A REVIEW OF THE GENUS *PRIMNOA* (OCTOCORALLIA: GORGONACEA: PRIMNOIDAE), WITH THE DESCRIPTION OF TWO NEW SPECIES

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ABSTRACT

The four species and one additional variety of the genus *Primnoa* are revised, including descriptions and illustrations of all taxa. Two new species are described, *Primnoa wingi* from the Aleutian Islands and *Primnoa notialis* from the Subantarctic. *Primnoa willeyi* Hickson, 1915 is considered to be a variety of *Primnoa pacifica* Kinoshita, 1907. *Primnoa* is known to occur in the northern boreal Atlantic and Pacific and Subantarctic South Pacific at depths of 9–1029 m. It is particularly common throughout the Aleutian Islands, where it is often a bycatch of fishery trawling and sometimes made into jewelry.

Primnoidae is probably the dominant gorgonian family in the Antarctic fauna, represented by many species in the genera *Thouarella, Primnoella, Convexella, Narella*, *Dasystenella, Parastenella, Callozostron, Ainigmaptilon, Fannyella, Ophidiogorgia*, and *Armadillogorgia*. However, until now *Primnoa*, the type genus of the family, has been known only from boreal and cold northern temperate waters. Operations by USNS Eltanin in Antarctic waters during 1964 obtained representatives of the genus from a seamount in the Subantarctic Pacific sector of the Southern Ocean. These have made it necessary to reevaluate the northern forms in order to determine the status of the Antarctic population. In doing so, the three previous taxa were reviewed and another species described from the Aleutian Islands.

Material and Methods

As the procedure for preparation of primnoid polyps with sclerites in place for examination by scanning electron microscope (SEM) has already been outlined (Bayer and Stefani, 1989: 451) it is unnecessary to do so again. However, because preparations of whole polyps and fragments of branches retain a large amount of dried organic material, deterioration might be expected to limit the durability of such mounts. Reexamination of old preparations to obtain additional views of polyps has shown that specimens mounted more than 20 yrs ago still give satisfactory results with SEM. This finding demonstrates that whole mounts for SEM remain useful for a considerable period of time and therefore merit long-term conservation. It should be noted that the material referred to above was not stored under any special conditions. Apart from protecting them from accumulation of dust, no unusual procedures were employed. Presumably, storage in sealed containers with desiccant would further extend durability of SEM whole mounts.

Twenty-two of the more recently collected samples of *Primnoa*, representing all five taxa, were submitted to S. France (University of Louisiana at Lafayette) for sequencing of the mitochondrial msh1 gene. He was successful in sequencing 13 specimens, which are indicated with an asterisk in the material examined sections: msh1, region 1 (about 800 bp): two samples; msh1, region 1 (about 340 bp): seven samples; and msh1, region 2 (about 300 bp): 10 samples. Sequences were obtained from four of the five taxa; none of which were obtained for *Primnoa notialis*. Additional specimens (one each of *Primnoa pacifica* Kinoshita, 1907, *Primnoa pacifica willeyi* Hickson, 1915, and *Primnoa wingi* sp. nov. from the Aleutian Ridge, and *Primnoa resedaeformis* (Gunnerus, 1763) from the Gulf of Maine), freshly collected spe-

cifically for genetic analysis by S. France, were amplified and sequenced to compare to the results from the older museum specimens. Although msh1 has been used successfully as a species level marker for some octocorals (France and Hoover, 2001; Lepard, 2003), all sequences obtained from these samples were identical within regions 1 and 2 (GenBank accession numbers AY968599-AY968601). This could be interpreted to mean that all four taxa are the same species, that the msh1 gene is not effective for discriminating species of *Primnoa* (see Lepard, 2003), or that a longer sequence is needed to show a difference. Given the extreme and consistent morphological differences among the putative *Primnoa* species and, in some cases, the vast unpopulated geographic distance between populations, and the evidence that mitochondrial mutation rate is extremely low in octocorals (France and Hoover, 2002; Shearer et al., 2002), we adopt the latter point of view. We suggest using a nuclear marker (S. France, University of Louisiana at Lafayette, pers. comm.) for future study.

The following abbreviations are used in the text: AB — Auke Bay Lab (NOAA), Juneau, Alaska (the following numbers are the last two numbers of the year of collection); Alb — USFCS Albatross; BMNH — British Museum of Natural History, London (now The Natural History Museum); MCZ — Museum of Comparative Zoology, Harvard, Cambridge; SEM — Scanning Electron Microscope stub number (unprefaced number pertains to series of Bayer, "C" to series of Cairns); USNM — U.S. National Museum (now the National Museum of Natural History), Smithsonian, Washington, D. C.

Subclass Octocorallia
Order Gorgonacea
Suborder Calcaxonia
Family Primnoidae Gray, 1858
Primnoa Lamouroux, 1812

Primnoa Lamouroux, 1812: 188; 1816: 442.—Kükenthal, 1919: 357–360; 1924: 265–266 (references).—Bayer, 1956: F220, fig. 157, 1.
Lithoprimnoa Grube, 1861: 174–175.
Type species.—Primnoa: Gorgonia lepadifera Linnaeus, 1767 (=*Gorgonia resedaeformis* Gunnerus, 1763), by monotypy.
Lithoprimnoa: Lithoprimnoa arctica Grube, 1861, by monotypy.

Diagnosis.—Dichotomously branched, arborescent Primnoidae with polyps not arranged in whorls but closely crowded on all sides of the twigs and branches; polyps distinctly curved downward toward the axis. Polyps adaxially naked or nearly so, abaxially armed with scales or plates of variable size, shape, and arrangement. Marginal scales eight, those of the adaxial side of the polyp smaller than those of the abaxial side and may be only indistinctly differentiated. Operculum strongly developed, the adaxial pair of scales smaller than the abaxials and laterals. Tentacles with small, thorny rods.

Remarks.—Kükenthal (1919) recognized only one species of *Primnoa, P. resedaeformis*, and a variety of it, *P. pacifica*, a view shared by Madsen (1944). Kükenthal later (1924: 267) treated *P. pacifica* as a subspecies of the North Atlantic *P. resedaeformis*: "*P. resedaeformis typica*." Both Kükenthal (1924) and Aurivillius (1931) treated *P. willeyi* as a dubious species, the former considering it probably synonymous with *P. resedaeformis*.

Broch (1935: 29–33) discussed the status of *P. pacifica* relative to *P. resedaeformis,* concluding that the Pacific species is a geographical form of the Atlantic species. His

investigation of Norwegian specimens from Trandhjemsfjord showed that the variability of polyp scales is considerably less than in Pacific colonies, and that strongly developed "Basalscleriten" are almost never ("fast nie") seen in Norwegian colonies.

While visiting the Natural History Museum, London, FMB was able to make a drawing of a branch of Hickson's original material of *P. willeyi* (Fig. 7C). No type material of *P. pacifica* is available to us, but samples collected in Japanese waters agree with Kinoshita's description in most respects and may be taken as representative of his concept.

Specimens of *Primnoa* trawled in the Pacific sector of the Southern Ocean by USNS Eltanin are the first record of the genus from Subantarctic waters, although this taxon was reported as a *nomen nudum* by Heikoop et al. (2002) and Risk et al. (2002). This material demonstrates unequivocally the bipolarity of the genus *Primnoa*. The few North Pacific specimens available for study show consistent differences from North Atlantic specimens. The numerous specimens from three stations in the Southern Ocean likewise differ somewhat from both North Pacific and North Atlantic specimens.

Kinoshita (1908a) already has remarked upon the *Narella*-like development of the basal scales in *P. pacifica*. Pacific specimens of *Primnoa* in the present collection carry the similarity of the two genera even further. Polyps of a very young colony from the Alexander Archipelago of southern Alaska (USNM 58397) are enclosed in a pair of large, *Narella*-like basal scales that form a pair of projecting flat horns, a pair of somewhat smaller medial scales, and a circle of buccal scales of which the abaxial pair commonly are the largest. These polyps (Fig. 5A–B, USNM 58397) have a strikingly *Narella*-like aspect, closely approaching in form the polyps of those *Narella* species having strongly developed adaxial buccal scales, such as *Narella megalepis* (Kinoshita, 1908). The most obvious distinction of *Primnoa* from *Narella* is the presence of more than four scales in the buccal ring, and the crowded, non-verticillate arrangement of polyps.

Most polyps of North Atlantic colonies of *P. resedaeformis* have two main rows of large abaxial scales between the marginal scales and the basal scales, the latter of which are not strongly developed and not especially conspicuous. The polyps of Pacific colonies have more numerous, more or less irregularly placed scales between the marginal and basal scales, which usually maintain or increase their size to a variable extent, commonly projecting outward as a pair of strong processes or flat spines.

Although interbreeding populations could be expected to exist around the northern perimeters of the North Pacific and North Atlantic, it is not known at present whether or not the two areas are linked by a continuous population around the Polar Sea (see Broch, 1949). Similarly, it is not known whether or not a continuous population extends from the North Pacific to the South Pacific. Not all possible localities have been sampled by dredge or observed by submersible at appropriate depths. However, the broad scope of explorations at low latitudes in both Pacific and Atlantic Oceans over the past century might have been expected to discover evidence of intermediate populations had such existed.

Key to Species and Varieties of *Primnoa*

1 . Basal scales of most polyps larger than medials, and usually with a prominent marginal spine (*Narella*-type scale) .....(*P. pacifica*) 2

1′. Basal scales roughly the same size as medials, never with marginal spines.....3

2 . Polyps long and fleshy, often twisted and lacking sclerites on lateral edges of polyps; ratio of mid- to distal polyp diameter 0.25–0.43..... *P. pacifica* var. *willeyi*

2′. Polyps more robust, straight, with small body wall sclerites on lateral surfaces of polyps; ratio of mid-distal polyp diameter 0.53–0.67 .....*P. pacifica* typical

3 . Abaxial medial scales large (to 1.5 mm wide), rectangular, and arranged in 2–5 pairs ....*P. resedaeformis*

3′. Abaxial medial scales smaller, elongate or elliptical, not arranged in pairs 4

4 . Medial scales elongate and slender (< 0.2 mm wide), restricted to a narrow abaxial tract that is immersed in tissue; operculars spatulate; marginals extremely concave; tentacular rods large and often curved; Aleutians .....*P. wingi* sp. nov.

4′. Medial scales elliptical to square (up to 1.0 mm wide), covering abaxial and lateral polyp surface; operculars isosceles-triangular; marginals flat; tentacular rods smaller and straight; Subantarctic.....*P. notialis* sp. nov.

Primnoa resedaeformis (Gunnerus, 1763)

(Figs. 1A, 2, 3)

Gorgonia resedaeformis Gunnerus, 1763: 321–329, pl. 9, figs. 1–2 (type locality: coast of Norway).

Gorgonia reseda Pallas, 1766: 204 (type locality: Norwegian Sea).—Gray, 1870: 44–45.

Gorgonia lepadifera Linnaeus, 1767: 1289 (type locality: Norwegian Sea).—Ellis and Solander, 1786: 84–85, pl. 13, figs. 1–2.—Esper, 1788, pl. 18, figs. 1–2 (polyps incorrectly illustrated as pointed up!).—Esper, 1791: 71–78 (extensive synonymy).—Houttuyn, 1792: 301–309.—Lamarck, 1815: 164.—Johnston, 1838: 185; 1847: 171–173, fig. 37.—Milne Edwards and Haime, 1857: 1: 139–140.—Grasshoff, 1991: 335.

Primnoa lepadifera.—Lamouroux, 1816: 442–443 (cites early literature, including pre-Linnaean).

Lithoprimnoa arctica Grube, 1861: 175, pl. 3, figs. 1–6 (type locality: off arctic Norway).

Primnoa reseda.—Verrill, 1862: 127–129; 1864: 9–10.–Versluys, 1906: 85.—Thomson, 1907: 65–72, pls. 1, 2 (photo of colony, and illustration of color in life).—Verrill, 1922: 14–15 (in part: pl. 4, figs. 4–6, not specimen from British Columbia; synonymy).—Opresko, 1980: B17–B18.

Primnoa resedaeformis.—Broch, 1912: 32–37, figs. 21–25 (synonymy; reproduces Gunnerus' original figure).—Schimbke, 1915: 17–22, text-fig. 4, pl. 1, figs. 1–2 (histology).—Jungersen, 1915: 1181–1183.—Kükenthal, 1919: 360–361 (synonymy!); 1924: 266–267, fig. 151.—Aurivillius, 1931: 293, fig. 58, 1–3.–Kramp, 1932: 16, fig. 7.—Deichmann, 1936: 157.—Kramp, 1939: 4.—Bayer, Grasshoff and Verseveldt, 1983: pl. 13, fig. 64.—Grasshoff and Zibrowius, 1983: 121–122, pl. 3, figs. 12–13.—Breeze et al. 1997: 22, fig. 9.—Heikoop et al. 2002: 117–123 (in part: specimens from N. Atlantic, isotopic paleotemperatures).—Risk, Heikoop, and Beukens, 2002: 126–130, figs. 1–6 (mineralogy, growth rate, longevity).—Willison, et al. 2002: pl. 1 (lower left), pl. 5 (upper), pl. 6.

Primnoa resedaeformis typica Kükenthal, 1924: 267.

Primnoae [sic] *resedaeformis*.—Madsen, 1944: 39 (in part: N. Atlantic records only).

