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Report on hydrozoans (Cnidaria), excluding Stylasteridae, from the Emperor Seamounts, western North Pacific Ocean

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Abstract

Fourteen species of hydroids, collected during August 2019 by ROV *SuBastian* of the Schmidt Ocean Institute, are reported from the Emperor Seamount chain in the western North Pacific Ocean. Two others, *Candelabrum* sp. and *Eudendrium* sp., were observed only on videos taken by the ROV. From collections and video observations, eight species of hydroids were found at Jingū Seamount, three at Yomei, Nintoku, and Annei seamounts, and one at Koko Seamount and Hess Rise. At Suiko and Godaigo seamounts, hydroids were seen in videos but they could not be identified. *Latebrahydra schulzei*, an endobiotic associate of the hexactinellid sponge *Walteria flemmingii* Schulze, 1886 from Annei Seamount and Hess Rise, is described as a new genus and species tentatively attributed to Hydractiniidae L. Agassiz, 1862. Another new species, *Hydractinia galeai*, is described from Jingū Seamount. Among its distinctive characters is a zooid termed a sellectozooid, likely serving in both food capture and defence. Hydroids examined from Yomei, Nintoku, and Jingū seamounts are elements of a cold-water fauna occurring in the North Pacific Boreal Bathyal province, while those of Annei and Koko seamounts, and Hess Rise, are part of the biota of the Central North Pacific Bathyal province. Hydroids identified as *Bouillonia* sp., from Nintoku Seamount, represent the first record of this predominantly deep water tubulariid genus in the North Pacific Ocean. *Bonneviella superba* Nutting, 1915, from Jingū Seamount, is reported for the first time outside the Aleutian Islands. *Bonneviella* cf. *gracilis* Fraser, 1939, known elsewhere only from Dease Strait in the western Canadian Arctic, was also collected on Jingū. In addition to hydroids, medusae of *Ptychogastria polaris* Allman, 1878 were observed on videos from Nintoku, Jingū, Annei, and Koko seamounts at depths between 2423–1422 m. An unidentified siphonophore was observed near bottom at 2282 m on Nintoku Seamount.

Key words: Anthoathecata, Hydroidolina, hydroids, Leptothecata, marine invertebrates, Medusozoa, taxonomy, Trachymedusae, zoological nomenclature

Introduction

The neritic hydroid fauna of the western North Pacific Ocean is relatively well-known (e.g., Stechow 1913a, b, 1923a; Yamada 1959; Naumov 1960, 1966; Hirohito 1988, 1995; Park 1990; Xu *et al*. 2014a, b; Antsulevich 2015). By contrast, that of the adjacent deep-sea has received scant attention. Publications such as those of Allman (1888), Stechow (1913b), Naumov (1960, 1966), Antsulevich (1987, 2015), Sheiko & Stepanjants (1997), Namikawa (2009), Stepanjants (2013a, b), and Stepanjants & Chernyshev (2015) provide records of species from bathyal and abyssal bottoms off the coasts of Japan and eastern Russia. Based on reports from these and other works, the hydroid fauna of seamounts to the east of the Asian continent in the North Pacific remain essentially unknown.

During the summer of 2019, a biological expedition was undertaken to the Emperor Seamounts in the western North Pacific Ocean. Its objective was to establish the location of a biogeographic transition zone between the North Pacific Boreal and the Central North Pacific bathyal provinces (Watling *et al*. 2013, 2020), with a primary focus on octocorals and sponges. The Emperors are a very old (42 to 85 Ma; Regelous *et al*. 2003) group of volcanic seamounts that are mostly flat-topped, having been islands early in their history (Koreneva 1980), but they are also highly eroded and of irregular shape due to massive slumping.

In addition to specimens of octocorals and sponges, a small collection of hydroids was also assembled. The goal of the present investigation was to provide a taxonomic account of hydroids found in the collection, and of those observed in videos from the expedition. Also observed in videos from the expedition were a benthic hydromedusa (*Ptychogastria polaris* Allman, 1878) and an unidentified siphonophore. This report simply represents a first step in knowledge of the hydrozoans of the Emperor Seamounts, the fauna of which remains poorly known. Stylasterids were not included as part of this work.

