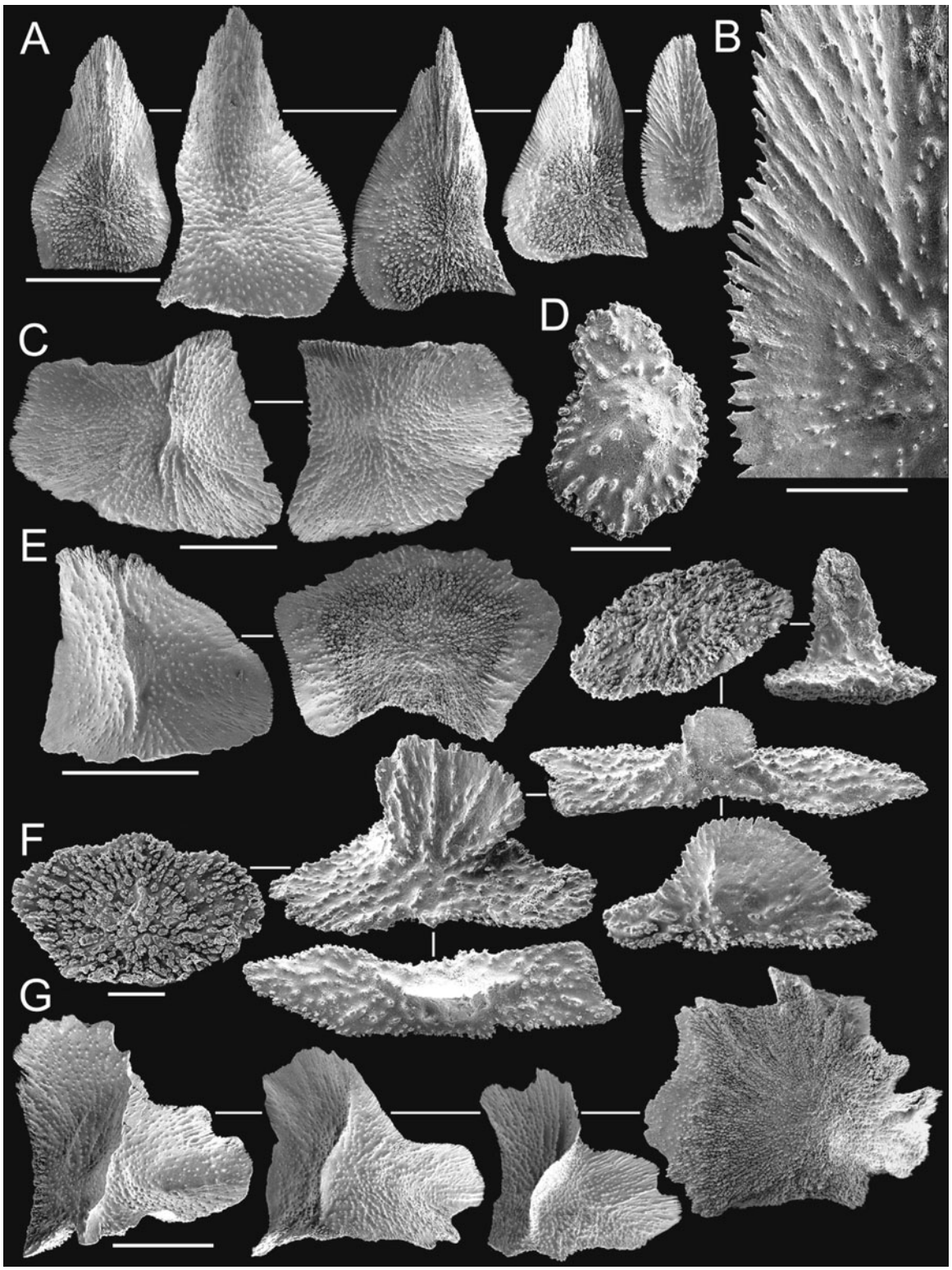

Figure 4 *Narella cristata*, holotype: A, opercular scales; B, laciniate edge of an opercular scale; C, abaxial buccal scales; D, adaxial buccal scale; E, medial scales; F, coenenchymal scales showing tall blades; G, ridged basal scales. Scale bares for A, C, E, G = 0.5 mm; B, D, F = 0.1 mm.

axis is golden yellow and quite brittle, 1.7 mm in maximum diameter; the basal attachment was not collected.

Polyps are arranged in whorls of only 2–4, 3 being the most common number; one face of the colony is usually devoid of polyps, the other three polyps of a whorl being disposed at right angles to each other. Whorls are well separated by 1.3–2.3 mm; invariably 9 whorls occur per 3 cm branch length. Polyps are compact (not flared), 1.9–2.4 mm in length and 1.0–1.3 mm in maximum width.

Each polyp is protected by four pairs of large abaxial body wall scales and 1–2 pairs of smaller adaxial buccal scales. The large basal scales stand perpendicular to the axis up to

