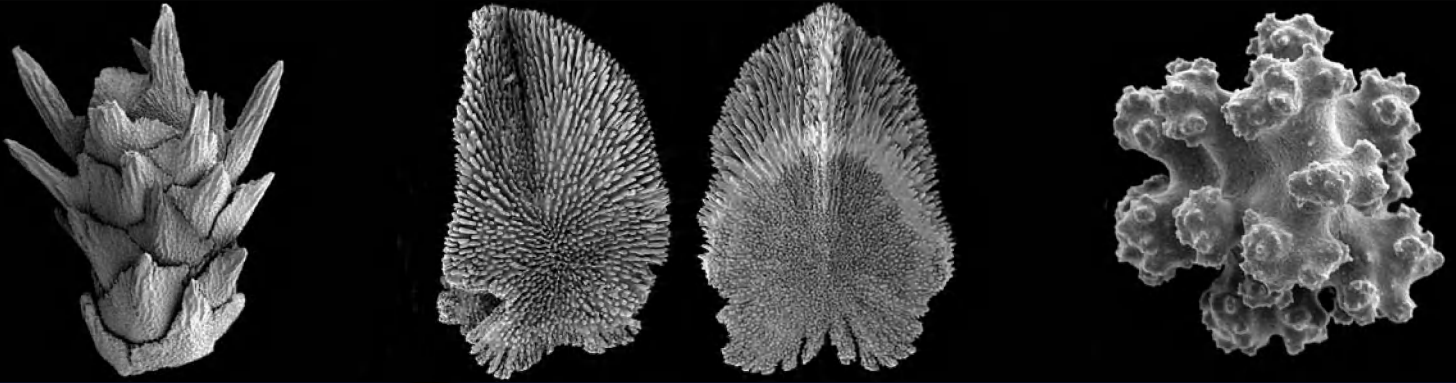




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A Revision of the Primnoidae
(Octocorallia: Alcyonacea)
from the Aleutian Islands
and Bering Sea

Stephen D. Cairns

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ABSTRACT

Cairns, Stephen D. A Revision of the Primnoidae (Octocorallia: Alcyonacea) from the Aleutian Islands and Bering Sea. *Smithsonian Contributions to Zoology*, number 634, vi + 55 pages, 17 figures, 3 tables, 2011.—Nineteen of the 31 octocoral species (61%) known from the Aleutian Islands belong to family Primnoidae, which form large deep-water (9–2,514 m) colonies providing habitat for one of the most productive fisheries in the North Pacific. These 19 species are described or redescribed and figured unless recent descriptions have been published. Eight new species are described, two in the genus *Thouarella* and six in the genus *Plumarella*. These two genera are redefined and differentiated by emphasizing the nature (keeled or not) of the inner side of their marginal scales and the inner side's articulation or lack thereof with the outer surface of the underlying opercular scales. *Dicholaphis* is proposed as a new subgeneric rank of the genus *Plumarella*, characterized by having polyps arranged on all sides of its branchlets, not on alternate opposite sides. A key is provided for the eight species of Aleutian *Plumarella*, and all 35 valid species in the genus are listed, including three new combinations: *P. superba*, *P. abietina*, and *P. recta*. A history of the Aleutian primnoids is recounted. Six primnoid species are reported from the Bering Sea, all of which also occur in the Aleutian Islands. Two-thirds of the Aleutian–Bering Sea primnoids are endemic to this region.

Cover images, from left to right: Figures 12b, 14d, and 13h (detail from each).

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A Revision of the Primnoidae (Octocorallia: Alcyonacea) from the Aleutian Islands and Bering Sea

INTRODUCTION

The Gulf of Alaska, particularly the Aleutian Islands, harbors one of the most productive fisheries in the world (Sanchez and Cairns, 2004; Stone and Shotwell, 2007). Their large size (some species up to 7 m; Krieger, 2001), longevity (some species over a hundred years; Andrews et al., 2002), and tendency to form high-density “coral gardens” make Aleutian deep-water octocorals important formers of habitat in deep water, providing vital refuges for fish and invertebrates (Heifetz, 2002; Krieger and Wing, 2002; Auster, 2005; Stone, 2006) but making them vulnerable to fishing impacts (Stone and Shotwell, 2007). Over the last decade, NOAA has sponsored research to determine the distribution, abundance, and species associations of these deep-water octocorals in an effort to assess their contribution to fisheries interactions and the need for conservation of these important ecosystems. However, the taxonomy of the Aleutian octocorals has not been revised since Nutting (1912), and most lists of species (e.g., Cimberg et al., 1981; Wing and Barnard, 2004; Heifetz et al., 2005; Stone and Shotwell, 2007) include a high percentage (almost half) of unidentified species as well as dated taxonomy. It is the purpose of this paper to taxonomically revise the Aleutian and Bering Sea primnoid species so that they can be discussed in a more meaningful way.

The Aleutian Islands certainly has the highest coral diversity in Alaska (Heifetz, 2002) relative to octocorals, stylasterids, and Scleractinia, but later claims of having “the highest abundance and diversity of coldwater corals in the world” (Heifetz et al., 2005:131; Stone, 2006) are overly exaggerated. In fact, using as a comparison the number of 31 as the total of valid, named nonpennatulacean octocoral species found in the Aleutian Islands (Stone and Shotwell, 2007; see below), there are 91 deep-water octocoral species known from the Hawaiian Islands (Cairns and Bayer, 2007), 89 species in Sagami Bay, Japan (A. K. Matsumoto

et al., unpublished poster [Bathymetric Distribution of the Deep-Water Octocorals (Cnidaria, Anthozoa) of Sagami Bay, Tokyo, Japan] presented at Third International Symposium on Deep-Sea Corals, Science and Management, University of Miami, 2005), 214 from the larger Japanese region (Imahara, 1996), and 166 deep-water species in the northwest Atlantic (Cairns, 2006, 2007a). However, the Aleutian Islands are distinctive in having a relatively high percentage of their octocoral fauna composed of primnoid species (i.e., 61%). The primnoid component of the Hawaiian Islands deep-water octocorals is only 31%, of Sagami Bay (36%), of the Japanese region (19%), and of the northwest Atlantic (22%). Of the 18 Aleutian primnoid species, seven also occur in the Bering Sea (Table 1). Twelve of the

19 (63%) are endemic to the Aleutian Islands–Bering Sea region (Table 1), whereas five species have broader distributions to the west (Okhotsk Sea, Sakhalin Island, Japan, and Indonesia), four have broader distributions to the east (two to the Alaskan coast, one to Panama, and one to California), and two are also found on Gulf of Alaska seamounts.

ABBREVIATIONS

The following abbreviations are used in the text.

Museums/Institution

AB Auke Bay Laboratory, Juneau, Alaska
BM The Natural History Museum, London

TABLE 1. The twenty-six primnoid species and one subspecies known from Alaska, including regions in which they have been collected (indicated with an x) and known depth range. A dash (–) indicates species is not known from that region; AI = Aleutian Islands.

Alaskan primnoid	West of Aleutians	AI	Gulf of Alaska seamounts	East of Aleutians	Bering Sea ^a	Depth range (m)
<i>Thouarella cristata</i> , n. sp.	–	x	–	–	x	94–768
<i>T. trilineata</i> , n. sp.	–	x	–	–	–	97–642
<i>Plumarella (Plumarella) spicata</i> Nutting, 1912	–	x	–	–	x	712–1,912
<i>P. (Dicholaphis) profunda</i> , n. sp.	–	x	–	–	–	2,514
<i>P. (D.) hapala</i> , n. sp.	–	x	–	–	–	120–384
<i>P. (D.) aleutiana</i> , n. sp.	–	x	–	–	x	79–517
<i>P. (D.) superba</i> (Nutting, 1912), n. comb.	x	x	–	–	x	29–888 (1,258) ^b
<i>P. (D.) nuttingi</i> , n. sp.	–	x	–	–	–	492–888
<i>P. (D.) echinata</i> , n. sp.	–	x	–	–	x	150–1,692
<i>P. (D.) robusta</i> , n. sp.	–	x	–	–	–	712–1,061
<i>Fanellia compressa</i> (Verrill, 1865)	–	x	–	–	–	82–1,061
<i>F. fraseri</i> (Hickson, 1915)	–	x	–	x	–	86–1,341
<i>Primnoa pacifica</i> Kinoshita, 1907	x	x	–	x	x	9–800
<i>P. pacifica</i> var. <i>willeyi</i> Hickson, 1915	–	x	x	x	–	27–863
<i>P. wingi</i> Cairns and Bayer, 2005	–	x	–	x	x	110–914
<i>Narella bayeri</i> Cairns and Baco, 2007	–	–	x	–	–	3,277–4,091
<i>N. arbuscula</i> Cairns and Baco, 2007	–	–	x	–	–	2,775–3,465
<i>N. cristata</i> Cairns and Baco, 2007	–	–	x	–	–	3,385
<i>N. abyssalis</i> Cairns and Baco, 2007	–	–	x	–	–	4,594
<i>N. alaskensis</i> Cairns and Baco, 2007	–	–	x	–	–	2,377–3,075
<i>Arthrogorgia utinomii</i> Bayer, 1996	–	x	–	–	–	163–882
<i>A. kinoshitai</i> Bayer, 1952	x	x	–	–	–	220–1,309
<i>A. otsukai</i> Bayer, 1952	–	x	–	–	–	1,359–1,372
<i>Calyptrophora laevispinosa</i> Cairns, 2007b	–	–	x	x	–	2,672–3,531
<i>Parastenella doederleini</i> (Wright and Studer, 1889)	x	x	–	–	–	400–3,423
<i>P. ramosa</i> (Studer, 1894)	x	x	x	x	–	665–1,766
<i>P. gymnogaster</i> Cairns, 2007b	–	–	x	x	–	1,962–2,869

^a Bering Sea (Bowers Bank, Pribilof Canyon, Zhemchug Canyon).

^b The depth of 1,258 m is for the pinnate growth form, which may be a station error (see text); 29–888 m is typical range.

CAS	California Academy of Sciences, San Francisco
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NOAA	National Oceanic and Atmospheric Administration
USNM	United States National Museum (now the NMNH)
ZMA	Zöologisch Museum, Amsterdam

Vessels

<i>Alb</i>	USFWS <i>Albatross</i>
<i>DW</i>	<i>Deep Worker</i> (submersible)
<i>MF</i>	R/V <i>Miller Freeman</i>

Other Terms

GOA	Gulf of Alaska
L:W	ratio of length to width of a polyp or coenenchymal scale
SEM	scanning electron microscope

HISTORY OF PRIMNOID OCTOCORALS FROM THE ALEUTIAN ISLANDS

The first primnoid reported from the Aleutian Islands, *Prymnoa verticillaris* by Ehrenberg (1834), is by inference only. Ehrenberg's account does not list a collecting locality, but Studer (1878), who examined and illustrated this specimen from the Chamisso collection in the Berlin Museum, stated that it was collected on the *Rurik* Expedition (1816–1817), which made collections in the Bering Sea and eastern Aleutian Islands. According to Studer, this species was the same as Verrill's (1865) *Primnoa compressa*, which was described from the Aleutian Islands and collected on the U.S. North Pacific Exploring Expedition but without precise locality or depth. *Primnoa compressa* has now been transferred to the genus *Fanellia*. According to Bayer (1982), Ehrenberg's specimens might have been either of the two *Fanellia* known from this region but more likely *F. fraseri*. It was not until 1915 that Hickson described *Caligorgia fraseri* (= *Fanellia fraseri*) from Albatross Bank in the Gulf of Alaska.

In his report on the octocorals collected by the *Albatross* in Japanese waters, Nutting (1912) also included nine extralimital records from the Aleutian Islands and Bering Sea, including three species of *Plumarella*, two of *Thouarella*, and a new genus and species, *Primnodendron superbum* (transferred to *Plumarella* herein). All of these records are discussed in the text below, but some samples of the specimens were too small or damaged to identify,

such as *P. flabellata* and *T. hilgendorfi*. Much later Bayer (1952) also reported two new species of *Arthrogorgia* from the same *Albatross* expedition of 1906, both from the Aleutian Islands.

In an infrequently cited "final report," Cimberg et al. (1981) listed all primnoids previously reported from Alaska and discussed some of the ecological factors (e.g., depth, substrate, temperature) that affect their distribution, but their taxonomy is uncritical and the publication is more similar to an informal agency report, and thus these references are not included in the species synonymies.

Bayer's (1982) second contribution to this topic was a redescription of the two species of *Fanellia* known from the Aleutian Islands, accompanied by detailed SEM illustrations and several new records for each species. He (Bayer and Stefani, 1989) later included these two species in a key to the species of *Fanellia*. Similar to his contribution of *Fanellia*, Bayer (1996) described three species (including one new) of *Arthrogorgia* from the Aleutian Islands, including copious SEM illustrations, several new records, and a key to the species in the genus.

In 2002, Heifetz listed and indicated coarse geographic abundance of the common primnoid octocorals collected by NOAA vessels from 1975 through 1998, showing a correlation to fish that were collected at the same stations. Many of the primnoids were not identified to species, and unfortunately voucher specimens were not indicated. Later Heifetz et al. (2005) amplified this discussion, listing 52 nonpennatulacean octocorals from Alaskan waters, 21 of which were primnoids. They also pointed out a zoogeographic and physical boundary at Samalga Pass (between Umnak and Chuginadak Islands) and that coral diversity was much higher to the west of this pass, an observation supported by the distributions of the primnoid species reported herein. Many of the specimens they used for their observations were collected by the *Delta* and *Jason II*, some of which are included in this study. And, although not taxonomic in nature, Stone (2006) studied the depth distribution of western Aleutian cold-water corals (including octocorals) and their fine scale associations with economically important fish species. Most of these specimens were collected by the *Delta* submersible, many of which are reported herein.

Wing and Barnard's (2004) field guide to the Alaskan corals listed 55 nonpennatulacean octocorals, 21 of which (38%) belonged to the family Primnoidae. They keyed all species and illustrated several, but, in general, their taxonomy was uncritical and voucher specimens were not designated.

In a revision of the genus *Primnoa*, Cairns and Bayer (2005) reported additional records of *Primnoa pacifica*

and the new species *P. wingi* from the Aleutian Islands. And, although not from the Aleutian Islands, Cairns (2007b) reported *Parastenella ramosa* and *P. gymnogaster* from seamounts in the adjacent Gulf of Alaska. Likewise, Cairns and Baco (2007) reported five species of *Narella* from deep seamounts in the Gulf of Alaska.

Finally, Stone and Shotwell (2007) provided a very useful status of the deep coral ecosystems of Alaska, and in their Appendix 2.1 list 68 nonpennatulacean octocorals from the Aleutian Islands, 21 of which were primnoids, however, almost half (31 taxa) of their listed taxa were undescribed, and their taxonomy was uncritical.

In summary, if one does not count unidentified species, only 14 (9 valid) primnoid species had been previously reported from the Aleutian Islands out of a total of 27 (22 valid) nonpennatulacean species (based on list of Stone and Shotwell, 2007). The addition of eight new species and a new record (*Parastenella doederleini*) increase the total number of valid Aleutian species to 31 and the number of primnoids to 19 species, or 61% (19/31 species) of the nonpennatulacean octocorals. Another eight primnoid species occur in the Gulf of Alaska, bringing the total of Alaskan primnoids to 26 (Table 1).

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MATERIAL AND METHODS

Specimens were examined from over 124 stations (see Appendix) and logged by 17 vessels, most of which were government research vessels and submersibles sponsored by NOAA, covering the entire length of the Aleutian Islands at depths of 40–2,514 m. Most of the specimens are deposited at the NMNH, but in some cases, especially

specimens from the *Jason IV* and *Delta*, only a small fragment is on deposit at the NMNH, with the main colony residing at Auke Bay Laboratory, Juneau, Alaska. Types of 21 of the 26 Aleutian species are deposited at the NMNH. Most of the SEM images were taken by the author (stub number prefaced with C), but 19 images were used from the Bayer archive (stub number prefaced with a B). In the material examined sections, specimens are presumed to be preserved in 70% ethanol unless otherwise noted. A “confirmed” depth range is reported for each species (i.e., the depths of the shallowest deep to the deepest shallow ranges of individual stations).

SYSTEMATIC ACCOUNTS

SUBCLASS OCTOCORALLIA

ORDER ALCYONACEA

SUBORDER CALCAXONIA GRASSHOFF, 1999

FAMILY PRIMNOIDAE MILNE EDWARDS, 1857

Genus *Thouarella* Gray, 1870

Thouarella Gray, 1870:45.—Kükenthal, 1919:405–408.—Bayer, 1956:F220.—Cairns, 2006:175–176.—Taylor et al., in press.

Rhopalonema Roule, 1908:2–3.

Thouarella (*Diplocalyptra*) Kinoshita, 1908a:454.—Cairns and Bayer, 2009:34–35.

Thouarella (*Euthouarella*) Kükenthal, 1915:149.—Cairns and Bayer, 2009:34.

Thouarella (*Parathouarella*) Kükenthal, 1915:150.

Thouarella (*Epithouarella*) Kükenthal, 1915:150–151.—Cairns and Bayer, 2009:35.

Thouarella (*Thouarella*).—Bayer, 1956:F220.—Cairns and Bayer, 2009:33–34.

DIAGNOSIS. Colonies bottlebrush, uniplanar pinnate, or dichotomous in branching. Polyps isolated, that is, occurring on all sides of branchlets (species Group 1 sensu Taylor et al., in press) or arranged in pairs or whorls on branchlets (species Group 2 sensu Taylor et al., in press), pointing upward. Polyps covered by 6 or 8 longitudinal rows of body wall scales, the scales of adaxial row often reduced in size and number to accommodate inward flexing of polyp. Marginal scales often arranged in 2 circlets of 4 scales that alternate with one another, the circumference of the distal polyp not being large enough to

accommodate 8 adjacent marginal scales. Each marginal bears a simple or ornate longitudinal keel or multiple keels that, when the marginals fold over the operculum, glide along outer concave surface of underlying opercular scales in a tongue-and-groove fashion.

DISCUSSION. The various subgenera of *Thouarella* were previously distinguished (see synonym above, especially Kükenthal, 1915, 1919, 1924; Bayer, 1956; Cairns, 2006; Cairns and Bayer, 2009) by the relative length of their marginal spines, and the grouping or nongrouping of polyps on the branchlets. However, Taylor et al. (in press) showed that the relative length of the marginal spine was a variable and continuous (nondiscrete) character. This led them to abandon that system of subgeneric differentiation in preference to dividing the 24 *Thouarella* species into two species groups, the groups based solely on the arrangement of polyps on the branchlets, a much easier character to interpret. Further differentiation of species within these groups is based on branching mode and characteristics of the polyp sclerites. The two new species of *Thouarella* described herein both belong to Group 1, that is, species having a random or isolated arrangement of polyps, which currently contains 18 of the 26 known species in this genus.

The specimen reported as *T. hilgendorfi* by Nutting (1912:66), Heifetz (2002), Wing and Barnard (2004:24), Heifetz et al. (2005), and Stone and Shotwell (2007) as questionably from the Bering Sea (*Alb*-4771: USNM 30133) could not be confidently identified. Likewise, *Thouarella* sp. A listed by Heifetz (2002) and Stone and Shotwell (2007) is uncertain.

DISTRIBUTION. Worldwide, from Antarctic to the Aleutian Islands, 73–2,100 m (Cairns and Bayer, 2009; Taylor et al., in press).

***Thouarella cristata*, new species**

FIGURES 1A, 3A–I

?*Plumarella* sp.—Wing and Barnard, 2004:24, 42, fig. 12.

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches, from which branchlets originate in an irregularly pinnate fashion also in plane of colony; however, associated with the presence of a commensal polychaete, which occasionally lives along one of the main branches, a third set of branchlets develop, causing the branches to appear somewhat bushy or bottlebrush in shape (Figure 1a). Branchlets up to 8 cm in length and not further subdivided, usually regularly arranged parallel

to one another. Largest colony (USNM 1010273) 50 cm in height, with a basal branch axis diameter of 11 mm. Holotype 32 cm tall and 16 cm wide, consisting of two main branches but lacking holdfast. Axis pale yellow to brown-black in color.

Polyps occurring on main stems and on all sides of branchlets in a crowded manner (Figure 3a), resulting in 24–26 polyps/cm, even more toward tips of branchlets. Polyps 1.7–2.5 mm in length and flared distally as well as curving upward along branchlet axis. Brooding polyps (or those with large eggs) common; these polyps cylindrical or basally swollen.

Polyps covered with 8 longitudinal rows of body wall scales: 6–9 scales in each abaxial row, 6–7 in each outer lateral row, 4–6 in each inner lateral row, and 3–4 in 2 adaxial rows, the proximal part of adaxial side of polyp being further covered with small elliptical scales 0.21–0.42 mm in diameter (Figure 3c, i). Opercular scales triangular, 0.47–0.69 mm in length (L:W = 2.0–2.45), forming a prominent, peaked operculum easily visible in lateral view (Figure 3b,e). Outer surface of operculars prominently ridged, the finely serrate ridges radiating from a central basal point; proximal inner surface tuberculate, but distal inner surface bearing prominent multiple longitudinal ridges; edge of operculars finely serrate. Marginal scales (Figure 3f) triangular and larger than operculars (0.53–0.73 mm in length) but with a smaller L:W (1.3–1.9), thus closer to an equilateral triangle. Outer surface of marginals prominently ridged, as the operculars, but distal inner surface bearing one or more prominent keels, easily visible in an opercular polyp view (Figure 3c, d); marginal scales flaring outward from polyp. The 2 adaxial marginals smaller than the other 6. Submarginal scales similar in shape to marginals, often flaring outward and having small keels, but shorter and with lower L:W ratio (0.9–1.5). Remaining body wall scales (Figure 3g) progressively shorter (L:W around 1) and less ornamented (smooth exteriorly) toward base of polyp. All body wall scales thick and robust.

Coenenchymal scales (Figure 3h) irregular in shape and flat, with a granular outer surface and a tuberculate inner surface; scales up to 0.9 mm in length.

REMARKS. According to the conventional organization of the genus (Cairns and Bayer, 2009), *Thouarella cristata* would fall within the nominate subgenus (i.e., those species having pointed marginal scales and isolated polyps) or according to the revised classification of the genus (Taylor et al., in press) as within species group 1 (i.e., those species having isolated polyps). Regardless, *T. cristata* differs from all previously described

species in having thick and highly ridged body wall and opercular scales, a relatively high number of polyps per centimeter, and a tendency to form quasi-bottlebrush colonies (i.e., main branches often having three distinct rows of branchlets).

TYPES AND TYPE LOCALITY. Holotype: *Delta* 6004-11C-6, 1 dry colony, 1 alcohol fragment, SEM stubs C1440-1443, USNM 1115600. Paratypes: 51°26.55'N, 179°21.62'E, 768 m, 7 Apr 2000, 1 dry colony, USNM 1006315 (exAB01-54); *Jason II* 2103-14-2, 1 fragment, USNM 1134916, and 1 dry colony, AB01-54 and AB10-0090; *Sea Storm* 116, 1 large dry colony and small colony in alcohol, USNM 1010273. Type Locality: 52°45'55"N, 179°19'42"W (southern Bowers Bank), 154 m.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Aleutian Islands: off Rat Islands: Kiska, Amchitka, and Semisopchnoi Islands, and southern Bowers Bank, 94–768 m.

ETYMOLOGY. Named *cristata* (Latin for crested or ridged), in allusion to the prominently ridged outer surfaces of the body wall scales and the ornate keels on the inner sides of the marginal scales.

***Thouarella trilineata*, new species**

FIGURES 1B, 4A–J

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches, from which branchlets originate usually in three rows giving the main branches a bushy (bottlebrush) appearance (Figure 1b). Branchlets up to 6 cm in length and not further subdivided, arranged in an alternating pinnate fashion on main branches. Largest colony (the holotype) 23 cm in height and 14 cm wide, consisting of only 2 main branches; basal branch axis 4.5 mm in diameter. Axis pale yellow.

Polyps occurring on main stems and on all sides of branchlets in a crowded manner (Figure 4a), resulting in 35–40 polyps/cm. Polyps 1.4–1.7 mm in length and are cylindrical to slightly flared distally, curving upward along branch axis. Modified brooding polyps not apparent, perhaps because eggs are fairly small.

Polyps covered with 6–8 longitudinal rows of body wall scales: 5–6 scales in the 2 abaxial rows, 4–6 in 2 outer lateral rows, 3–5 in 2 inner lateral rows, and only 6–10 randomly placed sclerites on adaxial side below adaxial marginals, hardly deserving of the name of row and not covering entire adaxial side (Figure 4b, c). Opercular scales triangular (Figure 4f), 0.35–0.52 mm in length (L:W = 2.0–2.5), and somewhat distally attenuate, such that the

8 operculars, when in closed position, do not form an entire operculum, allowing some space between opercular scales; adaxial operculars smaller than others (Figure 4c). Opercular scales curved inward, resulting in a low operculum (Figure 4b). Outer surface of operculars highly ridged, the finely serrate ridges originating from a central basal point; proximal inner surface tuberculate whereas distal inner surface bears multiple finely serrate ridges. Marginal scales triangular (pointed) to spinose (Figure 4g), except for the 2 adaxial marginals, which are rounded distally; otherwise, marginals about same height as operculars (0.42–0.55 mm) but have a broader base and thus a lower L:W of 1.0–1.5. Like opercular scales and all body wall scales, the outer surface of a marginal is highly ridged with deep valleys between the ridges; the distal inner surface bears multiple serrate keels. Submarginal scales (Figure 4h) similar to marginals but slightly less tall and thus having a smaller L:W of 1.0–1.25, and usually lack distinct keels. Remaining body scales (Figure 4i) progressively smaller toward base of polyp; those in lateral rows somewhat asymmetrical but all having tall ridges on their outer surface. Adaxial scales below marginals small (0.14–0.20 mm in diameter) and elliptical, not formed into rows, and exposing some of the adaxial side of polyp. All body wall scales rather thick, especially along longitudinal axis.