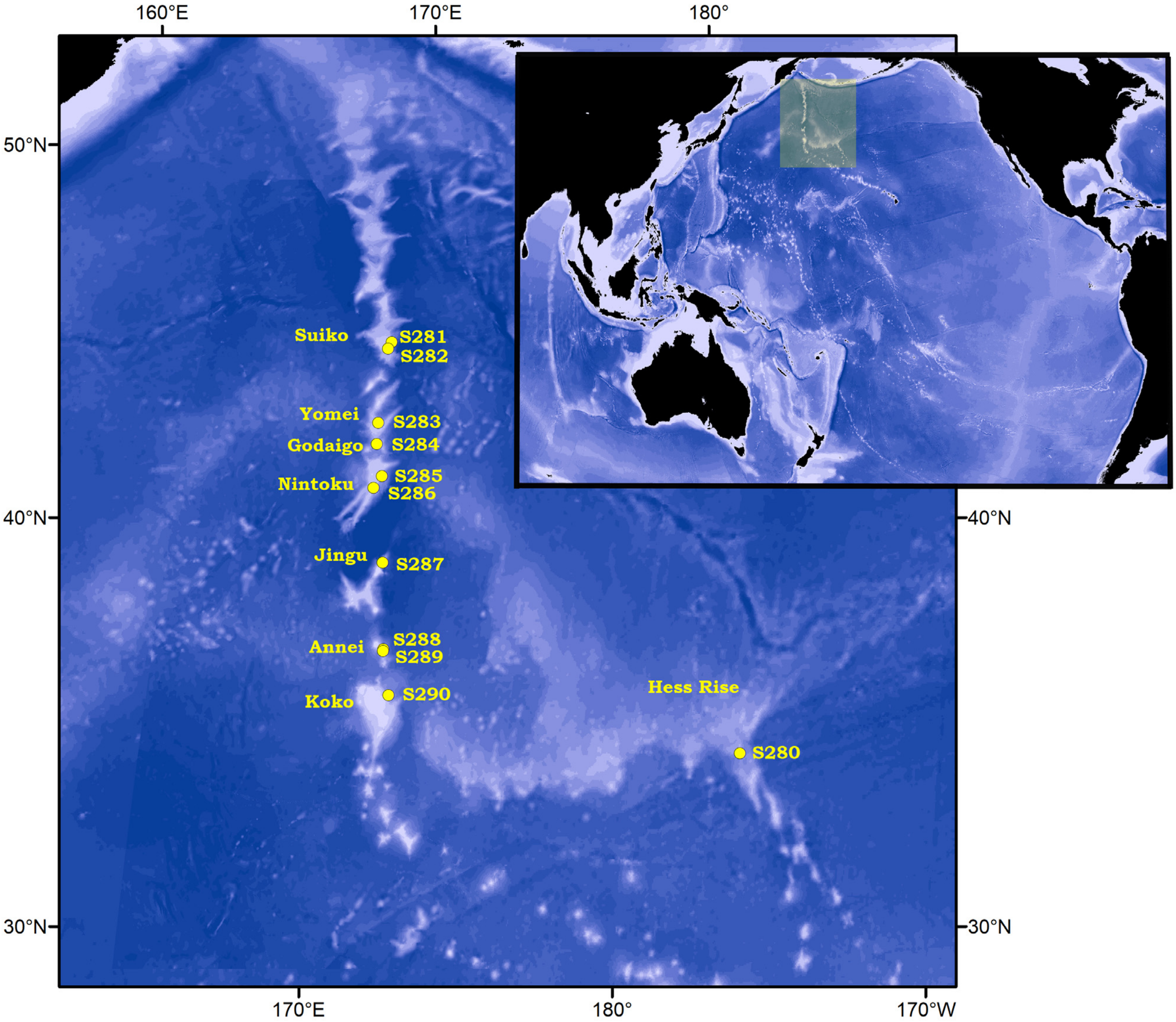

FIGURE 1. Map of the Emperor Seamount Chain, and Hess Rise, with dive locations and station numbers sampled by ROV *SuBastian* of the Schmidt Ocean Institute. Highlighted area of inset shows location of the seamounts in the western North Pacific Ocean.