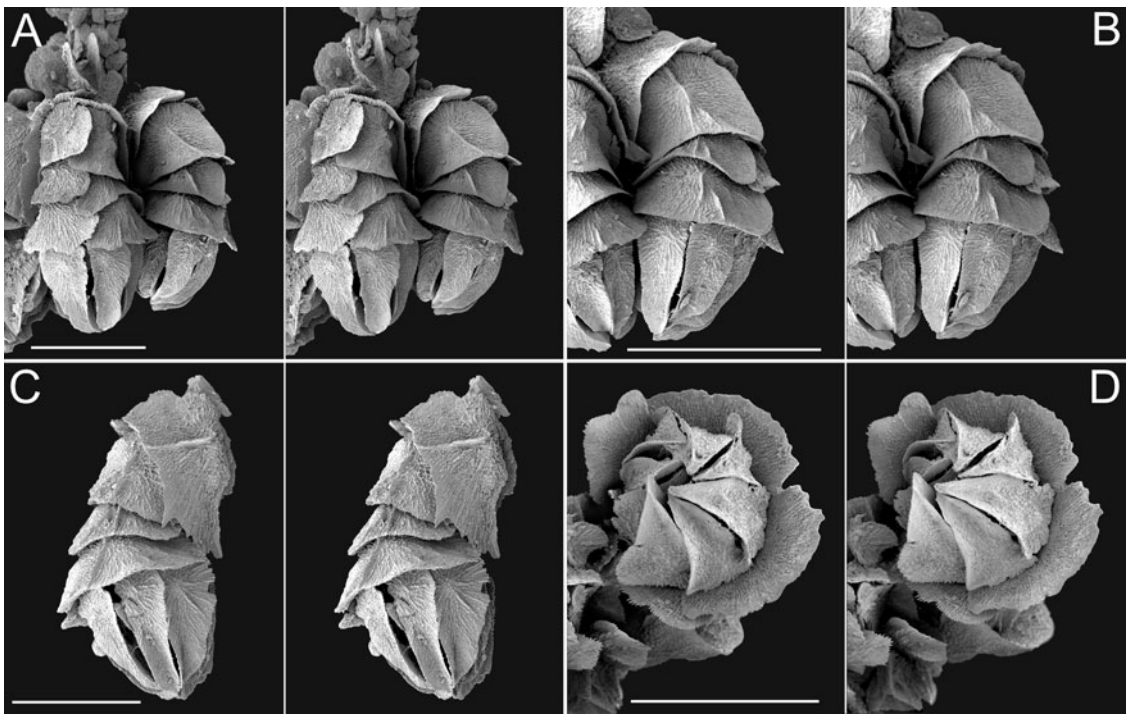

Figure 5 *Narella abyssalis*, holotype: A, stereo view of part of a whorl; B, stereo lateral view of a polyp; C, stereo lateral view of a polyp; D, stereo opercular view of a polyp. All scale bars are 1 mm.

0.95 mm in height, having a straight distal margin that does not rise far above its junction with the adjacent medial scale. The basolateral edge of each basal scale curves at a right angle and bears 1–3 prominent, finely serrate ridges up to 0.3 mm in height. The basal scales do not meet adaxially and thus do not form a closed ring. The two pairs of medial scales are much broader than long, each 0.4–0.6 mm in length. Like the basal scales, each lateral scale also curves in a right angle and bears low ridges on its basolateral edge, which are aligned with those of the basals. The abaxial buccal scales are slightly larger than the medials (up to 0.95 mm in length) and only slightly flared, producing a small cowl of about 0.25 mm; they also bear low basolateral ridges. In most cases, the basolateral ridges of the body wall scales bifurcate near the distal scale margin. Also, the distal margin of most body wall and coenenchymal scales are finely serrate. The small adaxial buccal scales occur as one or two pairs and are elliptical in shape, measuring about 0.3 mm in greater diameter; they are highly sculptured with ridges and granules.

The opercular scales are isosceles triangular in shape, the larger abaxial operculars symmetrical and up to 1.2 mm in length and 0.45 mm in basal width (H:W = 2.4–2.7). The lateral operculars are asymmetrical, often slightly longer than the abaxials (1.25 mm) having a H:W of 2–3.5, and the small symmetrical adaxial are rarely over 0.80 mm in length (H:W = 3.0–3.2). All operculars have a sagittally highly concave outer surface, which corresponds to a low blunt rill on the inner surface. The tips of the abaxial operculars are usually curved downward over the polyp, and the edges of all operculars are finely serrate. There is a small mound near the base of the outer surface of most operculars from which granules radiate (Fig. 6A).

Coenenchymal scales are fusiform and similar in shape to those described for other species, reaching up to 1.3 mm in length and 0.45 mm in blade height. Scales with taller blades are closest to the basal scales and seem to fit into notches of the basal scales, thus anchoring these large scales and restricting their lateral movement.

Comparisons

Only two other species of *Narella*, *N. laxa* Deichmann, 1936 and *N. spectabilis* Cairns and Bayer, 2003, both from the North Atlantic, consistently have four pairs of large abaxial body wall scales. All three species are found in relatively deep water, have few polyps per whorl, and whorls that are fairly well spaced. A. E. Verrill (see Bayer & Cairns, 2003) suggested that four pairs of body wall scales would constitute a generic difference, but he did not publish his results. Later authors did not follow that suggestion, and the presence of four pairs of body wall scales in a low percentage of polyps of *Narella bayeri*, *N. arbuscula* and *N. cristata* that otherwise have only three pairs of body wall scales argues for a transitional nature of this character. *Narella abyssalis* differs from *N. laxa* in having smaller polyps and consequently more whorls per cm, smaller basal scales without an apical spur, more elongate opercular scales, fewer pairs of adaxial buccal scales, and having low baso-lateral ridges on all body wall scales. However, *Narella abyssalis* is remarkably similar to *N. spectabilis*, a species thus far known from only one specimen from the Bahamas, differing only in having much smaller polyps, smaller adaxial buccal scales, and in being branched.

Distribution

Known only from the type locality of Derickson Seamount, 4594 m.