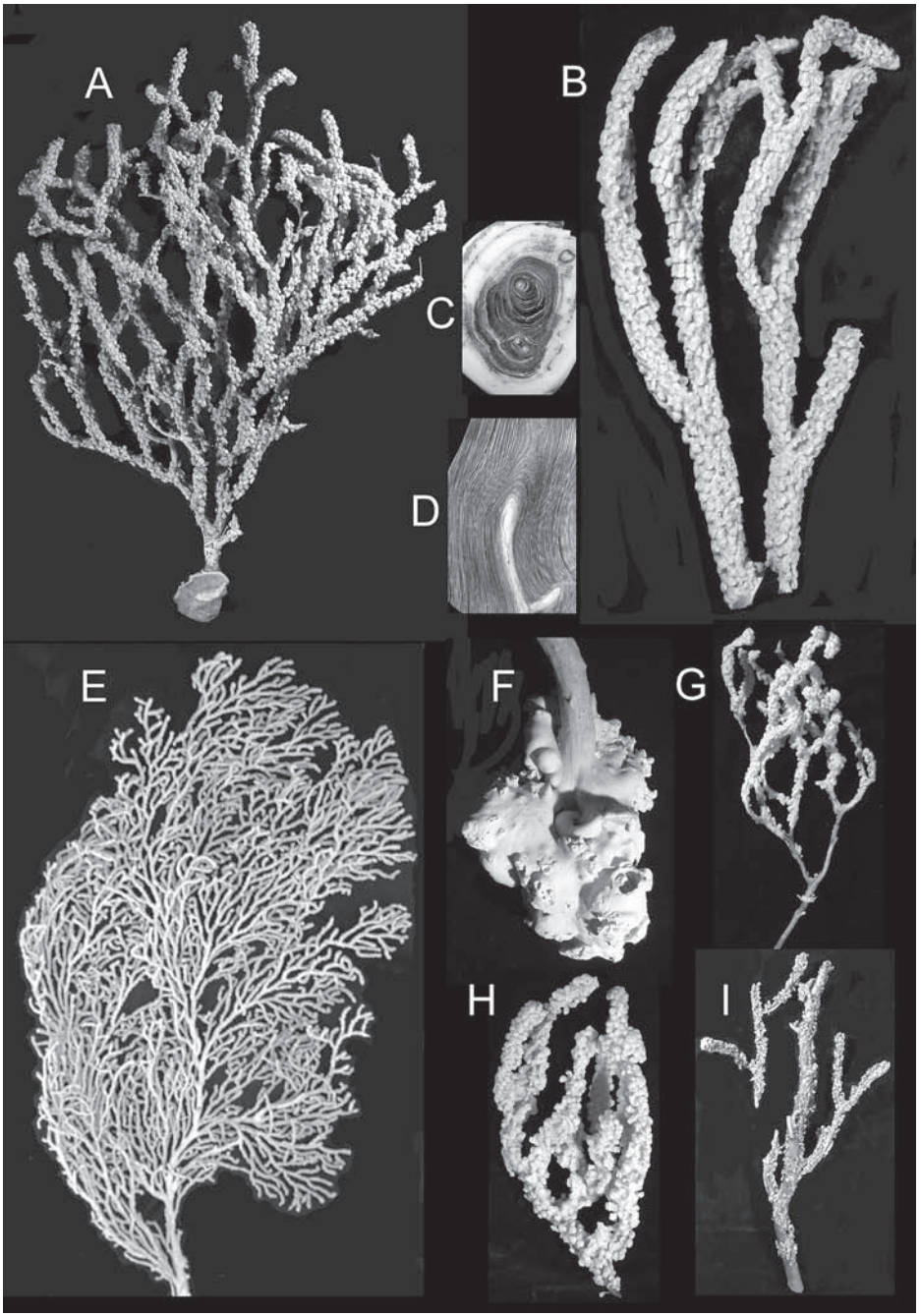

Figure 1. A, *Primnoa resedaeformis*, complete colony, USNM 4591, ×0.19; B, *Primnoa pacifica*, USNM 56993, distal branches, ×0.35; C–D, *P. pacifica* var. *willeyi*, USNM 44058, polished cross and longitudinal sections of a large-diameter stem, ×0.52, ×0.68, respectively; E, *P. p.* var. *willeyi*, large dry colony (USNM 58084), ×0.06; F, *P. notialis*, USNM 87625 (paratype), heavily calcified base, ×0.16; G, *P. notialis*, USNM 87621 (holotype), ×0.20; H, *P. wingi*, USNM 1012503 (paratype), distal branches, ×0.22; I, *P. wingi*, USNM 1010257 (holotype), dried colony, ×0.13.

Material Examined.—Alb-2068, one large colony in alcohol and SEM stubs 1423–1426, USNM 16946 and one dry colony, USNM 33577; Alb-2069, one colony in alcohol and SEM stubs 175, 185, USNM 17281; Alb-2070, one dry colony, USNM 33579; Alb-2072, two dry colonies without polyps, USNM 15875; Alb-2474, one branch in alcohol, USNM 11944; Alb-2480, one branch without polyps in alcohol, USNM 11942; Alb-2523, one branch in alcohol, USNM 11935; Alb-2527, 2–3 branches in alcohol and SEM stubs 1813–1823, C1117–1119, USNM 12262; Alb IV-00-06-23, two colonies in alcohol, USNM 1024423; Eastward 35982, one branch in alcohol and SEM stub 2554, USNM 80927; Eastward 36016, one branch in alcohol, *USNM 80929; Gilliss 7404-104, one large dry colony, *USNM 54269.

Nineteen lots from the northwest Atlantic, from Banquereau and Browns Bank off Nova Scotia south to Georges Bank off Massachusetts at 165–548 m, taken by the Gloucester fishing fleet 1879–1880 and numbered as "Gloucester donations:" 52, two dry colonies without polyps, USNM 4593; 66, one dry colony without polyps, USNM 4742; 194, one dry colony without polyps, USNM 4282; 322, one dry colony, USNM 4097; 346, two dry colonies, USNM 4285 and 4288; 347, one colony in alcohol, USNM 4142; 370, two dry colonies, USNM 4592; 383, two dry colonies, USNM 4589; 392, three dry colonies, USNM 4582; 485, seven dry colonies, USNM 4591 and 33580; 505, one dry colony, USNM 33576; 534, branches in alcohol, USNM 21837; 557, two dry colonies, USNM 4524; 683, one dry colony, USNM 4553; 733, one dry colony without polyps, USNM 4224; 752, two dry colonies, USNM 4544; 785, two dry colonies without polyps, USNM 4534; 797, one dry colony without polyps, USNM 4258; 869, one dry colony, USNM 4548.

Ten colonies are also deposited at the MCZ, most collected by the Albatross IV expeditions between Banquereau Bank and Norfolk Canyon, 144–275 m (not examined).

Diagnosis.—Both basal and medial scales large, square to rectangular, about the same size; basal scales without marginal spines; medial scales prominent, occurring in 2–5 pairs. Six large and two small, flat, rectangular marginal scales.

Short Description (based primarily on northwest Atlantic specimens).—Colonies planar to slightly bushy (arborescent); loosely and dichotomously branched; largest colonies up to 2 m in height with a massive basal main stem diameter up to 5.5 cm. Color in life bright pink. Terminal branches 9–11 mm in diameter. Polyps up to 6.0 mm in length and 3.2 mm in distal diameter, slightly flared (ratio of mid- to distal polyp diameter 0.6–0.7), and directed predominantly downward. Polyps densely and randomly arranged on all sides of branches, any free space on a branch soon occupied with a small developing polyp. Body wall scales consist of a pair of abaxial basals, 2–5 pairs of abaxial medials, and eight marginals. Body wall sclerites above this number usually the result of breakage. Basal scales square to rectangular in shape, slightly curved to encircle the greater circumference of the base of the polyp, and up to 2.0 mm in width, lacking marginal spines. Medials similar to basals, but flat and usually slightly smaller, the maximum size about 1.5 mm in width. Usually six large (up to 2.1 mm in height and 1.6 mm in width) rectangular marginals present in abaxial and lateral positions, one or two pairs of smaller scales occurring beneath each inner lateral marginal. Adaxial marginals smaller (1.0 mm in width), squarish, and often occurring as two pairs. All body wall scales granular above and tuberculate below, with a digitiform basal margin. Opercular scales isosceles-triangular in shape with a blunt apex and occasionally slightly constricted one third distance from the

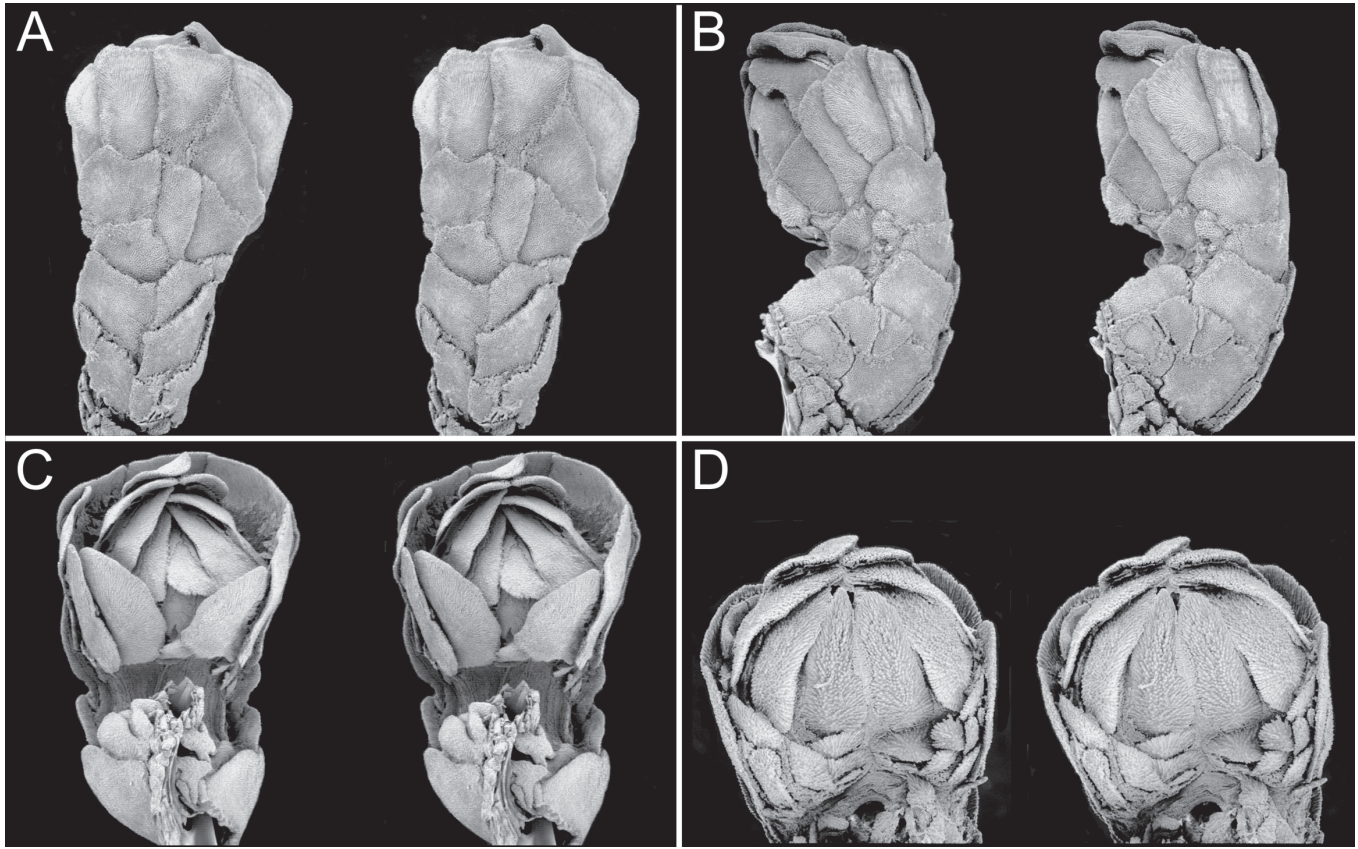

Figure 2. *Primnoa resedaeformis* (A–B, D, ALB-2068; C, ALB-2527): A, abaxial stereo view of polyp, ×11; B, lateral stereo view of polyp, ×11; C, adaxial stereo view of polyp, ×15; D, adaxial stereo view of opercular region of polyp, ×22.

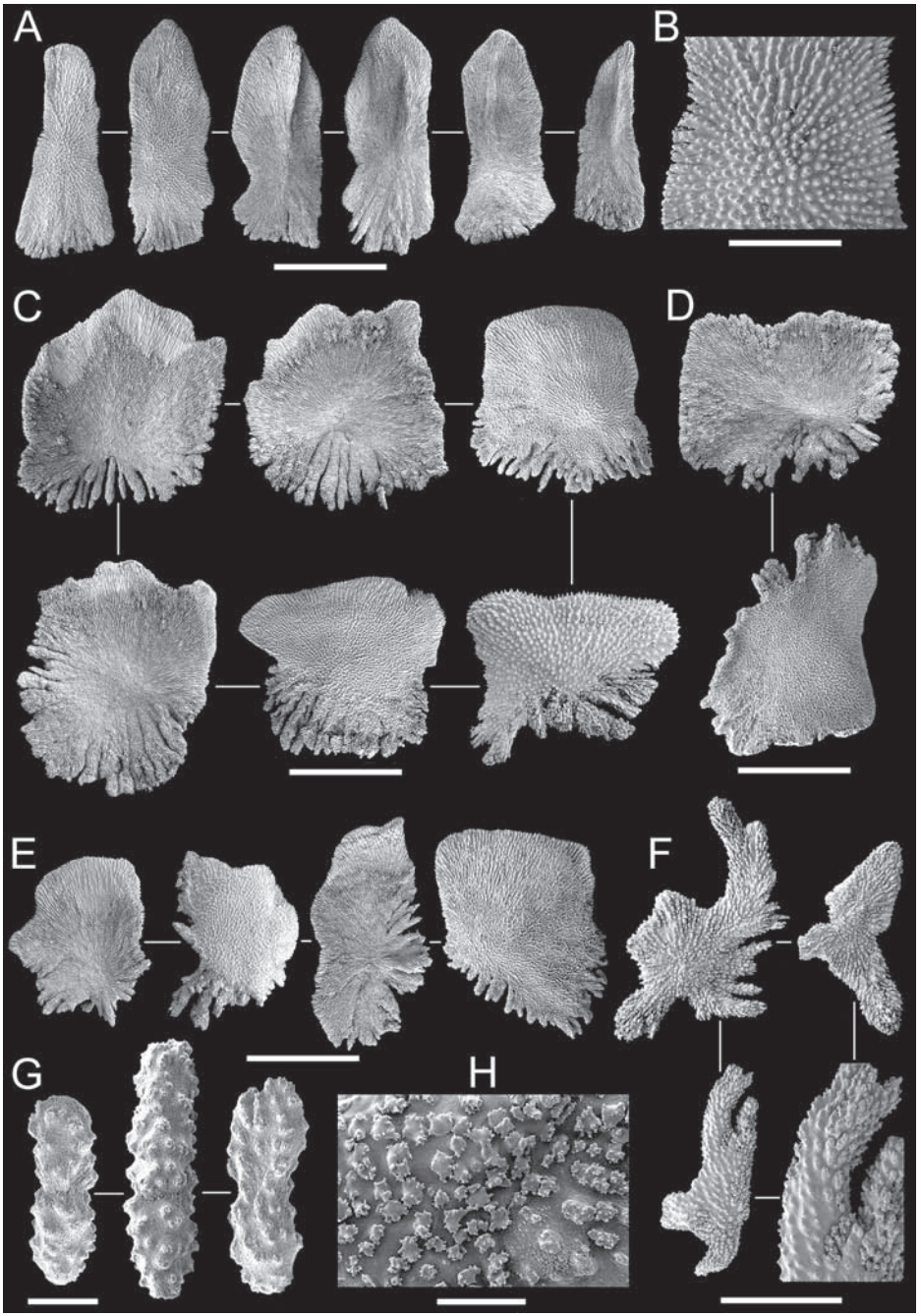

Figure 3. *Primnoa resedaeformis*, constituent sclerites from a colony from ALB-2527 (USNM 12262): A, opercular scales; B, granulation and edge serration of outer surface of an opercular scale; C, outer and inner surfaces of marginal scales; D, inner and outer surface of basal scales; E, body wall scales; F, H, coenenchymal scales and tubercles on inner side; G, tentacular rods. Scale bars: A, C–E = 1 mm, F = 0.5 mm (lower right = 0.17 mm), B = 0.2 mm, G–H = 0.05 mm.

base; lateral and apical edges finely serrate, edge of base produced into 5–7 slender lobes. Abaxial opercular up to 2.1 mm in height and 0.85 mm in basal width, the adaxial operculars being smaller. Middle to distal third of inner side of operculars bears a low blunt keel; tubercles present on lower half of inner side, whereas small granules (30 μm in height) are aligned in parallel rows on distal third. Outer surface of operculars covered with rounded granules that radiate from lower mid-line. Tentacles filled with small (up to 0.18 mm in length and usually 0.045 mm in diameter), cylindrical, blunt-tipped, longitudinally arranged, straight rods that are uniformly covered with tuberculate granules about 10 μm in diameter. Coenenchymal sclerites elongate, flat, often irregularly-shaped (straight, crescent-shaped, or irregular) scales up to 1.15 mm in length, granular above and tuberculate below.