Coenenchymal scales (Figure 4j) irregular in shape and flat, with a granular outer surface and tuberculate inner surface; scales up to 0.60 mm in length.

REMARKS. Small ophiuroids (disc diameter = 5–7 mm), the same color as the coenenchyme, are common commensals on this species.

Although similar in many ways to *Thouarella cristata*, *T. trilineata* differs in having smaller polyps, nonspinose adaxial marginals, reduced adaxial marginals such that part of the adaxial polyp face is bare, even more highly ridged body wall scales that extend to the base of polyp, and a less flared polyp shape.

TYPES AND TYPE LOCALITY. Holotype: *Dominator* 1997-01-39, 1 large colony in alcohol, SEM stubs C1425-1429, USNM 1010175. Paratypes: *Alb*-3330, 1 colony, USNM 49342; *Alb*-3331, 1 colony, USNM 49342; *Delta* 6199-5E-5, 1 branch, USNM 1135540, and 1 dry colony, AB10-0033; *Delta* 5993-7C-5, 1 dry fragment, USNM 1135538; *Dominator* 1997-01-49, 1 dry and 1 alcohol preserved colony, USNM 1009952 and 1009949, respectively; *Jason II* 2103-7-1A, fragment, USNM 1135539; *Let's Go* 861-50, 1 branch, USNM 1135541; *Pacific Knight* 941-38, 1 colony, USNM 100798; *Sea Storm* 148, 1 colony, USNM 1009943; *Starlight* 84-1-7, 1 colony, USNM 100753; *Vesteraalen* 941-36, 2 colonies,

USNM 100754 and 100746. Type Locality: 53°01'11"N, 170°18'49"W (northwest of Carlisle Island, Islands of Four Mountains), 202 m.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Aleutian Islands from Amchitka Pass to Unalaska, 97–642 m.

ETYMOLOGY. Named *trilineata* (Latin for “three lines”) for the trilinear arrangement of the branchlets from the main branches.

Genus *Plumarella* Gray, 1870

Plumarella Gray, 1870:36.—Cairns and Bayer, 2009:39 (revision).

DIAGNOSIS. Colonies usually uniplanar and alternately pinnately branched but may also be dichotomously branched and bottlebrush in shape. Polyps arranged in alternate biserial fashion on branchlets or crowded on all sides of branchlets in no order. Polyps covered by 8 longitudinal rows of body wall scales, the adaxial rows sometimes reduced in number and size. Marginal scales arranged in one cirlet of scales, which do not fold over the operculum; marginals variable in shape, their distal edges being spinose, pointed, or straight; inner surface of marginals may be smooth, ridged, or spiny but never keeled.

DISCUSSION. The 35 species currently assigned to genus are listed in Table 2. The genus was recently revised by Cairns and Bayer (2009).

The dry specimen of *P. flabellata* reported by Nutting (1912:63), Heifetz (2002), Wing and Barnard (2004:24), Heifetz et al. (2005), and Stone and Shotwell (2007) based on specimens from *Alb-4784* (Attu Island, Near Islands, Aleutians), USNM 91438, was too damaged to properly identify.

The Alaskan listing of *P. longispina* by Wing and Barnard (2004), Heifetz et al. (2005), and Stone and Shotwell (2007:107) could not be confirmed.

The species listed as *Amphilaphis* A, B, and C by Heifetz (2002), Heifetz et al. (2005), and Stone and Shotwell (2007:106) may be the species of *Plumarella* (or *Thouarella*) discussed below. Similarly, the Alaskan listing of *Plumarella* sp. 1 or A by Heifetz (2002) and Stone and Shotwell (2007), respectively, cannot be confirmed.

DISTRIBUTION. Indo-Pacific, western Atlantic, Subantarctic; 10–3,182 m.

Subgenus *Plumarella* (*Plumarella*) Gray, 1870

DIAGNOSIS. *Plumarella* in which polyps occur on alternating sides of branchlets.

DISCUSSION. See discussion of subgenus *Dicholaphis*.

DISTRIBUTION. As for genus.

Plumarella (*P.*) *spicata* Nutting, 1912

FIGURES 1f, 5A–H

Plumarella spicata Nutting, 1912:64–65, pl. 8: figs. 2, 2a, pl. 18: fig. 6.—Kükenthal, 1919:350; 1924:261.—Wing and Barnard, 2004:24 (listed).—Heifetz et al., 2005:132 (listed).—Stone and Shotwell, 2007:107 (listed).—Cairns and Bayer, 2009:29 (listed).

Plumarella spinosa.—Nutting, 1912:63 (in part: *Alb-4781*).—Heifetz, 2002:26 (listed).—Wing and Barnard, 2004:24 (listed).—Heifetz et al., 2005:132 (listed).—Stone and Shotwell, 2007:107 (listed).

DESCRIPTION. Colonies uniplanar, consisting of numerous branches arranged in a quasi-dichotomous manner, from which branchlets diverge in a quasi-dichotomous to loosely alternate pinnate fashion (Figure 1f), branchlets on same side of a branch being 8–15 mm apart. Colonies delicate and flimsy, quite flexible; adjacent branchlets not held rigidly parallel to one another. Largest colony (holotype fragment) 14 cm tall and 7 cm in width, with a basal branch diameter of only 1.2 mm. Branch axis straw yellow in color.

Polyps occurring on main branches and branchlets in an alternating biserial arrangement in plane of colony flabellum, although occasional polyp diverging out of the flabellar plane; polyps sparse, about 12–14/cm branchlet length. Polyps of moderate size, 1.4–1.6 mm in length, slightly flared distally; polyps oriented perpendicular to branchlets, although distal ends curved slightly upward.

Polyps covered with 8 longitudinal rows of body wall scales: 5 or 6 scales in each abaxial row, 5–6 in outer lateral rows, 4–6 in inner lateral rows, and 4–6 small scales in reduced adaxial rows (Figure 5c). Opercular scales (Figure 5e) isosceles triangular in shape, elongate, and pointed, 0.32–0.70 mm in length (L:W = 2.7–3.7), the adaxial operculars being shortest and often having rounded tips. Outer surface of operculars smooth to slightly granular proximally; inner surface tuberculate proximally, smooth medially, and ridged distally. All 8 marginals (Figure 5c, d, f) prominently spinose, consisting of a rectangular (wider than tall) to crescent-shaped basal part that is clearly demarcated from the distal spine, the spine approaching 70% length of scale. Marginal scales up to 0.80 mm in length, the adaxial marginals being smaller, and have an L:W of 2.1–2.8. Outer surface of basal portion of marginals smooth to granular, inner surface tuberculate; distal spine

TABLE 2. List of the 35 species of *Plumarella* Gray, 1870, arranged by subgenus and indicating location data. A dash (–) indicates species not found.

Species	Distribution	Depth (m)
Subgenus <i>Plumarella</i> (<i>Plumarella</i>)		
<i>P. penna</i> (Lamarck, 1815) (type species)	Australia	10–60+
<i>P. laevis</i> Thomson and Mackinnon, 1911	Australia	90–115
<i>P. dentata</i> Thomson and Russell, 1910	Providence, Indian Ocean	229
<i>P. flabellata</i> Versluys, 1906	Japan	unknown
<i>P. spinosa typica</i> Kinoshita, 1907	Japan	237–330
<i>P. s. brevispina</i> Kükenthal, 1919	Japan	50
<i>P. alba</i> Kinoshita, 1908	Japan	550
<i>P. gracilis</i> Kinoshita, 1908	Japan	unknown
<i>P. longispina</i> Kinoshita, 1908	Japan	604
<i>P. acuminata</i> Kinoshita, 1908	Japan	330
<i>P. dofleini</i> Kükenthal and Gorzawsky, 1908	Japan	80–250
<i>P. d.</i> var. <i>boninensis</i> Aurivillius, 1931	Bonin Island	128
<i>P. lata</i> Kükenthal and Gorzawsky, 1908	Japan	200–300
<i>P. rigida</i> Kükenthal and Gorzawsky, 1908	Japan	180–600
<i>P. adhaerans</i> Nutting, 1912	Japan	180
<i>P. recta</i> (Nutting, 1912), n. comb.	Japan	869–924
= <i>P. alternata</i> (Nutting, 1912) n. comb.	Japan	934
= <i>P. attenuata</i> Kükenthal, 1924:301 (misspelling of <i>alternata</i>)	–	–
<i>P. spicata</i> Nutting, 1912	Aleutian Islands	712–1,912
<i>P. circumoperculum</i> Cairns, 2010	Hawaiian Islands	432–1,373
<i>P. abietina</i> (Studer, 1894), n. comb.	Off Ecuador	3,182
<i>P. delicatissima</i> Wright and Studer, 1889	Patagonia	256
<i>P. undulata</i> (Zapata-Guardiola and López-González, 2010)	South Georgia	306–343
<i>P. bayeri</i> (Zapata-Guardiola and López-González, 2010)	South Georgia	306–343
<i>P. diadema</i> (Cairns, 2006)	Brazil, South Georgia	278–1,000
= <i>T. sardana</i> Zapata-Guardiola and López-González, 2010	–	–
<i>P. pourtalesii</i> (Verrill, 1883)	Western Atlantic	231–950
<i>P. p.</i> forma <i>robusta</i> Deichmann, 1936	–	–
<i>P. p.</i> forma <i>obtusata</i> Cairns and Bayer, 2004	–	–
<i>P. pellucida</i> Cairns and Bayer, 2004	North Carolina	549–1,160
<i>P. laxiramosa</i> Cairns and Bayer, 2004	North Carolina	348–625
<i>P. dichotoma</i> Cairns and Bayer, 2004	South Carolina to Florida	494–1,065
<i>P. aurea</i> (Deichmann, 1936)	Florida	574
<i>P. aculeata</i> Cairns and Bayer, 2004	Florida, Bahamas	400–900
Subgenus <i>Plumarella</i> (<i>Dicholaphis</i>)		
<i>P. delicata</i> (Kinoshita, 1907)	Japan	731
<i>P. profunda</i> , new species	Aleutian Islands	2,514
<i>P. hapala</i> , new species	Aleutian Islands	120–384
<i>P. aleutiana</i> , new species	Aleutian Islands	79–517
<i>P. superba</i> (Nutting, 1912), n. comb.	Aleutian Islands	40–1,258
<i>P. nuttingi</i> , new species	Aleutian Islands	492–888
<i>P. echinata</i> , new species	Aleutian Islands	150–779
<i>P. robusta</i> , new species	Aleutian Islands	712–1,746

circular in cross section and covered with small spines that are often aligned in discontinuous rows (not keeled, Figure 5f). Abaxial submarginals often highly spinose like marginals but otherwise remaining body wall scales (Figure 5g) elliptical to crescent shaped with a rounded, pectinate distal edge, only 0.18–0.29 mm in height, and having L:W ratios of 0.66–1.3. Their inner surface is tuberculate, but their outer surface is spiny with short ridges at their distal edges that project as short points. Distal edges of operculars and marginals finely serrate, whereas edges of body wall and coenenchymal scales pectinate. Tentacular rodlets absent.

Coenenchymal scales (Figure 5h) small (0.10–0.19 mm diameter) elliptical scales, coarsely granular above and tuberculate below.

REMARKS. Among the 27 species in the nominate subgenus (Table 2), only four have dichotomous branching: *P. spicata*, *P. bayeri* (Zapata-Guardiola and López-González, 2010), *P. dichotoma* Cairns and Bayer, 2004, and *P. aurea* (Deichmann, 1936). *Plumarella spicata* differs from the other three in having spinose marginal scales that are covered with small spines. *Plumarella spicata* is also the only Pacific dichotomously branching species and the deepest dwelling of all in the subgenus.

Similar to *Acanthoprinnia* in having coarsely granular coenenchymals and pectinate scale edges, *P. spicata* differs in having tubercles on its inner scale surfaces.

TYPE AND TYPE LOCALITY. The holotype, preserved in alcohol, is now broken into at least 15 fragments, also SEM stubs B720 and C1437-1439, USNM 30050. Type locality: Alb-4780, 52°01'N, 174°39'E (Passage between Near Islands and Rat Islands, Aleutians), 1912 m.

MATERIAL EXAMINED. Type; Alb-4771, colony, USNM 80926 (reported by Nutting, 1912); Alb-4781, 1 branch, USNM 30058 (reported by Nutting, 1912, as *P. spinosa*); Jason II 2100-3-1, 1 dry colony, AB10-0075; Jason II 2100-4-8, 1 colony, USNM 1134070; Jason II 2101-7-9, 1 colony, USNM 1134071; Jason II 2104-5-2, 1 dry branch, USNM 1134073, and 3 dry colonies, AB10-0091; Jason II 2104-5-3, 1 branch, USNM 1134072.

DISTRIBUTION. Aleutian Islands from Near Islands to Adak Canyon, including Bowers Bank, 712–1912 m.

***Plumarella (Dicholaphis) Kinoshita, 1907,*
new subgenus rank**

Dicholaphis Kinoshita, 1907:230-231; 1908b:24-27.—Cairns and Bayer, 2009:26.

Primnodendron Nutting, 1912:70.

DIAGNOSIS. *Plumarella* in which polyps occur on all sides of branchlets.

DISCUSSION. In our revision of the primnoid genera (Cairns and Bayer, 2009), *Dicholaphis* was kept as a separate genus, distinguished from *Plumarella* because of the isolated nature of its polyps, not arranged in alternate biserial fashion as in all other *Plumarella* species (see Cairns and Bayer, 2009:21, key). The discovery of a clade of seven Aleutian species having a similar polyp placement but being otherwise similar to *Plumarella*, has caused a reevaluation of the genus, leading to incorporating *Dicholaphis* as a subgenus of *Plumarella*. The primary difference of this subgenus is that the polyps are arranged on all sides of the branchlets, not in alternating biserial fashion. Nutting (1912:70) also established a new genus for this primnoid ground plan, *Primnodendron* (type species, *P. superbum*), which he differentiated from *Plumarella* by its “bearing secondary branching from the terminal twigs,” but *P. superbum* fits nicely within the *Dicholaphis* subgenus.

The placement of *Primnodendron* as a junior synonym of *Thouarella* by Cairns and Bayer (2009) was a mistake. In retrospect, the genera *Plumarella* and *Thouarella* are much more difficult to distinguish than one might expect, despite the seemingly distinctive characters used by Cairns and Bayer (2009:20–21). Indeed, it is often difficult to determine if the marginal scales fold over the base of the opercular scales or not, the primary differentiating character used by Cairns and Bayer (2009) to distinguish the two genera. A more reliable character to differentiate the two genera is the nature of the marginal scales. In *Thouarella* the inner surface of the marginal scales are keeled, the keels gliding along the outer concave surface of the underlying opercular scales in a tongue-and-groove fashion, allowing the marginals to fold and slide over the opercular scales. In *Plumarella*, the inner marginal surfaces are smooth, spiny, or lightly ridged (never keeled) and do not fold over or in any way articulate with the outer surface of the opercular scales. Thus the marginals of *Thouarella* fold and those of *Plumarella* are fixed. Another difference is that in *Thouarella* the eight marginals tend to form two quartets of four scales, whereas the eight marginals of *Plumarella* are usually in one cirlet. This redefining of the two genera has led to the reassignment of several species in both genera (see Table 2).

The species in this subgenus are arranged herein in order of increasing length of their marginal scales.

DISTRIBUTION. Aleutian Islands and off Japan, 40–2514 m.

Key to the Species of the Subgenus *Plumarella* (*Dicholaphis*)

1. Colonies dichotomously branching; species occurs only off Japan *P. delicata*
- 1'. Colonies pinnately branched or shaped as a bottlebrush; occurs only off Aleutian Islands 2
2. Colonies bottlebrush in branching 3
- 2'. Colonies pinnately branched 4
3. Polyps large (3.0–3.6 mm), 9–15 polyps/cm; tentacular rodlets present; coenenchymal membrane often present between bases of branchlets *P. nuttingi*
- 3'. Polyps small (1.0–1.4 mm), 30–35 polyps/cm; tentacular rods absent; no coenenchymal membrane between branchlets *P. superba*
4. Marginal scales (exclusive of adaxials) bear elongate spines consisting of over 60% of length of scale; marginal spine spiny or ridged on all surfaces 5
- 4'. Marginal scales (exclusive of adaxials) have a pointed or straight distal edge but never produced into an elongate spine; inner surface of marginal spines smooth 6
5. Colonies consists of a single branch from which branchlets originate in a pinnate manner; marginal spines finely ridged; tentacular rodlets present; species occurs deeper than 800 m *P. robusta*
- 5'. Colonies consists of several major branches from which branchlets originate in a pinnate manner; marginal spines coarsely spiny; tentacular rodlets absent; species occurs at depths shallower than 700 m *P. echinata*
6. Marginal scales rectangular, with a straight distal edge; opercular scales quite elongate, with a L:W over 2.5; species occurs deeper than 2500 m *P. profunda*
- 6'. Marginal scales triangular, with a pointed distal edge; opercular scales triangular but with a L:W less than 2.5; species occurs at depths shallower than 500 m 7
7. Polyps small (0.9–1.2 mm); body wall scales thick and coarsely serrate; tentacular rodlets absent *P. aleutiana*
- 7'. Polyps larger (2.0–2.4 mm); body wall scales thin, concave above, and finely serrate; tentacular rodlets present *P. hapala*

***Plumarella* (*D.*) *profunda*, new species**

FIGURES 1E, 6A–F

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches from which branchlets originate in a loose, alternating, pinnate manner (Figure 1e), the distance between adjacent branchlets on one side of a branch 6–12 mm. Branchlets up to 9 cm in length, the entire colony being fairly flexible. Holotype 18 cm in height and 11 cm in width, with a basal axis diameter of 1.8 mm. Branch axis and polyps pale yellow.

Polyps occurring on all sides of the branches and branchlets; however, occasional branchlets in an alternate biserial arrangement. Polyps 1.5–1.9 mm in length, standing perpendicular to branchlets but often slightly turned upward at their tip; polyps widely spaced, only 10–14/cm on a branchlet.

Polyps covered with 8 longitudinal rows of body wall scales: about 5 in each abaxial and outer lateral row, 4 in inner lateral rows, and a variable number of smaller scales in the reduced adaxial rows. Opercular scales (Figure 6c) isosceles triangular in shape, brittle, and pointed:

0.47–0.86 mm in length (L:W = 2.5–4.1). Outer opercular surface smooth to mildly granular and longitudinally concave near tip; inner surface tuberculate proximally and covered with low longitudinal ridges distally. There is little difference between marginal and remaining body wall scales, all being roughly rectangular, with a straight (not pointed or spinose), slightly serrate distal edge (Figure 6d). Body wall scales 0.32–0.42 mm in length, with an L:W of 1.0–1.6. Outer surface of body wall scales smooth to mildly granular; inner surface tuberculate. Tentacular rodlets common (Figure 6f): cigar shaped, 0.083–0.105 mm in length (L:W = 3.6–5.2).

Coenenchymal scales (Figure 6e) elliptical to circular, 0.11–0.31 mm in diameter; outer surface bear low granules, inner surface tuberculate.

REMARKS. This species is unique within the subgenus in having rectangular body wall scales, including the marginal scales, and in having such elongate opercular scales (L:W up to 4.1). It is also the deepest known species within its subgenus.

TYPES AND TYPE LOCALITY. Holotype: *Jason II* 2098-2-1, dry colony and alcohol fragment, SEM stubs C14553-1455, USNM 1134074. Paratype: *Jason II*

2098-2-2, 1 small colony, USNM 1134075. Type locality: 51°23.404'N, 177°04.549'W (south of Kanaga I., Aleutian Islands), 2514 m.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Known only from type locality.

ETYMOLOGY. Named *profunda* (Latin for deep) for its relatively deep capture depth.

***Plumarella (D.) hapala*, new species**

FIGURES 1C, 7A–K

?*Amphilaphis* sp. Wing and Barnard, 2004:24, 41, fig. 11.

DESCRIPTION. Colonies uniplanar, consisting of a small number of branches from which branchlets originate in an alternate pinnate manner (Figure 1c), the distance between branchlets on one side of a main branch ranging from 7 to 11 mm. Holotype 26 cm tall and 22 cm wide, with a basal branch diameter of 3.7 mm. Branchlets 4–5 cm in length, occasionally with secondary branching. Branch axis yellow-brown and relatively stiff.

Polyps occurring on all sides of main branches and branchlets in a crowded manner (Figure 7a), with 18–25 polyps/cm toward branchlet tip. Polyps rather large, 2.0–2.4 mm in length, slightly flared distally, and curved upward along branch. Many polyps containing an egg, with each egg ~0.9 mm in diameter, and thus considerably swelling polyp's body cavity (Figure 7e). Polyps rather fragile, often compressed during collection, and covered with mucous.

Polyps encased with 8 longitudinal rows of body wall scales: 6–8 in each abaxial row, 5–7 in outer lateral rows, 3–6 in inner lateral rows, and 5–8 smaller scales in foreshortened adaxial rows (Figure 7b). Opercular scales isosceles triangle in shape (Figure 7f), and 0.55–0.80 mm in length (L:W = 2.1–2.5), forming a conical operculum over polyp. Outer surface of operculars covered with small spines arranged in lines radiating from a common proximal point; lower part of inner surface tuberculate but distal surface covered with rows of spines as on outer side. Six of 8 marginal scales (Figure 7g) pointed (not spinose), the 2 adaxial marginals having a rounded distal edge. Pointed marginals up to 0.62 mm in length with an L:W of 1.3–1.6; adaxial marginals shorter, with an L:W of about 1. Outer surface of marginals smooth to faintly striate whereas proximal inner surface tuberculate and distal pointed region smooth and thickened longitudinally but not keeled (Figure 7h). Remaining body wall scales (Figure 7i) pointed but progressively shorter toward base of

polyp, ranging in size from 0.88 to 1.2 mm in length (adaxial scales smaller, only about 0.2 mm in diameter), with a L:W of 0.9–1.2. Body wall scales thin, with a relatively smooth outer surface, contributing to fragility of polyp; distal edges of all polyp scales finely serrate. Tentacular rodlets common (Figure 7j), cigar shaped, ranging from 0.080 to 0.110 mm in length (L:W = 3.5–5.0).

Coenenchymal scales (Figure 7k) elliptical to rectangular, having a smooth outer surface, up to 0.6 mm.

REMARKS. Within the subgenus, *P. hapala* is perhaps most similar to *P. aleutiana* (see Key) but distinctive in having thin, outwardly concave body wall scales that contribute to a relatively weak polyp body wall. The polyps are also relatively large and often contain an egg, which increases the size of the polyp (Figure 7e).

TYPES AND TYPE LOCALITY. Holotype: *Ocean Olympic*, 1 dry colony, SEM stubs C1449-1452, USNM 1006310, and dry branches, AB00-22. Paratypes: *Alaska Sea* about 52°N, about 175° E, 183 m, 26 Jan 2000, 1 dry colony, USNM 1006334; *Alaskan Leader* 35-2, 1 dry colony, AB02-23; *Delta* 5997, 1 dry colony, USNM 1011096; *Delta* 5597-8C-1, 1 large dry colony, AB10-0024; *Delta* 6004-11C-1A, B, fragment, USNM 1134095, and 2 dry colonies, AB10-0026; *Delta* 6005-11B-1, fragment, USNM 1134212, and a dry colony, AB10-0029; *Dominator* 1997-01-49, 1 dry colony, USNM 1134093; *Jason II* 2102-12-1A, fragment, USNM 1134094 and AB10-0087; *Jason II* 2102, 12-1B, fragment, USNM 1134213; *Vesteraalen* 941-186, 4 colonies, USNM 100796; *Western Alaska*, 52°11.54'N, 176°07.77'E, 183 m, 25 Jan 2000, 1 dry colony, AB00-36. Type locality: 52°11.89'N, 176°17.30'E (off Buldir Reef, west of Kiska Island), 20 Oct 2000, 366 m.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Throughout Aleutian Islands from western Rat Islands to Islands of Four Mountains, 120–384 m.

ETYMOLOGY. Named *hapala* (Latin for soft to the touch, delicate) because the thin body wall scales produce a relatively weak body wall, which is often crushed or collapsed during collection.

***Plumarella (D.) aleutiana*, new species**

FIGURES 1D, 8A–K

?*Thouarella* sp. Wing and Barnard, 2004:24, 43, fig. 13.

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches from which branchlets

originate in an alternate pinnate manner, the holotype (the largest specimen) colony being 50 cm in height and 36 mm in width, consisting of 10 main stems or fronds (Figure 1d); base of colony 7.5×6.5 mm in diameter. Branchlets 4–9 cm in length, only rarely with secondary branching, arranged parallel to one another on each side of a main branch every 4–6 mm. Branch axis brown to black in color, toward base of large colonies elliptical or flattened in cross section (up to 10 mm), the greater axis of ellipse in plane of flabellum. Branches and colonies somewhat stiff in tension.

Polyps occurring on main stems and all sides of branchlets in a crowded manner, with 20–35 polyps/cm toward distal end of a branchlet. Polyps small, 0.9–1.2 mm in length, and cylindrical to slightly flared distally, curving upward along the branches.

Polyps covered with 8 longitudinal rows of body wall scales: 5–9 in each abaxial row, 4–6 in outer lateral rows, 2–5 in inner lateral rows, and 2–4 in adaxial rows (Figure 1d). Opercular scales (Figure 8e) triangular and curved inward, 0.25–0.41 mm in length (L:W = 1.4–1.9), the adaxial operculars always the smallest (Figure 8c); operculum low owing to downward curvature of opercular scales. Outer surface of operculars quite spiny and even longitudinally ridged; inner surface tuberculate proximally and smooth distally; edges finely serrate. Marginal scales (Figure 8g, h) variable in shape, on some polyps spinose (H:W about 1.6) and on other polyps simply triangular (H:W = 1.1–1.3), but in all cases, adaxial marginals low and rounded distally (H:W about 1.0). Outer surface of marginals bearing low ridges and granules; inner surface tuberculate proximally and smooth distally. Remaining body wall scales (Figure 8i) progressively less tall but wider toward base, with H:W ratios of 0.5–0.7, and having coarsely serrate distal edge. Outer surface of body wall scales usually longitudinally ridged but occasionally smooth, polyps of both types directly adjacent to one another. Tentacular rodlets absent.