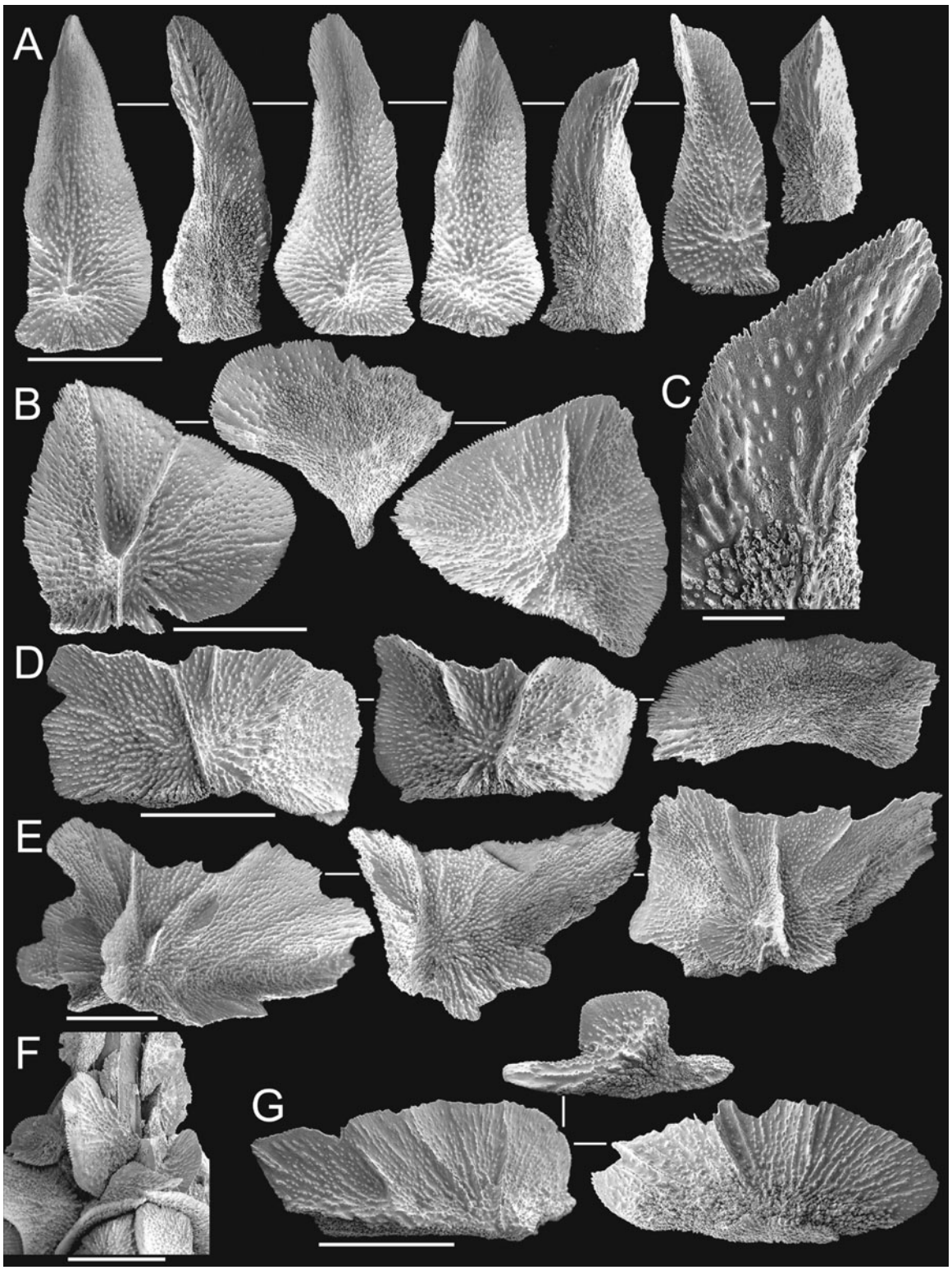

Figure 6 *Narella abyssalis*, holotype: A, opercular scales; B, adaxial buccal scales; C, distal inner surface of an opercular scale; D, medial scales; E, basal scales; F, coenenchymal scales in situ; G, coenenchymal scales showing tall blades. Scale bars for A-B, D-G = 0.5 mm; C = 0.1 mm.

Etymology

The species name *abyssalis* (Latin: *abyssus*, deep sea, abyss + *alis*, an adjectival suffix meaning pertaining to) is an allusion to the great depth at which this species was collected, the deepest of any known *Narella*.

Narella arbuscula sp. nov.

Figs 7–8

Material examined/Types

Holotype: *Jason II*-93-29, 20 branches in alcohol and three branches dry, SEM stubs 1143–1149, USNM 1080451, and