Remarks.—Primnoa resedaeformis has been known since the early days of science, having been poorly described but remarkably well illustrated as early as 1605 by Clusius and described under at least four different names (see synonymy). It is one of the most often reported deep-water octocorals, probably because it is found in relatively shallow-water fishing beds and occurs off northern Europe, an active region for early taxonomic descriptions of all kinds. Although the synonymy is long, it is certainly not complete, including only those references of historical, taxonomic, and biological value. One of the best English descriptions is that of Aurivillius (1931), however our illustrations are believed to be the first detailed SEM of the sclerites and polyps of this important species.

Young polyps, which occur on the coenenchyme between fully developed individuals, have four pairs of large abaxial scales and a number of smaller scales around the oral end of the body in their early stages. Subsequently, the latter probably differentiate into opercular, lateral, and adaxial marginal scales.

According to Breeze et al. (1997), this species is known to Canadian fisherman under the common names of: seacorn, popcorn coral, bush coral, and spruce trees.

Distribution.—Eastern Atlantic: off the coast of Norway from 70°N (Kramp, 1939) to the coast of Scotland, Faroe Islands, Iceland; 95–1020 m (Grasshoff and Zibrowius, 1983); reputed to occur off Setubal, Portugal (Gray, 1870), but this record is unconfirmed. Western Atlantic: west coast of Greenland to 63°N (Kramp, 1939); Banquereau Bank; Nova Scotia; Sable Island Bank; Browns Bank; Gulf of Maine (Verrill, 1922); Georges Bank; Lydonia, Oceanographer and Baltimore Canyons; south to off Virginia Beach, Virginia (37°03′N) (Heikoop et al., 2002); 91–548 m.

Primnoa pacifica Kinoshita, 1907

(Figs. 1B, 4–6)

Primnoa pacifica Kinoshita, 1907: 232 (type locality: Mochiyama, Sagami Bay, depth unknown); 1908a: 42–45, text-figs. 8–9, pl. 3, figs. 19–20, pl. 6, fig. 49; 1908b: pl. 18, fig. 3; 1909: 2–3, text fig.—Wing and Barnard, 2004: 24, fig. 15.

Primnoa resedaeformis var. *pacifica*.—Kükenthal, 1915: 146; 1919: 361–362.—Aurivillius, 1931: 295–296 (Sagami Misaki, Okinose, 600 m).

Primnoa japonica Verrill, 1922: 15 (*nom. nud.*).

Primnoa resedaeformis pacifica.—Kükenthal, 1924: 267, fig. 152.

Primnoa resedaeformis forma *pacifica*.—Broch, 1935: 29–33, figs. 17a–e, 18a (Okhotsk Sea, 335 m; Tatar Sound, 600–700 m; Japan Sea, 780–832 m); Broch, 1940: 20–21.—Naumov, 1955: 66, pl. 11, fig. 5.

Primnoa resedaeformis.—Andrews et al. 2002: 101–110, figs. 1–3 (age and growth estimates).—Heikoop et al. 2002: 119 (in part: specimen from Prince William Sound, mineralogy).

?Primnoa sp. Cimberg et al. 1981: 13–16, figs. 2–3, 5–7.—Heifetz, 2002: 22 (conservation).—Krieger and Wing, 2002: 83–90 (faunal associations).—Krieger, 2002: 106–115, figs. 1–5 (conservation).

Material Examined.—ALB-4239, five dichotomous branches and fragments of a large colony, dry, USNM 58396, and one young dry colony, USNM 58397; ALB-4329, one incomplete dry specimen possibly only a branch of a large colony, SEM 1390, USNM 57557; ALB-4982, six branches from a large colony in alcohol, SEM 1391, USNM 56993; RV MILLER FREEMAN 93-9-10, one large dry branch, possibly of large colony, SEM 2533, USNM 1006140; north of Hinomisaki, Shimane Prefecture, Honshu, Sea of Japan, 145 m, coll. Katsuchiyo Ito, Japan Sea Fisheries Research Laboratory, 1956, one branch with four bifurcations, obviously from a much larger colony, preserved dry, SEM 1639-1642, USNM 85281; Okushiri Island, off southwestern Hokkaido, Sea of Japan, 800 m, November 1985, received from K. Muzik, five small branchlets from a large colony in alcohol, SEM 1389, C1120-1123, *USNM 84870; Jack Bay, Prince William Sound, Alaska, 64 m, bottom mud and rocks, Alaska King Crab Investigations, M/V LOCKS, C.J. Pertuit coll., 28 May 1941, branches of a large colony in alcohol, SEM 176, 1619, 1620, USNM 51283; Strait of Georgia, British Columbia, 6.5 km NE of Entrance Island, 350 m on submerged cable, Neil McDaniel coll., 14 August 1973, one decalcified branch in alcohol, USNM 57980; R/V PACIFIC LADY (AB70-270), one branch in alcohol, USNM 1011028; R/V JOHN COBB (AB94-21), one branch in alcohol, *USNM 1011074; F/V TRITON (AB01-50), two dry branches, USNM 1004617; F/V PATRICIA LEE (AB01-47), one dry branch, *USNM 1004659; "Southeast Alaska," 274 m, coll. E. Payn, 1924, one complete dry colony, USNM 1024425; Boutillier 10, 54°20′15″N, 133°03′19″W, 457–466 m, one branch, *USNM 1016354.

Diagnosis.—Most polyps with a pair of massive basal scales, each basal bearing a prominent marginal spine. Medial scales usually fusiform and unpaired. Five marginal scales of large size, remaining three marginals much smaller. Operculars often with more than one keel.

Short Description.—Colonies planar to slightly bushy in shape with a stiff/rigid axis, loosely and dichotomously branched, the largest colony (the holotype) 68 cm in height, but surely larger colonies exist as evidenced by basal axis diameters of up to 24 mm (USNM 1024425, Payn). Terminal branch diameter (including polyps) 7.5–9.0 mm. Living colonies pink. Polyps stout and straight, 5.0–6.5 mm in length, and only slightly flared, having a ratio of mid- to distal polyp diameter of 0.53–0.67. Polyps densely and randomly arranged on all sides of branches, except in part of one colony (see Remarks) in which the polyps are arranged in whorls of five. Basal scales of most polyps paired, quite large (massive), and curved to surround most of the base of the polyp: up to 3.1 mm in height, including the marginal spines, considerably larger than any medial or marginal scale; however, in some polyps these large basals are missing. Each basal usually bears a prominent spine up to 1.5 mm in height on their outer distal margin, projecting like a horn (*Narella*-like basals); in some cases two spines project from each basal. Outer surface of basals covered with mammiform granules 25–30 μm in diameter; inner surfaces tuberculate. Medial body wall scales variable in size and position (Figs. 4A, 5B), but usually not paired, occurring 2–5

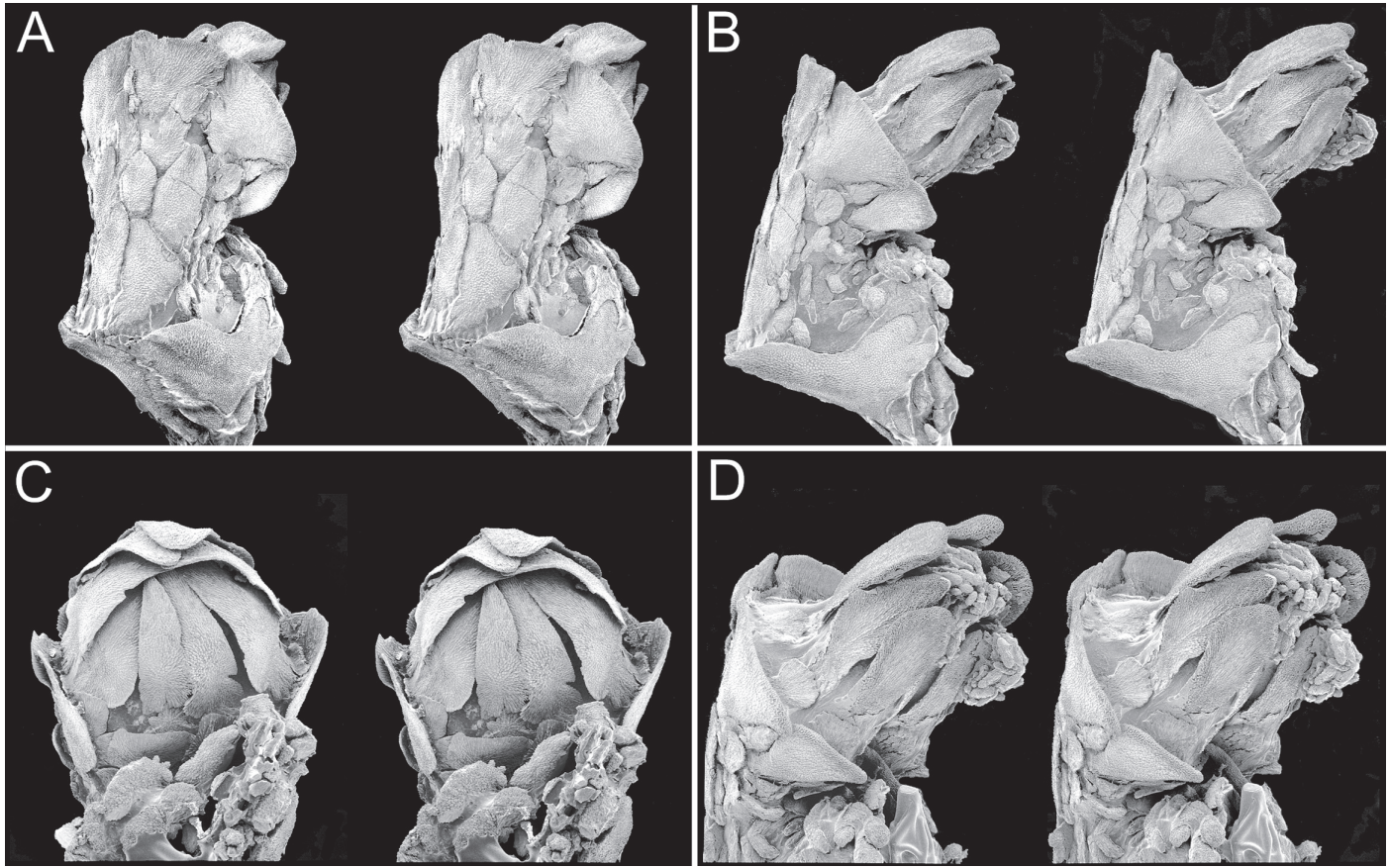

Figure 4. *Primnoa pacifica* (A–B, D, from Hokkaido, USNM 84870; C, Sea of Japan, USNM 85281): A–B, lateral stereo views of polyps showing large spined basals and abaxial scales, ×11; C, adaxial stereo view of opercular region of a polyp, ×15; D, lateral stereo view of opercular region of a polyp, ×14.

across the abaxial and lateral polyp surface in roughly three indistinct and overlapping tiers. Medial body wall scales elongate (often fusiform), up to 1.5 mm in length and usually 0.5–0.6 mm in width, those on the lateral polyp surfaces always much smaller and irregular in shape. Usually five large (up to 1.4 m in height and 1.8 mm in width), slightly curved marginal scales present in abaxial and lateral positions, the three adaxial marginals considerably smaller (0.85 mm square). Distal third of inner surface of marginals bear aligned granules (not tubercles), projecting above base of operculars as a collar. A small (0.5 mm) squarish "supporting scale" (Fig. 4D) often present between each marginal and corresponding opercular scales. Opercular scales isosceles-triangular, the widest portion often slightly above base or even at opercular tip; lateral and apical edges finely serrate, basal edge digitiform. Abaxial operculars up to 2.8 mm in height, adaxials only about 1.5 mm. All operculars bear at least one and sometimes up to four parallel ridged keels on distal half of their inner sides. Otherwise ornamentation is as in *P. resedaeformis*. Tentacular sclerites straight, rotund rods up to 0.32 mm in length and 0.12 in diameter. Coenenchymal sclerites elongate, somewhat rounded in cross section, and up to 1.5 mm in length, often irregular in shape, sometimes curved.

Remarks.—The sample from Hokkaido (USNM 84870) agrees in general appearance with the original material of *P. pacifica* illustrated by Kinoshita (1908a), but the polyps are not as similar to *P. resedaeformis* in appearance as is implied by Kinoshita's fig. 49 on plate 6. The colonies from the Sea of Japan (USNM 56993, 85281) have branches much stouter than the illustrated type; the polyps are virtually indistinguishable from those of Alaskan colonies, and the young polyps are very *Narella*-like. In all of the present material but not mentioned by Kinoshita, the marginal scales have a wide free margin that flares cape-like around the base of the folded operculum, a condition uncommon in Atlantic *P. resedaeformis*. However, this feature is obscured by a thick external layer of tissue covering the sclerites and in some cases is difficult to see unless the polyp is carefully cleaned. The large abaxial basal scales described by Kinoshita as being similar to those of *Stachyodes (=Narella*) are developed in many, but not all, polyps. This character strongly suggests a close relationship of *Primnoa* with *Narella*, the latter differing principally in having only four marginal scales (two large abaxials, two small adaxials), only one or two pairs of abaxial scales between the marginals and the basals, and in having the polyps arranged in regular whorls. The opercular scales as described by Kinoshita (1908a: 44) are "verlängert elliptis[c]h, an der Apex stumpf-spitzig," but in the present material they commonly are hastate in outline, somewhat constricted above the base; they often have a small scale (termed "supporting scales" by Aurivillius 1931: 295) located below each.

One of the two branches from AB01-47 (USNM 1004659) has its polyps arranged in discrete whorls of five polyps each for a distance of at least 9 cm.

Specimens from Prince William Sound, Alaska (USNM 51283) and the Strait of Georgia (USNM 57980) are in good agreement with Japanese specimens, although the opercular scales are more nearly triangular. Clearing some polyps with carbolxylol reveals that the sclerites are situated essentially as in Japanese material.