Materials and methods

Hydroids examined here were sorted from collections of invertebrates, especially octocorals and sponges, obtained during an expedition to the Emperor Seamounts (https://schmidtocean.org/technology/live-from-rv-falkor/rov-dives-deep-coral-diversity-at-the-emporer-seamount-chain-2019). Sampling was undertaken during August 2019 using ROV *SuBastian* from R/V *Falkor* of the Schmidt Ocean Institute, Palo Alto, California, USA. In all, dives were undertaken with *SuBastian* on seven seamounts in the chain (Suiko, Yomei, Godaigo, Nintoku, Jingū, Annei, and Koko), as well as on an unnamed seamount on nearby Hess Rise (Fig. 1).

The hydroid collection was small, comprising specimens recovered from substrates on Yomei, Nintoku, Jingū, Annei, and Koko seamounts, as well as Hess Rise, at depths ranging from 1236 m (Annei) to 2030 m (Koko). Data on depth, salinity, and water temperature were recorded for each sample. Specimens were preserved in 95% ethanol.

To complement the specimen collection, searches were made for both hydroids and benthic hydromedusae in videos from dives by the ROV. In being mostly small, hydrozoans were difficult or impossible to detect and identify in them. However, hydroids and hydromedusae were occasionally visible in close-ups of the bottom, adding to the total number of species reported from the seamounts.

The classification system for hydrozoans adopted here generally follows Schuchert (2012, 2021) for anthoathecates and Maronna *et al*. (2016) for leptothecates. A synonymy list accompanying each species includes the original binominal name together with its author and date. Also cited are works providing primary records of these species from the North Pacific Ocean. All of the cited references in the work have been examined as part of the study. Except for a figure by Schulze (1887) of *Latebrahydra schulzei*, gen. nov., sp. nov. in the sponge *Walteria flemmingii* Schulze, 1886, illustrations are based on specimens studied herein. Examinations of nematocysts were made at 1000× using a Zeiss Axioscop microscope from material preserved in ethanol. All figures of nematocysts herein are to the same magnification, and all measurements were made on undischarged capsules.

Results

Systematic Account

Phylum Cnidaria Verrill, 1865

Class Hydrozoa Owen, 1843

Subclass Hydroidolina Collins, 2000

Order Anthoathecata Cornelius, 1992

Suborder Aplanulata Collins, Winkelmann, Hadrys & Schierwater, 2005

Family Candelabridae Stechow, 1921b

Genus *Candelabrum* de Blainville, 1830

Candelabrum sp.

Fig. 2a

Observed on video. Yomei Seamount, ROV *SuBastian* Dive 283, within 2–3 m of Sta. YOM103-1A, 42°25'54.8694"N, 170°26'06.5424"E, 09 August 2019, 1472 m, 2.4°C, 34.5 psu, one polyp, in small cavity in rock, with gonophores.—Nintoku Seamount, ROV *SuBastian* Dive 286, ca. 40°45'N, 170°35'E, 12 August 2019, 1439 m, 2.5°C, one polyp, on vertical rock face, with gonophores.

Remarks. Hydroids of *Candelabrum* sp. were observed only in videos from Yomei and Nintoku seamounts. They could not be reliably identified based on available images.

A review of the genus *Candelabrum* de Blainville, 1830 has been given by Segonzac & Vervoort (1995), including accounts of *C. phrygium* (Fabricius, 1780) and *C. serpentarii* Segonzac & Vervoort, 1995) from the Mid-Atlantic Ridge. *Candelabrum phrygium*, a putatively circumpolar hydroid, is the only species of the genus reported to date from the northwest North Pacific Ocean. The species has been reported from eastern Russia at depths of 64–145 m off the island of Paramushir (Naumov 1960; Antsulevich 1987, 2015), from 8–24 m in Avacha Bay on the east coast of the Kamtchatka Peninsula (Schuchert *et al*. 2016), and from Matua Island (Sanamyan & Sanamyan 2020). Meanwhile, Rybakova *et al*. (2020) reported *Candelabrum* sp. from video surveys of the northern slope of Volcanologists Massif, southwest Bering Sea, at bathyal and abyssal depths (3450–3610 m; 4277–4278 m).