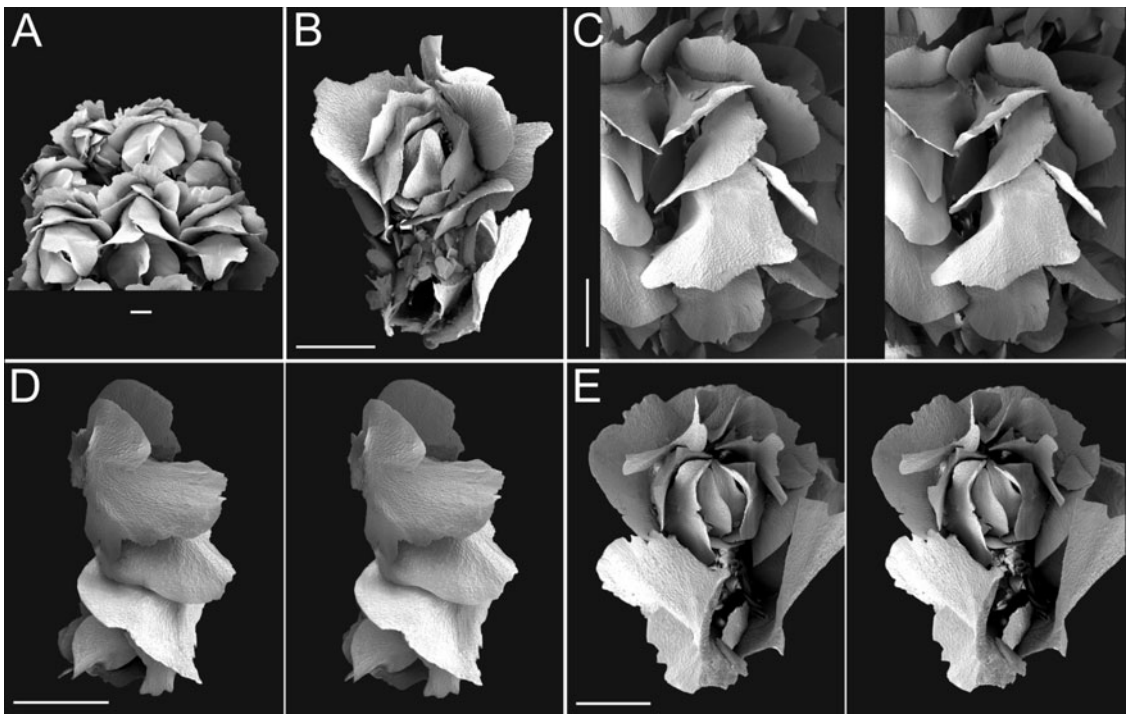

Figure 7 *Narella arbuscula*, holotype: A, abaxial-opercular view of part of a whorl; B, adaxial view of a polyp; C-E, stereo abaxial, lateral, and adaxial views (respectively) of polyps. All scale bars are 1 mm.

one dry fragment, BM (NHM 2005.2344). Paratypes: *Jason II*-93-20, one colony in alcohol and one dry branch, USNM 1080452; *Alvin* 4041-3, one colony in alcohol, USNM 1075465; *Alvin* 4041-7, one colony in alcohol, USNM 1075466; *Alvin* 4041-9, four branches in alcohol and one dry, USNM 1075467.

Type locality

52°59.032′N, 161°14.941′W (Derickson Seamount, Gulf of Alaska), 2775 m.

Description

The holotypic type series consists of 23 branch fragments, all presumably from the same colony; the largest fragment consists of seven terminal branches and a total height of 10 cm. Colonies are sparsely and dichotomously branched, appearing to be bushy in shape, the large fragment showing three-dimensionality. Terminal branches are long, up to 12 cm in length. No colonies were collected with an intact base. The axis is golden yellow in colour and rather rigid, 1.8 mm in diameter in the holotype.

Polyps are arranged in whorls of 6–7, but predominantly 6, each whorl directly adjacent to the next (crowded) or separated by less than 1 mm; 6–8 whorls occur per 3 cm. Polyps are 3.4–4.7 mm in length and rather wide, 2.5–3.5 mm in the highly flared basal and buccal regions.

Each polyp is protected by three pairs of large abaxial body wall scales and one pair of smaller adaxial buccal scales, as well as several dozen even smaller adaxial scales that are irregularly arranged and attach directly to the adaxial body wall. Rarely an additional unpaired medial scale will be present. The basal scales are quite large, up to 2.9 mm in height, the uppermost lobe of each scale projecting up to 0.90 mm above its connection to the adjacent medial scale. Basal scales do not have a right angle basolateral edge, but rather gently curve around the polyp. This region of curvature of the basal is either smooth or occasionally may bear a tall (up to 1 mm) slender ridge (Figs 7D, 8E) proximally. The basal scales do not meet adaxially and thus do not form a closed ring. Medial scales are up to 1.8 mm in length, and, like the basals, curve around the basolateral edge of the polyp and are rarely ridged; they are also flared outward like the basals. The abaxial buccals are slightly larger (1.7–2.2 mm in length), have rounded basolateral edges, and rounded, highly flared distal margins, which produce a cowl 0.9–1.0 mm in height surrounding the lower edges of the opercular scales; they are never ridged. The rounded, almost flattened, nature of the basolateral edges of the body wall scales and their flared distal margins produce a 'fluted' or open nature to the polyp. There is usually one pair of smaller, rectangular (0.5–0.8 mm in greater width) adaxial buccal scales, as well as several dozen smaller elliptical to oval scales (0.2–0.3 mm in greater diameter) attached directly to the otherwise naked/unprotected adaxial side of the body wall.

The opercular scales are triangular in shape, but are quite broad. The primary (or sagittal) abaxial opercular is the largest of the operculars, symmetrical, spade-shaped, up to 1.7 mm in length, and usually broader than long (H:W = 0.85–1.0). It is widest at mid-height and is highly concave along the sagittal axis. The lateral operculars are narrower (also up to 1.7 mm in length, but only about 1 mm wide, H:W = 1.5–1.7) and asymmetric; the adaxial operculars are the smallest (only 1.0–1.1 mm in length and about 0.45 mm in width, H:W = 2.3–2.4) and are symmetric. Although the outer sagittal axis of all operculars is concave, the corresponding mound on the inner