A colony from the southern coast of California (USNM 57557) differs in having the projections of the basal scales more or less subdivided and the margins of some of the other abaxial scales armed with strong marginal spines. The opercular scales are roughly triangular. Obtained some 2000 km south of the Strait of Georgia, it is the southernmost record for the species.

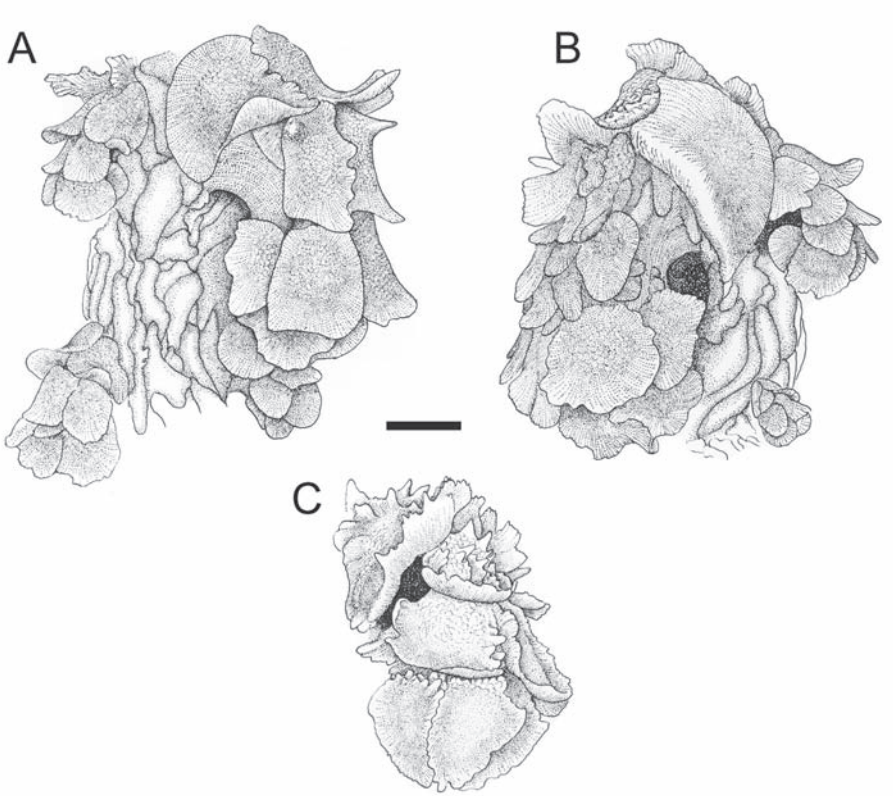

Figure 5. *Primnoa pacifica*, polyps of small colony from Alexander Archipelago, Alaska, USNM 58397: A, one fully developed *Narella*-like polyp and three young polyps; B, one fully developed polyp with many medial body scales nearly as narrow as in *P. p. willeyi*, and two young polyps; C, one fully developed *Narella*-like polyp with strongly ornamented scales. Scale bar = 1 mm.

A small colony from Alb-4239 (USNM 58396, 58397) in the Alexander Archipelago of southern Alaska is the most remarkable specimen in the collection. It is a young colony 7 cm tall with only four bifurcations, the first immediately above the base, and three very short new branchlets. Although branched nearly in one plane, the smallest branches originate out of the original plane indicating that a more bushy growth form probably would result as size increased. At its small size, the polyps of this colony retain the basic arrangement of body scales, which on large colonies is more or less obscured through breakage and repair of scales or intercalation of supernumerary scales between the original sclerites. Its polyps vary from almost perfectly *Narella*-form (Fig. 5A) to nearly typical *pacifica*-form (Fig. 5B), with body scales ranging from practically smooth to elaborately sculptured (Fig. 5C). Very young polyps (Fig. 5A) usually have three pairs of large abaxial body scales (including the abaxial marginal/buccal scales), closely resembling the adult condition in *Narella*. Considered independently, it could be regarded as a morphologically distinct species, but when assessed in the context provided by fully developed colonies from Prince William Sound southward to California and from Hokkaido south to Kyushu, it can only be regarded as a young colony of the same species of *Primnoa* inhabiting the northern perimeter of the Pacific. The variation in armature present on polyps of this colony spans the range demonstrated by various colonies throughout the geographical

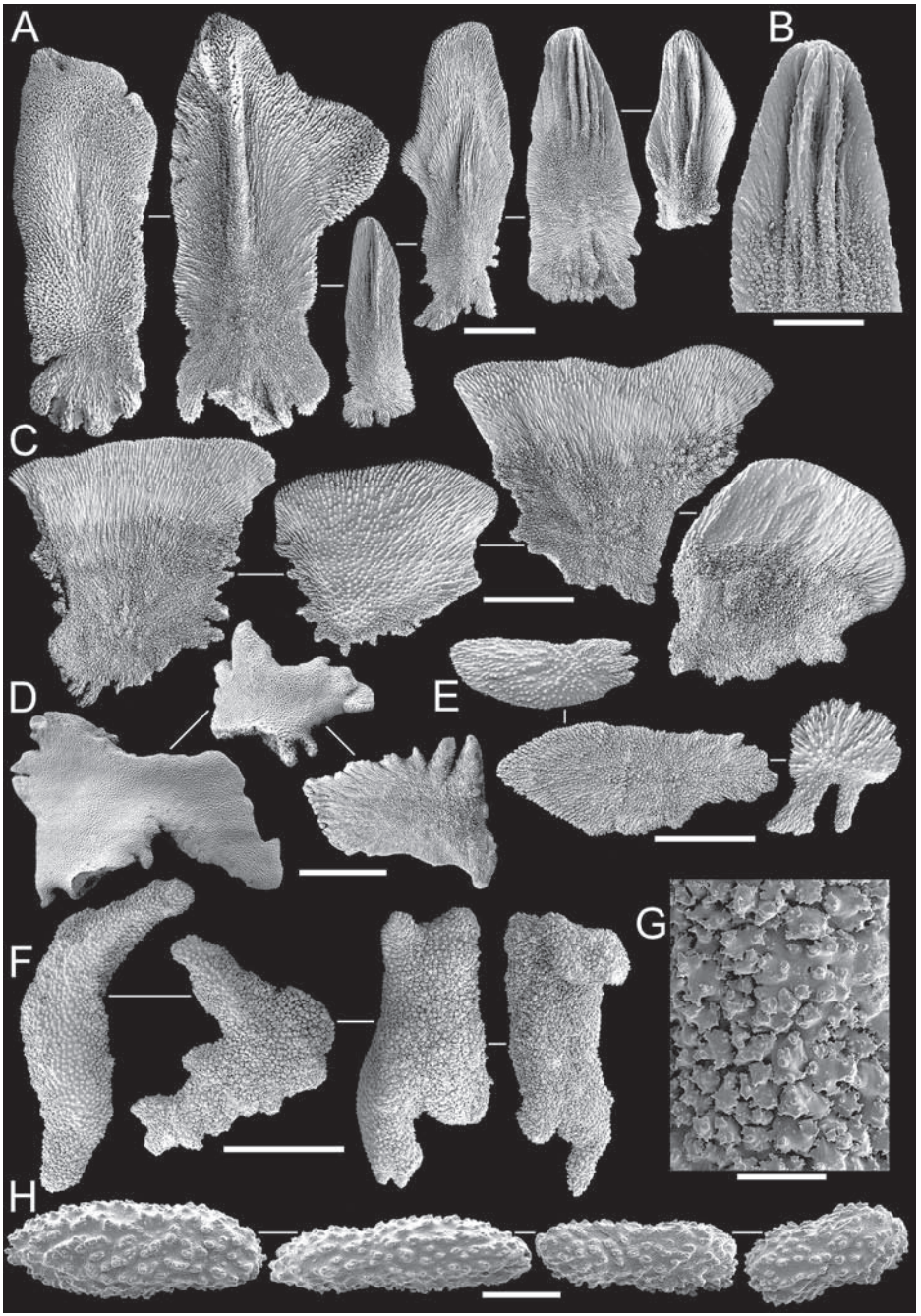

Figure 6. *Primnoa pacifica pacifica*, constituent sclerites from a colony from Hokkaido (USNM 84870): A, opercular scales; B, inner distal surface of an opercular showing a double ridge; C, marginal scales; D, basal scales; E, body wall scales; F, coenenchymal scales; G, tubercles on inner surface of a coenenchymal scale; H, tentacular rods. Scale bars: D = 1 mm, A, C, E–F = 0.5 mm, B = 0.25 mm, H = 0.10 mm, G = 0.05 mm.

range represented, and provides evidence that the variation seen in Japanese and northeastern Pacific colonies of *Primnoa* lacks taxonomic significance.

Cimberg et al. (1981, App. 3) reported 94 Alaskan occurrences of *Primnoa* from Dixon Entrance to Amchitka at depths of 10–800 m, but most of these records are personal communications from fishermen and thus no vouchers exist to determine which of the three Alaskan *Primnoa* they represent, although most of these records are probably *P. pacifica*. They conclude that *Primnoa* occurs only on hard substrates (e.g., large boulders, exposed bedrock), in areas of low turbidity, and at a minimum yearly temperatures of 3.7 °C.

Comparisons.—Primnoa pacifica is distinguished from *P. resedaeformis* primarily by its possession of prominent, often spinose, basal scales, which are by far the largest sclerite on the polyp (Table 1). Also, *P. pacifica* usually has narrower and thus more numerous unpaired medial scales, five (not six) large marginal scales, and supporting scales between the marginals and opercularis.

Commercial Exploitation.—When cut and polished (Figs. 1C–D), cross sections of main stem —which may be up to 6 cm in diameter— resemble agate or petrified wood in medium and pale brown tones. As a by-product of halibut fishing, this coral yielded $20–$25 per lb to the fishermen and found a substantial market until about 1980. As colonies large enough to be useful probably are very old, it is likely that the standing crop on productive trawling grounds would soon be exhausted during routine fishing operations, sharply limiting supply. As has occurred with commercial red corals (*Corallium* spp.), intensive over-fishing can be expected to deplete the stock of colonies of usable size locally, but it is unlikely to threaten the species with extinction. A reservoir of small but already reproductive colonies can be expected to avoid capture even on trawling grounds, and large colonies certainly will persist on bottom too rough for trawling. More recently, Krieger and Wing (2002) report a negligible jewelry harvest of only 200 kg yr^{-1}.

Distribution—Sea of Japan (Kinoshita, 1907; Broch, 1935), Sagami Bay, Japan (Kinoshita, 1907), Sea of Okhotsk (Broch, 1935), Aleutian Islands, Gulf of Alaska, Alexander Archipelago to Dixon Entrance, off La Jolla, California; 64–800 m. R. Stone (Auke bay Lab, Juneau, pers. comm.) reports specimens from 9 m from Glacier Bay, Alaska. Numerous other records from the Aleutians and Gulf of Alaska reported as *Primnoa* sp. (e.g., Cimberg et al., 1981) remain unconfirmed.

Primnoa pacifica var. *willeyi* Hickson, 1915
(Figs. 1C–E, 7–8)

Primnoa willeyi Hickson, 1915: 551–553, text fig. 3 (type locality: wsw Moreseby Island, British Columbia, 183 m).—Kükenthal, 1924: 267.—Aurivillius, 1931: 296 (comparisons).—Cimberg et al. 1981: 8, 10, 12 (remarks).—Heifetz, 2002: 22, 26 (listed).—Krieger and Wing, 2002: 83 (mention).—Andrews et al. 2002: 102 (comment).—Wing and Barnard, 2004: 24 (listed).

Material Examined.—"taken by fishermen out of Petersburg, Kupreanof I., Alexander Archipelago, Alaska," exact locality not recorded, 146 m, one nearly complete colony 2.2 m tall, preserved dry and a small piece rehydrated in alcohol, SEM 1828-1831, C1123-1127, USNM 58084; vicinity of Petersburg, Kupreanof I., Alexander Archipelago, exact locality and depth not recorded, 19 August 1947, one small branch

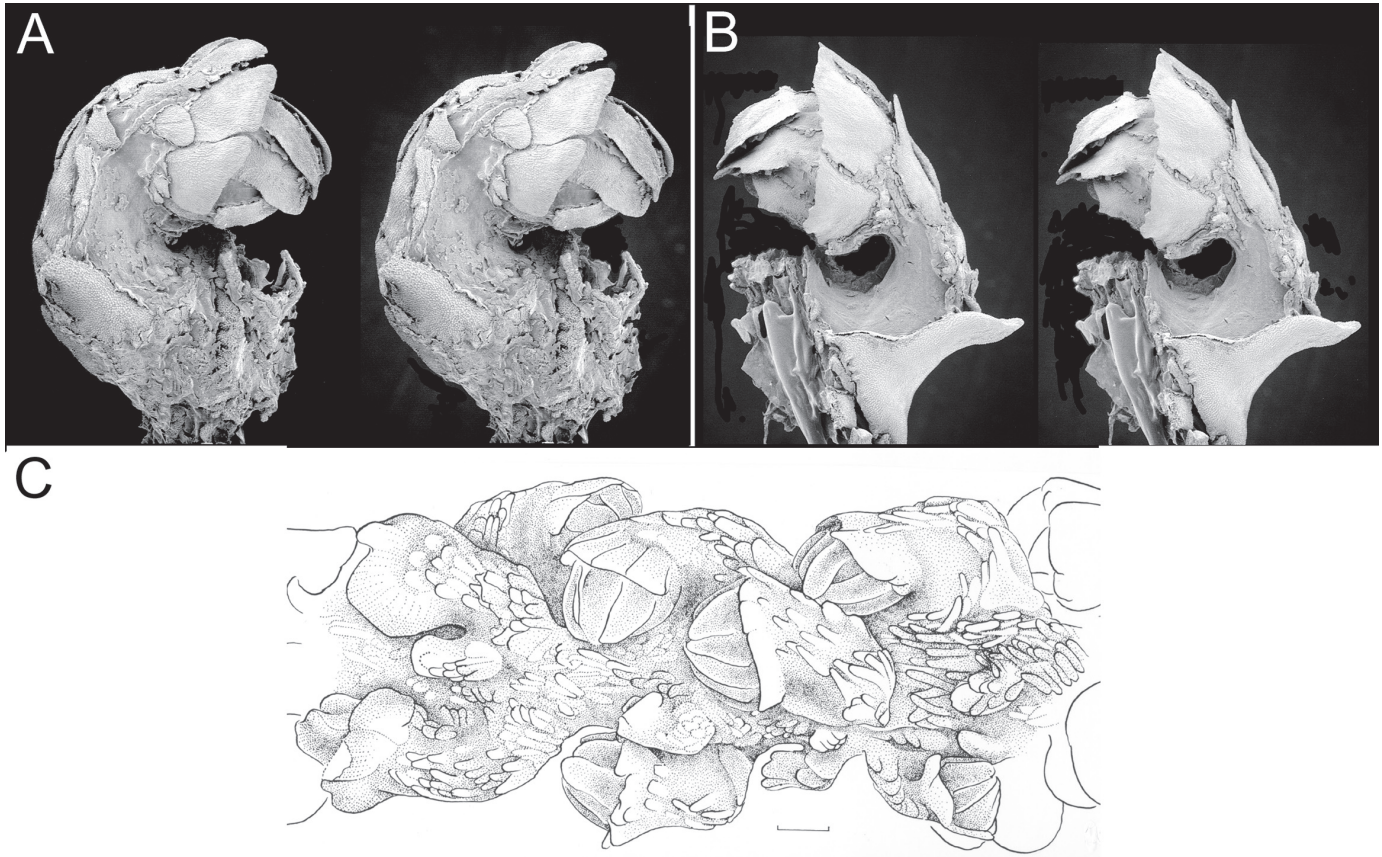

Figure 7. *Primnoa pacifica* var. *willeyi* (A–B, Kupreanof Island, USNM 58084; C, polyps of syntype, BMNH 1962.7.20.188): A, B, lateral stereo views of polyps with large-spined basals, ×11; C, drawing of a branch fragment, scale bar = 1 mm.