Coenenchymal sclerites (Figure 8j) irregular in shape but usually elongate, up to 0.6 mm in length, their outer surface coarsely granular. Coenenchymal sclerites, which cover older large-diameter branches, consisting of much smaller spiny spheroids 0.050–0.090 mm in diameter (Figure 8k), probably the result of degeneration of once larger sclerites.

REMARKS. *Plumarella aluetiana* is similar to *P. superba* in many characteristics but differs in colony shape (pinnate versus bottlebrush), having coarsely serrate body wall scales, opercular scales with a highly spiny outer surface and smooth inner surface, and curved operculars, resulting in a lower operculum. Also, the outer surface of most body wall scales of *P. aluetiana* is ridged, whereas it is smooth in *P. superba*.

TYPES AND TYPE LOCALITY. Holotype: *Delta* 5590, 1 large dry colony, SEM C1421-1424, USNM 1011356. Paratypes: *Alaska Sea*, 52°13'52"N, 175°09'32"E, 183 m, 26 Jan 2000, 1 dry colony, USNM 1006333, and 1 dry branch, AB00-38; *Alb*-3319, 1 branch, USNM 51322; *Alb*-3500, several large colonies, alcohol and dry, USNM 49975; *Alb*-4779, 1 colony, USNM 49579; *Dominator* 1997-01-49, 1 colony, USNM 1134746; *Let's Go* 861-52, 1 colony, USNM 1134754; *Let's Go*, 861-57, 3 dry colonies, USNM 1134508; *MF (Harvester)* 802, VH80-30, 1 colony, USNM 82125; *MF* 833-16, 1 colony, USNM 1134538; *Pacific Knight* 941-29, 1 branch, USNM 100808; *Pacific Knight* 941-73, 1 branch, USNM 100842; *Pacific Knight* 941-204, 2 colonies, USNM 100752 and 100847; *Patricia Lee*, 51°18'42"N, 179°30'04"E, 329 m, 20 Oct 2000, 1 dry colony, USNM 1006302; *Vesteraalen* 2001-01-5, dry colony and alcohol fragment, USNM 1006032, and 1 dry branch, AB00-40; *Vesteraalen* 941-15, 1 colony, USNM 1012501; 51°43'52"N, 178°43'31"W, 256 m, 2 Apr 2000, 1 dry colony, USNM 1006739; 51°32', 179°15'W, col. K.K.Chew, 278–289 m, Sep 1968, 5 large dry colonies, USNM 60344 and 60345; 51°55'05"N, 176°38'13"E, 14 Feb 2000, 1 dry colony, USNM 1006246. Type locality: 51°43'22"N, 176°29'10"W (off Beyer Bay, Adak Island), 85 m.

MATERIAL EXAMINED. Types; Nontypes: *Alaskan Leader* 35, 1 dry colony, AB10-0019; *Delta* 5600, 4 dry colonies, AB02-116; *Delta* 5989-14B-1, fragment, USNM 1134747, and 1 dry colony, AB; *Delta* 5993-7C-4 and 6, fragments, USNM 1134504, and 1 dry branch, AB10-0021, 23; *Delta* 6007-13C-2, dry fragment, USNM 1135852, and 1 dry colony, AB10-0067; *Delta* 6199-5E-7, fragment, USNM 1134537, and 2 dry colonies, AB; *Delta* 6202-14D-4, fragment, USNM 1134753, and 2 dry colonies, AB; *Delta* 6208-21D-5, fragment, USNM 1134748, and 2 dry branches, AB10-0042; *Delta* 6209-21C-1, 1 dry colony, AB; *Delta* 6219-3B-2, fragment, USNM 1135874, and 1 dry branch, AB10-0058; *Delta* 6221-2B-9, fragment, USNM 1134755, and 1 large dry colony, AB10-0060; *Jason II* 2095-2-1-2, 1 dry colony, AB10-0069; *Jason II* 2102-6-5, 1 branch, USNM 1135289 and AB10-0085; *Jason II* 2102-7-1C, D, E, 3 fragments, USNM 1134507, 1134539, and 1 dry colony, AB10-0086.

DISTRIBUTION. Common throughout Aleutian Islands from Near Island in the west to Unalaska to the east, and Pribilof Canyon, 79–517 m.

ETYMOLOGY. Being the most commonly collected *Plumarella* in the Aleutian Islands, the species is named for the island group.

***Plumarella (D.) superba* (Nutting, 1912),
new combination**

FIGURES 2C, 9A-L

Primnodendron superbum Nutting, 1912:71–72, pl. 9, figs. 2, 2a, pl. 19, fig. 4.

Thouarella striata.—Nutting, 1912:69, pl. 10, figs. 2, 2a.—Heifetz, 2002:26 (listed).—Wing and Barnard, 2004:24 (listed).—Heifetz et al., 2005:133 (listed).—Stone and Shotwell, 2007:107 (listed).

Thouarella (Amphilaphis) superba.—Kükenthal, 1919:412–413; 1924: 291.

Thouarella superba.—Wing and Barnard, 2004:24, 44, fig. 14.—Heifetz et al., 2005:133 (listed).—Dautova, 2007:299, fig. 2.—Stone and Shotwell, 2007:107 (listed).

Thouarella (Thouarella) superba.—Cairns and Bayer, 2009:28 (listed).

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches from which numerous branchlets originate in a modified bottlebrush arrangement (Figure 2c), i.e., short branches (1.5–2 cm in length) diverge from both sides of main branches in plane of colony, whereas even shorter branches (0.5–1.0 cm) diverge from anterior and posterior faces of flabellum, often slightly longer on the anterior face (by definition). The larger branchlets and sometimes even the shorter ones usually bifurcate or give off several still shorter branchlets. Because of the unequal lengths of the branchlets on the main branches, the bottlebrush form is described as modified. Branches of colony somewhat rigid and wiry. Holotype now in 3 pieces, the largest 14 cm tall and 9 cm wide; largest specimen examined (USNM 1011277) 26 cm tall and 32 cm wide (Figure 2c), with a basal branch diameter of 8.3 mm. Axis black and woody in texture.

Polyps occurring on main stems and on all sides of branchlets in a crowded manner, with ~30–35/cm. Polyps small, 1.0–1.3 mm in length (not 2 mm as reported by Nutting, 1912), and slightly larger at their distal end (but not flared), facing upward.

Polyps covered with 8 longitudinal rows of body wall scales: 5–7 scales in abaxial rows, 4–6 in outer lateral rows, 3 or 4 in inner lateral rows, and only 1 or 2 in adaxial rows, the adaxials being reduced in number and size (Figure 9c, k). Opercular scales (Figure 9e) triangular, 0.20–0.38 mm in length (L:W = 1.3–2.0), the adaxial operculars usually smallest. Outer surface of operculars smooth to mildly spinose; inner surface longitudinally ridged as well as tuberculate. Marginal scales (Figure 9g) triangular (pointed) to spinose, the distal spine decreasing in size toward adaxial side, where adaxial marginals (and sometimes the inner lateral marginals) have only rounded distal edges (Figure

9h). Abaxial marginal scales 0.33–0.48 mm in length (L:W = 1.2–1.8), with a smooth outer surface and a tuberculate inner surface, the distal spine being circular in cross section and smooth all around; scales thick. Adaxial marginals only about 0.35 mm in length, with a low L:W of about 0.75). Abaxial submarginal scales similar to abaxial marginals, bearing distal spines; otherwise, distal margin of remaining body wall scales transition from spinose to pointed to rounded moving toward base of polyp, and L:W ratios vary from 0.8 to 1.1. Adaxial body wall scales (Figure 9j) much smaller and elliptical in shape, having a greater diameter of 0.11–0.17 mm (Figure 9k). Edges of all scales slightly serrate, and outer surface of all body wall scales proximal to operculars quite smooth (but see below). Tentacular rodlets absent.

Coenenchymal sclerites (Figure 9l) irregular in shape but usually elongate, rarely over 0.45 mm in length, their outer surface bearing coarse granules.

REMARKS. The species was originally placed in a separate genus, *Primnodendron*, Nutting (1912) noting that it had strong affinities to both *Plumarella* and *Thouarella*. Kükenthal (1919, 1924) later placed it in *Thouarella*, probably because it has a bottlebrush arrangement of branchlets, a common arrangement for *Thouarella*. Cairns and Bayer (2009) followed suite, officially, but incorrectly, synonymizing *Primnodendron* with *Thouarella*. However, emphasizing the characteristic of the inner marginal keel of *Thouarella* (see description of subgenus above and Taylor et al., in press), this species must be transferred to *Plumarella*, and to the subgenus *Dicholaphis*, as discussed above. It is one of only two species in the genus to have a bottlebrush arrangement of branchlets (see Key), and is distinguished from *P. nuttingi* by its smaller polyps and lack of a coenenchymal membrane at the base of its branchlets.

Although most of the specimens examined have very smooth outer surfaces of the body wall scales (Figure 9a, e, h, j), six lots (USNM 1009951, 100814, 1006323, 1135292, 1135852, and 1135265) are identical in all respects but have radiating ridges on their body wall scales (Figure 9b, f). These specimens were collected somewhat deeper (to 888 m) than the other specimens (40–102 m). Furthermore, two other specimens (USNM 57527, 57536) are also otherwise identical but are pinnately branched and were collected from an even greater depth of 882–1258 m. A station error cannot be ruled out.

The specimen reported as *Thouarella striata* by Nutting (1912) from *Albatross* 4778 could not be found, but a small vial of several hundred disarticulated sclerites was found labeled as such in Nutting's handwriting, which are

consistent with an identification of *P. superba*. They were also collected at the type locality of *P. superbum*.

TYPES AND TYPE LOCALITY. The holotype, now in three pieces, two small vials of sclerites, and SEM stubs C1430-1432, are deposited at the USNM (30691). Type locality: *Alb-4778*: 52°612'N, 179°52'E (Petrel Bank north of Semisopochnoi Island), 60–79 m.

MATERIAL EXAMINED. TYPES. *Alb-3501*, 1 branch (pinnate form), USNM 57527; *Alb-4777*, 1 colony, SEM stub B280, C1433, USNM 50150, and another colony, USNM 57535; *Alb-4778*, sclerites only (*T. striata* of Nutting, 1912), USNM 1135267; *Alb-4781*, 1 colony (pinnate form), USNM 57536; *Delta 5993-7C-4*, fragment, USNM 1135265, and 1 dry colony, AB; *Delta 6199-5E-1*, fragment, USNM 1134506; *Delta 6199-5E-7*, dry colony, AB10-0068; *Delta 6199-5E-8*, 1 dry colony, AB; *Delta 5E-9*, fragments, USNM 1135266, and 5 dry colonies, AB; *Delta 5199-5E-14*, 1 dry colony, AB10-0031; *Delta 6199-5E-15*, fragment, USNM 1134756; *Delta 5591*, 1 colony, USNM 1011276, and 1 dry colony, AB02-144; *Delta 5604*, 1 colony, USNM 1011277; *Delta 6203-18-1*, fragment, USNM 1134749 and AB10-0039; *Delta 6206-18-2*, fragments, USNM 1135287; *Delta 6209-21C-7*, fragments, USNM 1135278 and AB10-0049; *Dominator-1997-01-49*, 4 alcohol-preserved colonies, 6 dry colonies, SEM stubs C1464-1466, USNM 1009951, 1135264, respectively; *Esperanza PC 7-3-6-3*, 1 branch, USNM 1116845; *Let's Go 861-79*, fragments, USNM 1135290; *MF 833-24*, 1 branch, USNM 1135292; *Spirit of the North*, 51°21.66'N, 178°31.99'W, depth unknown, 20 Oct 2000, 1 dry colony, AB00-68; *Vesteraalen 941-36*, 4 dry colonies, USNM 100814; *Vesteraalen 941-94*, 5 colonies in alcohol, 1 dry colony, USNM 100845; *Vesteraalen 2001-01-5*, 1 colony, USNM 1006027; *Western Alaska*, 52°11.54'N, 176°07.77'E, 183 m, 12 Jul 2000, 1 dry colony, USNM 1006323.

DISTRIBUTION. Aleutian Islands: from eastern Near Islands to Umnak Island, including Petrel Bank and Pribilof Canyon, 40–1258 m. Also, off southeastern Sakhalin Island, 29 m (Dautova, 2007).

***Plumarella (D.) nuttingi*, new species**

FIGURES 2D, 10A–K

DESCRIPTION. Colonies uniplanar, consisting of relatively few main branches from which branchlets diverge from all sides in a bottlebrush fashion (Figure 2d); however, longer branchlets growing in plane of flabellum producing a compressed bottlebrush form. Largest colony

(holotype) 19 cm in height and width, with a basal branch diameter of 4.4 mm; axis pale yellow, polyps white. Branchlets up to 7 cm in length, usually not subdivided. Basal 6–8 mm of each branchlet often immersed in a thin coenenchymal membrane that is continuous with main branch; coenenchymal scales present in this membrane (Figure 10i, k).

Polyps usually occurring on all sides of branches and branchlets, occasionally in an alternate biserial manner. Polyps large (3.0–3.6 mm in length), standing perpendicular to branchlets, having a slightly upturned distal end, and slightly flared distally. Because of large size of polyps, only 9–14/cm on a branchlet. Polyps fleshy, the tissue often preventing the operculars from closing in the preserved condition; operculars also appearing to unite basally in a fleshy internal web.

Polyps covered with 8 longitudinal rows of body wall scales: 7 or 8 in each abaxial and outer lateral row, 6 or 7 in inner lateral rows, and 6 or 7 smaller scales in reduced adaxial rows (Figure 10c). Opercular scales (Figure 10e) isosceles triangular in shape, with an elongate distal spine and thus a high L:W ratio (1.0–1.5 mm in length, L:W = 2.9–5.0). Outer surface of operculars longitudinally ridged and quite spiny, especially on distal region; inner surface tuberculate proximally and ridged distally; edges of scales finely serrate. Marginals (Figure 10f, g) shorter and squatter, more equilateral triangular in shape, their distal margin pointed to spinose, the spine consisting of 25–40% length of scale. Marginals 0.70–1.1 mm in length with an L:W ranging from 1.0 to 1.6. Outer surface of marginals relatively smooth, sometimes with a longitudinal ridge; inner surface largely tuberculate, the distal edge and spine being smooth or bearing a low ridge but not keeled (Figure 10g). Remaining body wall scales (Figure 10h) thin, elliptical in shape, with finely serrate distal edges that flare outward; height of body wall scales 0.45–0.55 mm, with an L:W of 1.0–1.25. Outer edges of body wall scales smooth with low ridges; inner surface tuberculate. Tentacular rodlets (Figure 10j) common, 4 to 5 across at base of a tentacle, 2–3 across distally. Rodlets cigar shaped (Figure 10j,k), 100–0.185 mm in length (L:W = 3.5–6.2).

Coenenchymal scales (Figure 10i) 0.2–0.4 mm in diameter, elliptical, and flat, with a granular outer surface and a tuberculate inner surface.

REMARKS. Within the subgenus this species has the largest polyps and consequently the fewest polyps per centimeter, the longest and most slender opercular scales (L:W = 5), and a distinctive coenenchymal membrane that often occurs at the bases of branchlets, this membrane containing coenenchymal sclerites.

TYPES AND TYPE LOCALITY. Holotype: *Spirit of the North*, 1 dry colony and many separate polyps, SEM stubs C1444-1448, 1462-1463, USNM 1006317; *Jason II* 2102-6-4, fragment, USNM 1134464, and 1 dry colony, AB10-0084; *Western Viking*, 52°07.7'N, 176°00.11'W, depth unknown, 8 Feb 2000, 1 dry colony, USNM 1006331, and 1 dry branch, AB. Type Locality: 51°59.32'N, 177°41.33'W (off Kanaga Island, Andreanof Islands), 492 m, 20 Oct 2000.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Aleutian Islands from Amchitka Pass to Great Sitkin Island, 492–888 m.

ETYMOLOGY. Named in honor of Charles C. Nutting, specifically in recognition of his revision of the North Pacific deep-water octocorals (Nutting, 1912).

***Plumarella (D.) echinata*, new species**

FIGURES 2A, 11A–K

Plumarella spinosa. —Nutting, 1912:63, in part (Alb-4769).

DESCRIPTION. Colonies uniplanar, consisting of a moderate number of branches (fronds) from which branchlets originate in an alternate pinnate manner, the largest colony examined (the holotype) 25 cm in height and 28 cm in width, consisting of 13 fronds; basal branch diameter 3.8 mm (Figure 2a). Branchlets relatively short, usually 2–5 cm in length but up to 6 cm long toward base of colony, the distal ends of branchlets from adjacent fronds slightly overlapping such that the full plane of the colony sieves the passing water current. Branchlets rarely secondarily branched, arranged parallel to one another on each side of a main branch at intervals of 3–4 mm. Branch axis bronze, polyps white. Colony branches fairly flexible.

Polyps occurring on main branches and all sides of branchlets in a crowded manner (Figure 11a), with 20–30 polyps/cm toward distal end of a branchlet (Figure 11a). Polyps small, 1.1–1.4 mm in length, and slightly flared distally, curving upward along branch.

Polyps covered with 8 longitudinal rows of body wall scales: only 3–5 in each abaxial row, 3 or 4 in outer lateral rows, 2 or 3 in inner lateral rows, and 2–4 smaller scales in adaxial rows (Figure 11c, d, j). Opercular scales (Figure 11e) isosceles triangle in shape and slightly curved over the polyp (Figure 11c), the abaxial and outer lateral operculars being so long (up to 0.77 mm, L:W = 2.5–3.9) that they do not form a cohesive operculum; instead, steeped above other opercular scales (Figure 11c, d). Adaxial operculars

shorter (0.35 mm) and lying flat over polyp. Outer surface of operculars highly spiny and longitudinally ridged; inner surface smooth to faintly ridged. Six of 8 marginal scales (all but the adaxials) prominently spinose (Figure 11f), consisting of a square to diamond-shaped basal region clearly demarcated from the distal spine, the latter circular in cross section (Figure 11g) and constituting as much as 2/3 length of scale (Figure 11f). Marginal scales up to 0.90 mm in length, with an L:W = 2.0–3.1, the larger marginals obscuring view of underlying operculum. Adaxial marginals much smaller (about 0.25 mm in diameter), circular to square (L:W = 1), with a straight distal edge (Figure 11c, d). Outer surface of marginals spiny; inner surface of basal portion tuberculate, whereas inner distal spine covered with low, discontinuous, spiny ridges (Figure 11g). Submarginals (Figure 11h) bear shorter distal spines, 0.45–0.50 mm in length (L:W = 1.3–1.5). Remaining body wall scales rather thick, (Figure 11i) with pointed to rounded distal edges and large granules on outer surface, about 0.4 mm in length, with L:W ratios ranging from 0.98 to 1.4; adaxial body wall scales smaller than others. Outer edges of all polyp scales finely serrate. Tentacular rodlets absent.

Coenenchymal sclerites (Figure 11k) irregular in shape, usually elongate, up to 0.55 mm, and coarsely granular on outer surface.

REMARKS. *Plumarella echinata* is distinctive among the species in the subgenus in having elongate marginal spines that are spiny (not ridged or smooth) and in having relatively few scales in the body wall rows.

TYPES AND TYPE LOCALITY. Holotype: MF-833-38, 1 colony, SEM stubs C1434-1436, USNM 1135009. Paratypes: *Alaska Sea*, 52°N, 175°W, depth unknown, 1 dry colony, USNM 1006227; *Alb-3480*, 1 branch, USNM 57546; *Alb-4769*, 1 colony, USNM 43107; *Alb-4771*, 1 branch, USNM 57534; *Delta 6199-5E-14*, fragment, USNM 1135006; *Esperanza* PC 7-4-6-3, 2 dry colonies, AB10-0097; *Jason II* 2095-2-1-2, fragment, USNM 1135010; *Jason II* 2095-2-7-3, 1 dry colony, AB10-0068; *Jason II* 2100-4-2, fragment, USNM 1135993; *Jason II* 2104-10-2, fragment, USNM 1135995, and dry colony, AB10-0092; *Let's Go* 861-57, 4 colonies, USNM 1134976; *Let's Go* 861-58, 2 dry colonies, USNM 1134975; MF-833-15, 3 colonies, USNM 1134974; *Western Viking*, 52°17'N, 176°14'E, 284 m, 1 dry colony, USNM 1002569. Type locality: 51°42.9'N, 178°51.5'W (Gareloi Island [Delarof Islands], Aleutians), 582 m.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Aleutian Islands from off Buldir Reef (Rat Islands) to Amukta Pass, and Bowers Bank, 150–1,692 m.

ETYMOLOGY. Named *echinatus* (Latin for spiny) because not only are the marginal scales spinose, but the marginal spines also bear smaller spines.

***Plumarella (D.) robusta*, new species**

FIGURES 2E, 12A–J

DESCRIPTION. Colonies consisting of one main branch, a uniplanar pinnate frond, from which branchlets originate in alternating pinnate fashion (Figure 2f), spaced approximately 3–3.5 mm apart on one side of main branch in parallel fashion. Branchlets 7–8 cm long toward base of colony, gradually increasing in length toward middle of colony and then decreasing to about 4 cm at branch tip; all branchlets simple. Largest colony examined (the holotype) 25 cm tall and 13 cm in width, with a basal branch diameter of 1.7 mm. Colony fairly flexible and pale yellow in life.

Polyps occurring on main stem and all sides of branchlets in a crowded manner (Figure 12a), with ~20 polyps/cm near branchlet tips. Polyps moderate in size, 1.4–1.8 mm in length, cylindrical to slightly flared distally, and curving upward along branchlets.

Polyps covered with 8 longitudinal rows of body wall scales: 4 or 5 in each abaxial row, 3 or 4 in outer lateral rows, 3 or 4 in inner lateral rows, and several smaller scales on adaxial face. Opercular scales (Figure 12e) triangular to somewhat rectangular (some operculars within same operculum with a pointed tip, others rounded), 0.30–0.67 mm in length (L:W = 2.0–2.6), curved inward over polyp, and with a concave outer surface. Outer surface of operculars bearing low spiny ridges that radiate from a proximal point; inner surface tuberculate proximally but bearing multiple ridges distally (Figure 12e). Marginal scales (Figure 12d, f, g) prominently spinose, with a rectangular basal portion wider than tall and clearly demarcated from distal spine, the latter circular in cross section and constituting as much as 60% length of scale. Marginal scales up to 0.77 mm in length (L:W = 1.4–2.6), the adaxial marginals much smaller (Figure 12d), only 0.35–0.50 mm in length, but also bearing a short distal spine. Outer surface of basal portion of marginals granular, inner surface tuberculate. Distal spine circular in cross section and bearing 7 or 8 elongate spiny longitudinal ridges, the space between ridges deeply channeled, the ridges occurring uniformly on all sides of spine (Figure 12g). Occasional marginal bearing a short (0.1 mm) spur on proximal edge (Figure 12f). Remaining body wall scales (Figure 12i) spinose to pointed (sometimes

bifid), often irregular in shape (0.31–0.56 mm in length, L:W = 0.70–2.2), quite thick and distinctly convex; adaxial body wall scales much smaller. Outer and inner surfaces of body wall scales similar to that of marginals. Distal edges of all polyp scales finely serrate. Tentacular rodlets (Figure 12j) common: cigar shaped, 0.055–0.065 mm in length (L:W = 4.0–4.5).

Coenenchymal sclerites (Figure 12h) elongate, up to 0.6 mm (L:W = 1.5–2.5), but plate-like: outer surface covered with spiny ridges radiating from a central point, inner surface tuberculate.

REMARKS. Although similar to *P. echinata* in marginal spine length, *P. robusta* differs in having ridged marginal spines and in having much thicker body wall scales that are markedly convex and commonly spinous (also see Key). This species co-occurs with *P. spicata* at two stations.

TYPES AND TYPE LOCALITY. Holotype: *Jason II* 2104-11-1, a dry colony and a small fragment in alcohol, SEM stubs C1456-1459, USNM 1135992. Paratypes: *Jason II* 2101-4-3, dry colony, USNM 1135884; *Jason II* 2101-7-7, 1 dry colony and a fragment in alcohol, USNM 1135991; *Jason II* 2102-6-2, 1 dry colony and a fragment in alcohol, USNM 1135987.

MATERIAL EXAMINED. Types.

DISTRIBUTION. Aleutian Islands from a relatively circumscribed region from Amchitka Pass to Adak Canyon, 712–1,061 m.

ETYMOLOGY. Named *robusta* (Latin for hard, strong, robust), for the robust polyps produced by its thick body wall scales.

Genus *Fanellia* Gray, 1870

Fanellia Gray, 1870: 46.—Bayer, 1982:134–135 (key).—Bayer and Stefani, 1989:470–471 (key).—Cairns and Bayer, 2009:40–41, fig. 12e–m.—Cairns, 2010:433.

DIAGNOSIS. Colonies usually uniplanar, branchlets arranged dichotomously or in pinnate fashion. Polyps arranged in pairs or whorls, the polyps facing upward. Polyps protected by 4–8 rows of thick body wall scales, in some cases the adaxial and inner lateral scales being absent below the marginals resulting in a naked adaxial side. Outer surface of body wall scales covered with prominent tubercles, arranged in ridges. Marginal scales not folded over operculars, the latter bearing a longitudinal keel or set of ridges on inner surface. Coenenchymal scales consisting of an inner layer of tuberculate spheroids covered by thick polygonal scales.

DISCUSSION. The eight species known in the genus are keyed by Bayer and Stefani (1989). Recent works discussing species in this genus are included in the synonymy above.

DISTRIBUTION. Western and central Pacific from New Caledonia to Alaska, 82–1,341 m.