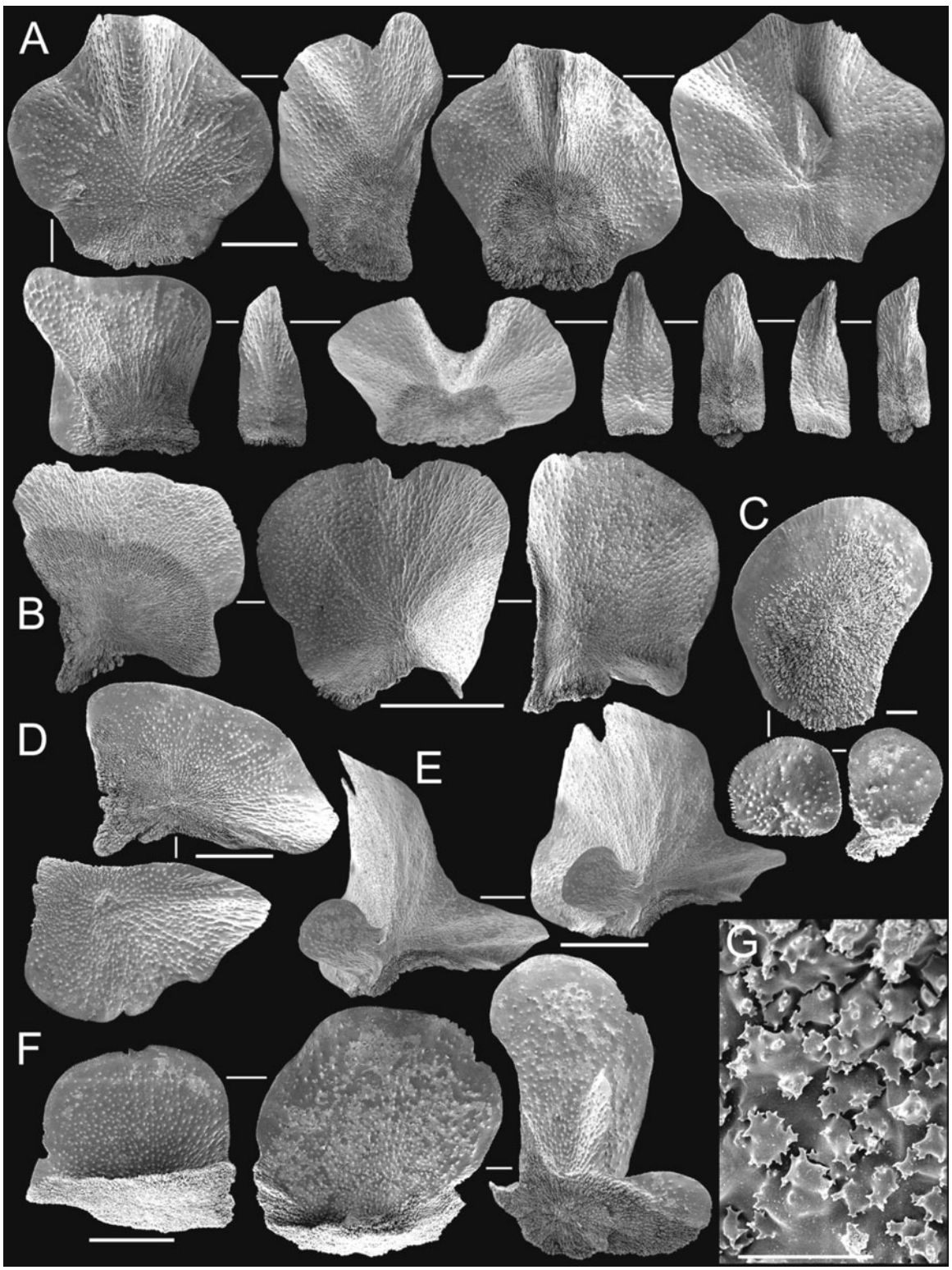

Figure 8 *Narella arbuscula*, holotype: A, opercular scales, the smaller ones in the adaxial position; B, abaxial buccal scales; C, adaxial buccal scales; D, medial scales; E, basal scales; F, lateral view of coenenchymal scales showing tall blades; G, tubercles on inner side of a coenenchymal scale. Scale bars for A, D = 0.5 mm; B, E = 1.0 mm; C = 0.1 mm; F = 0.5 mm; G = 50 Φm.

side is not expressed as a sharp keel, but rather as an elongate rounded ridge.

The coenenchymal scales are similar in size and shape to those of *Narella bayeri*, consisting of a thick basal portion from which one or two tall (up to 1.3 mm), thin, translucent blades originate perpendicular to the branch axis. Specific tentacular sclerites were not noted. All sclerites are tuberculate on their inner surfaces.