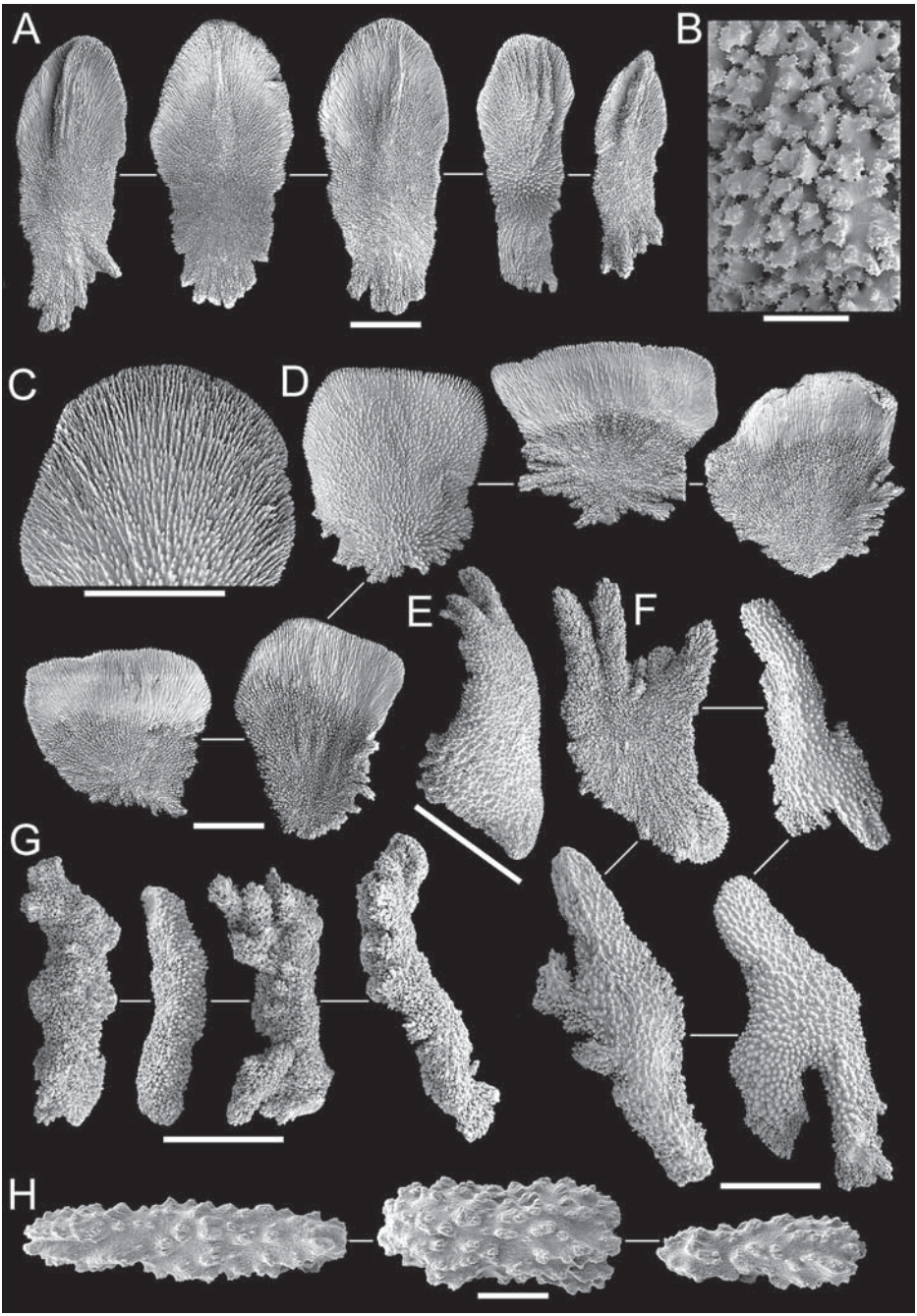

Figure 8. *Primnoa pacifica* var. *willeyi*, constituent sclerites from a colony from Kupreanof Islands (USNM 58048): A, opercular scales; B, tubercles on inner surface of a coenenchymal scale; C, spination on outer distal surface of an opercular scale; D, marginal scales; E, one basal scale; F, body wall scales; G, coenenchymal scales; H, tentacular rods. Scale bars: E = 1 mm, A, C–D, F–G = 0.5 mm, B, H = 0.05 mm.

of a large colony preserved dry, and three pieces of axis, one cut longitudinally and another transversely and polished, USNM 44058; off Petersburg, Alexander Archipelago, Kupreanof I., coll. Titus Ulke, date not recorded, branches from a large dry colony, USNM 40066; Chatham Sound, B. C., depth not recorded, coll. B. Eggleston, date not recorded, incomplete dry colony in very poor condition, identification questionable, USNM 52199; "Halibut fishing grounds," B. C., exact location not recorded, coll. Michaud Bros., 4 March 1922, one incomplete dry specimen, USNM 42135; Alb-4239, six dry branches, USNM 58396; Alb-4302, one colony in alcohol, USNM 1024424; Miller Freeman 93-9-10, one dry branch probably of a large colony, SEM 2507-2509, USNM 100834; Miller Freeman 01-04-01, one branch in alcohol and one dry, *USNM 1010785; FV Pat San Marie (AB78-119), SW of Dall Island, Dixon Entrance, B. C., depth unknown, July 1978, one branch in alcohol, USNM 111073; FV Aleutian No.1 (AB01-51), one dry branch, USNM 1004603; off British Columbia, depth unknown, about 1938, one dry branch, MCZ 3855; Alvin 4028, branches in alcohol, USNM; syntypic branches of *P. willeyi*, probably from one colony (in alcohol transferred from formalin), BMNH 1962.7.20.188.

Diagnosis.—Differs from the typical form in having twisted polyps with a narrow mid section and a bulbous distal end, and medial body wall sclerites that are restricted to the abaxial side.

Remarks.—Variety *willeyi* differs from the typical variety by having basal scales that are usually smaller than their marginals, often the same size as the medials or quite inconspicuous, but occasionally quite large and spined, just as large as those in the typical variety. Variety *willeyi* also differs from the typical variety in having more slender and often twisted, even recurved polyps that support a bulbous, flared distal end, evidenced by its having a much smaller mid- to distal polyp diameter ratio (Table 1). Also, its medial body wall scales cover only the abaxial body wall, not the lateral body wall, resulting in a larger exposed naked region of the polyp on the lateral and adaxial sides. Nonetheless, these differences are more of a matter of degree than kind, some specimens of variety *willeyi* having a range of basal scale size and shape that overlaps that of the typical form. The only consistent difference between the two taxa is the shape of the polyps, which, because the distribution of both taxa overlap (in two cases occurring at the same station), is considered herein to be only a varietal difference.

Kükenthal (1924) stated that *P. willeyi* is distinguished from *P. resedaeformis* by its somewhat smaller polyps and the weaker scale covering of the adaxial [sic] side of the polyps; the latter statement is probably an error for "abaxial," as the adaxial sides of polyps in all *Primnoa* are devoid of scales below the adaxial marginals.

Distribution.–Most verified records are from off British Columbia and contiguous Alexander Archipelago, Alaska, but it is also known from western Gulf of Alaska (Dickens Seamount) and Aleutian Islands (Amchitka); 183–755 m.

Primnoa wingi new species
(Figs. 1 H–I, 9–10)

Material Examined/Types.—Holotype: one dry colony, a smaller fragment in alcohol, SEM C1128-1130, C1132-1133, R/V Sea Storm 150, *USNM 1010257. Paratypes: FV Spirit of the North (AB01-67), one dry colony, USNM 1006247; FV Alaskan Beauty (AB01-68), one dry colony and branches, USNM 1004613; FV Patricia Lee (AB01-69), two dry branches, USNM 1004616; FV Patricia Lee (AB01-70), one dry branch, USNM 1004601; RV Verstraalen 941-53, two branches in alcohol, *USNM 100741; RV Verstraalen 941-118, five branches in alcohol, SEM 1131, *USNM 100740, 100844, and 1012503.

Type Locality.—52°30′57″N, 173°29′35″W (north of Amlia Island, Andreanof Islands, Aleutians), 213–220 m.

Diagnosis.—Basal scales inconspicuous; medial scales elongate, rarely over 0.2 mm wide, occurring in a narrow abaxial tract and immersed in tissue, often not seen. Marginal scales highly concave, forming a discrete girdle around polyp. Opercular scales uniquely shaped (see text), resulting in a porous operculum. Tentacular rods large (up to 0.5 mm) and often curved. Polyps very fleshy.

Description.—Colonies are roughly planar in shape and dichotomously branched, although the frequency of branching is low, the largest specimen (the holotype) having only seven branch axils in its 35 cm height. The holotype is only a partial colony, lacking its base and distal branches; its axis is 14.5 mm in basal diameter, rigid, striate, and black in color. No colonies were collected with an intact base. Terminal branches, which are always covered with polyps, are 13–15 mm in diameter. The color of the living colony is reddish-orange.

Polyps are densely crowded on all branch surfaces and usually directed downward, but because of their elongate shape and flaccid nature, they often curve or corkscrew in various directions, often resulting in an upward or sideways orientation. Polyps are long (8–12 mm) and slender, supporting a bulbous apical end, the ratio of mid- to apical polyp diameters being 0.25–0.36.

The medial sclerites form a narrow strip 2–4 across along the abaxial midline of the polyp, these sclerites being elongate, flattened scales up to 1.5 mm in length and only 0.17–0.19 mm in width. In a dried and partially bleached polyp the medial sclerites (Fig. 10F) can be seen to form a narrow abaxial "spine" within the abaxial polyp wall, but afford little actual support for the polyp. The polyp body wall tissue on both sides of the abaxial midline, as well as the lateral and adaxial surfaces, are naked and quite fleshy, sometimes appearing translucent. There are no definable basal scales, the medial scales indistinguishably merging with the coenenchymal scales of the axis. The eight marginal scales are by far the largest sclerites, rectangular to squarish in shape, the six abaxial and lateral marginals up to 2.1 mm in height and 2.0 mm in width, the adaxial marginals about 1.4 mm in both dimensions. Altogether the eight marginals form a prominent circular and continuous collar that envelopes the lower opercular scales. The inner surface of the marginals is highly concave (almost hemispherical), tuberculate only on their proximal half and striate on their distal. The outer surface is covered with sharp, aligned spines, those toward the apical end up to 50 μm in length (Fig. 9F). The opercular scales are uniquely shaped, composed of a rectangular but often bifid base comprising the lower 25% of the scale and being about 0.4 mm wide; a narrow neck region comprises the next 10% of the scale, which

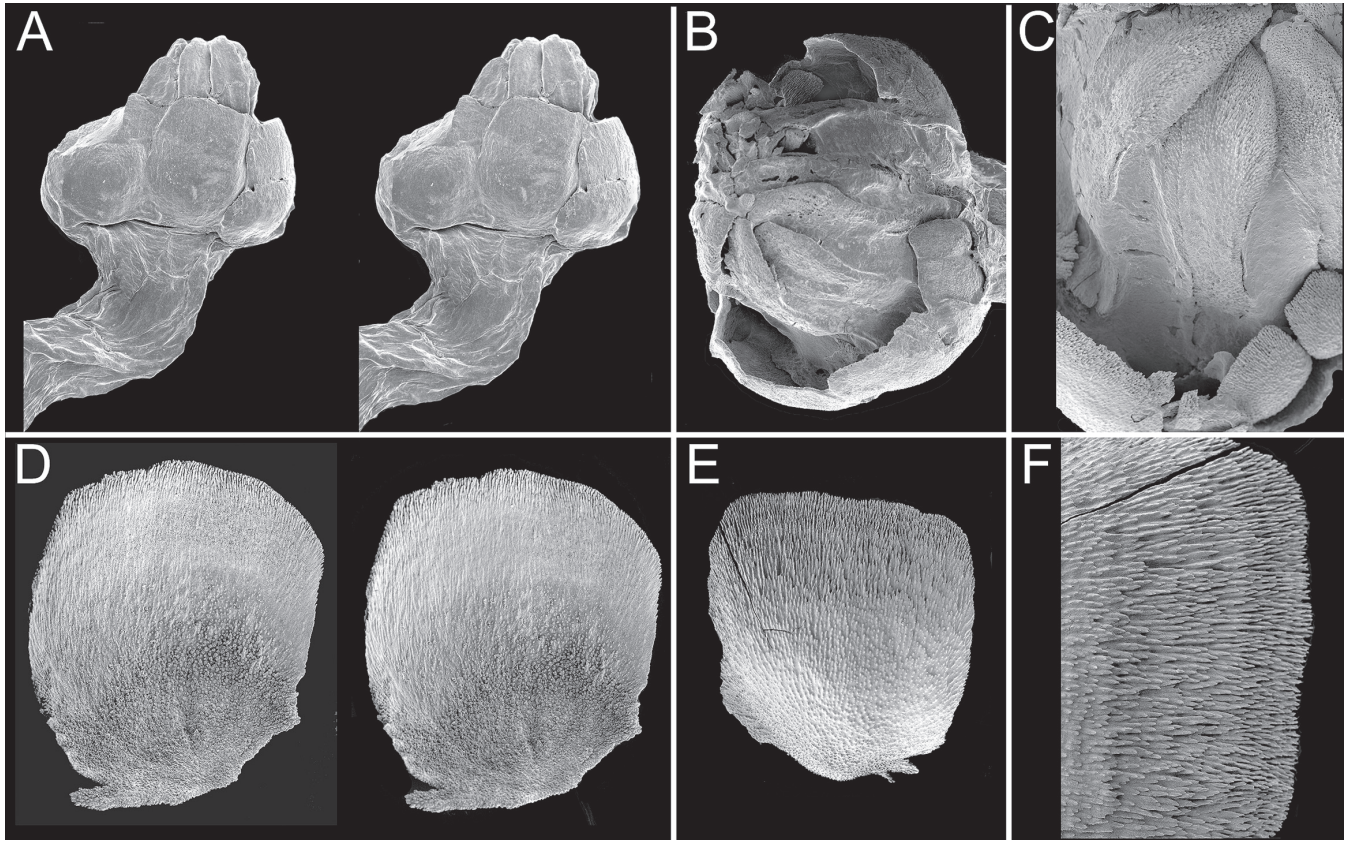

Figure 9. *Primnoa wingi,* sp. nov., holotype: A, lateral stereo view of polyp, ×8; B, opercular view of a polyp, ×11; C, opercular view of a polyp showing naked region (dried tissue) between opercular bases, ×22; D, stereo view of highly concave inner surface of a marginal scale, ×22; E, outer surface of an adaxial marginal scale, ×22; F, spination on distal outer edge of a marginal scale, ×45.