***Fanellia compressa* (Verrill, 1865)**

FIGURE 13A–D, H

?*Prymnoa verticillaris*.—Ehrenberg, 1834:357 (not *Gorgonia verticillata* Pallas, 1766).

Primnoa compressa Verrill, 1865:189.

Fanellia compressa.—Gray, 1870:46.—Bayer, 1982:136–140, figs. 11–14.—Bayer and Stefani, 1989:471 (key).—Heifetz, 2002:22.—Not Wing and Barnard, 2004:fig. 16 (= *F. fraseri*).—Stone and Shotwell, 2007:106 (listed).—Cairns and Bayer, 2009:30 (listed).

Calligorgia compressa.—Studer, 1878:647.—Heifetz, 2002:26 (listed).

Caligorgia compressa.—Wright and Studer, 1889:80.—Verssluys, 1906:81–82.—Kükenthal, 1919:379; 1924:276.

DESCRIPTION. Colonies uniplanar, up to 80 cm in height and 40 cm in width, with a basal branch diameter up to 1.8 mm (USNM 60281). Branching dichotomous, occurring every 3–5 cm but largely restricted to proximal third of colony, the end branches being straight and up to 50 cm in length; branches on edge of colony sometimes divided into a series of smaller branches in quick succession producing a lyrate arrangement in those regions. Dried tissue pale gray, branch axis metallic bronze.

Polyps occurring in close-spaced whorls on all branch surfaces: 8–12 polyps per whorl on distal branches (Figure 13c) and up to 25 polyps per whorl on larger-diameter basal branches; 4–6 whorls/cm. Polyps sometimes obliquely arranged in whorls approximating a spiral arrangement. Polyps cylindrical, closely spaced within whorl (Figure 13c), as well as abutting to polyps in adjacent whorls, with little intervening coenenchyme. Polyps 1.6–2.0 mm in length.

Polyps covered with 8 longitudinal rows of body wall scales: 7–10 scales in each abaxial row, 5–7 in outer lateral rows, 2 or 3 in inner lateral rows, and usually only 1 pair adaxially. Opercular scales triangular, abaxial operculars up to 0.50 mm in length, adaxial much smaller (only about 0.25 mm in length); L:W = 1.4–1.6. Marginal body wall scales not significantly different from other body wall scales. Distal abaxial body wall scales roughly square in shape but toward polyp base becoming progressively wider and ultimately on the seventh to tenth abaxial

scale away from operculum bearing elongate extensions or spurs on their adaxial side some of which extend to adaxial polyp face (Figure 13a, b). All outer lateral scales roughly the same size, but those in third to sixth position also bearing adaxial extensions (Figure 13a,b). Inner lateral and adaxial scales much smaller and without extensions. Although abaxial and outer lateral scales bearing elongate adaxial extensions, adaxial side of polyp mostly unprotected because of small size and number of inner lateral and adaxial scales (Figure 13d). Outer surfaces of all body wall and opercular scales covered with tall spiny (aculeate), discontinuous ridges separated by deep furrows, characteristic of the genus.

Coenenchymal scales consisting of closely fitting polygonal plates and numerous tuberculate spheroids, the latter 0.060–0.090 mm in diameter (Figure 13h).

REMARKS. *Fanellia compressa* was well described and illustrated by Bayer (1982), but he neglected to include opercular and adaxial polyp views and coenenchymal tuberculate spheroids, which are included herein. This report also adds 30 new records for this species, which previously had been known from only three specific localities, extending its known range east to the Islands of Four Mountains.

Fanellia compressa is quite similar to *F. fraseri* and is sympatric for much of its distribution, although it occurs farther west and not as far east as the known distribution of *F. fraseri*. *Fanellia compressa* differs in having more outer lateral body wall scales (5–7 versus 2–3, respectively), which usually have adaxial extensions (*F. fraseri* does not have these extensions), larger polyps (1.6–2.0 versus 1.1–1.5 mm), longer distal branches (up to 50 versus 15 cm), dichotomous branching (versus pinnate), 4–6 whorls/cm (versus 6–7/cm for *F. fraseri*), and a tendency to be taller than broad, whereas *F. fraseri* is usually equally tall as broad.

Both species carry commensal ophiuroids of the same color of the coenenchyme, having a disc diameter of 7–8 mm.

TYPES AND TYPE LOCALITY. The type is presumed to be lost (Cairns and Bayer, 2009). Type locality: “Aleutian Islands,” depth unknown.

MATERIAL EXAMINED. *Alaska Sea*, 52°09'24"N, 173°44'19"E, 318 m, 5 Feb 2000, 1 dry branch, USNM 1006336, and 1 dry colony, AB00-39; *Alaskan Trojan*, 51°32'07"N, 177°56'42"W, 346 m, 1 dry colony, USNM 1006152; *Delta 5E-2*, 1 branch, USNM 1123883, and 1 dry colony, AB10-0054; *Delta 5E-3*, 1 branch, USNM 1123884, and 1 dry colony, AB10-0100; *Delta 5E-5*, 1 branch, USNM 1123885, and 1 dry colony, AB10-0054; *Delta 5615*,

51°53.52'N, 176°11.294'E, 156 m, 22 Jul 2002, 1 large dry colony, AB02-134; *Delta* 6199-5E-9, dry branch, USNM 1123886, and 1 dry colony, AB10-0110; *Delta* 6221-2B-1, branch, USNM 1123874, and 1 dry colony, AB10-0061; *Delta* 6223-2D-1, 1 branch, USNM 1123382, and dry branches, AB10-0062; *Dominator* 1997-01-49, 3 colonies, USNM 1009944; *Dominator* 1997-01-78, 1 large colony, USNM 1009942; *Dominator* 2000-01-156, 1 dry colony, USNM 1010176; *Jason II* 2101-1-5, 1 branch, USNM 1123878, and 1 dry colony, AB10-0077; *Jason II* 2101-4-1, 1 branch, USNM 1123879, and 1 dry colony, AB10-0078; *Jason II* 2101-7-6, 1 branch, USNM 1123880, and 1 dry colony, AB10-0124; *Jason II* 2101-10-3, 1 branch, USNM 1123881, and 1 dry colony, AB10-0081; *Jason II* 2102-14-1, 1 branch, USNM 1136354; *Let's Go* 861-50, 1 dry branch, USNM 1136353; *Let's Go* 861-79, 1 branch, USNM 1123873; *MF* 833-3, 1 branch, USNM 82122; *MF* 833-47, 2 large colonies, USNM 1123826; *North Pacific*, 51°50.33'N, 174°15.82'W, 443 m, 20 Oct 2000, 2 dry colonies, USNM 1006337; *Pacific Knight* 941-204, 1 dry colony, USNM 100810; *Sea Storm* 116, 2 dry colonies, 3 branches, 1010256; *Starlight* 84-1-7, 1 colony, USNM 100747; *Vesteraalen* 941-51, 1 dry colony, USNM 100833; *Vesteraalen* 941-153, 1 large dry colony, USNM 100813; *Vesteraalen* 941-163, 1 large dry colony, USNM 100811; *Western Viking*, 52°17'09"N, 176°13'57"E, 265 m, 25 Jun 2000, 1 dry colony, USNM 1006321; 52°11.17'N, 176°17.00'E, 220 m, 20 Oct 2000, 1 dry colony, AB00-22; 53°04'N, 170°12'W, depth unknown, 4 Aug 2002, 1 colony in alcohol, AB02-24; specimens reported by Bayer (1982).

DISTRIBUTION. Known only from the Aleutian Islands from the Near Islands to Islands of Four Mountains, 82–1,061 m, although most records are from 150 to 300 m.

Fanellia fraseri (Hickson, 1915)

FIGURE 13E–G, I

?*Prymnoea verticillaris*.—Ehrenberg, 1834:357 (not *Gorgonia verticillata* Pallas, 1766).

Caligorgia fraseri Hickson, 1915:553–554, pl. 1, fig. 2, text fig. 5; 1917:23 (listed).—Kükenthal, 1924:279.

Fanellia fraseri.—Bayer, 1982:140–144, figs. 15–17.—Bayer and Stefani, 1989:471 (key).—Heifetz, 2002:22 (listed).—Wing and Barnard, 2004:24 (listed).—Heifetz et al., 2005:132, 136.—Stone and Shotwell, 2007:106 (listed).—Cairns and Bayer, 2009:30 (listed).

?*Fanellia compressa*.—Wing and Barnard, 2004:fig. 16.

DESCRIPTION. Colonies uniplanar and approximately equally tall as wide: up to 36 cm in height and 32 cm in width, with a basal branch diameter of 9.5 mm (USNM 82123). Branching loosely alternate pinnate, the main branch being straight (not geniculate), branchlets originating from the same side of a main branch separated by 6–15 mm. Branching throughout colony, resulting in relatively short end branches, i.e., usually less than 15 cm. Dried tissue a pale gray but pink when alive; branch axis a brownish-yellow.

Polyps occurring in closely spaced whorls on all branch surfaces: 5–8 polyps per whorl on distal branches, increasing to 12 on larger-diameter branches (Figure 13g); 6–7 whorls/cm. Polyps slightly clavate and closely spaced within and between whorls. Polyps 1.1–1.5 mm in length.

Polyps covered with 6 to 8 longitudinal rows of body wall scales: 7–8 scales in each abaxial row, 2–3 in outer lateral rows, 1 in inner lateral rows, and 0–1 adjacent to adaxial operculars, resulting in a naked adaxial side (Figure 13f). Opercular scales triangular, the abaxial operculars up to 0.45 mm in length, the adaxial operculars much smaller (Figure 13f); L:W = 1.4–2.0. Each abaxial body wall scale in the third through sixth position from operculum bearing a short adaxial wing-like extension; however, no other body wall scales with a similar spur (Figure 13e). As with *F. compressa*, the outer surfaces of all scales covered with spiny ridges.

Coenenchymal scales consisting of tuberculate spheroids (Figure 13i) 0.075–0.120 mm in diameter.

REMARKS. As with *Fanellia compressa*, *F. fraseri* was fairly well described and illustrated by Bayer (1982), but he also neglected to include opercular and adaxial polyp views and coenenchymal tuberculate spheroids, which are included herein. Otherwise, see Remarks for *F. compressa*.

MATERIAL EXAMINED. *Delta* 5592, 1 dry colony, USNM 1011274; *Delta* 6199-5E-13, 1 branch, USNM 1123888, and 1 dry colony, AB10-0044; *Delta* 5E-4, 1 branch, USNM 1123889, and 1 dry colony, AB10-0054; *Delta* 6206-18-14, 1 branch, USNM 1123890, and 1 dry colony, AB10-0041; *Delta* 6209-21C-2, 1 branch, USNM 1123891, and 1 dry colony, AB; *Delta* 6209-21C-4, 1 branch, USNM 1123892; *Jason II* 2101-1-1, 1 branch, USNM 1123877, and 1 dry colony, AB10-0071; *Jason II* 2104-2-2, 1 branch, USNM 1123887; *MF* 802-VH-80-30, 1 colony, USNM 82123; *Starlight* 84-1-7, 1 colony, USNM 1013158; *Vesteraalen* 5, 1 dry colony and 1 alcohol branch, USNM 1006138; 53°04'N, 170°12'W, depth unknown, 4 Jun 2002, 1 dry colony, AB02-24; specimens reported by Bayer (1982).

TYPES AND TYPE LOCALITY. Two syntypes, both dry, are deposited at the BM (1962.7.20.821-822). Type localities: Albatross and Portland Banks (just northeast of Kodiak Island), Gulf of Alaska, 92–183 m.

DISTRIBUTION. Known only from Alaska from Amchitka Pass to the Albatross Bank northeast of Kodiak Island, 86–1,341 m, although most records are from 100 to 150 m.

Genus *Primnoa* Lamouroux, 1812

Primnoa Lamouroux, 1812:188.—Cairns and Bayer, 2005:226–228 (genus revision and key to species); 2009:41–42, fig. 13h–p.

DIAGNOSIS. Colonies dichotomously branched and usually bushy. Polyps closely spaced and randomly arranged (not in pairs or whorls) but usually facing downward. Polyps fleshy, each covered with 6 longitudinal rows of scales, the adaxial side largely naked; 8 highly concave marginal scales, the adaxials often quite small. Well-developed operculum present, the operculars keeled on inner surface. Tentacular rodlets common.

DISCUSSION. The four species in this genus were revised by Cairns and Bayer (2005), which also includes a key to the species.

DISTRIBUTION. North Pacific, North Atlantic, Subantarctic South Pacific, 6–1,020 m.

***Primnoa pacifica* Kinoshita, 1907**

Primnoa pacifica Kinoshita, 1907:232.—Cairns and Bayer, 2005:233–239, figs. 1C, 4–6 (synonymy, key, description).—Stone and Shotwell, 2007:72, 93, 107, *in situ* fig. 2.23.—Whitmire and Clarke, 2007:152 (listed).—Cairns and Bayer, 2009:30 (listed).

Primnoa resaediformis pacifica.—Heifetz et al., 2005:132.

REMARKS. The typical form of *Primnoa pacifica* was recently described and figured by Cairns and Bayer (2005) and thus will not be redescribed herein. It differs from the other species in the genus by having prominently spined basal abaxial body wall scales and from variety *willeyi* in having thicker, more robust polyps and sclerites on the lateral surface of the polyps.

This account reports 28 new records of the species, but only one additional from the Aleutian Islands (USNM 1115517), the others being from the Bering Sea, and the northeast Pacific coast from Alaska to Washington.

TYPE LOCALITY. Mochiyama, Sagami Bay, depth unknown.

MATERIAL EXAMINED. *Cobb* TA-06-1, 3, 4, 6, 13, 14, 15, 16, and 17, Stephen's Passage, Alexander Archipelago, 12–27 m, 9 branches, USNM 1099633-1099636, 1099638-1099642; *DW* 6-1-1, 3 branches, USNM 1130914 and 1130920; *DW* 6-7-1, 1 branch, USNM 1130918; *DW* 7-1-1, 1 branch, USNM 1130922; *DW* 7-2-1, 1 branch, USNM 1130917; *DW* 7-4-1, 3 branches, USNM 1130921; Fiber Optic Monitoring Cruise-1159, 3 branches, USNM 1122474 and 1122478; *Esperanza* ZC-7-7-7-5 (Zhemchug Canyon, Bering Sea), 1 branch, USNM 1116849; *Quest* GB-06-1to 5, Glacier Bay, 9.5-18 m, 25 branches, USNM 1099628-1099632; 51°38'18"N, 179°34'37"W (Amchitka Pass), 395 m, 3 branches, USNM 1115517; 59°01'N, 136°10'26"W, 25 m, 1 branch, USNM 1115518; 50°41'03"N, 125°59'48"W, 20 m, 28 Jun 2008, 1 dry branch, USNM 1120445; specimens listed by Cairns and Bayer (2005);

DISTRIBUTION. Sea of Japan, Sea of Okhotsk, Aleutian Islands (Amchitka Pass), Bering Sea (Zhemchug Canyon), northeast Pacific coast from Alaska to La Jolla, California, 9–800 m.

***Primnoa pacifica* var. *willeyi* Hickson, 1915**

Primnoa willeyi Hickson, 1915:551–553, text fig. 3.

Primnoa pacifica var. *willeyi*.—Cairns and Bayer, 2005:239, figs. 1C–E, 7–8 (synonymy, key, description).—Stone and Shotwell, 2007:107 (listed).—Cairns and Bayer, 2009:30 (listed).

Primnoa resaediformis willeyi.—Heifetz et al., 2005:132.

REMARKS. *Primnoa pacifica* var. *willeyi* was recently described and figured by Cairns and Bayer (2005) and thus will not be redescribed herein. It differs from the other species in the genus by having prominently spined basal abaxial body wall scales and from the typical form in having a more slender polyp and lacking sclerites on the lateral surface of the polyps (see Cairns and Bayer, 2005:228 [key], 252 [table]).

This account reports three new records of the species, adding a second record to the Aleutian Islands (also from the Rat Islands), documenting the record from Dickens Seamount reported by Cairns and Bayer (2005), and a third very shallow record (27 m) from Stephen's Passage, Alexander Archipelago.

TYPES AND TYPE LOCALITY. Syntypes deposited at the BM (1962.7.20.188). Type locality: WSW Moresby Island, British Columbia, 183 m.

MATERIAL EXAMINED. *Alvin* 4028 (Dickens Seamount), 1 branch, USNM 1075478; *Cobb*

TA-06-09 (Stephen's Passage), 2 branches, USNM 1099637; 51°50'26"N, 179°52'41"E (Rat Islands), 863 m, 2 branches, USNM 1115516; specimens listed by Cairns and Bayer (2005);

DISTRIBUTION. Most records are from off British Columbia and the adjacent Alexander Archipelago, Alaska, as well as adjacent Dickins Seamount (GOA), but also known from Semidi Island (off Alaska Peninsula), and from two records in the Aleutian Rat Islands, 27–863 m.

***Primnoa wingi* Cairns and Bayer, 2005**

Primnoa wingi Cairns and Bayer, 2005:243–246, figs. 1h–i, 9–10; 2009: 30 (listed).—Stone, 2006:233 (listed).—Stone and Shotwell, 2007:90, 107 (listed).—Cairns and Bayer, 2009:30 (listed).

REMARKS. *Primnoa wingi* was recently described and figured by Cairns and Bayer (2005) and thus will not be redescribed herein. Keys to the species within the genus are also found in Cairns and Bayer (2005). It differs from the other species in the genus by having inconspicuous body wall scales that are immersed in polyp tissue, spatulate operculars, and large curved tentacular rodlets.

This account reports six new records of the species, extending its known distribution to the west (to the Near Islands), to the east (to Chatham Strait, Alexander Archipelago), and far to the north into the Bering Sea (Zhemchug Canyon), as well as broadening its known bathymetric range.

TYPES AND TYPE LOCALITY. The holotype (USNM 1010257) and paratypes are deposited at the USNM. Type locality: *Sea Storm*-150, 52°30'57"N, 173°29'35"W (north of Amlia Island, Andreanof Islands, Aleutians), 213–220 m.

MATERIAL EXAMINED. Type material; *Esperanza* ZC-7-2-ROV-1, 1 branch, USNM 1116847; *Jason II* 2104-11-2, 1 dry colony, AB10-0093; *Sea Storm* 95, 1, USNM 1123872; 51°39'24"N, 179°35'02"W, 712 m, 2 branches, USNM 1115519; 57°13'52"N, 134°04'21"W, 110 m, 4 branches, USNM 1115520, and AB01-88, 1 colony; 52°38'59"N, 172°15'30"E, 382 m, 1 branch, USNM 1115521; 51°50'26"N, 179°52'41"E, 863 m, 5 branches, USNM 1115550.

DISTRIBUTION. Aleutian Islands from Near Islands to Amukta Pass, Chatham Strait, and the Bering Sea (Zhemchug Canyon), 110–914 m.

Genus *Arthrogorgia* Kükenthal, 1908

Arthrogorgia Kükenthal in Kükenthal and Gorzawsky, 1908:625.—Bayer, 1996:605.—Cairns and Bayer, 2009:43.

DIAGNOSIS. Colonies with pinnate or dichotomous branching. Polyps arranged in whorls, the polyps pointing downward. Polyps protected by 8 keeled operculars (sometimes with small accessory operculars on inner side of opercular scales), a pair of buccal and basal scales, as well as a variable number of infraopercular scales that may or may not be visible in abaxial view. Several transverse rows of strongly curved, unpaired infrabasal scales also present. Tentacular rodlets common.

DISCUSSION. Four species occur in the genus (Cairns and Bayer, 2009), three of them found in the Aleutian Islands. The specific identity of *Arthrogorgia* sp. (Heifetz, 2002; Stone, 2006) is unknown.

DISTRIBUTION. North Pacific; Japan to Aleutian Islands, 163–1,359 m.

***Arthrogorgia utinomii* Bayer, 1996**

FIGURE 14A–L

Arthrogorgia utinomii Bayer, 1996:619–628, figs. 13–20.—Wing and Barnard, 2004:24, fig. 17.—Heifetz et al., 2005:132.—Stone and Shotwell, 2007:106 (listed).—Cairns and Bayer, 2009:31 (listed).

DESCRIPTION. Colonies uniplanar, branching equal dichotomous, the distal branches up to 30 cm in length. Largest colony (*Alb*-4781) 30 cm tall. A thin web of tissue occurring at each branching axil, which contains coenenchymal sclerites. Axis brown to bronze in color; colony orange in life.

Polyps arranged in whorls of 7–10, directed downward; 7–9 whorls per 3 cm branch length. Polyps 3.0–3.5 mm in length.

Each polyp protected by 8 opercular scales, a variable number of infraopercular scales, 1 pair of buccal scales, 1 pair of basal scales, and 2–4 transverse rows of infrabasal scales. Opercular scales (Figure 14d) triangular to tongue shaped but with a somewhat blunt distal tip. Abaxial operculars up to 2.0 mm in length, but operculars decreasing in length toward adaxial side, the adaxial operculars (Figure 14c) only 0.5 mm in length; L:W = 1.5–2.0. Inner surface longitudinally keeled, corresponding to a longitudinal crease on outer side. Infraopercular scales (Figure 14e) square to rectangular in shape, 1–2 pairs occurring proximal to each abaxial, inner, and outer lateral opercular (Figure 14a, b, e), these scales 0.5–1.0 mm in width, and easily visible just anterior to distal edge of buccal scales. On adaxial side of polyp stand a pair of square adaxial buccal scales 0.35–0.65 mm in width, and often a series of smaller adaxial body wall scales proximal to

those (Figure 14c, j). The two large abaxial buccal scales (Figure 14f) as much as 2.2 mm in length, terminating in a rounded or moderately pointed distal edge. The two basal scales (Figure 14h) as much as 3 mm in height (including the spine), each with a thick longitudinally ridged spine on their anterolateral edges that may constitute up to 45% of length of scale. Proximal to basal scales 2–4 transverse rows of thin, curved infrabasal scales (Figure 14b, i), each layer consisting of about 4 scales (Figure 14b), giving greater flexibility to polyp. Outer surface of all body wall and coenenchymal scales covered with radiating lines of small spines (Figure 14g).

Outer layer of coenenchyme composed of elongate, irregularly shaped sclerites (Figure 14k) up to 0.65 mm in length; inner coenenchymal layer composed of tuberculate spheroids 0.09–0.18 mm in diameter. Tentacular rodlets cigar shaped, 0.085–0.110 mm in length, and about 0.030 mm in diameter (Figure 14l).

Yellow eggs common in many polyps, each egg measuring about 0.65 mm in diameter.

REMARKS. This species was well described and copiously figured by Bayer (1996), but he did not provide images of individual sclerites, even though he had compiled a finished plate of sclerites that for unknown reasons was not included in his publication. Images of individual sclerites are provided herein, as well as an amplified description, and records of additional specimens.

Arthrogorgia utinomii is very similar to *A. kinoshitai*, and the species are sympatric for a large part of their ranges. *Arthrogorgia utinomii* differs in having slightly shorter (up to 2.2 mm) buccal scales, which reveal the distal edges of the underlying infraopercular scales on the abaxial, outer, and inner lateral positions; the buccal scales of *A. kinoshitai*, however, are slightly longer (up to 2.5 mm) and terminate in an extended lobate edge, both of which together form a protective cowl that mostly covers the infraopercular scales. Furthermore, infraopercular scales are less common and may even be absent in some polyps of *A. kinoshitai*. Otherwise, the two species are quite similar.

TYPES AND TYPE LOCALITY. The holotype, collected at R/V *Starlight* 84-1-36, is deposited at the USNM (97198). The two other specimens listed by Bayer (1996) in the original description are not designated as types and thus are not considered as paratypes. Type locality: 52°28'N, 172°30'W (not E as reported by Bayer, 1996), off Seguam Island, 234 m.

MATERIAL EXAMINED. Holotype; non-type specimens reported by Bayer (1996); *Arctic Dawn*, 51°32.42'N, 177°45.29'W, 402 m, 25 Dec 1999, dry branches, USNM 1006335; *Dominator*-5159, 1 colony,

USNM 1009950; *Jason II* 2104-5-1, branch, USNM 1115598, and 1 dry colony, AB10-0104; *North Pacific*, 52°04.36'N, 176°58.01'E, 384 m, 20 Oct 2000, dry branches, USNM 1006329; 52°27.633'N, 175°09.417'E, depth unknown, 4 Aug 2005, 1 dry colony, AB05-57.

DISTRIBUTION. Aleutian Islands from the Near Islands to off Amuka Island, 163–882 m, although most records from 250 to 700 m.

Arthrogorgia kinoshitai Bayer, 1952

FIGURE 15 A–J

Calyptrophora ijimai.—Broch, 1935:26, figs. 15–16; 1940:12, 20.

Arthrogorgia kinoshitai Bayer, 1952:64–65, pl. 2: figs. 1–8, pl. 3: figs. 1–12; 1996:606–619, figs. 5–12.—Heifetz, 2002:26 (listed).—Cairns and Bayer, 2009:31 (listed).

Arthrogorgia kinoshita.—Heifetz et al., 2005:132, 136.—Wing and Barnard, 2004:24 (listed).—Stone and Shotwell, 2007:106 (listed).

?*Arthrogorgia ijimai*.—Stone and Shotwell, 2007:106 (listed).

DESCRIPTION. See Remarks.

REMARKS. This species was well described by Bayer (1952) and profusely illustrated by him (Bayer, 1996) using SEM, but SEM-quality images of individual sclerites have never been published and are provided herein. Four new records are also reported.

The species is so similar to *A. utinomii* that it would be redundant to describe it in full. It is illustrated herein and distinguished from *A. utinomii* in the account of that species. The colony from *Jason II* 2107-5-1 displays extreme webbing of the coenenchyme between its basal branches.

TYPES AND TYPE LOCALITY. The holotype, collected at Alb-4781, is deposited at the USNM (49978) and consists of one colony preserved in alcohol, SEM stubs B2499-2500, 2548, C 1414-17, and two “exploded” polyps, all the sclerites of which have been glued to a slide by F. M. Bayer to approximate their relative position in the polyp. Type locality: 52°14'30"N, 174°13'E (west of Agattu Island, Near Islands), 882 m.