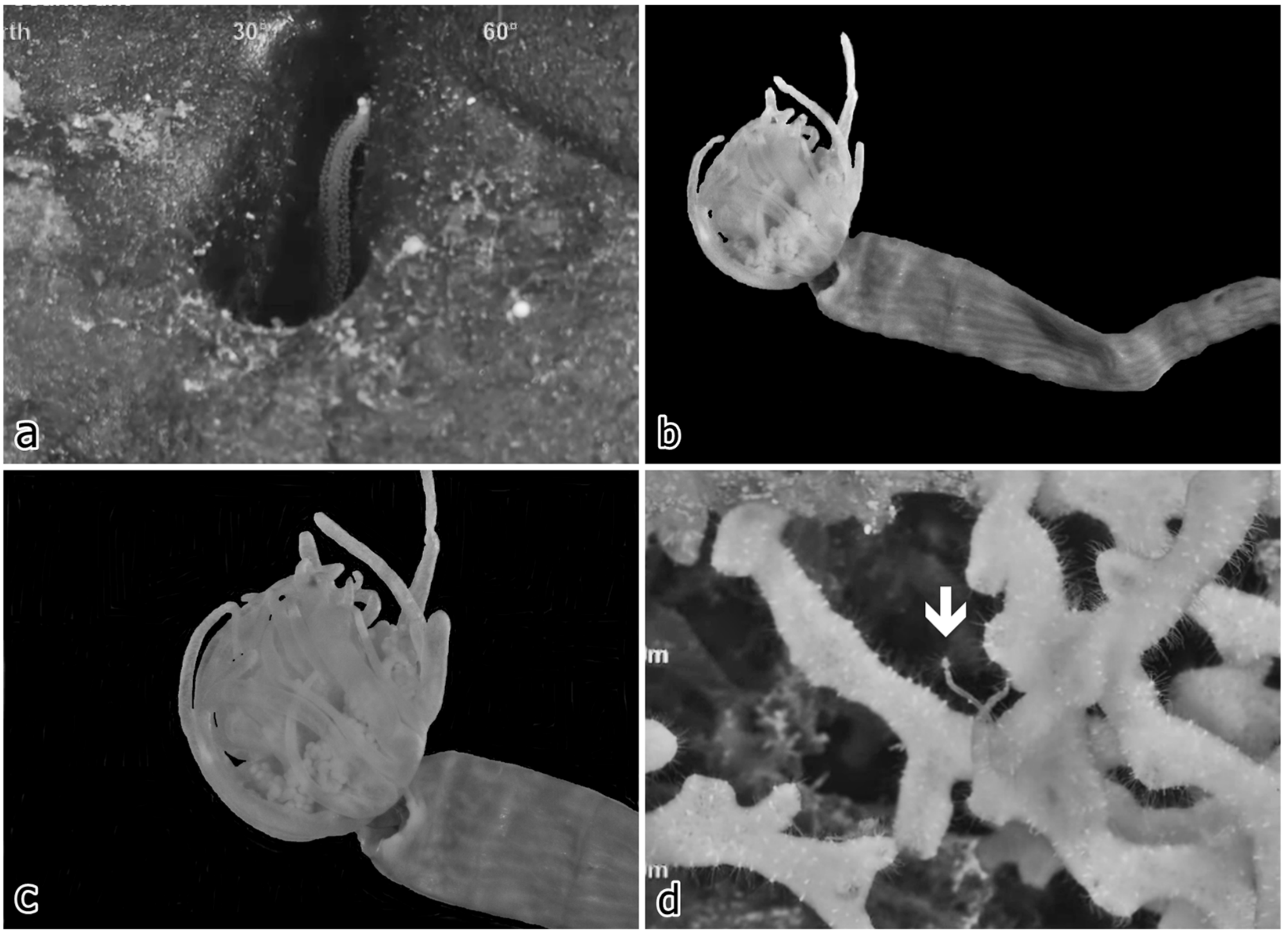

FIGURE 2. Anthoathecata: Candelabridae and Tubulariidae. a, *Candelabrum* sp., hydroid in crevice on rock, Yomei Seamount, adjacent to Sta. YOM103-1A. **b, c, *Bouillonia* sp.,** polyp with hydranth, gonophores, and part of hydrocaulus, this specimen (ROMIZ B5345) examined and described herein, Nintoku Seamount, Sta. NIN205-1. **d, Tubulariidae (undetermined),** hydroids on hexactinellid sponge, Annei Seamount, Sta. ANN217-1.

Family Tubulariidae Goldfuss, 1818

Genus *Bouillonia* Petersen, 1990

Bouillonia sp.