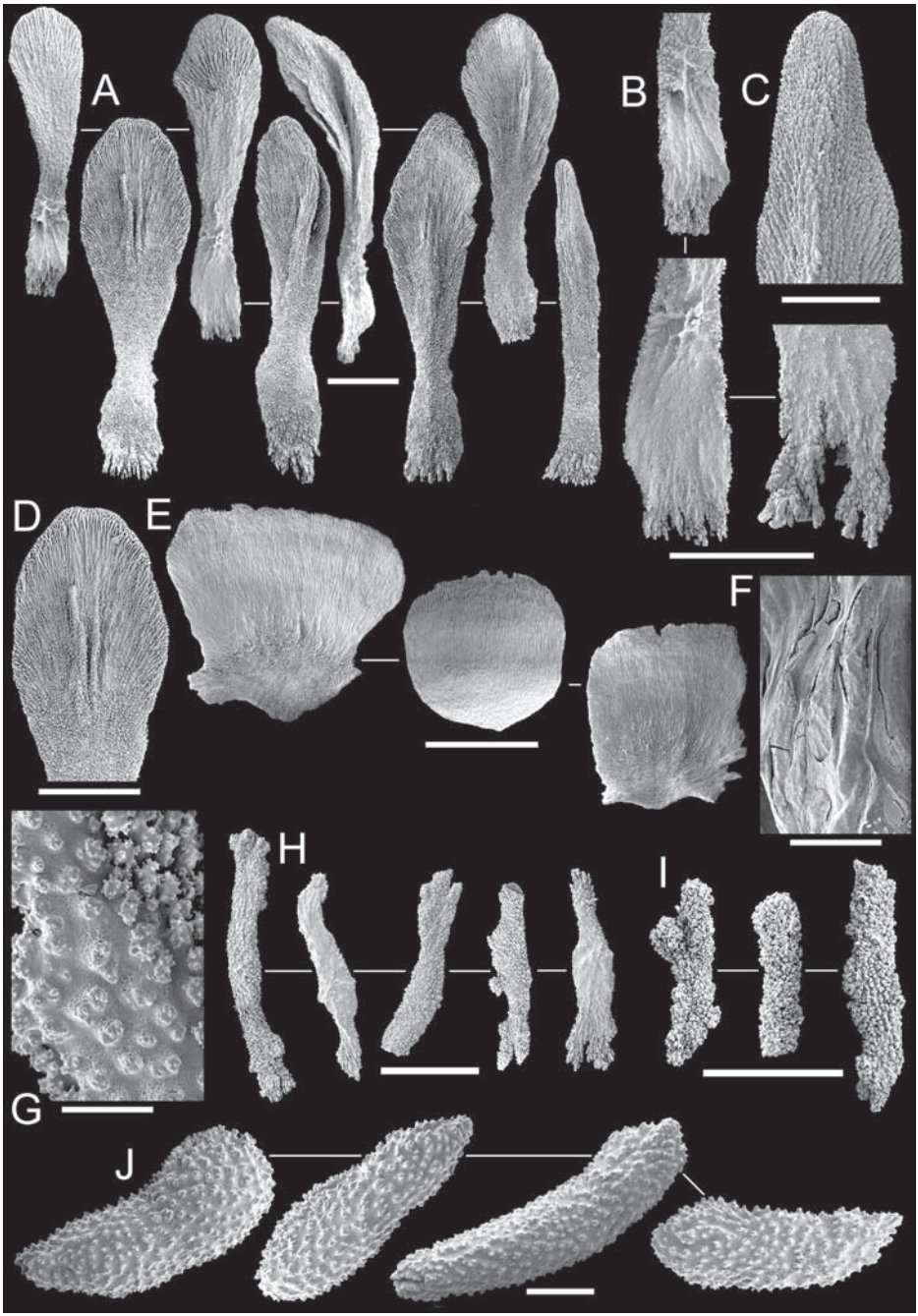

Figure 10. *Primnoa wingi*, sp. nov., constituent sclerites from the holotype: A, opercular scales; B, slender outer proximal regions of opercular scales; C–D, inner distal region of two opercular scales; E, marginal scales; F, several body wall sclerites in situ; G, tubercles on inner surface of a coenenchymal scale; H, body wall sclerites; I, coenenchymal sclerites; J, tentacular rods. Scale bars: E = 1 mm, A–B, D, F, H–I = 0.5 mm, B (lower right), C = 0.25 mm, J = 0.10 mm, G = 0.05 mm.

is about 0.25 mm in width; and a large distal spatulate region comprises the remaining 65% of the scale, which is up to 0.70 mm wide, an entire abaxial opercular being up to 2.6 mm in length. The opercular are strongly curved to arch over the top of the polyp. The neck region is quite fragile and often breaks in sclerite preparations. The inner surface of the opercular is tuberculate, the tubercles measuring 11–15 μm in diameter, the distal region bears one or two low longitudinal keels, and the tip of the distal region bears numerous low ridges that extend to the edge of the scale (Fig. 10D). The outer surface of the opercular basal region is fairly flat and unornamented, whereas the short neck region bears tall reticulate ridges; the distal region is covered with small spines and occasionally also bears a prominent longitudinal ridge. Because the operculars are so narrow basally (i.e., the neck region) they do not overlap or even meet laterally, thus the operculum has eight elongate, ovoid, naked regions devoid of sclerites (Fig. 9C) but held together with tissue. The tentacular sclerites are straight to slightly curved, rotund rods, measuring up to 0.5 mm in length and 0.17 mm in diameter, but most smaller; i.e., 0.40 × 0.15 mm. Coenenchymal sclerites are elongate and somewhat irregular in shape but with few bifurcations, and rarely over 0.9 mm in length and 0.15 mm in width.

Remarks.—Judging from the way in which the polyps adhere to one another and to the branch when dried, it would appear that this species produces large quantities of mucous during collection. According to B. Wing (Auke Bay Lab, Juneau, pers. comm) this species attains a height of 5 m.

Comparisons.—*Primnoa wingi* is most similar to *P. pacifica* var. *willeyi*, particularly in its slender adaxial body wall sclerites, but *P. wingi* has unique features that easily distinguish from all other congeners (Table 1), including its distinctive spoon-shaped opercular scales; highly concave marginal scales; large curved tentacular rods; relatively short coenenchymal sclerites; large, extremely fleshy, flaccid polyps; and large distal branch diameter. Furthermore, distinctive basal scales are not present.

Etymology.—Named in honor of Bruce Wing, strong advocate of invertebrate zoology in the Gulf of Alaska.

Distribution.—Aleutian Islands, Alaska: Rat Islands, Andreanof Islands, south of Yunaska Island; 208–512 m.

Primnoa notialis new species

(Figs.1 F–G, 11–13)

Primnoa resedaeformis notialis.—Heikoop et al. 2002: 118 (*nom. nud.*).—Risk et al. 2002: 126 (*nom. nud.*).

Material Examined/Types.—Holotype: *Eltanin*-1346, one colony in alcohol (SEM 1812, 1824-1827, 1832-1834), USNM 87621. Paratypes: *Eltanin*-1343, many large branches and smaller fragments, all paratypes preserved in alcohol (SEM 177, 187, 290, 1392-1393, 1400, 1470), USNM 58169-58172; young variant form (SEM 2558-2559), USNM 87623; *Eltanin*-1345, one branch (paratype) in alcohol, USNM 98264; *Eltanin*-1346, one colony devoid of polyps but with many individual detached polyps, in alcohol, USNM 87624, and a massive dry calcified basal branch without polyps USNM 87625, and one large colony and many smaller branches (most in alcohol, some branched dried) (SEM C1113-C1116), USNM 87627, and one small variant

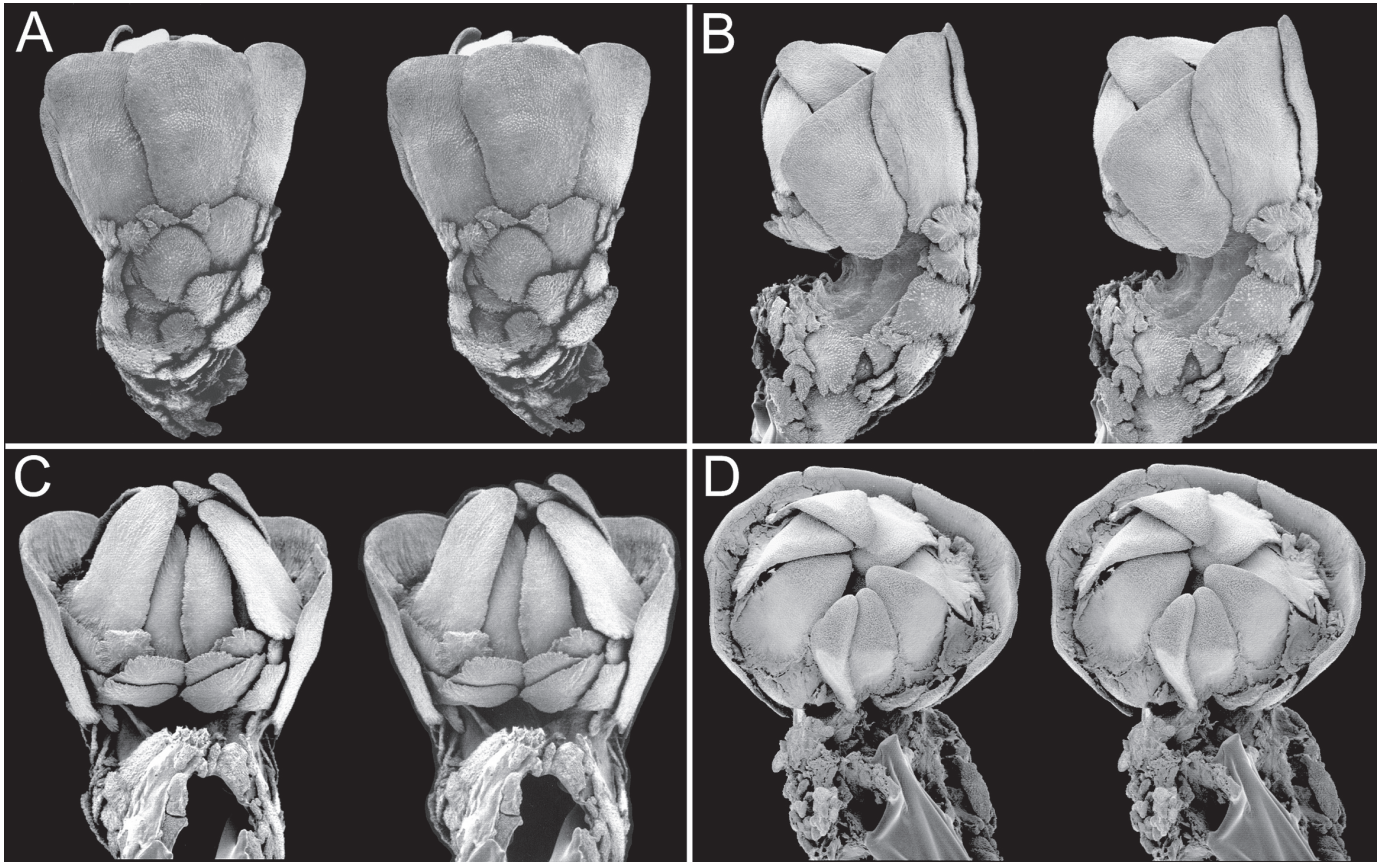

Figure 11. *Primnoa notialis*, sp. nov., holotype: A, abaxial stereo view of a polyp, ×13; B, lateral stereo view of a polyp, ×13; C, adaxial stereo view of a polyp showing pairs of adaxial opercular scales, ×15; D, opercular stereo view of a polyp, ×13.

colony attached to *Solenosmilia variabilis* (Duncan, 1873) (SEM 1394-1397, 2557), USNM 87622.

Type Locality.—54°49′S, 129°48′W (Subantarctic seamount on the Heezen Fracture Zone of the Eltanin Fracture Zone System), 549 m.

Diagnosis.—Primnoa with basal body scales not strongly developed, without conspicuous projecting marginal processes or spines; medial body wall scales irregularly arranged; 4–5 large marginal scales, the remaining marginals much smaller.

Description.—The growth form of the colonies is similar to that of typical *resedaeformis*. The largest fragments are about 40 cm tall, indicating that complete colonies would be much larger, possibly a meter or more in height; the holotype is a branch fragment 23 cm in length. The stoutest main stem is about 15 mm in diameter, hence much smaller than the trunk of fully developed colonies from the North Pacific. A main stem with holdfast (USNM 87624) has a calcareous basal thickening like that of *P. resedaeformis*, and another massive calcareous holdfast from *Eltanin*-1346 (USNM 87625) gives rise to a very large stout main trunk axis 23.5 mm in diameter, spreading over the substrate to a radius of 15 cm and to a thickness of 13 mm in places. Although this specimen is devoid of polyps, the axial material is identical with that of the other specimens and could hardly by anything but *P. notialis*. In thinner branches and twigs the axis has a brilliant golden sheen but in most places is brown with a dull metallic luster; in some places it may be very dark brown, almost black, with no gloss. The axial surface is longitudinally grooved. Branching is irregularly dichotomous and roughly in the same plane; the terminal branchlets curve upward and often are rather sinuous, some of them with a prominent apex devoid of polyps, others with a blunt tip about 9 mm in diameter formed by the bases of the uppermost polyps. Branchlets originating from the lower side of more or less horizontal branches turn upward through as much as 180°.

The polyps are densely crowded all around the branches, most of them bent downward, but individuals directed upward and obliquely in various directions are not uncommon. They are so closely and irregularly placed that usually no verticillate arrangement is obvious, but areas showing a tendency toward arrangement in whorls can be found here and there throughout the colonies (see "variation"). Depending upon girth, the circumference of the axis accommodates from five or six to up to ten or more polyps. For the most part the polyps are only slightly flared distally (mid-to distal ratio of polyp diameter 0.5–0.6), having a campanulate aspect. They are 3–5 mm in length, 1.5–2.0 mm in diameter near the middle, and 2–3 mm across the marginal scales.