MATERIAL EXAMINED. Holotype (USNM 49978) and specimens (USNM 100748-9, SEM stubs B2510, 2125, 2143-47) reported by Bayer (1996); *Delta* 5993-7C-1, 1 dry colony, AB10-0020; *Jason II* 2103-5-1, 1 branch, USNM 1115594, and 1 dry colony, AB10-0117; *Ocean Olympic*, 52°11'10"N, 176°17'00"E, 220 m, 20 Oct 2000, 1 dry colony, USNM 1006150; *Pacific Knight* 941-204, 1 dry colony, USNM 100812 (from same station reported by Bayer, 1996); coll. by Renfro, 51°41'46"N, 178°20'30"W, 280 m, 8 Mar 2000, 1 dry colony, USNM 1006248.

DISTRIBUTION. Sea of Okhotsk (Broch, 1935), western Aleutian Islands from Near Islands to Tanaga Pass, 220–1,309 m.

***Arthrogorgia otsukai* Bayer, 1952**

FIGURE 16 A–J

Arthrogorgia otsukai Bayer, 1952:65–69, pl. 2, figs. 9–12, pl. 3, figs. 13–27; 1996:606, figs. 3–4.—Heifetz, 2002:26 (listed).—Wing and Barnard, 2004:24 (listed).—Heifetz et al., 2005:132.—Stone and Shotwell, 2007:106 (listed).—Cairns and Bayer, 2009:31 (listed).

DESCRIPTION. Colonies uniplanar, branching equal dichotomous, the distal branches 4–15 cm in length. Largest colony (*Jason II* 2102-4-1) only 20 cm in height and 10 cm width. Axis dark brown.

Polyps arranged in whorls of 5–7, directed downward; 11–13 whorls per 3 cm branch length. Polyps 2.3–2.75 mm in length.

Each polyp protected by 8 opercular scales (an occasional accessory opercular scale), a variable number of infraopercular scales, 1 pair of buccals and basals, and 4–5 transverse rows of infrabasal scales. Opercular scales triangular (Figure 16d), but with an elongate, cylindrical, distal blunt spine having numerous prominent, parallel, serrate ridges. Operculars decreasing progressively in size toward axial side (Figure 16c), the abaxials as much as 1.5 mm in length, the adaxials only 0.6–0.7 mm in length; L:W = 2.0–2.7. Occasionally, much smaller infraoperculars occurring on inner side of adaxial and inner lateral opercular scales (Figure 16c). Infraopercular scales (i.e., marginals and submarginals) square to rectangular in shape, 0–1 pair occurring proximal to each abaxial opercular (Figure 16a, g), 1–2 pairs adjacent to outer and inner lateral operculars, and 4–6 pairs on adaxial face (Figure 16c). These scales often visibly protruding from beneath distal margin of covering buccal scale (Figure 16a). Adaxial infraoperculars as much as 0.5 mm in width, others as much as 0.8 mm in width. The two large abaxial buccal scales (Figure 16b, e) as much as 1.4 mm in length terminating in a gently rounded margin. The two basal scales (Figure 16f) rarely more than 1 mm in height, terminating in a small distal lobe or nub, not a spine. Infrabasal scales (Figure 16a, h) not arranged in pairs but in 4 or 5 transverse rows of 4 or 5 thin, curved scales. Outer surface of all scales covered with radiating lines of small spines.

Coenenchymal scales (Figure 16i) thin, flat, polygonal scales as much as 0.5 mm in width. Coenenchymal

webbing present between basal branches of colony from *Jason II* 2102-4-1. Tentacular rodlets (Figure 16j) 0.10–0.13 mm long and 0.030 mm in width, usually slightly flattened.

REMARKS. This species was well described by Bayer (1952) and partially illustrated by him (Bayer, 1996) using SEM, but SEM-quality images of individual sclerites and various polyp views have never been published and are provided herein. One new record is reported here; it is the only record known having a specific locality.

Arthrogorgia otsukai is distinguished from other Aleutian congeners by lacking spines on its basal scales and in having smaller polyps. It also has multiridged opercular tips (ridges occurring even on the outer surface), flattened tentacular rodlets, and lacks coenenchymal tuberculate spheroids.

TYPES AND TYPE LOCALITY. The types (16 colonies) are deposited at the USNM (49979) and also includes SEM stubs B2561-2, C1419, 1420, and an “exploded” polyp, all the sclerites of which have been glued to a slide by F. M. Bayer to approximate their relative position in the polyp. Although Bayer (1952) referred to a holotype, no particular specimen in the type lot was segregated or specified in the text as the unique type; thus all 16 colonies are considered to be syntypes, as implied by Bayer (1996). Type locality: Somewhere between Aangan River, Kamchatka and Bowers bank, depth and *Albatross* station unknown.

MATERIAL EXAMINED. Syntypes; *Jason II* 2101-2-1, 1 branch, USNM 1115557, and 1 dry colony, AB10-0111; *Jason II* 2102-4-1, 1 branch, USNM 1115597 and AB10-0112; *Jason II* 2102-4-2, 2 branches, USNM 1115595, and 1 dry colony, AB10-0118.

DISTRIBUTION. Amchitka Pass and south of Kanaga Island, Aleutian Islands, 1,359–1,372 m. The type locality is too generalized to be of use.

Genus *Calyptrophora* Gray, 1866

Calyptrophora Gray, 1866:25.—Bayer, 2001:367–368.—Cairns, 2007b: 527.—Cairns and Bayer, 2009:44–45, figs. 15i–n.—Cairns, 2009:420–426 (key to species).

DIAGNOSIS. Colonies uniplanar, branched or unbranched. Polyps arranged in whorls, facing upward in most species, but downward in some. Polyps composed of 2 annular sclerite rings (basal and buccal), each composed of 2 inseparably fused scales; crescent-shaped infrabasals also present. Buccal and basal scales often bearing

distal cylindrical spines or flattened teeth. Opercular scales keeled. Coenenchymal scales granular, sometimes ridged. Tentacular rodlets often present.

DISCUSSION. The 16 valid species in the genus were listed, keyed, and phylogenetically analyzed by Cairns and Bayer (2009).

DISTRIBUTION. Pacific Ocean and western Atlantic, 229–3,531 m.

***Calyptrophora laevispinosa* Cairns, 2007**

FIGURE 2E

Calyptrophora laevispinosa Cairns, 2007b:536–537, figs. 1G, 14–15.—Cairns and Bayer, 2009:31 (listed).

REMARKS. This species was recently described and illustrated, and thus little can be added to its characterization; however, a picture of a large colony (40 cm in height, Figure 2e) is provided and six additional localities are provided, extending its known distribution throughout the Gulf of Alaska and to a depth of 3,531 m, the greatest depth recorded for a species of *Calyptrophora*.

The specimens from *Alvin* 3802 and 4037 are identical to *C. laevispinosa*, differing only in having ridged basal spines. Ironically, this was the character used to key various species (Cairns and Bayer, 2009) and to name the species (Cairns, 2007b), and thus it may be necessary to re-evaluate the consistency of this character among the *Calyptrophora* species or to reevaluate this particular specimen, perhaps using molecular analyses.

Galls containing a vermiform parasite are common in holotype and USNM 1075477.

TYPES AND TYPE LOCALITY. The holotype is deposited at the USNM (1102462), and a piece is also at the CAS (175310). Type locality: 46.683°N, 126.782°W (Gorda 1996 Flow off Washington), 3,107 m.

MATERIAL EXAMINED. *Alvin* 3802, 8 branches, USNM 1082615–1082617; *Alvin* 4033, 1 branch, USNM 1075472; *Alvin* 4037, 1 large colony and several branches, USNM 1075473–1075475; *Alvin* 4041, 1 dry colony and 1 alcohol preserved branch, USNM 1075476 and 1075477, respectively; *Jason II*-93-18, 1 dry colony, USNM 1081195; *Jason II*-93-23, 1 dry colony and 1 alcohol-preserved branch, USNM 1081196.

DISTRIBUTION. Gorda Flow off Washington, GOA (Derickson, Patton, Giacomini, and Welker Seamounts), 2,672–3,531 m. Not known from the Aleutian Islands, rather only from the closely adjacent GOA.

Genus *Parastenella* Versluys, 1906

Stenella (*Parastenella*) Versluys, 1906:39, 45.

Candidella (*Parastenella*).—Bayer, 1956:F222.

Parastenella.—Bayer, 1961:295.—Cairns, 2007a:245–247; 2007b:518 (tabular key).—Cairns and Bayer, 2009:45–46.—Cairns, 2010:434 (key to species).

DIAGNOSIS. Colonies flabellate or slightly bushy, dichotomously or irregularly branched, usually fairly stiff. Polyps occurring in whorls, pairs, or individually, oriented perpendicular to branch. Body wall scales arranged in 5–8 longitudinal rows, the 8 marginal scales elongate and often (most commonly those on abaxial side) extending as a semicircular to tubular flute; each marginal flute bearing a concentrated patch of nematocysts (a nematocyst pad) on their distal inner side. Opercular scales offset in alignment from marginal scales. Opercular scales keeled on inner surface. Tentacular rodlets common.

DISCUSSION. Seven species are known in the genus (Cairns and Bayer, 2009; Cairns, 2010), which are keyed and discussed in the papers cited above. The genus is easily distinguished by having its opercular scales offset from its marginals (see below). Cairns (2010) suggested that marginal nematocyst pads were characteristic of the genus, as he reported them from *P. bayeri* and *P. gymnogaster*. They are herein confirmed from *P. doederleini* and *P. ramosa*, and are retrospectively noted in *P. atlantica* (see Cairns, 2007a:fig. 3). Thus they need only be confirmed in *P. pacifica* and *P. spinosa*.

In most primnoids, there are two rows of abaxial scales that cover the abaxial side of the polyp, the adjacent abaxial edges of these scales abutting or overlapping along the sagittal axis of the polyp, which is also the case in *Parastenella*. In most primnoid genera a set of eight opercular scales are in directly alignment with the body wall scales; however, in *Parastenella* the opercular scales are uniquely offset from the marginal scales such that each opercular scale is aligned with the space between two adjacent marginals (see Cairns, 2007a:fig. 5, and Figure 17c herein). This results in one large abaxial opposing a small adaxial scale and aligned with the sagittal axis, and three couples of lateral opercular scales that are paired across the sagittal axis. These three pairs may be termed the outer lateral, transverse lateral, and inner lateral pairs.

DISTRIBUTION. Known from all ocean basins except eastern Atlantic and off continental Antarctica, 330–3,470 m.

***Parastenella doederleini*
(Wright and Studer, 1889)**

FIGURES 2B, 17A–J

- Stenella doederleini* Wright and Studer, 1889:58, pl. 20, fig. 7.—Not Studer, 1894:64 (= *P. ramosa*).—Kükenthal, 1915:152 (key to species); 1919:446–447; 1924:304–305 (key to species).—Aurivillius, 1931:290–291.
- Stenella (Parastenella) doederleini*.—Versluys, 1906:45–47, pl. 1 fig. 3, text figs. 49–54.—Kinoshita, 1908b:28–30, pl. 2, fig. 12, text figs. 4–7.
- Candidella (Parastenella) doederleini*.—Bayer, 1956:F222, fig. 159-4a.
- Parastenella doederleini*.—Bayer, 1981:934, 936, fig. 69.—Cairns, 2007b:518–519 (tabular key), 523, fig. 4B.—Whitmire and Clarke, 2007:152 (listed).—Cairns and Bayer, 2009:31, 45–46, fig. 16a–b.—Cairns, 2010:435 (key to species).

DESCRIPTION. Colonies bushy, dichotomously branched, and rather small, the largest Aleutian colony only 6 cm in height (Figure 2b), whereas other colonies reported to be (Aurivillius, 1931) as much as 25 cm in height. Axis dark brown, usually visible through single thin, translucent white layer of coenenchymal scales. Polyps occurring singly, in pairs, and occasionally in whorls of 3, projecting perpendicular to branch surface, slightly clavate, and 2.1–2.5 mm in length.

Each polyp covered with 8 opercular scales, 8 marginal scales, and 5 or 6 longitudinal rows of body wall scales. As is typical for the genus, 1 pair of opposing symmetrically shaped abaxial and adaxial opercular scales separated by 3 pairs of asymmetrical lateral opercular scales (Figure 17c). Whereas length of the operculars (Figure 17e) not varied much (0.71–0.92 mm), the basal width increasing progressively from adaxial to abaxial side, such that abaxials L:W = 1.7 and adaxials about 2.1. Outer surface of operculars deeply longitudinally creased and covered with tiny spines; inner surface prominently keeled. The 8 marginal scales forming an asymmetrical rosette (Figure 17c) when viewed from above, the 5 marginals on abaxial and lateral sides bearing elongate flutes, whereas the 3 on adaxial side lacking flutes (Figure 17c). Fluted marginals (Figure 17d) consisting of a broad rectangular base supporting a projecting semi-circular to tubular flute, the flutes quite narrow (0.10–0.15 mm or ¼ width of the base), 50–55% length of the scale, bearing a nematocyst pad in their distal inner surface (Figure 17c, j). Nematocysts closely packed, each uniformly 0.021 mm in length and 0.003 mm in diameter. Nonfluted adaxial marginals with a rounded distal margin. Body wall scales arranged in roughly 6 rows: 2 abaxial rows of 5 or 6 scales, 2 short lateral rows of 2 or 3 scales,

and 2 adaxial rows of 5 or 6 scales, the latter (Figure 17f) roughly square (0.35–0.45 mm in width) and completely covering adaxial polyp surface. Abaxial body wall scales (Figure 17g) proximal to marginals also bearing flutes, but progressively smaller toward base of polyp.

Coenenchymal scales (Figure 17h) irregular in shape, up to 0.55 mm in length, flat, and often bearing a boss or ridge on center of outer surface. Tentacular rodlets (Figure 17i) cigar shaped, 0.070–0.082 mm in length (L:D = 5.1–5.8).

REMARKS. *Parastenella doederleini* is quite similar to *P. ramosa* as is discussed by Cairns (2007b) by narrative and tabular key and by Cairns (2010) in a key to the species in the genus. In summary, *P. doederleini* is distinguished by having smaller, more delicate polyps; more slender and shorter marginal and submarginal flutes; and by having a tendency to have bosses or ridges on its coenenchymal scales. Their distributions do not quite overlap in that, whereas *P. ramosa* is known from the Gulf of Alaska and the closely adjacent Commander Islands to the west, it has not yet been collected from the Aleutian Islands; *P. doederleini* also tends to be found in deeper water than *P. ramosa*. *Parastenella doederleini* is the type of the genus and has been redescribed several times based on new material by Versluys (1906), Kinoshita (1908b), Kükenthal (1919), and Aurivillius (1931). It is a new record for Alaska and the Aleutian Islands.

The presence of nematocyst pads on the inner surface of the marginal scales is confirmed in this species (Figure 17c,j), as suggested might be the case for all the species within the genus (Cairns, 2010).

TYPES AND TYPE LOCALITY. The holotype is deposited at the BM (1889.5.27.37) and a fragment also at the ZMA (Coel. 3085, see van Soest, 1979). Type locality: *Challenger*-237, 34°37'N, 140°32'E (off Yokohama, Japan), 3423 m.

MATERIAL EXAMINED. *Jason II* 2098-2-2, branch, USNM 111556; *Jason II* 2100-3-2, branches, USNM 1115561; *Jason II* 2100-3-3, branch, SEM stubs C1478-1481, USNM 1115560.

DISTRIBUTION. Indonesia, Japan, Aleutian Islands (Adak Canyon), 400–3,423 m.

***Parastenella ramosa* (Studer, 1894)**

- Stenella ramosa* Studer, 1894:64–65.
- Stenella doederleini*.—Studer, 1894:64.
- Stenella (Parastenella) ramosa*.—Versluys, 1906:47–48.—Kükenthal, 1919:445; 1924:303.

Parastenella ramosa.—Cairns, 2007b:518–523, figs. 1E, 4, 5.—Cairns and Bayer, 2009:31 (listed).

REMARKS. *Parastenella ramosa* has recently been described and figured by Cairns (2007b), and thus will not be redescribed herein. Keys to the species within the genus are found in Cairns (2007b, 2010), and comparison to *P. doederleini* is made above. This account reports six new records of the species, extending its known distribution west to the Commander Islands, Russia, and Adak Canyon in the Aleutian Islands.

The presence of nematocysts pads in the inner surface of the marginal scales is confirmed in this species, as suggested might be the case for all the species within the genus (Cairns, 2010).

TYPES AND TYPE LOCALITY. Holotype lost (see Cairns, 2007b). Type locality: *Albatross* 3384: 7°31'30"N, 79°14'W (Gulf of Panama), 837 m.

MATERIAL EXAMINED. *Alvin* 3798, branch, USNM 1082596; *Alvin* 3799, branch, USNM 1082601; *Alvin* 3806, branches, USNM 1082639, -2633, -2641; *Alvin* 4028, branch, USNM 1075358; *Jason II* 2099-18-1, 1 dry colony, AB10-0074; *R/V Keldysh (Mir 2)* 22, branches, USNM 1106689; specimens reported by Cairns (2007b).

DISTRIBUTION. Gulf of Panama, various seamounts off western USA and Canada (e.g., Rodriguez, Davidson, Axial 1998 South Flow, Welker, and Dickins), Gulf of Alaska (Giacomini, Pratt, Murray, and Warwick Seamounts), Pip Volcano (Commander Islands, off Kamchatka, Russia), Adak Canyon, 665–1,766 m.

***Parastenella gymnogaster* Cairns, 2007**

Parastenella gymnogaster Cairns, 2007b:523–526, figs. 1B, 6–7.—Cairns and Bayer, 2009:31 (listed).

REMARKS. *Parastenella gymnogaster* has recently been described and figured by Cairns (2007b) and thus will not be redescribed herein. Keys to the species within the genus are found in Cairns (2007b, 2010). In summary, it differs from other species in having broad, short marginal flutes, only six rows of body wall scales (the scales of the abaxial rows being quite broad and linearly arranged), ornately ridged coenenchymal scales, and a naked adaxial polyp face. This account reports three new records of the species from three additional seamounts in the Gulf of Alaska, although it is not known from the Aleutian Islands.

TYPES AND TYPE LOCALITY. The holotype and paratypes are deposited at the USNM (holotype = 1075464). Type locality: *Alvin* 4033-23, 54°59'01"N, 140°23'59"W (Welker Seamount off British Columbia), 2,634 m.

MATERIAL EXAMINED. Types; *Alvin* 3803, branches, USNM 1082619; *Alvin* 3804, branches, USNM 1082620, -2624, -2626, -2628, -2630, -2632; *Alvin* 4029, branches, USNM 1075359-1075361, 1075363.

DISTRIBUTION. Juan de Fuca Ridge off Oregon and seamounts off Oregon and British Columbia, Gulf of Alaska (Derickson, Chirikof, Marchand Seamounts), 1,962–2,869 m.

FIGURES 1-17

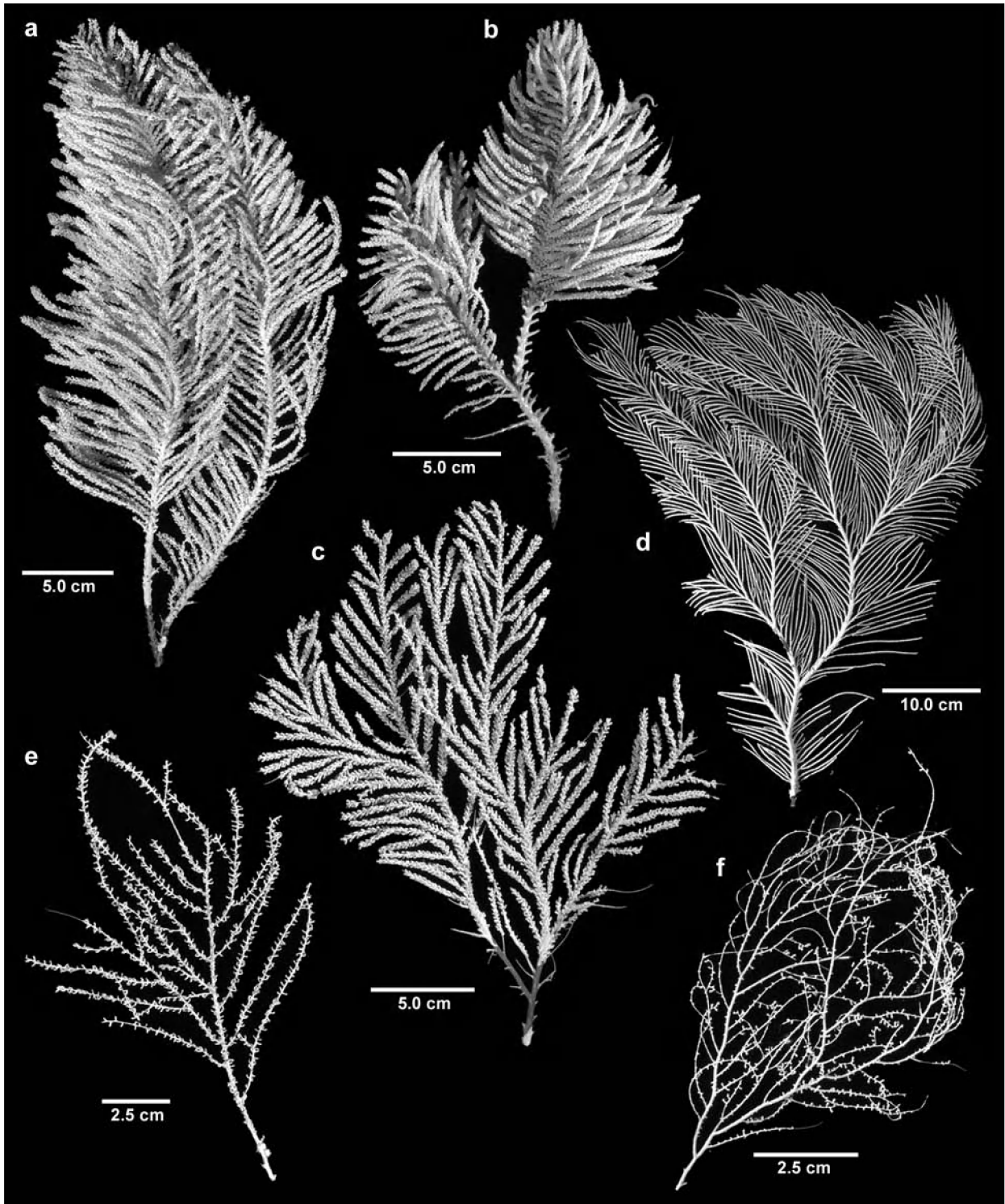


FIGURE 1. Colonies of various species: (a) *Thouarella cristata*, holotype (USNM 1116600), dry; (b) *T. trilineata*, holotype (USNM 1010175), in alcohol; (c) *Plumarella hapala*, holotype (USNM 1006310), dry; (d) *P. aleutiana*, holotype (USNM 1011356), dry; (e) *P. profunda*, holotype (USNM 1134074), dry; (f) *P. spicata*, holotype (USNM 30050), in alcohol. Scale bars: a-c, 5 cm; d, 10 cm; e-f, 2.5 cm.

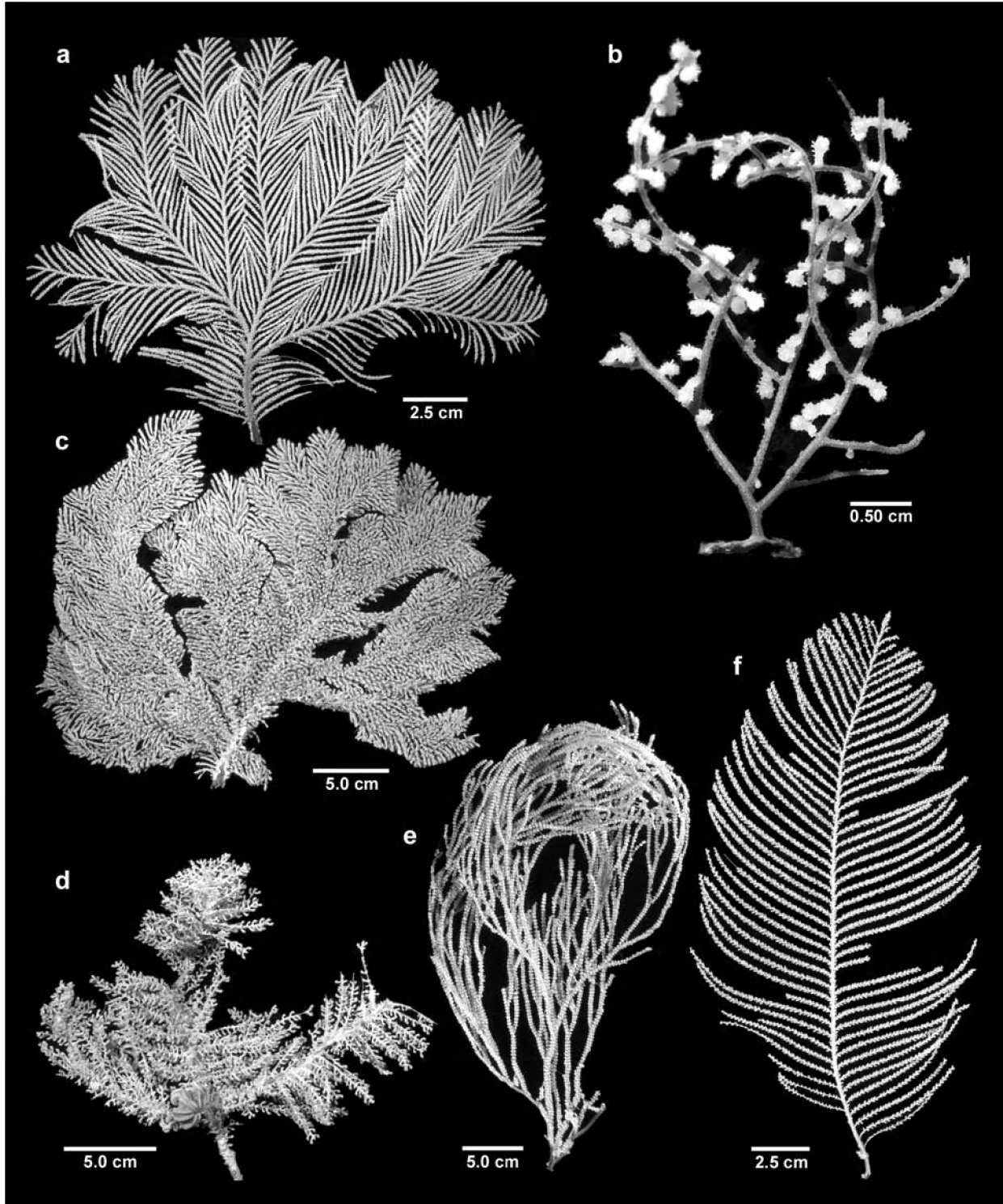


FIGURE 2. Colonies of various species: (a) *Plumarella echinata*, holotype (USNM 1135009), in alcohol; (b) *Parastenella doederleini*, Jason IV 2100-3-3, USNM 1115560, in alcohol; (c) *Plumarella superba*, Delta 5604 (USNM 1011277), dry; (d) *P. nuttingi*, holotype (USNM 1006317), dry; (e) *Calyptrophora laevispinosa*, Alvin 4037 (USNM 1075475), in alcohol; (f) *Plumarella robusta*, holotype (USNM 1135992), dry. Scale bars: a, f, 2.5 cm; b, 0.5 cm; c–e, 5 cm.