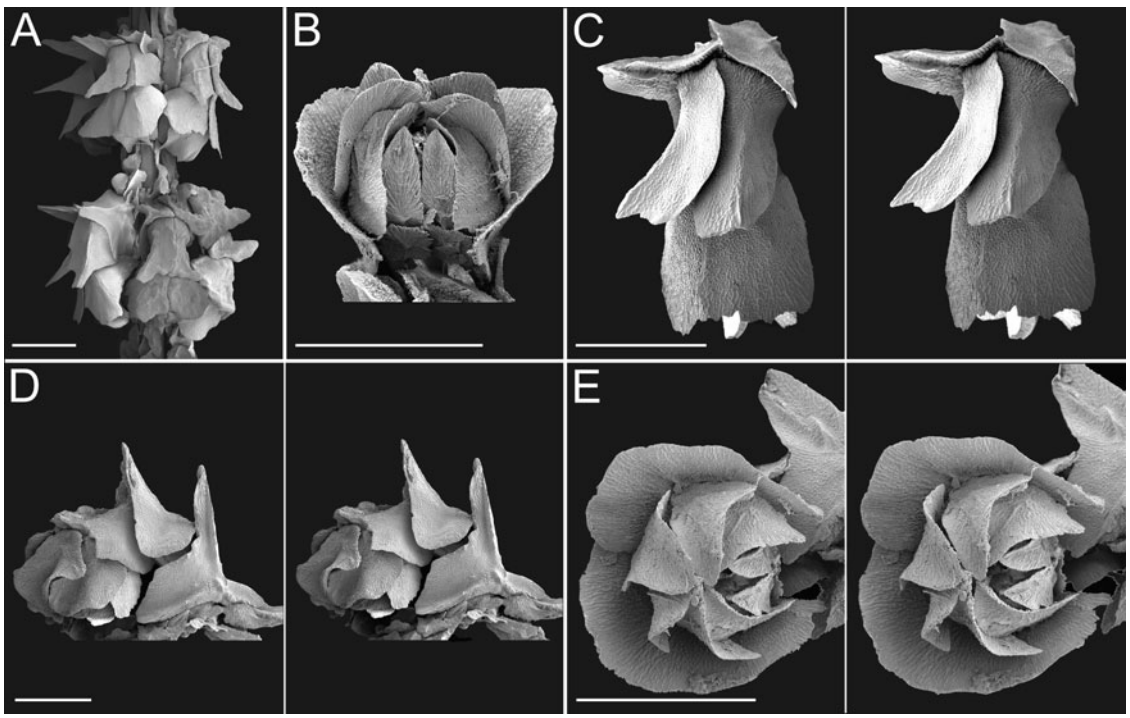

Figure 9 *Narella alaskensis* (A-B, E, paratype from 4027-10; C-D, holotype): A, lateral view of two whorls; B, adaxial opercular view; C, stereo abaxial view of a polyp; D, stereo lateral view of a polyp; E, stereo opercular view. Scale bars for A-C, E = 1.0 mm; D = 0.5 mm.

Comparisons

Narella arbuscula is distinguished from other congenerics in the Gulf of Alaska (Table 2) by having almost flat (concave) and thus highly flared body wall scales that do not have a sharp basolateral edge, as well as having the largest polyps of any species. But a similar polyp morphology is shared with at least two species from Indonesian waters, *N. obscura* (Versluys, 1906) and *N. dichotoma* (Versluys, 1906), which are similar to each other. *Narella arbuscula* is distinguished from both species by having larger polyps, a bushy colony (not uniplanar), and by having a tall ridge (Figs 7D, 8E) on the proximal basolateral margin of the basal scales. It is further differentiated from *N. obscura* by having elongate, ridged coenenchymal scales (those of *N. obscura* are polygonal and not ridged) and from *N. dichotoma* in having more polyps per whorl and more closely spaced whorls.

Distribution

Derickson and Giacomini Seamounts, Gulf of Alaska; 2775–3465 m

Etymology

The species name *arbuscula* (Latin: *arbuscula*, small tree) refers to the three dimensional, bushy shape of the colonies.

Narella alaskensis sp. nov.

Figs 9–10

Material examined/Types

Holotype: *Alvin* 4033–23, three branches (one dry, one in alcohol), SEM stubs 1159–1163, USNM 1075470, and 1 alcohol branch at BM (NHM 2005.2347). Paratypes: *Alvin* 3797, two branch fragments in alcohol, USNM 1080453; *Alvin* 3803-4-5, four branch fragments in alcohol, USNM 1080454; *Alvin* 4033-28, three branch fragments in alcohol, USNM 1075471; *Alvin* 4027-10, eight branches (six in alcohol, two dry), USNM 1075468; *Alvin* 4029-16, three branch fragments in alcohol, one dry, USNM 1075469.

Type locality

54°59.24′N, 140°23.99′W (Welker Seamount, Gulf of Alaska), 2634 m.

Description

The holotype is a branch segment only 11 cm long and 7 mm in branch diameter, showing only one bifurcation; the paratypes show the species to have a uniplanar colony. Branching appears to be sparse with long terminals. No specimens were collected with an intact base. The axis is golden yellow, up to 1.33 mm in diameter in the holotype.

Polyps on large diameter branches are arranged in whorls of 7–9, but predominantly 8, the polyps of each whorl tightly packed one against another and contiguous with those of adjacent whorls, showing no intervening branch coenenchyme. This extremely crowded polyp arrangement results in about 10.5 whorls per 3 cm, and thick cylindrical branches with a whorl diameter of up to 7.5 mm. On smaller-diameter branches there are only 4 or 5 polyps per whorl and whorls are spaced about 0.5 mm apart. Polyps are 2.7–3.2 mm in length and 1.3–2.1 mm in maximum width.