Sclerites are fully developed only on the abaxial side of the polyp, usually only indistinctly arranged in two rows if at all. The unpaired basal scales are slightly or not at all larger than the medials and do not have marginal projections. In by far the vast majority of polyps, the medial abaxial scales, which occur in 3–6 indistinct tiers, are irregularly disposed. They consist of larger elliptical to rhomboidal-shaped scales 0.8–1.1 mm in width and numerous tiny supernumerary irregularly-shaped sclerites 0.15–0.40 mm in width arranged around the edges of the larger scales. The larger medial scales are rather thick and slightly convex above, often with irregular digitiform edges. The marginal scales differ in size, each polyp usually having five large, slightly convex, rectangular marginal scales in the abaxial and outer lateral positions, these scales up to 2.3 mm in height and 1.7 mm in width, their distal edges projecting well above (0.50–0.75 mm) the insertion of the proximal edges of the

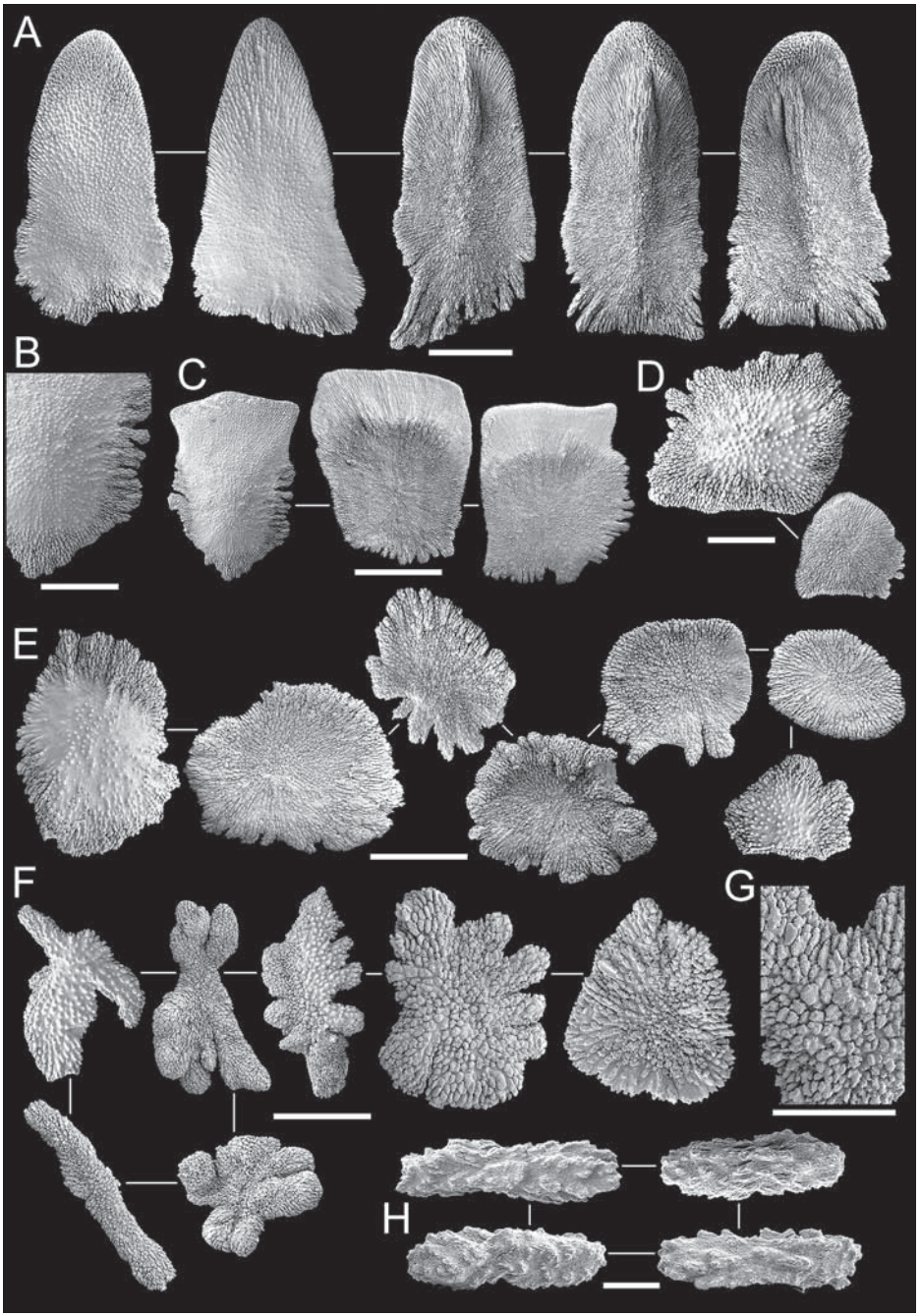

Figure 12. *Primnoa notialis*, sp. nov., constituent sclerites from a paratype from *Eltanin*-1346 (USNM 87627): A, opercular scales; B, edge of outer surface of a marginal scale; C, marginal scales; D, adaxial marginal scales; E, body wall scales; F, coenenchymal scales; G, tubercles on inner surface of a coenenchymal scale; H, tentacular rods. Scale bars: C = 1.0 mm, A–B, D–F = 0.5 mm, G = 0.20 mm, H = 0.05 mm.

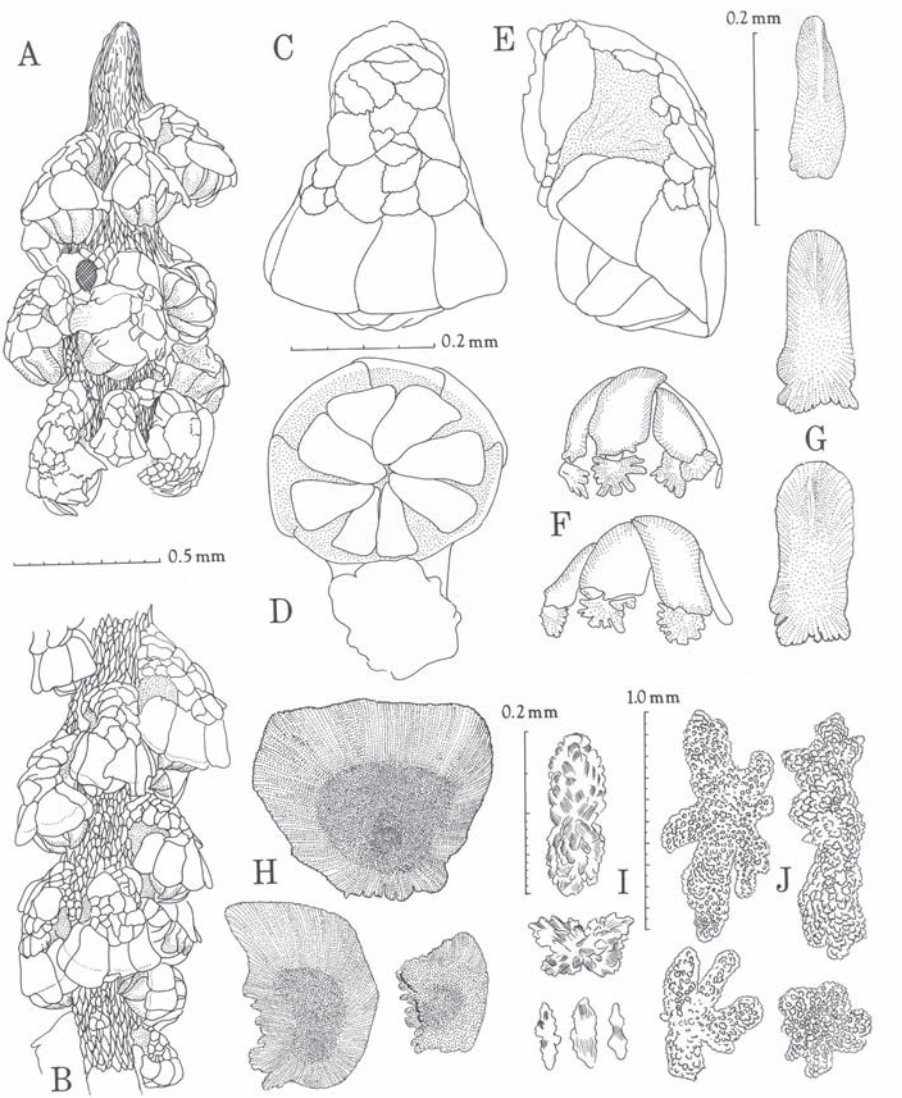

Figure 13. *Primnoa notialis*, sp. nov., drawings of the holotype: A, branch tip with terminal growing point; B, part of branch showing irregular arrangement of polyps; C–E, abaxial, opercular, and lateral views of a polyp; F, lateral view of operculum of two polyps showing fracture of basal part of opercular scales; G, adaxial (top), outer lateral (middle) and adaxial opercular scales; H, abaxial, outer lateral, and adaxial marginal scales; I, tentacular sclerites; J, coenenchymal sclerites. Scale as indicated.

opercular scales, together forming a prominent hood for the operculum. Their distal and lateral edges are finely serrate, their proximal edges digitiform. The lower two-thirds of the inner surface is tuberculate, the upper third striate; the outer surface is granular. Two pairs of smaller (0.75–1.0 mm in width), squarish marginal scales occur in the inner lateral position and 2–3 pairs of slightly smaller marginal scales also occur in the adaxial position (Fig. 12D). The opercular scales curve slightly to mold to the curvature of the polyp, forming an operculum consisting of eight isosceles-tri-

angular shaped scales with a rounded apex, when folded together forming a compact, prominent blunt cone. The abaxial operculars of fully developed polyps are 1.8–1.9 mm in height and 0.8–1.0 mm wide at the base; the adaxial operculars are 1.2–1.4 mm in height and 0.6–0.7 mm wide at the base. The operculars have a low, blunt longitudinal keel on their inner surface as well as being covered with tubercles on the proximal portion and striate towards the tip. The outer opercular surfaces are covered with granules, which are developed into small spines toward the tip. The outer and lateral edges of the operculars are finely serrate, the proximal edge digitiform. Often a small, rounded scale lies beneath each of the operculars, as was noted also in *P. pacifica* by Kinoshita (1908a: 44, pl. 6, fig. 49). The outer surfaces of all body wall and opercular scales are covered with a low, fine granulation, the granules measuring 15–20 μm in diameter, and arranged in radiating lines from an origin point about one-third up from the base of each sclerite. Tentacular rods are straight, rotund and up to 0.17 mm in length and 0.035–0.045 in diameter. Coenenchymal sclerites are thick, elongate rods, irregularly rounded plates, and scales with lobed margins, varying from about 0.5 to a little more than 1 mm in greatest length. Their outer surfaces are covered with granules 25–28 μm in diameter whereas their inner surfaces are covered with complex tubercles, some of which are as large as 35 μm in diameter.

Many polyps contain several dozen small yellow eggs, each about 0.45 mm in diameter.

Variation.—In a few specimens (USNM 87622, 87623), unfortunately in damaged condition, the body scales of the polyps are larger, thinner, and more regularly arranged, and the opercular scales are more sharply pointed. As these specimens are small colonies attached by their holdfasts to branches of scleractinian coral, it is possible that their polyps retain the basic arrangement of body scales that is disrupted on large colonies, as was noted in the young colony of *P. pacifica*. The arrangement of body scales is similar to that of some specimens of typical North Atlantic *resedaeformis*.

Although the predominant arrangement of polyps is random, in fact, in small colonies the polyps are often arranged in whorls, but these become disrupted almost at once by asymmetrical growth and the production of young polyps between older ones. The polyps on the branch tip illustrated on Figure 13B clearly shows the polyps arranged in a somewhat oblique whorl. But, in most cases, the polyps are much more crowded near the branch tips where the whorls are completely obscured and the branches are distinctly clavate.

Comparisons.—*Primnoa notialis* most closely resembles *P. pacifica* in the irregular size and arrangement of the medial body scales, but no polyps with large, *Narella*-like basal scales have been found in the present material. In this respect, *P. notialis* is more like typical *resedaeformis* of the North Atlantic (Table 1).

Etymology.—The species is named *notialis* (Latin: southern) for the only known species of *Primnoa* south of the equator.

Distribution.—Known only from a Subantarctic seamount on the Heezen Fracture Zone of the Eltanin Fracture Zone System at depths of 549–915 m, the site of a deep-water coral bank composed primarily of the scleractinian coral *S. variabilis* (see Cairns, 1982).

Table 1. Distinguishing characteristics of the species of *Primnoa*.

	P. resedaeformis	*P. pacifica* typical	*P. pacifica* var. *willeyi*	*P. wingi*	*P. notialis*
Color alive	Bright pink.	Pink.	"Scarlet," orange.	Reddish-orange.	Unknown.
Terminal branch diameter (including polyps)	9–11 mm.	7.5–9.0 mm.	6–9 mm.	13–15 mm.	8–9 mm.
Polyp length; ratio of mid- to distal polyp diameter	5–6 mm; 0.6–0.7	5–6.5 mm; 0.53–0.67	5–6 mm; 0.25–0.43	8–12 mm; 0.25–0.36	3–5 mm; 0.5–0.6
Body wall basal scales: size and shape; marginal spines; paired	Same size or slightly wider but shorter than medials; no marginal spines; paired.	Largest of sclerites (massive); often with a large marginal spine (*Narella*-like); paired.	Variable: large and spined (*Narella*-like) or small; paired.	Inconspicuous, same as medials; no marginal spines; unpaired.	Small, size and shape of medial scales; no marginal spines; unpaired.
Body wall medial abaxial scales: shape; mx. width; number; paired	Rectangular, flat; to 1.5 mm width; 2–5 linearly arranged pairs.	Variable: rec-tangular to elongate; up to 1.5 mm in length and 0.5–0.6 mm wide; 2–5 across in three irregular tiers; usually not paired.	Like typical form, but do not occur on lateral edges of polyp.	Elongate, embedded in tissue along abaxial spine; up to 1.5 mm long and less than 0.2 in width; 2–3 across; not paired.	Elliptical, square; 1.0–1.1 mm wide; numerous, including supernumerary; unpaired, irregularly disposed.
Body wall marginal scales: shape; number and size	Rectangular, flat; usually six large and two smaller adaxial.	Rectangular; usually five large and three smaller adaxial plus "support scales".	Like typical form.	Rectangular to square; six large and two smaller adaxial, highly concave.	Rectangular; five large and 3–4 smaller adaxial.
Opercular scales: shape and size of abaxial opercular; keel	Isosceles, blunt- tipped, 2.1 mm; low, blunt keel.	Isosceles or hastate, blunt tipped, up to 2.8 mm; 1–4 prominent, ridged keels.	Isosceles; up to 2.3 mm; one or more ridged keels.	Uniquely shaped (see text), up to 2.6 mm; 1–2 blunt keels.	Isosceles, blunt-tipped, up to 1.9 mm; low keel.
Tentacular rods: size and shape	Straight; 0.18 × 0.045 mm.	Straight, rotund; 0.32 × 0.12 mm.	Straight, rotund; 0.22 × 0.07 mm.	Straight to curved, rotund; 0.50 × 0.17 mm.	Straight, rotund; 0.16 × 0.045 mm.
Distribution; depth range	North Atlantic: Virginia Beach to Greenland (91–548 m); Eastern Atlantic: Greenland to Scotland; 95–1,020 m.	Honshu, Japan to California; 9–800 m.	Aleutian Islands to British Columbia; 183–755 m.	Aleutian Islands; 208–512 m.	Subantarctic seamount; 549–915 m.