Figs. 2b, c, 3a, 4a–l

Material examined. Nintoku Seamount, Sta. NIN205-1, 40°45’6.8412”N, 170°35’32.2494”E, 12 August 2019, 1490 m, 2.4°C, 34.5 psu, on octocoral *Chrysogorgia* sp., three twisted stems, to 1.6 cm high, only one with a hydranth, with gonophores, ROMIZ B5345.

Observed on video. Nintoku Seamount, ROV *SuBastian* Dive 286, Sta. NIN205-1, 40°45’6.8412”N, 170°35’32.2494”E, 12 August 2019, 1489 m, 2.4°C, 34.5 psu, on octocoral *Chrysogorgia* sp., specimen collected and listed above under “Material examined”.—Nintoku Seamount, ROV *SuBastian* Dive 286, 12 August 2020, one polyp, on lost or discarded gillnet, 1326 m, 2.9°C.

Description. Specimens solitary, comprising fragments of three hydrocauli, only one of them with a hydranth. Hydrocauli unbranched, curved, with a few distinct bends at some points, gradually increasing in diameter from proximal to distal ends, longitudinal peripheral canals ribbon-like, between 15 and 20 in number. Single hydrocaulus bearing a hydranth broken off at base, 8 mm long, maximum diameter 1.6 mm, minimum diameter 0.7 mm. Hydrocauli without hydranths up to 16 mm long, maximum diameter 1.0 mm, minimum diameter 0.45 mm, attached to substrates by short stolons. Perisarc encasing hydrocauli mostly smooth, of moderate thickness except at distal end, appearing as a thin film adhering closely to a neck region and not inflated, terminating at base of hydranth, tan-coloured in thicker areas, thin and clear over neck region. Hydranth pear-shaped with broad hypostome, separated from neck region by a prominent circumferential groove, reaching 2.5 mm high from groove to tip of hypostome, maximum diameter, at base of hydranth, 2.5 mm; tentacles occurring in aboral and oral whorls. Aboral tentacles filiform, about 30 in number, crowded and laterally flattened at proximal ends, about 0.25 mm in diameter at base, gradually tapering to tip, up to 4.7 mm long. Oral tentacles filiform, in a scattered row around hypostome, about 30 in number, 0.13 mm at base, tapering from proximal end to tip, to 1.8 mm long. Color of preserved hydranth white; appearing to be slightly pinkish in specimens seen on videos.