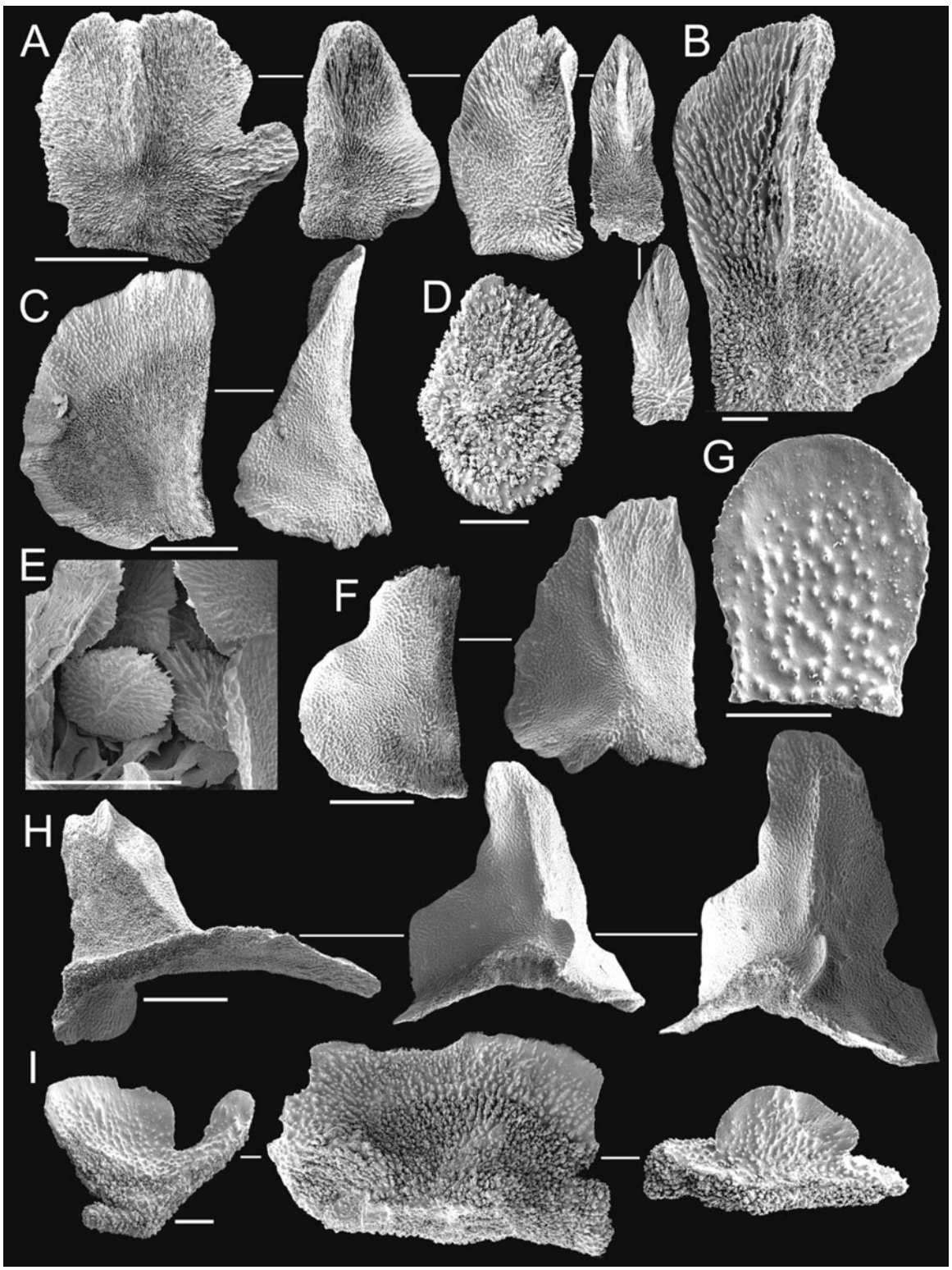

Figure 10 *Narella alaskensis*, holotype: A, opercular scales; B, inner surface of an opercular scale; C, abaxial buccal scales; D, an adaxial buccal scale; E, adaxial buccal scales in situ; F, medial scales; G, an adaxial body wall scale; H, basal scales; I, coenenchymal scales showing tall blades. Scale bars for A, C, E-F, H = 0.5 mm; B, D, G, I = 0.10 mm.

Each polyp is protected by three pairs of large abaxial body wall scales, 1–2 pairs of smaller (0.30–0.40 mm in width), oval adaxial buccal scales, and a variable number of even smaller (0.12–0.20 mm) scales that are directly attached to the adaxial body wall. The large basal scales stand perpendicular to the branch and reach as much as 2.0 mm in height, the distal most 0.6–1.0 mm rising well above the junction with the adjacent medial scales as a sharp to blunt projecting spine or spur. These spines are often broken off or worn down in older polyps. The basolateral edge of the basal scale curves at

a right angle and sometimes bears a ridge up to 0.25 mm in height near the coenenchyme, but may just as often lack the ridge. Occasionally there is a short, low longitudinal ridge on the inner surface of the projecting spur. The basal scales do not meet adaxially and thus do not form a closed ring. The medial scales are up to 1.6 mm in length, highly flared distally, and also usually bear a low, smooth ridge at their basolateral edge. Each medial scale also bears a prominent sharp spine on its basolateral margin. The large abaxial buccal scales are up to 1.8 mm in length, gently curved at the basolateral edge, and do not bear ridges. Their margins project outward up to 0.5 mm as a cowl surrounding the bases of the opercular scales.

The opercular scales are triangular in shape, the single large symmetrical abaxial opercular up to 1.1 mm in length and often of the same width (H:W = 0.9–1.0). The five lateral operculars are asymmetrical in shape, up to 1.0 mm in length and about 0.4–0.6 mm in width (H:W = 1.7–2.3); the small symmetrical pair of adaxial operculars are only 0.6–0.8 mm in length and 0.24–0.34 mm in width (H:W = 2.2–2.8). All operculars are highly concave on their outer surfaces and tuberculate and distally keeled on their inner surfaces.

Coenenchymal scales are fusiform and similar in shape to those described for other species, reaching up to 0.9 mm in length and 0.50 mm in blade height.

Discussion

Some of the distinguishing characters used in Table 2 vary for this species depending on the location of the polyp within the colony. For instance, polyps on terminal branches are somewhat smaller, occurring only 4 or 5 per whorl, the whorls only slightly spaced from one another, altogether producing a whorl diameter of only 3–4 mm. These polyps also have well-developed spines on the margins of both basal and medial scales (Fig. 9D). Polyps on larger-diameter (to 7 mm) proximal branches are larger and more crowded, with as many as 9 polyps per whorl, and the whorls are very closely spaced. The spines on the basals and medials are present but somewhat blunt as though through wear over time (Fig. 9C). At first these isolated branches were thought to represent two closely related species, thus underscoring the importance of having a complete colony or colonies for examination.

Comparisons

Narella alaskensis is readily distinguished from other congenerics from the Gulf of Alaska (Table 2) by its possession of prominent spines on the distal margin of the basolateral edge of the basal and medial scales. But several other species in the genus have such spination, one of which *N. parva* (Versluys, 1906), known only from Indonesia at 1300–1595 m, has a remarkably similar polyp morphology. *Narella alaskensis* differs from that species in having more polyps per whorl (*N. parva* has only 3–4 per whorl) and in having very crowded (contiguous) whorls (those of *N. parva* are separated by as much as 1 mm). Furthermore, it is unlikely that a species would have such broad distribution and bathymetric ranges, encompassing the tropical west Pacific and boreal Gulf of Alaska. But, as *N. parva* is known from only several poorly preserved specimens, future comparisons are encouraged between Indonesian and Alaskan faunas.