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Literature Cited

Andrews, A. H., E. E. Cordes, M. M. Mahoney, K. Munk, K. H. Coale, G. M. Cailliet, and H. Heifetz. 2002. Age, growth and radiometric age validation of a deep-sea, habitat-forming gorgonian (*Primnoa resedaeformis*) from the Gulf of Alaska. Hydrobiologia 471: 101–106.

Aurivillius, M. 1931. The Gorgonarians from Dr. Sixten Bock's expedition to Japan and Bonin Islands 1914. K. Svenska Vetensk.-Akad. Handl. (3)9(4): 337 p.

Bayer, F. M. 1956. Octocorallia. Pages F166–189, 192–231 *in* R. C. Moore, ed. Treatise on invertebrate paleontology. University of Kansas Press, Lawrence. 498 p.

_____ and J. Stefani. 1989. Primnoidae (Gorgonacea) de Nouvelle-Calédonie. Mém. Mus. natn. Hist. nat., Paris, (4)10(A no. 3): 449–476.

_____, M. Grasshoff, and J. Verseveldt (eds.). 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. E. J. Brill, Leiden. 75 p.

Breeze, H., D. S. Davis, and M. Butler. 1997. Distribution and status of deep sea corals off Nova Scotia. Ecology Action Centre, Halifax. 58 p.

Broch, H. 1912. Die Alcyonarien des Trondhjemsfjordes II. Gorgonacea. K. Norske Vidensk. Selsk. Skr. 1912, No. 2: 48 p.

_____. 1935. Oktokorallen des Nördlichsten Pazifischen Ozeans und ihre Beziehungen zur Atlantischen Fauna. Avh. norske VidenskAkad., Oslo Matematisk- naturvidenskapelig Klasse 1935 1: 53 p.

_____. 1940. Anthozoa, mainly from Pacific waters, collected by USSR Expeditions 1930-1932. Explorations des Mers de l'USSR 23: 5–22.

_____. 1949. Post-glacial interchange between Pacific and Atlantic deeper living boreal faunas? Norsk geogr. Tidsskr. 12: 126–141.

Cairns, S. D. 1982. Antarctic and Subantarctic scleractinia. Antarctic Res. Ser. 34: 74 p.

Cimberg, R. L., T. Gerrodette, and K. Muzik. 1981. Habitat requirements and expected distribution of Alaska coral. Final report, Research Unit 601, VTN Oregon, Inc., U. S. Dept. of Commerce, NOAA, Anchorage. 54 p.

Clusius, C. 1605. Exoticorum libri decem: quibus animalium, plantarum, aromatum, aliorumque perigrinorum fructuum historiae discribuntur. Officina Plantiniana Raphelengii, Antverpiae. 10, 378, 5 p.

Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean. Mem. Mus. comp. Zool. Harv. 53: 317 p.

Ellis, J. and D. Solander. 1786. The natural history of many curious and uncommon zoophytes ... systematically arranged and described by the late Daniel Solander. Benjamin White and Son, London. 208 p.

Esper, E. J. C. 1788. Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. Theil 1. Raspichen Buchhandlung, Nürnberg. 97–192 p.

_____. 1791. Die Pflanzenthiere in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. Theil 2. Raspischen Buchhandlung, Nürnberg. 97–180 p.

France, S. C and L. L. Hoover. 2001. Analysis of variation in mitochondrial DNA sequences (ND3, ND4L, MSH) among Octocorallia (=Alcyonaria)(Cnidaria: Anthozoa). Bull. Biol. Soc. Wash. 10: 110–118.

_____ and _____. 2002. DNA sequences of the mitochondrial COI gene have low levels of divergence among deep-sea octocorals (Cnidaria: Anthozoa). Hydrobiologia 471: 149–155.

Grasshoff, M. 1991. Die von E. J. C. Esper 1788-1809 beschriebenen Anthozoa (Cnidaria). Senckenberg. biol. 71(4/6): 325–368.

_____ and H. Zibrowius. 1983. Kalkkrusten auf Achsen von Hornkorallen, rezent und fossil. Senckenberg. marit. 15(4/6): 111–145.

Gray, J. E. 1857 (1858). Synopsis of the families and genera of axiferous Zoophytes or barked corals. Proc. Zool. Soc. Lond. 1857: 278–294.

_____. 1870. Catalogue of the lithophytes or stony corals in the collection of the British Museum. British Museum, London. 51 p.

Grube, E. 1861. Beschreibung einer neuen Coralle (*Lithoprimnoa arctica*) und Bemerkungen über ihre systematiche Stellung. Breslau Schles. Ges. vaterländ. Cultur. 1: 167–176.

Gunnerus, J. E. 1763. Om en Søevext, allevegne ligesom besat med Frøhuuse, *Gorgonia resedaeformis.* Trondhjem. Selsk. Skr. 2: 321–329.

Hickson, S. J. 1915. Some Alcyonaria and a *Stylaster* from the west coast of North America. Proc. Zool. Soc. Lond. 1915: 541–557.

Heifetz, J. 2002. Coral in Alaska: distribution, abundance, and species associations. Hydrobiologia 471: 19–28.

Heikoop, J. M., D. D. Hickmott, M. J. Risk, C. K. Shearer, and V. Atudorei. 2002. Potential climate signals from the deep-sea gorgonian coral *Primnoa resedaeformis*. Hydrobiologia 471: 117–124.

Houttuyn, M. 1792. De Zee-Gewassen. Pages I–vii+1–614, pls. 126–138 *in* Natuurlyke Historie of uitvoerige Beschryving der Dieren, Planten en Mineraalen, volgens het Samenstel van den Heer Linnaeus, 1(17). F. Houttuyn, Amsterdam.

Johnston, G. 1838. A History of the British zoophytes. W. H. Lizars, Edinburgh. 341 p.

_____. 1847. A History of the British Zoophytes, 2nd ed. John Van Voorst, London. Vol. 1, 488 p.

Jungersen, H. 1915. Alcyonaria, Antipatharia og Madreporaria. Conspectus Faunae Groenlandicae. Meddr Grønland 23: 1156–1212.

Kinoshita, K. 1907. Vorläufige Mitteilung über einige neue japanische Primnoidkorallen. Annotnes zool. jap. 6: 229–237.

_____. 1908a. Primnoidae von Japan. J. Coll. Sci. Imp. Univ. Tokyo, Japan 23: 74 p.

_____. 1908b. Gorgonacea no ikka Primnoidae ni tsuite. Zool. Mag. (Dobutsugaku Zasshi) 20: 517–528 (in Japanese).

_____. 1909. Gorgonacea no ikka Primnoidae ni tsuite, Zool. Mag. (Dobutsugaku Zasshi) 21: 1–10 (in Japanese).

Kramp, P. L. 1932. The Godthaab Expedition 1928. Alcyonaria, Antipatharia, and Madreporaria. Meddr Grønland 79: 20 p.

_____. 1939. Octocorallia. Zool. Iceland 2: 13 p.

Krieger, K. J. 2002. Coral (*Primnoa*) impacted by fishing gear in the Gulf of Alaska. Pages 106–116 *in* Willison, J. H. M. et al. eds. Proc. 1st Int. Symp. Deep-Sea Corals. Ecology Action Centre, Halifax.

_____ and B. L. Wing. 2002. Megafauna associations with deepwater corals (*Primnoa* sp.) in the Gulf of Alaska. Hydrobiologia 471: 83–90.

Kükenthal, W. 1915. System und Stammesgeschichte der Primnoidae. Zool. Anz. 46: 142–158.

_____. 1919. Gorgonaria. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "*Valdivia*", 1898-1899. 13: 946 p.

_____. 1924. Coelenterata: Gorgonaria. Das Tierreich 47. Walter de Gruyter and Co., Berlin. 478 p.

Lamarck, J. B. P. A. d. M. 1815. Sur les polypiers corticifères. Mém. Mus. Natl. Hist. Nat., Paris 1–2: 401–416, 467–476, 76–84, 157–164, 227–240.

Lamouroux, J. V. F. 1812. Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. Nouv. Bull. Sci. Soc. Philomatique, Paris 3: 181–188.

_____. 1816. Histoire des polypiers coralligènes flexibles, vulgairement nommés Zoophytes. F. Poisson, Caen. i-lxxxiv + 560 p.

Lepard, A. 2003. Analysis of variation in the mitochondrial encoded msh1 in the genus *Leptogorgia* (Cnidaria: Octocorallia) and implications for population and systematics studies. MS Thesis, College of Charleston.

Linnaeus, C. 1767. Systema naturae. Editio duodecima, reformata. Impensis Direct. Laurentii Salvii, Holmiae, 1: 533–1327.

Madsen, F. J. 1944. Octocorallia. Dan. Ingolf-Exped. 5: 70 p.

Milne Edwards, H. 1857. Histoire naturelle des coralliaires ou polypes proprement dits. Librairie Encyclopédique de Roret, Paris. 1: 326 p., 8 pls. # A1–6, B1–2.

Naumov, D. V. 1955. Species of coelenterates. Pages 51–68, pl. 7–11 *in* Atlas of the invertebrates of fareastern seas of U.S.S.R. Academy of Sciences, Moscow. (in Russian)

Opresko. D. M. 1980. Appendix B: Taxonomic description of some deep-sea octocorals of the Mid and North Atlantic. Pages B1–B30 *in* B. Hecker. Epifaunal zonation and community structure in three mid- and North Atlantic Canyons. Lamont-Doherty Geological Observatory, Palisades.

Pallas, P. S. 1766. Elenchus zoophytorum. Apud Franciscum Varrentrapp, Hagae Comitum. [1]–xvi, [17]–28, 451 p.

Risk, M. J., J. M. Heikoop , M. G. Snow, and R. Beukens. 2002. Lifespans and growth patterns of two deep-sea corals: *Primnoa resedaeformis* and *Desmophyllum cristagalli*. Hydrobiologia 471: 125–131.

Schimbke, G. O. 1915. Studien zur Anatomie der Gorgonaceen. Arch. Naturgesch. 80 Jahrg. 1914 (Abt. A) 11: 81 p. (Also issued separately as Inaugural-Dissertation zur Erlangung der Doktorwürde der Hohen Philosophischen Fakultät der Schlesischen Friedrich-Wilhelms-Universität zu Breslau. Nicolaische Buchhandlung R. Stricker, Berlin.)

Shearer, T. L., M. J. H. van Oppen, S. L. Romano, and G. Wörheide. 2002. Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). Molec. Ecol. 11: 2475–2487.

Thomson, J. A. 1907. Note on *Primnoa reseda* from the Faeroe Channel, and on its embryos. Proc. Roy. Phys. Soc. Edinb. 17: 65–72.

Verrill, A. E. 1862. Notice of a *Primnoa* from Georges Bank. Proc. Essex Inst. 3: 127–129.

_____. 1864. Revision of the polypi of the eastern coast of the United States. Mem. Boston Soc. Nat. Hist. 1: 1–45.

_____. 1922. Alcyonaria and Actiniaria. Rep. Can. arct. Exped. 1913-18, 8(G): 164 p.

Versluys, J. 1906. Die Gorgoniden der Siboga-Expedition. II. Die Primnoidae. Siboga-Exped. 13a: 187 p.

Wing, B. L. and D. R. Barnard. 2004. A field Guide to Alaskan Corals. NOAA Tech. Memo. NMFS-AFSC-146: 67 p.

Willison, J. H. M. et al. (eds.). (2001) 2002. Proc. 1st Int. Symp. Deep-Sea Corals. Ecology Action Centre, Halifax, 231 p.

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Appendix 1. Station data

Station	Latitude	Longitude	Depth (m)	Date
		Alvin		
AD-4028	54°33.17′N	136°50.64′W	755	4 Aug 2004
		Auke Bay (AB) stations		
AB-70-270	59°42′24″N	149°06′40″W	170	1 Oct 1970
AB-94-21	57°22.86′N	136°22.38′W	276	3 Jun 1994
AB-01-47	51°50.53′N	176°00.14′E	362	5 Dec 2000
AB-01-50	51°24.79′N	178°50.03′W	640	2 Feb 2001
AB-01-51	51°13.14′N	179°25.42′E	399–501	June 2000
AB-01-67	51°59.25′N	176°49.52′W	512	9 Mar 2000
AB-01-68	52°07.44′N	177°51.05′E	208–435	6 Feb 2000
AB-01-69	51°58.45′N	177°32.85′E	411	3 Dec 2000
AB-01-70	52°08.11′N	176°07.29′E	475	14 Dec 2000
		U.S.F.C.S Albatross (Alb)		
2068	42°03′00″N	65°48′40″W	239	1 Sep 1883
2069	41°54′50″N	65°48′35″W	183	1 Sep 1883
2070	41°55′30″N	65°47′10″W	207	1 Sep 1883
2072	41°53′00″N	65°35′00″W	?1,477	2 Sep 1885
2474	44°18′30″N	57°10′40″W	243	4 Jul 1885
2480	44°06′00″N	57°16′30″W	346 m	5 Jul 1885
2523	41°48′30″N	65°44′30″W	203	13 Jul 1885
2527	41°59′N	65°35′30″W	214	13 Jul 1885
4239	Guard I., Behm Canal, B.C.		377–454	9 Jul 1903
4302	Pt. Amelius, Shakan, Sumner Str		309–388	24 Aug 1903
4329	Soledad Hill, La Jolla, CA		205–234	8 Mar 1904
		RV Albatross IV (Alb IV)		
IV-00-06-23	37°03.94′N	74°39.55′W	375–489	8 Sept 2000
		RV Eastward		
35982	40°23′42″N	68°07′53″W	415–680	15 May 1979
36016	40°24′49″N	67°41′37″W	182–612	23 May 1979
		RV Eltanin		
1343	54°50′S	129°50′W	567–604	7 Nov 1964
1345	54°51′S	129°46′W	915–1153	7 Nov 1964
1346	54°49′S	129°48′W	549	7 Nov 1964
		RV Gilliss		
7404-104	37°03′36″N	74°34′06″W	237–385	24 Nov 1974
		RV Miller Freeman		
MF93-9-10	54°36.25′N	133°21.2′W	329	24 Jul 1993
MF01-04-01	55°43′41″N	156°32′04″W	235	Oct 2000
		FV Sea Storm		
150	52°30′57″N	173°29′35″W	213–220	21 Jul 2002
		RV Verstraalen		
941-53	52°20′N	170°42′W	224	13 Jun 1994
941-118	51°32′04″N	176°35′55″W	427	2 Jul 1994