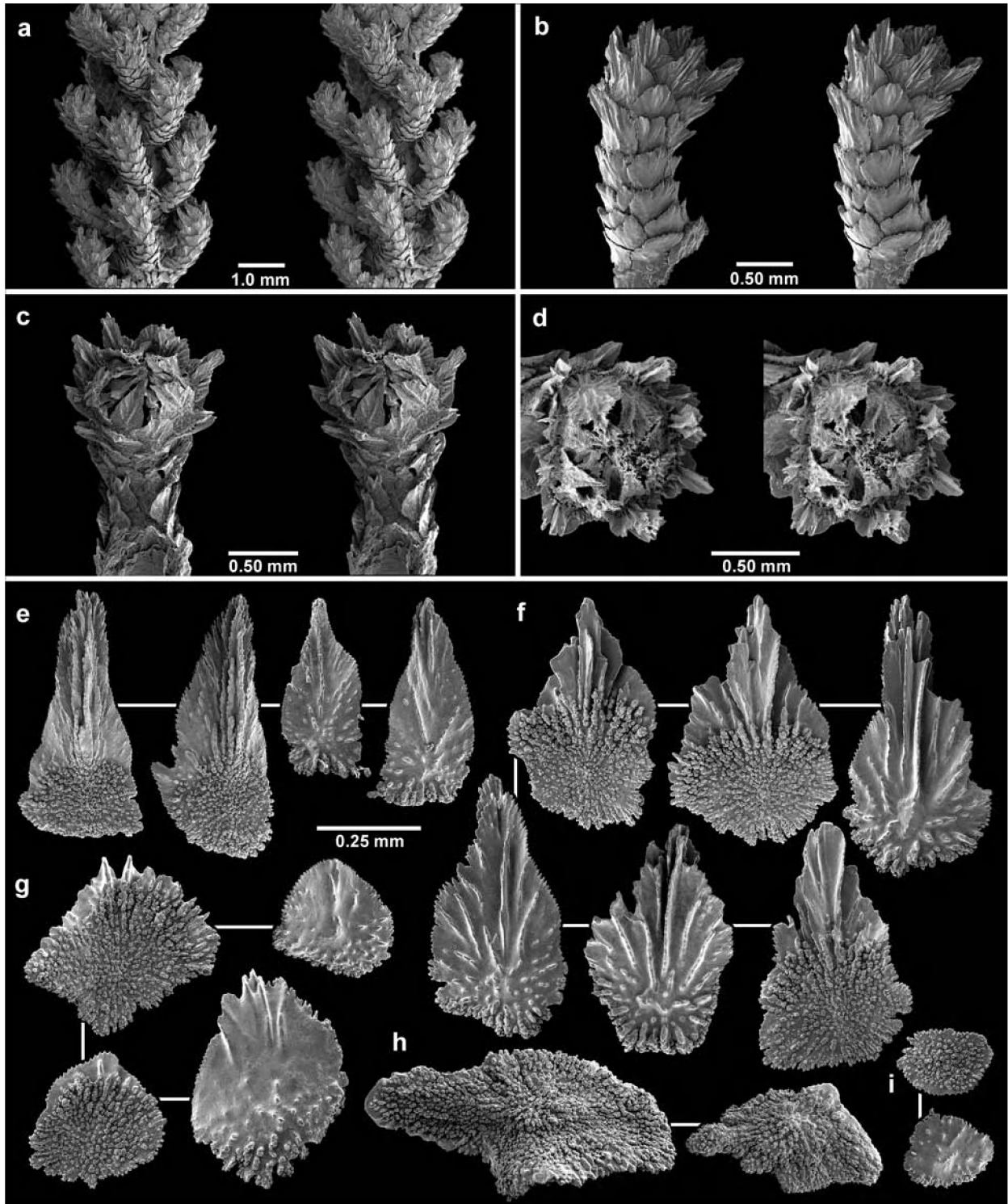


FIGURE 3. Polyps and scales of *Thouarella cristata* from the holotype (USNM 1115600), a–d are stereo views: (a) lateral view of branchlet showing randomly arranged polyps; (b–d) abaxial, adaxial, and opercular views of polyps, respectively; (e) opercular scales; (f) marginal scales; (g) abaxial body wall scales; (h) coenenchymal scales; (i) adaxial body wall scales. Scale bars: a, 1 mm; b–d, 0.5 mm; e–i, 0.25 mm.

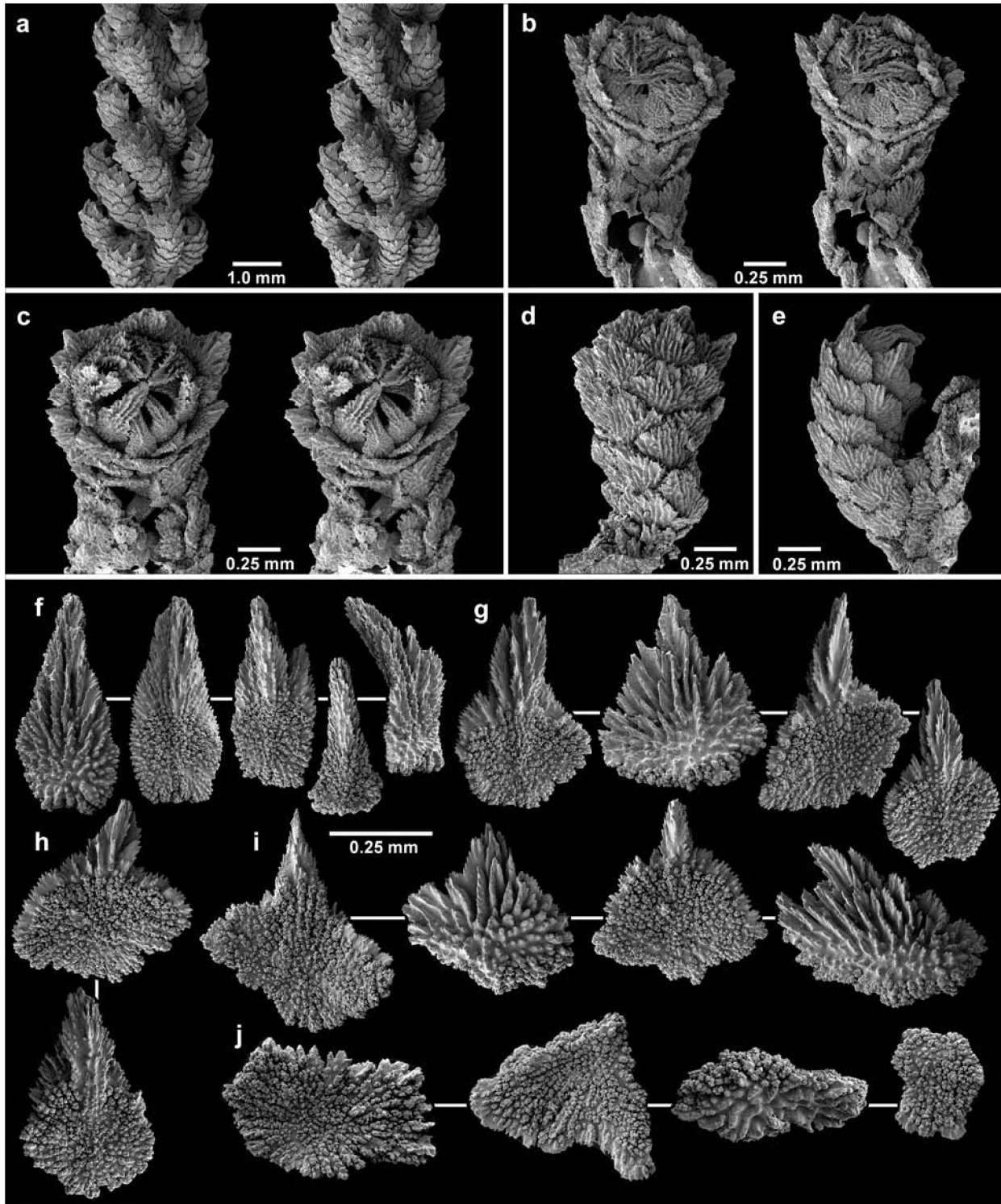


FIGURE 4. Polyps and scales of *Thouarella trilineata* from the holotype (USNM 1010175), a–c are stereo views: (a) lateral view of branchlet showing randomly arranged polyps; (b–c) two opercular views of polyp, also showing adaxial polyp face; (d) adaxial side of polyp (m = marginal scales); (e) lateral view of polyp; (f) opercular scales; (g) marginal scales; (h) submarginal scales; (i) body wall scales; (j) coenenchymal scales. Scale bars: a, 1 mm; b–e, 0.5 mm; f–j, 0.25 mm.

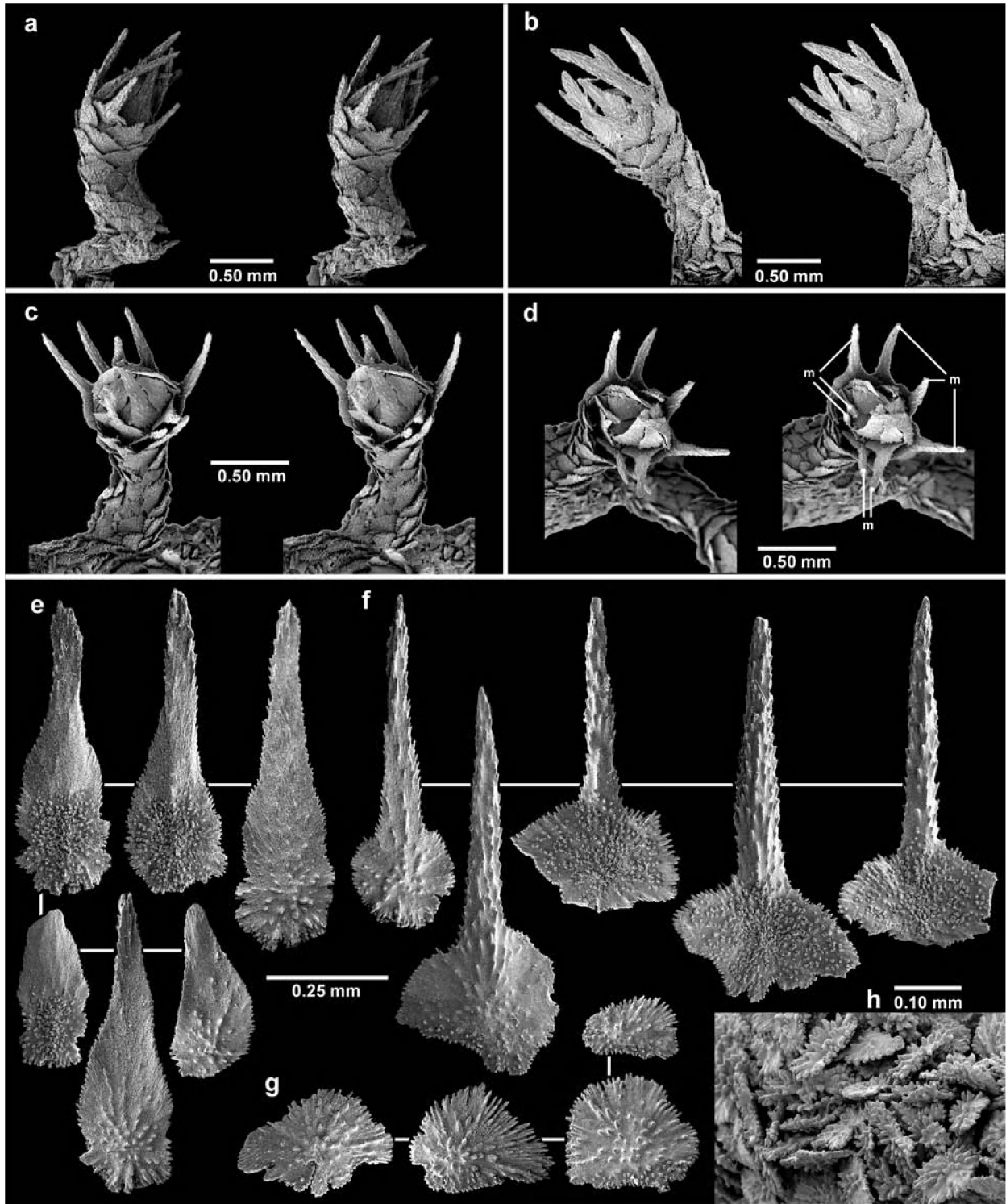


FIGURE 5. Polyps and scales of *Plumarella spicata* from the holotype (USNM 30050), a–d are stereo views: (a) adaxial view of polyp; (b) lateral view of polyp; (c) adaxial view of polyp; (d) opercular view of polyp; (e) opercular scales; (f) marginal scales; (g) body wall scales; (h) outer surface of coenenchymal scales, in situ. Scale bars: a–d, 0.5 mm; e–g, 0.25 mm; h, 0.10 mm.

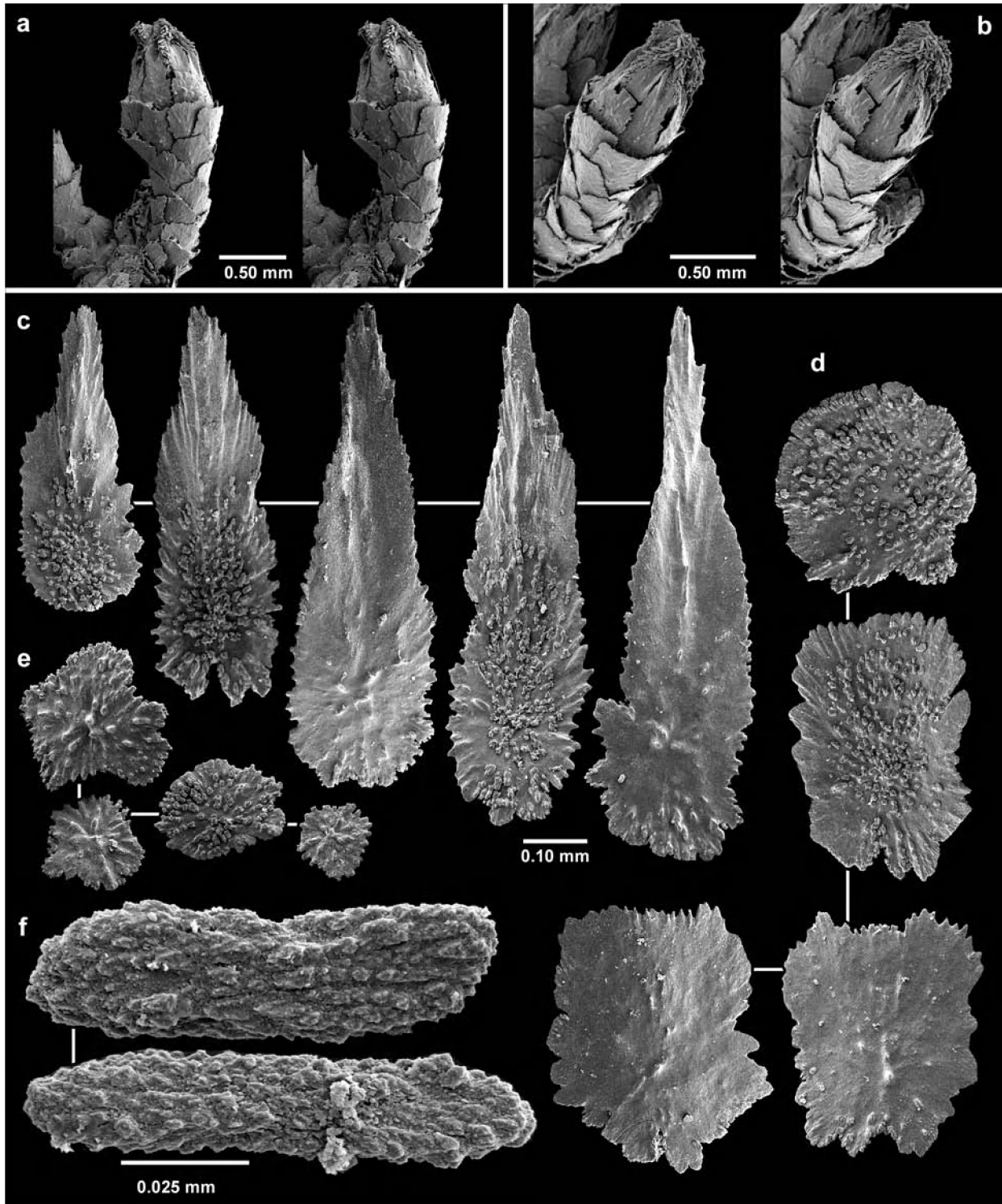


FIGURE 6. Polyps and scales of *Plumarella profunda* from the holotype (USNM 1134074), a–b are stereo views: (a–b), lateral and abaxial views of polyps; (c) opercular scales; (d) body wall scales; (e) coenenchymal scales; (f) tentacular rodlets. Scale bars: a–b, 0.5 mm; c–e, 0.10 mm; f, 0.025 mm.

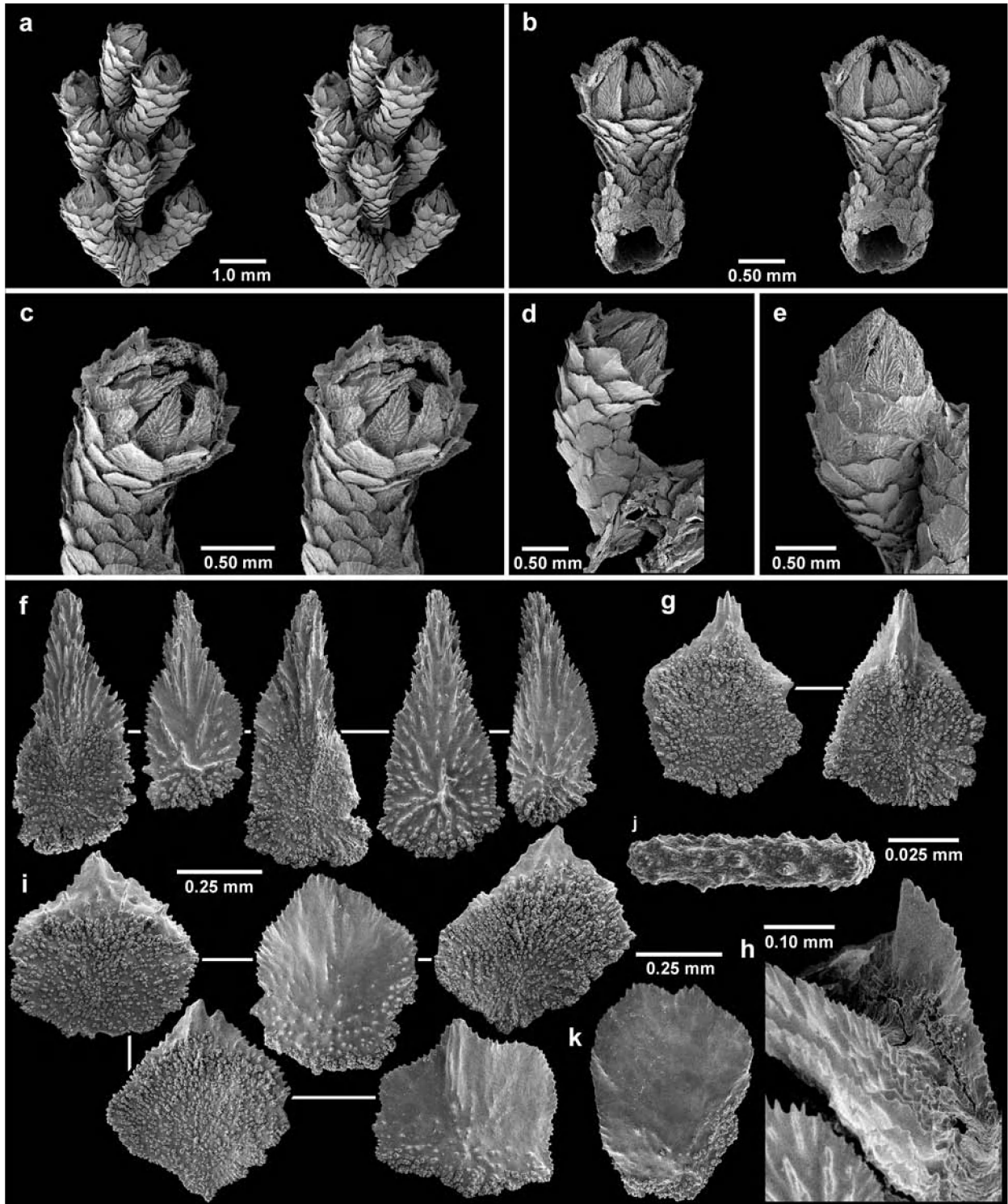


FIGURE 7. Polyps and scales of *Plumarella hapala* from the holotype (USNM 1006310), a–c are stereo views: (a) lateral view of branchlet showing randomly arranged polyps; (b–c) adaxial view of polyps; (d) lateral view of polyp; (e) lateral view of gravid polyp; (f) opercular scales; (g) marginal scales; (h) smooth inner surface of a marginal scale, in situ; (i) body wall scales; (j) a tentacular rodlet; (k) a coenenchymal scale. Scale bars: a, 1 mm; b–e, 0.5 mm; f–g, i, k, 0.25 mm; h, 0.10 mm; j, 0.025 mm.

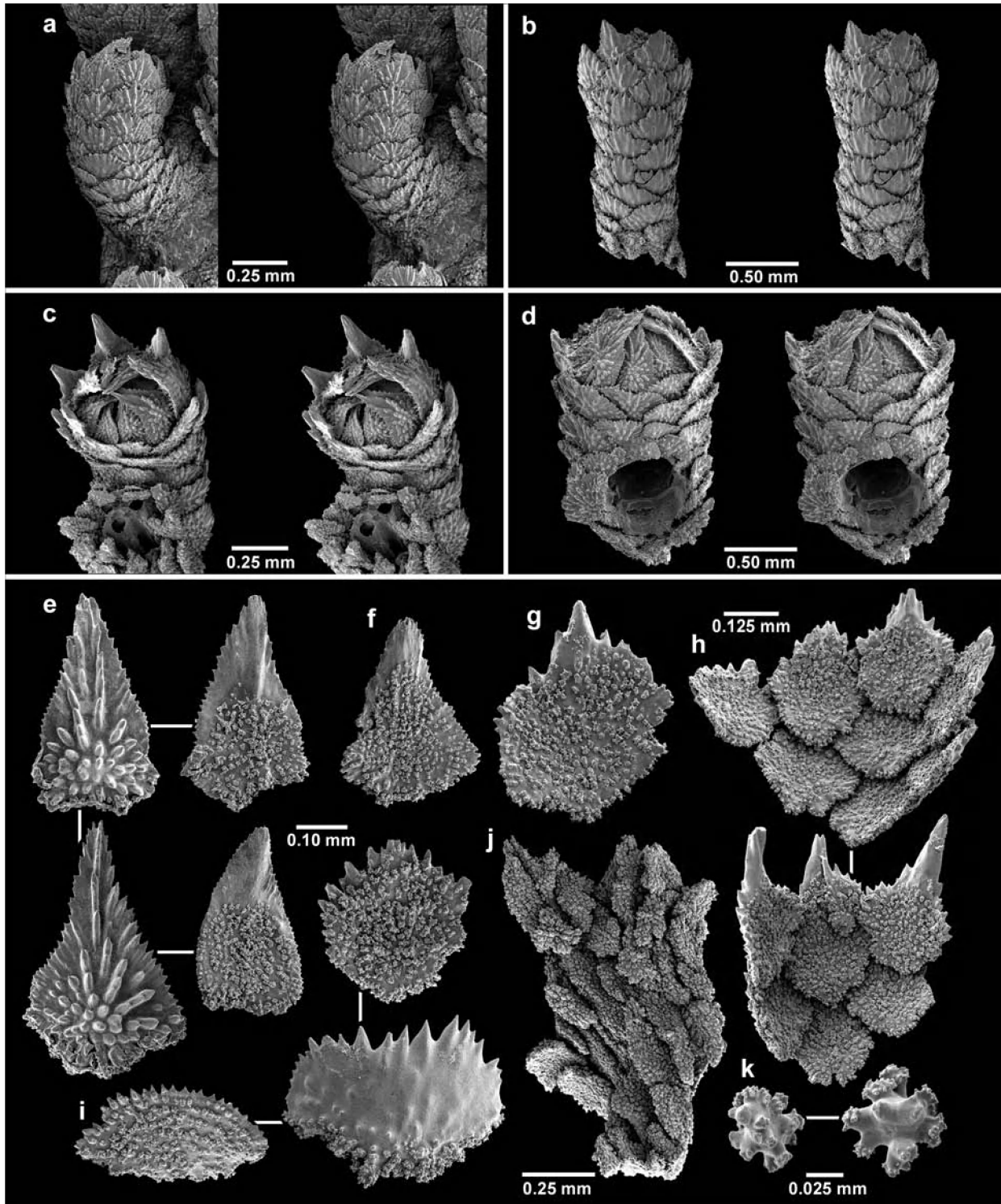


FIGURE 8. Polyps and scales of *Plumarella aleutiana* from the holotype (USNM 1011356), a–d are stereo views: (a–b) lateral and abaxial views of polyps; (c–d) adaxial opercular views of two polyps; (e) opercular scales; (f) submarginal scale; (g) marginal scale; (h) inner surface of several smooth-tipped marginal scales, in situ; (i) body wall scales; (j) inner surface of coenenchymal scales, in situ; (k) coenenchymal tuberculate spheroids. Scale bars: a, c, 1.0 mm; b, d, h, 0.5 mm; e–g, i, 0.10 mm; j, 0.25 mm; k, 0.025 mm.