Distribution

Chirikof, Murray, Welker, Denson, and Dickins Seamounts, Gulf of Alaska; 2377–3075 m, the most widespread and shallowest of the *Narella* in the Gulf of Alaska.

Etymology

This species is named for the Gulf of Alaska, being the most widespread *Narella* collected from the Gulf thus far.

Genetic data

Seven hundred and eighty-six base pairs of msh1 and 610 bp of ND6 were compared for these species. Other Alaskan primnoids given the preliminary identifications of *Calyptrophora japonica*, and *Primnoa pacifica var. willeyi*, were used as outgroups. Table 3 summarizes the uncorrected 'p' pairwise distances between each species for msh1. Only a single haplotype was obtained for each species except *Narella arbuscula*, which had two haplotypes that differed by one base pair. One haplotype was represented by individuals collected on Derickson Seamount, and the other by individuals from Giacomini Seamount. Interspecific distance ranged from 0% to 1.39%. The distance between the species of *Narella* and the outgroup species ranged from 1.39% to 3.68%. The two outgroup species also had a pairwise distance of 3.68%.

Variation in ND6 was very low, with only three variable positions within the Alaskan *Narella*, and an additional two variable positions when the outgroups were added. Table 4 summarizes the pairwise distances between each species for ND6. Among the five new *Narella* species, pairwise distances ranged from 0 to 0.33%. Comparisons of the *Narella* species to the outgroup species ranged from 0.33% to 0.49%. These results suggest that ND6 is not variable enough to be useful for intraspecies or intrageneric differences within the octocoral Family Primnoidae.

Three species *N. bayeri, N. cristata* and *N. abyssalis*, showed no sequence differentiation between species for either gene. All three species were collected from Derickson Seamount. It has been suggested that seamounts may act as hot spots for speciation due to their isolation (e.g. Parker & Tunnicliffe, 1994; Rogers, 1994; DeForges *et al*., 2000), and these three species may represent a relatively recent radiation of *Narella* on Derickson Seamount. Sanchez *et al*. (2003) point out that these genes may provide limited resolution for recently evolved species, however, it is also likely that msh1 and ND6 simply have too low variation levels to distinguish all species within this genus. Five species in the octocoral genus *Corallium* (Family Coralliidae), showed no sequence variation in the first 100 bp of the msh1 gene (France & Hoover, 2002). Two species of Hawaiian *Narella* differed by 2.8% in the same 100 bp region of msh1 (France & Hoover, 2002). Other published data on this region of the msh1 with multiple species in a single genus include those of Sanchez *et al*. (2003) and Wirshing *et al*. (2005), but unfortunately, they did not include pairwise distances in their results. The only

	N. bayeri (AK-21, 18, and 17)	*N. cristata* (AK-20)	*N. abyssalis* (AK-15)	*N. arbuscula* haplo 1 (AK 16 and 19)	*N. arbuscula* haplo 2 (AK 41, 42, and 109)	*N. alaskensis* (AK 36, 37, 38, WPC 1, 8)	*Calyptrophora japonica* (Ak-94)	*Primnoa pacifica* var. *willeyi* (AK-107)	Gen Bank # for Haplotype
N. bayeri (AK-21, 18, and 17)	–								DQ234754
N. cristata (AK-20)	0.0	–							DQ234753
N. abyssalis (AK-15)	0.0	0.0	–						DQ234755
N. arbuscula haplo 1 (AK 16 and 19)	0.507	0.507	0.507	–					DQ234751
N. arbuscula haplo 2 (AK 41, 42, and 109)	0.634	0.634	0.634	0.127	–				DQ234752
N. alaskensis (AK 36, 37, 38, WPC 1, 8)	1.394	1.394	1.394	1.141	1.267	–			DQ234750
Calyptrophora japonica (Ak-94)	2.788	2.788	2.788	2.788	2.915	3.676	–		DQ234756
Primnoa pacifica var. *willeyi* (AK-107)	1.394	1.394	1.394	1.394	1.521	2.281	3.676	–	DQ234757

Table 3 Uncorrected 'p' pairwise distances (%) for new species of *Narella*, based on MutS sequences.

	N. bayeri (AK-21, 18, and 17)	*N. cristata* (AK-20)	*N. abyssalis* (AK-15)	*N. arbuscula* (AK 16 and 19, 41, 42, and 109)	*N. alaskensis* (AK 36, 37, 38, WPC 1, 8)	*Calyptrophora japonica* (Ak-94)	*Primnoa pacifica* var. *willeyi* (AK-107)	Gen Bank # for Haplotype
N. bayeri (AK-21, 18, and 17)	–							DQ234762
N. cristata (AK-20)	0.0	–						DQ234761
N. abyssalis (AK-15)	0.0	0.0	–					DQ234763
N. arbuscula (AK 16 and 19, 41, 42, and 109)	0.328	0.328	0.328	–				DQ234760
N. alaskensis (AK 36, 37, 38, WPC 1, 8)	0.328	0.328	0.328	0.164	–			DQ234759
Calyptrophora japonica (Ak-94)	0.492	0.492	0.492	0.492	0.492	–		DQ234764
Primnoa pacifica var. *willeyi* (AK-107)	0.328	0.328	0.328	0.328	0.328	0.492	–	DQ234765

Table 4 Uncorrected 'p' pairwise distances (%) for new species of *Narella*, based on ND6 sequences.

estimate of the mutation rate for the msh1 gene in octocorals is 0.2% per million years (LePard, 2003). Although msh1 is considered the most rapidly evolving mitochondrial protein-encoding gene for octocorals (France & Hoover, 2002), clearly there is still a need for a more informative marker at the species level.

Acknowledgements

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