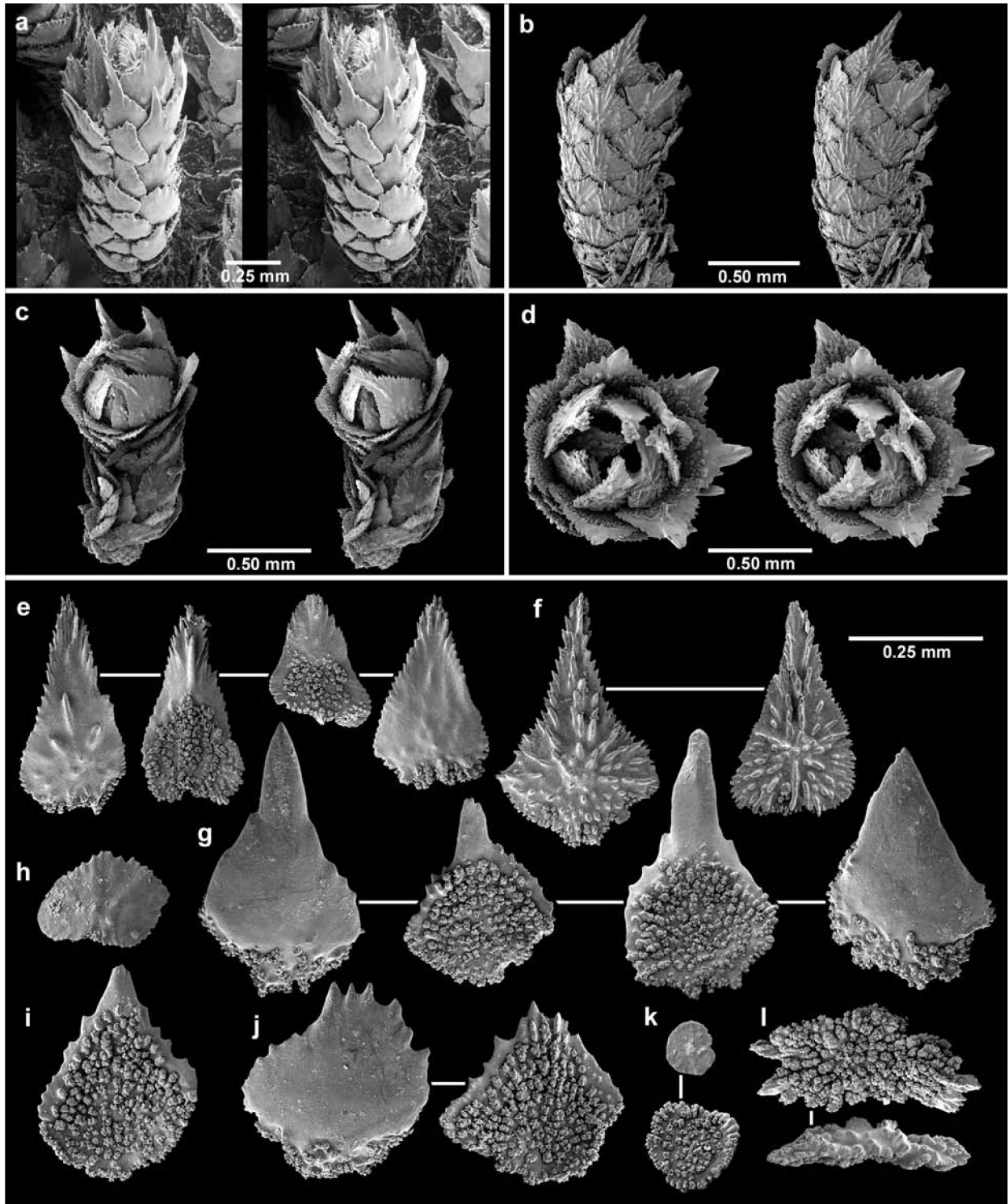


FIGURE 9. Polyps and scales of *Plumarella superba* (a, e, g-l, holotype, USNM 30691; b, f, USNM 1009951; c-d, USNM 50150), a-d are stereo views: (a) abaxial view of a typical polyp with smooth scales; (b) abaxial view of a polyp with ridged body wall scales; (c-d) adaxial and opercular views of polyps, respectively; (e) typical opercular scales with smooth outer face; (f) variant opercular scales with ridged outer surface; (g) abaxial marginal scales; (h) adaxial marginal scale; (i) submarginal scale; (j) smooth body wall scales; (k) adaxial body wall scales; (l) coenenchymal scales. Scale bars: b-d, 0.5 mm; a, e-l, 0.25 mm.

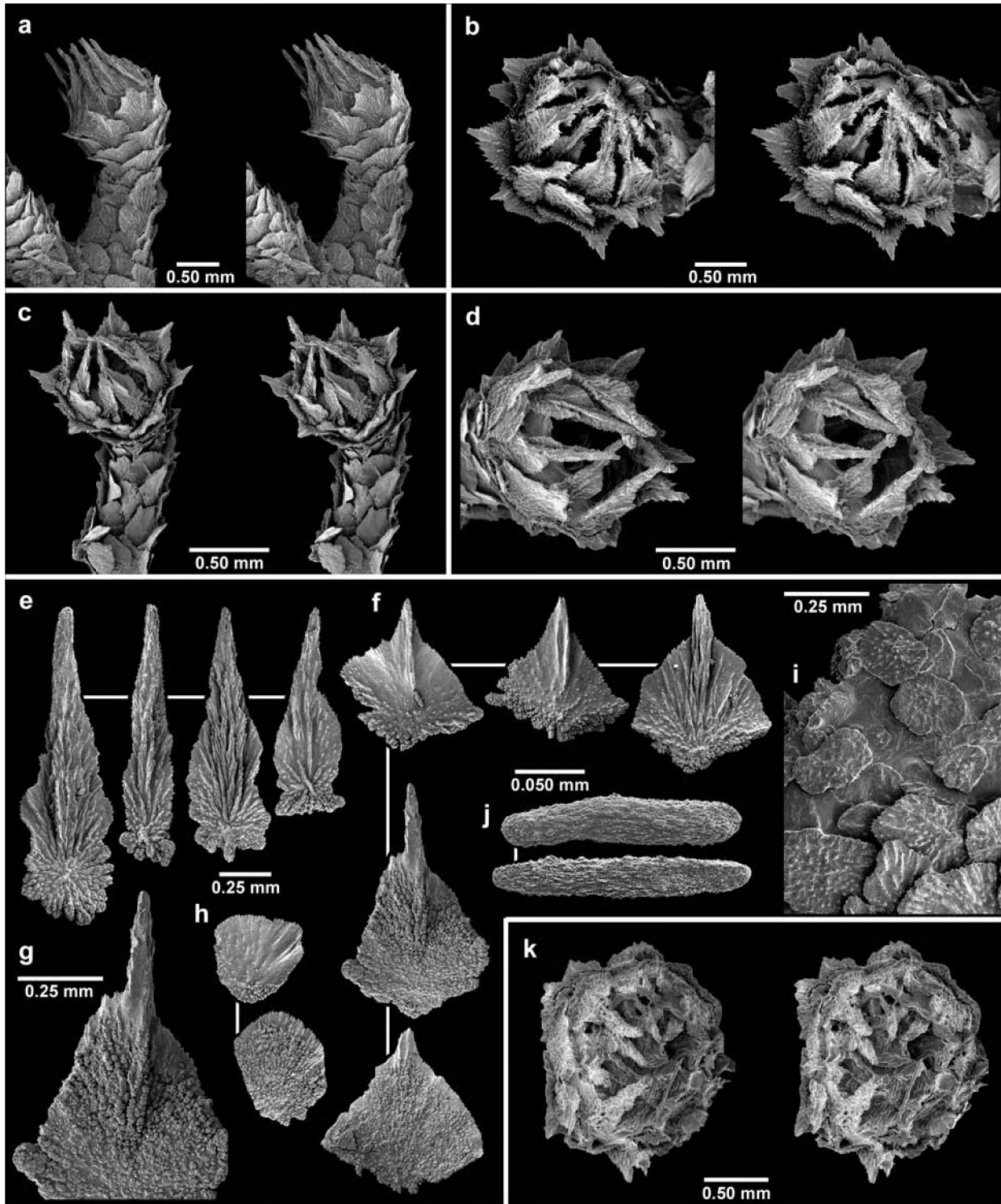


FIGURE 10. Polyps and scales of *Plumarella nuttingi* from the holotype (USNM 1006317), a–d, k are stereo views: (a, c) lateral and adaxial view of polyps, respectively; (b–d) opercular view of polyps; (e) opercular scales; (f) marginal scales; (g) inner face of a marginal scale; (h) body wall scales; (i) coenenchymal scales in situ in web; (j) tentacular rodlets; (k) tentacular rodlets, in situ. Scale bars: a–d, k, 0.5 mm; e–i, 0.25 mm; j, 0.05 mm.

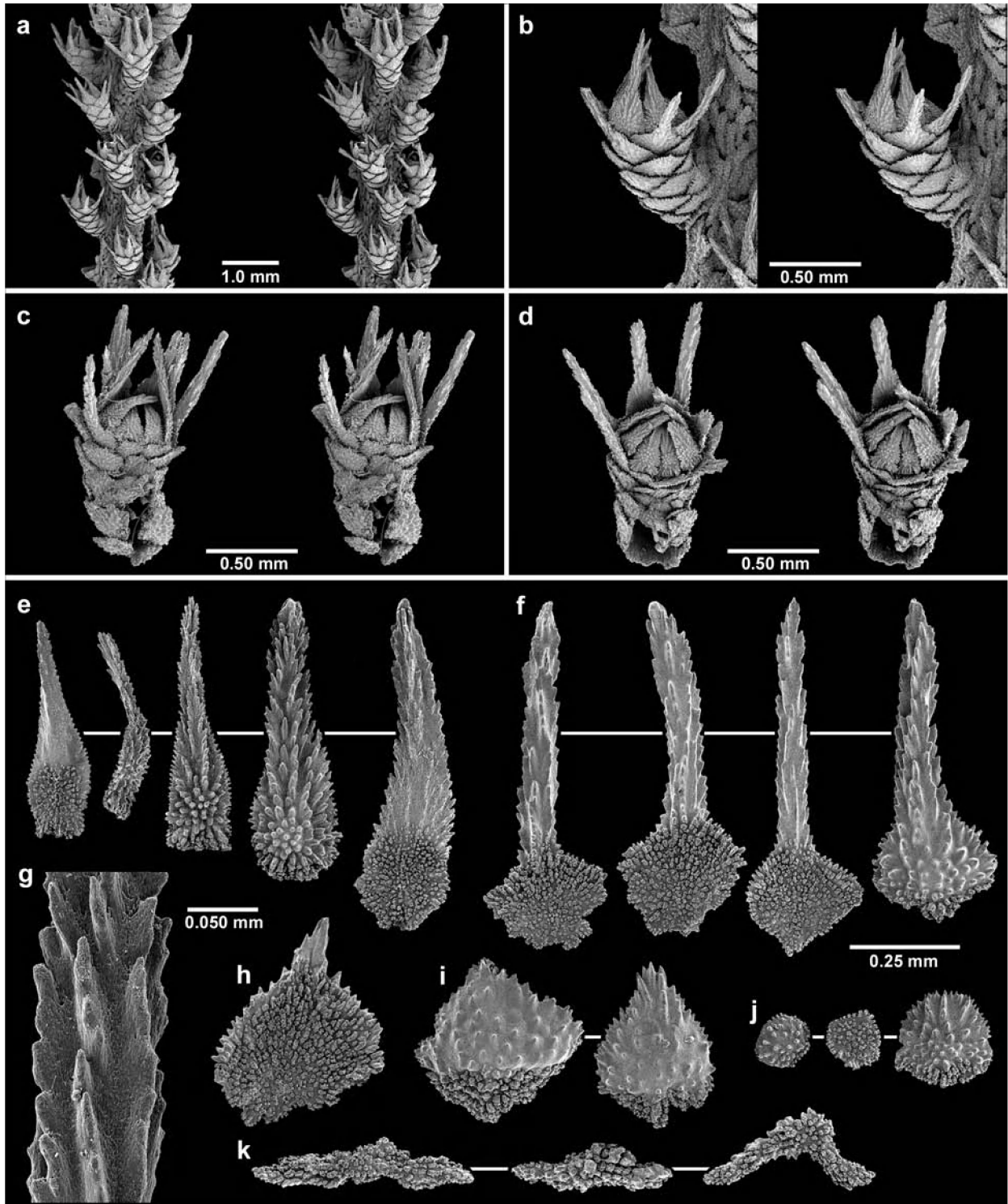


FIGURE 11. Polyps and scales of *Plumarella echinata* from the holotype (USNM 1135009), a–d are stereo views: (a) lateral view of branchlet showing randomly arranged polyps; (b) view of outer lateral face of a polyp; (c–d) adaxial and opercular views of polyps, respectively (m = marginal scales); (e) opercular scales; (f) marginal scales; (g) spination on a marginal spine; (h) submarginal scale; (i) abaxial body wall scales; (j) adaxial body wall scales; (k) coenenchymal scales. Scale bars: a, 1 mm; b–d, 0.5 mm; e–f, h–k, 0.25 mm; g, 0.05 mm.

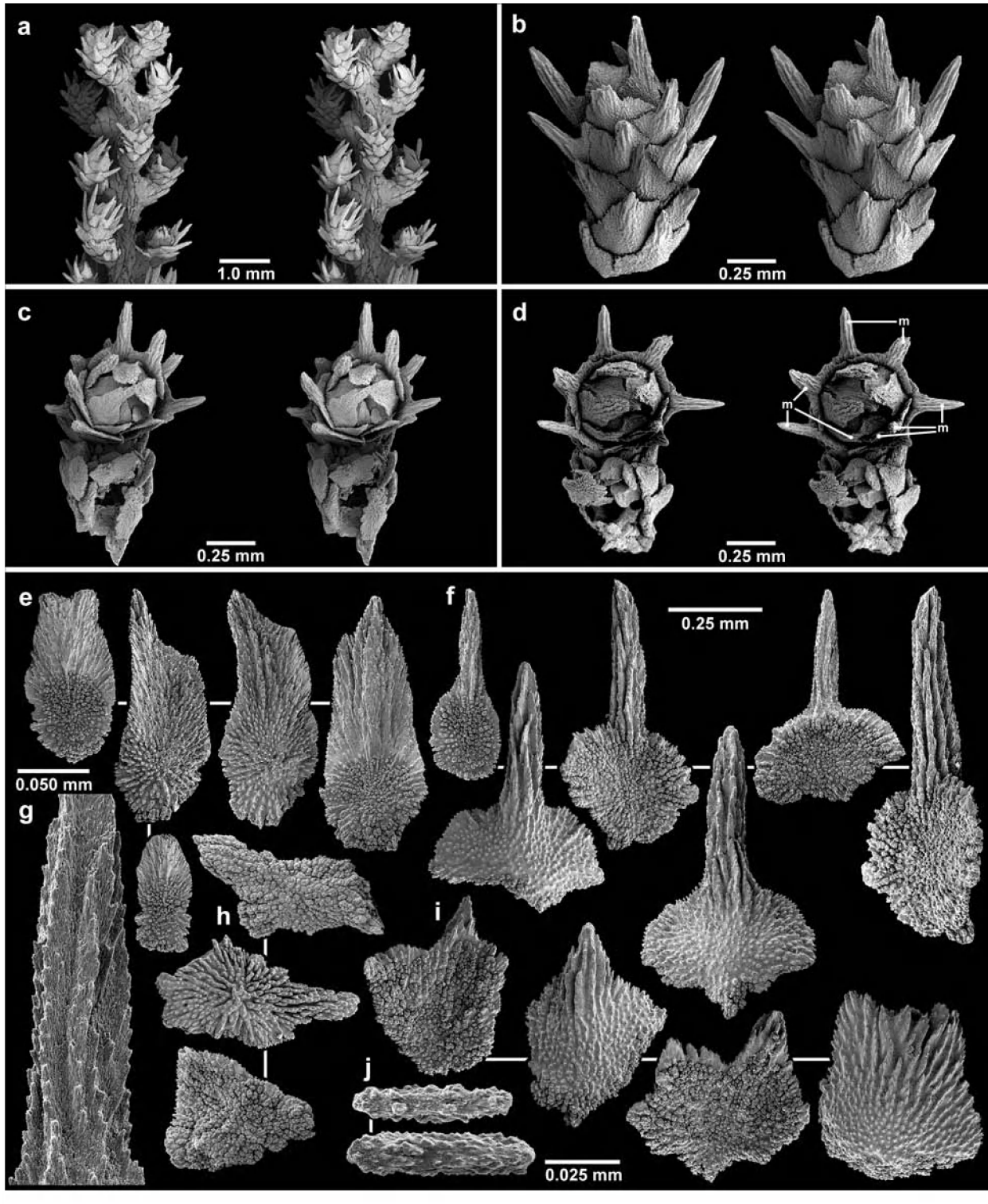


FIGURE 12. Polyps and scales of *Plumarella robusta* from the holotype (USNM 1135992), a–d are stereo views: (a) lateral view of branchlet showing randomly arranged polyps; (b) abaxial view of a polyp; (c–d) adaxial opercular view of two polyps ($m = 8$ marginal scales); (e) opercular scales; (f) marginal scales; (g) spination on a marginal spine; (h) coenenchymal scales; (i) body wall scales; (j) tentacular rodlets. Scale bars: a, 1 mm; b–f, h–i, 0.25 mm; g, 0.05 mm; j, 0.025 mm.

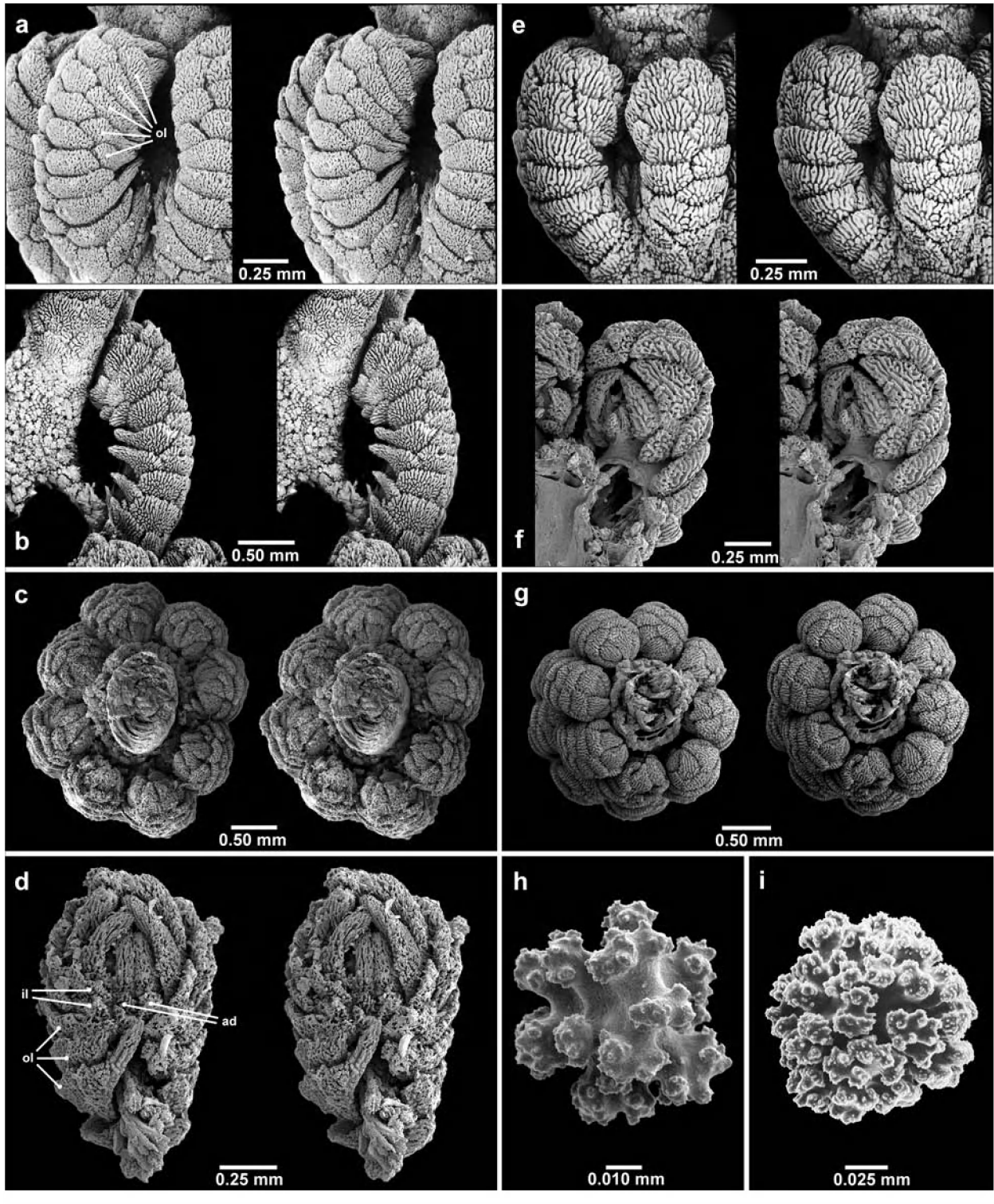


FIGURE 13. Polyps and sclerite of *Fanellia compressa* (a, c–d, h, USNM 57543; b, USNM 57542), a–d are stereo views: (a–b) oblique view of two polyps showing outer lateral body wall scales with lateral extensions (ol = outer lateral scales); (c) opercular view of a polyp whorl; (d) adaxial view of a polyp (il = inner lateral scales, ol = outer lateral scales, ad = adaxial scales); (h) coenenchymal tuberculate spheroid. Polyps and sclerite of *Fanellia fraseri* (e–g, i, USNM 51284), e–g are stereo views: (e) adaxial and lateral views of polyps; (f) adaxial opercular view of a polyp; (g) opercular view of a polyp whorl; (i) coenenchymal tuberculate spheroid. Scale bars: a, d–f, 0.25 mm; b–c, g, 0.5 mm; h, 0.01 mm; i, 0.025 mm.

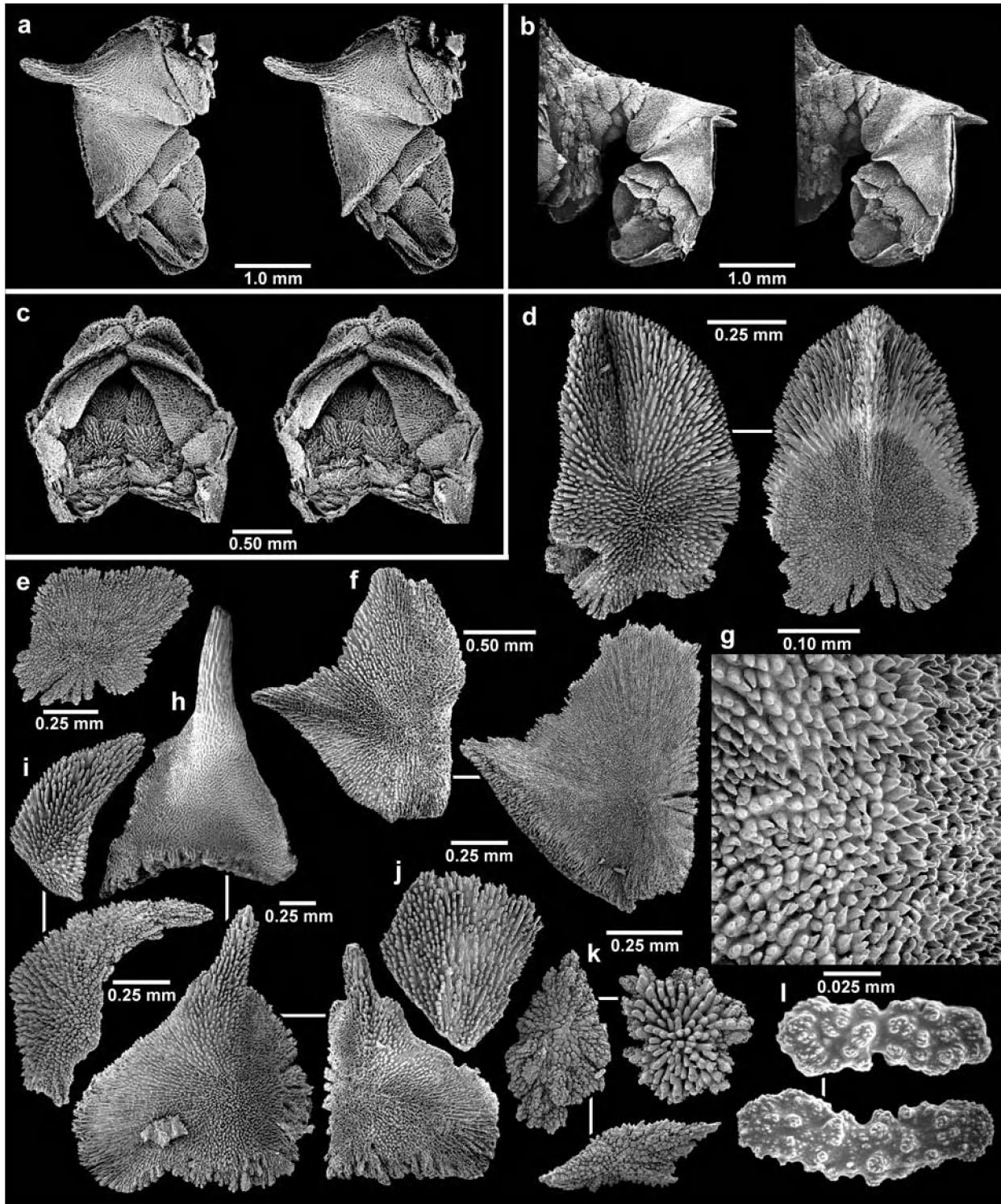


FIGURE 14. Polyps and scales of *Arthrogorgia utinomii* (a, f–h, paratype, USNM 80829; b–e, i–k, paratype, USNM 58168; l, holotype), a–c are stereo views: (a–b) lateral view of two polyps showing infraopercular scales; (c) adaxial view of a polyp; (d) opercular scales; (e) infraopercular scale; (f) buccal scales; (g) spination on outer surface of body wall scale; (h) basal scales; (i) infrabasal scales; (j) adaxial body wall scale; (k) coenenchymal scales; (l) tentacular rodlets. Scale bars: a–b, 1 mm; c, f, 0.5 mm; d–e, h–k, 0.25 mm; g, 0.01 mm; l, 0.025 mm.

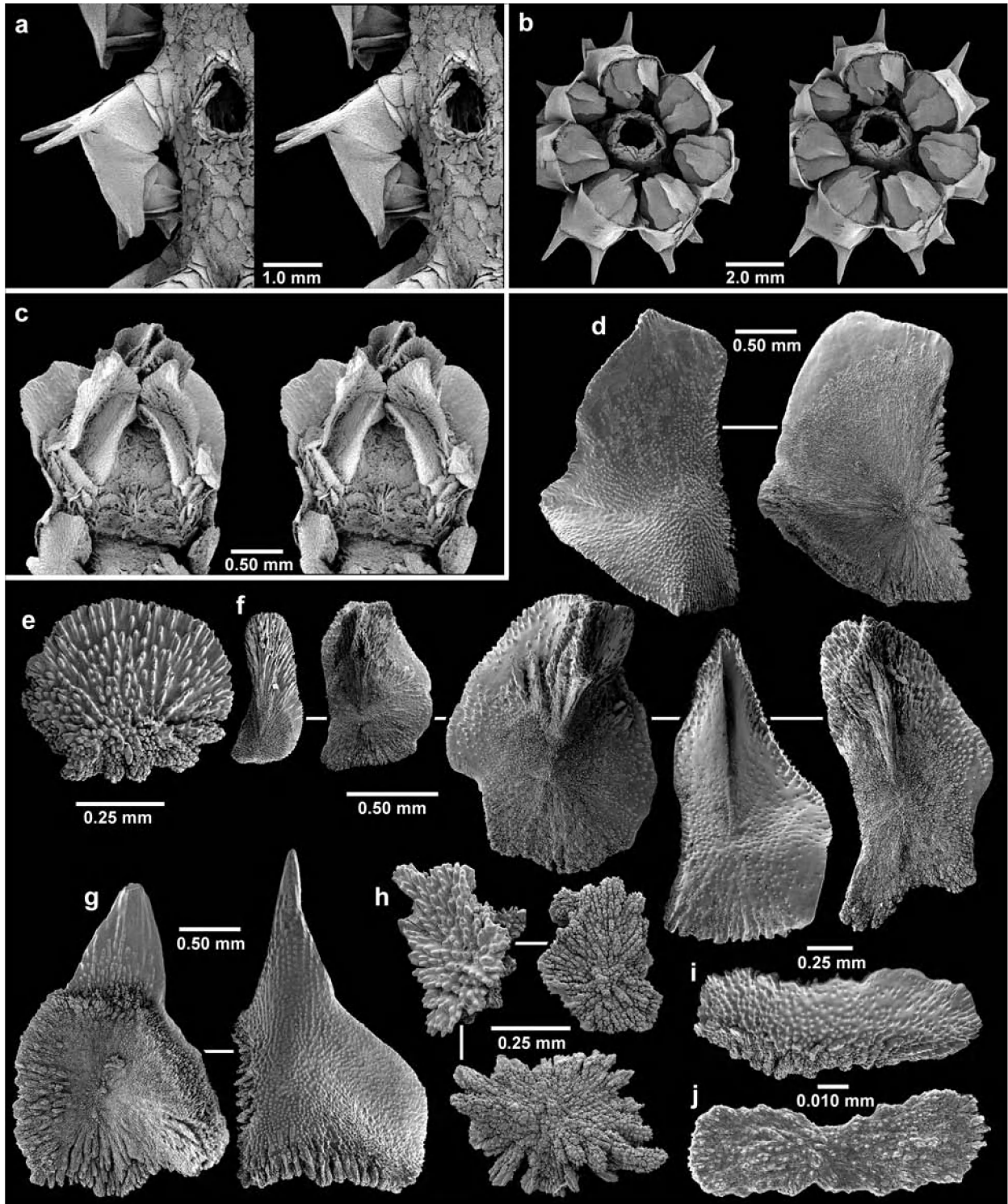


FIGURE 15. Polyps and scales of *Arthrogorgia kinoshitai* (a, c, *Pacific Knight* 941-204, USNM 100748; b, d–j, holotype, USNM 49978), a–c are stereo views: (a) lateral view of a polyp showing infrabasal and accessory infraopercular scales; (b) opercular view of a polyp whorl; (c) adaxial view of a polyp showing small adaxial body wall scales and other accessory infraopercular scales; (d) buccal scales; (e) infraopercular scale; (f) opercular scales; (g) basal scales; (h) coenenchymal scales; (i) infrabasal scale; (j) tentacular rodlet. Scale bars: a, 1 mm; b, 2 mm; c–d, g, f, 0.5 mm; e, h–i, 0.25 mm; j, 0.01 mm.

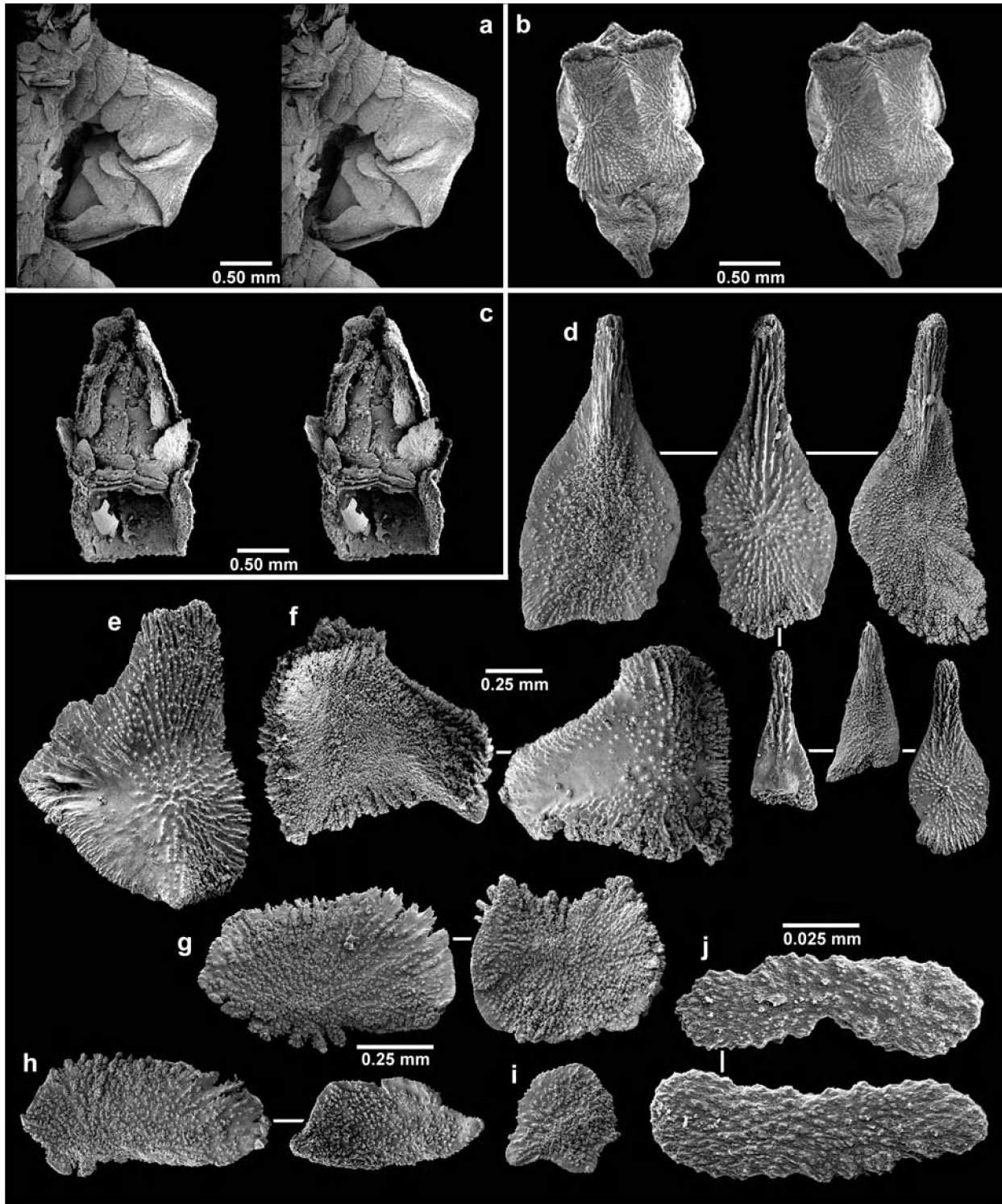


FIGURE 16. Polyps and scales of *Arthrogorgia otsukai* from a syntype colony (USNM 49979), a–c are stereo views: (a) lateral view of polyp showing both infrabasal and infraopercular scales; (b) abaxial buccal view of a polyp; (c) adaxial polyp view; (d) opercular scales; (e) outer surface of a buccal scale; (f) basal scales; (g) outer lateral infraopercular scales; (h) infrabasal scales; (i) coenenchymal scale; (j) tentacular rodlets. Scale bars: a–c, 0.5 mm; d–i, 0.25 mm; j, 0.025 mm.

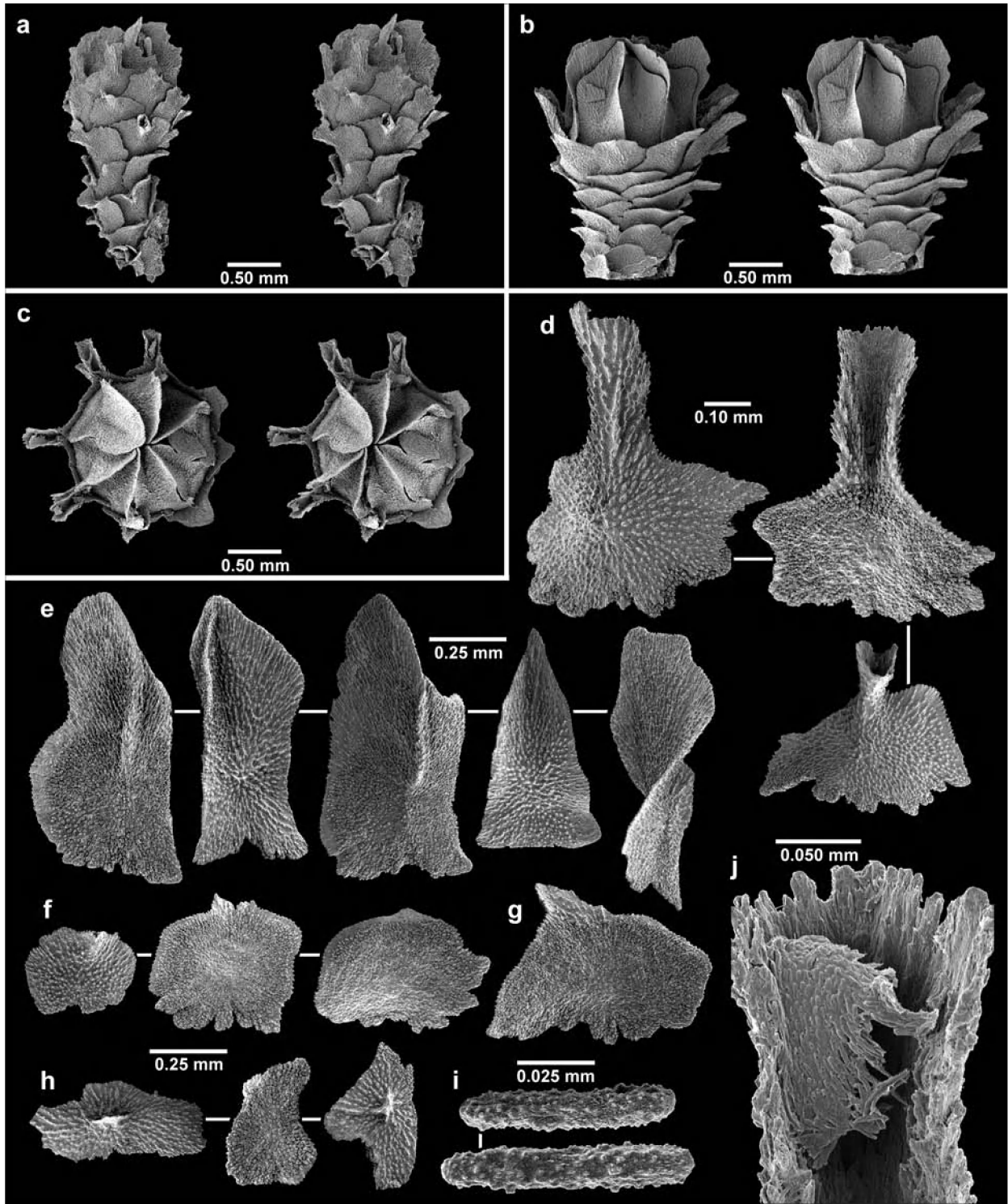


FIGURE 17. Polyps and scales of *Parastenella doederleini* from Delta J2100-3-3 (USNM 1115560), a–c are stereo pairs: (a) outer lateral view of a polyp; (b) adaxial view of a polyp; (c) opercular view of a polyp (adaxial side on right); (d) fluted marginal scales; (e) opercular scales; (f) adaxial body wall scales; (g) abaxial body wall scale; (h) coenenchymal scales; (i) tentacular rodlets; (j) clustered nematocysts of a nematocyst pad on inner side of a marginal flute. Scale bars: a–c, 0.5 mm; d, 0.1 mm; e–h, 0.25 mm; i, 0.025 mm; j, 0.05 mm.

Appendix: Station List

Details on all the stations where specimens for this study were recorded are provided in Table A.1.

TABLE A.1. List of data stations, their locations, and date data were recorded at each. A question mark (?) indicates lack of information.

Research vessel and station no.	°N Latitude	° Longitude	Depth (m)	Date
<i>Alaskan Leader</i>				
35	53°04'	170°12'W	?	4 Jun 2002
35-2	53°03.7'	170°12'W	182–630	4 Jun 2002
<i>Albatross (Alb)</i>				
3319	53°40'30"	167°30'00"W	108	18 Jun 1890
3330	54°00'45"	166°53'50"W	642	21 Jun 1890
3331	54°01'40"	166°48'50"W	840	21 Jun 1890
3480	52°06'00"	171°45'00"W	518	8 Jul 1893
3500	56°02'00"	169°30'00"W	221	17 Jul 1893
3501	55°51'00"	169°18'00"W	1,258	17 Jul 1893
4769	54°30'40"	179°14'00"E	433–446	3 Jun 1906
4771	54°30'00"	179°17'00"E	779	4 Jun 1906
4777	52°11'00"	179°49'00"E	79–95	5 Jun 1906
4778	52°12'00"	179°52'00"E	60–79	5 Jun 1906
4779	52°11'00"	179°57'00"W	99–102	5 Jun 1906
4781	52°14'30"	174°13'00"E	882	7 Jun 1906
<i>Alvin</i>				
3798	53°53'34"	148°31'56"W	855	27 Jun 2002
3799	53°59'32"	148°30'14"W	1,308	28 Jun 2002
3802	54°31'50"	150°18'13"W	1,778–1,993	1 Jul 2002
3803	54°48'31"	152°55'44"W	2,869	2 Jul 2002
3804	54°56'50"	151°19'11"W	2,417	5 Jul 2002
3806	48°05'21"	132°50'38"W	815	10 Jul 2002
4028	54°33.17'	136°50.64'W	755	4 Jun 2004
4029	54°37.18'	136°42.54'W	2,704–2,789	5 Jun 2004
4033	54°59.24'	140°23.99'W	2,635–2,665	9 Jun 2004
4037	56°22.18'	142°25.62'W	2,783	13 Jun 2004
4041	56°21.03'	146°22.82'W	2,803	17 Jun 2004
<i>Cobb, John</i>				
TA-6-1 and 9	57°53'39"	133°20'12"W	27	22 Mar 2006
<i>DW (Deep Worker)</i>				
6-1-1	54°37.55'	130°57.0'W	247	19 Jun 2009
6-7-1	52°31.36'	131°23.16'W	351	20 Jun 2009
7-1-1	54°37.84'	130°57.05'W	242	19 Jun 2009
7-2-1	51°45.26'	130°44.24'W	500	12 Jun 2009
7-4-1	52°31.32'	131°22.33'W	320	16 Jun 2009
<i>Delta</i>				
5E-2-5, 7, 9	51°37.322'	177°14.35'W	155	?
5590	51°43'22"	176°29'10"W	85	13 Jul 2002
5591	51°47'29"	176°15'34"W	79	13 Jul 2002
5592	51°47'29"	176°15'34"W	165	13 Jul 2002
5597	52°45'18"	179°19'47"W	145	15 Jul 2002
5997-8C-1	51°21.822'	179°29.07'W	185	?
5600	52°32.7351'	177°33.7975'E	87	15 Jul 2002
5604	52°13'27"	179°53.17'W	40	16 Jul 2002
5989-14-B-1	51°57.094'	176°50.3431'W	134	1 Jul 2003
5993-7C-1,4,5,6	51°24.082'	178°34.479'W	100	3 Jul 2003

TABLE A.1. *continued*

Research vessel and station no.	°N Latitude	° Longitude	Depth (m)	Date
6004-11C-1,6	52°45.913'	179°19.701'W	154	6 Jul 2003
6005-11B-1	51°43.986'	179°19.188'W	120	6 Jul 2003
6007-13C-2	51°55.214'	177°28.281'W	150	7 Jul 2003
6199-5E-1,5,7,8,9,13,14,15	51°37.117'	177°13.853'W	135–175	26 Jun 2004
6202-14D-4	51°57.715'	176°50.004'W	165	27 Jun 2004
6203-18-1	51°52.226'	176°15.996'W	138	28 Jun 2004
6206-18-2,14	51°51.97'	176°15.13'W	98–100	29 Jun 2004
6007-13C-2	51°55.214'	177°28.281'W	150	?
6208-21D-5	51°51.97'	176°15.13'W	100	30 Jun 2004
6209-21C-1,2	51°43.178'	176°17.944'W	100	30 Jun 2004
6209-21C-4	51°43.582'	176°17.540'W	95	30 Jun 2004
6209-21C-7	51°43.983'	176°17.021'W	52	30 Jun 2004
6219-3B-2	51°52.374'	175°15.695'W	154	5 Jul 2004
6221-2B-1	51°54.117'	173°52.462'W	142	6 Jul 2004
6221-2B-9	51°54.819'	173°53.139'W	119	6 Jul 2004
6221-2D-1	51°56.744'	173°55.306'W	82	6 Jul 2004
<i>Dominator</i>				
1997-1-39	53°01'11"	170°18'49"W	202	19 Jun 1997
1997-1-49	52°22.45'	170°34.25'W	231–277	21 Jun 1997
1997-1-78	51°58'40"	172°35'24"W	173	28 Jun 1997
2000-1-156	51°51'01"	178°25'57"E	388–395	1 Jul 2000
5159	52°26'02"	179°56'29"E	170	21 Jul 2000
<i>Esperanza</i>				
PC 7-3-6-3	56°09'37"	168°48'40"W	310	30 Jul 2007
PC 7-4-6-3	55°58.98'	170°00.79'W	300	1 Aug 2007
ZC 7-2-ROV-1	58°23'27"	174°59'22"W	914	5 Jun 2007
ZC 7-7-7-5	58°36.195'	174°45.195'W	520	8 Sep 2007
<i>Fiber Optic</i>				
1159	48°07'47"	125°05'41"W	272–279	10 Jul 2008
<i>Jason II</i>				
93-18	53°00'58"	161°13'42"W	3,531	21 Jul 2004
93-23	53°00'44"	161°14'25"W	3,442	22 Jul 2004
2095-2-1-2	51°43.311'	173°46.879'W	2,828	25 Jul 2004
2095-2-7-3	51°48.693'	173°49.965'W	843	25 Jul 2004
2098-2-1, 2	51°23.404'	177°04.549'W	2,514	29 Jul 2004
2099-18-1	51°30.164'	177°02.332'W	1,429	?
2100-3-1,2,3	51°31.582'	177°05.506'W	1,746	1 Aug 2004
2100-4-2, 8	51°31.607'	177°05.568'W	1,692	1 Aug 2004
2101-1-1, 5	51°28.954'	177°53.438'W	1,341	2 Aug 2004
2101-2-1	51°28.996'	177°53.530'W	1,332	2 Aug 2004
2101-4-1, 2, 3	51°30.059'	177°55.461'W	1,061	2 Aug 2004
2101-7-6,7,9	51°30.56'	177°55.357'W	824	2 Aug 2004
2101-10-3	51°31.488'	177°57.513'W	490	2 Aug 2004
2102-4-1, 2	51°17.521'	179°32.532'W	1,359	3 Aug 2004
2102-6-2 4,5	51°18.549'	179°31.693'W	888	3 Aug 2004
2102-7-1C,D,E	51°19.624'	179°30.771'W	248	3 Aug 2004
2102-12-1A,B	51°19.886'	179°30.599'W	192	3 Aug 2004

continued

TABLE A.1. *continued*

Research vessel and station no.	°N Latitude	° Longitude	Depth (m)	Date
2102-14-1	51°19.969'	179°30.194'W	176	3 Aug 2004
2103-5-1	51°47.85'	179°57.255'E	1,309	4 Aug 2004
2103-7-1A	51°47.898'	179°57.169'W	1,267	4 Aug 2004
2103-14-2	51°50.972'	179°51.191'E	746	4 Aug 2004
2104-2-2	51°43.825'	179°35.034'W	1,009	5 Aug 2004
2104-5-1,2,3	51°43.302'	179°34.928'W	712	5 Aug 2004
2104-10-2	51°39.403'	179°35.041'W	713	5 Aug 2004
2104-11-1,2	51°39.397'	179°35.028'W	712	5 Aug 2004
<i>Keldysh (Mir)</i>				
22	55°13'12"	167°14'04"E	1,200	31 Jul 1990
<i>Let's Go</i>				
861-50	51°16.6'	179°14.6'W	97	14 Jun 1986
861-52	51°14.46'	179°11.84'E	241	17 Jun 1986
861-57	51°29.85'	178°39.59'E	154	18 Jun 1986
861-58	51°35.88'	178°17.01'E	371	18 Jun 1986
861-79	52°03.9'	177°13.84'E	93	28 Jun 1986
<i>Miller Freeman (MF)</i>				
802-VH-80-30	52°52'34"	168°47'43"W	86	5 Jun 1980
833-3	51°43.0'	177°20.8'E	567	28 Jul 1983
833-15	51°29.8'	178°39.0'E	185	30 Jul 1983
833-16	51°25.8'	178°50.5'E	205	30 Jul 1983
833-24	51°17.8'	179°24.8'E	229	31 Jul 1983
833-38	51°42.9'	178°51.5'W	582	3 Jun 1983
833-47	51°56.6'	176°52.8'W	201	5 Jun 1983
<i>Pacific Knight</i>				
941-29	53.06917°	169.93°W	145	10 Jun 1994
941-38	52.4685°	170.56°W	319	6 Jun 1994
941-73	52.34783°	174.57°W	112	19 Jun 1994
941-204	53.0965°	171.7°E	455	31 Jul 1994
<i>Sea Storm</i>				
95	51°55'29"	178°14'59"E	234	5 Jul 2002
116	52°04'10"	177°14'25"E	87-94	11 Jul 2002
148	52°28'16"	173°34'31"W	194-201	21 Jul 2002
150	52°30'47"	173°29'35"W	213-220	21 Jul 2002
<i>Starlight</i>				
84-1-7	52°36'	172°20'W	238	12 Jul 1984
84-1-36	52°28'	172°30'W	234	13 Jul 1984
<i>Vesteraalen</i>				
941-15	54°04'46"	166°23'43"W	79	6 Jun 1994
941-36	52°56'	169°31'W	227	10 Jun 1994
941-51	53°	171°W	126	13 Jun 1994
941-94	52°	174°W	91	26 Jul 1994
941-153	52°10'	179°43'E	94	11 Jul 1994
941-163	51°37'	178°25'W	155	18 Jul 1994
941-186	52°	176°W	254	24 Jul 1994
2001-1-5	52°40'43"	169°07'01"W	102	21 May 2001

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