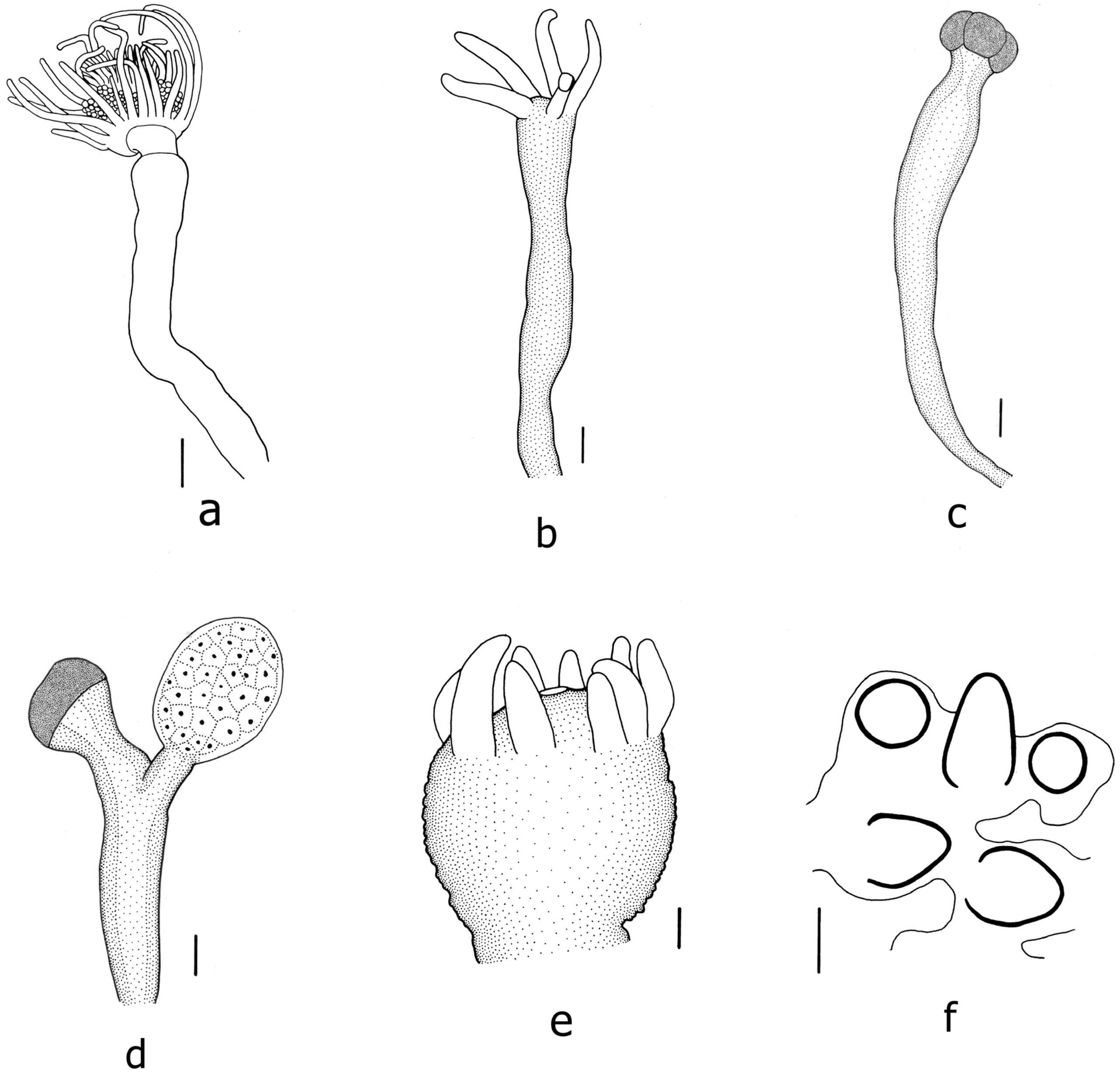

FIGURE 3. Anthoathecata: Tubulariidae and Hydractiniidae. a, *Bouillonia* sp., one polyp, with hydranth, gonophores, and part of hydrocaulus, Nintoku Seamount, Sta. NIN205-1, ROMIZ B5345. Scale equals 1.0 mm. **b, *Hydractinia galeai*, sp. nov.,** tall, slender sellectozooid, Jingū Seamount, Sta. JIN 110-1, ROMIZ B5347. Scale equals 0.2 mm. **c, *Hydractinia galeai*, sp. nov.,** defensive zooid, Sta. JIN 110-1, ROMIZ B5347. Scale equals 0.2 mm. **d, *Hydractinia galeai*, sp. nov.,** gonozooid with female gonophore, Jingū Seamount, Sta. JIN 110-1, ROMIZ B5347. Scale equals 0.1 mm. **e, *Hydractinia galeai*, sp. nov.,** short, robust gastrozooid, Jingū Seamount, Sta. JIN 110-1, ROMIZ B5347. Scale equals 0.1 mm. **f, *Hydractinia galeai*, sp. nov.,** small chitinous spines, Sta. JIN 110-1, ROMIZ B5347. Scale equals 0.05 mm.

Gonophores fixed sporosacs, borne on about 10 short, bifurcated blastostyles arranged in a whorl around base of hydranth just above aboral tentacles; sporosacs small, in dense clusters on blastostyles, apparently juvenile and styloid, arising from short pedicels.

Nematocysts.

Aboral tentacles:
desmonemes (n = 10): 5.4–7.1 µm long × 3.6–4.4 µm wide
microbasic mastigophores (n = 10): 12.5–15.9 µm long × 8.7–10.2 µm wide
stenoteles, small oval (n = 10): 10.6–12.0 µm long × 8.4–9.4 µm wide
stenoteles, small subspherical (n = 10): 9.0–10.7 µm long × 7.4–9.3 µm wide

Oral tentacles:
desmonemes (n = 10): 5.4–6.0 µm long × 3.5–4.2 µm wide (undischarged)
stenoteles, small subspherical (n = 10): 8.8–10.0 µm long × 7.4–8.8 µm wide
stenoteles, large oval (n = 3): 17.5–18.0 µm long × 12.5–13.5 µm wide
stenoteles, large subspherical (n = 10): 17.3–18.2 µm long × 16.0–16.5 µm wide

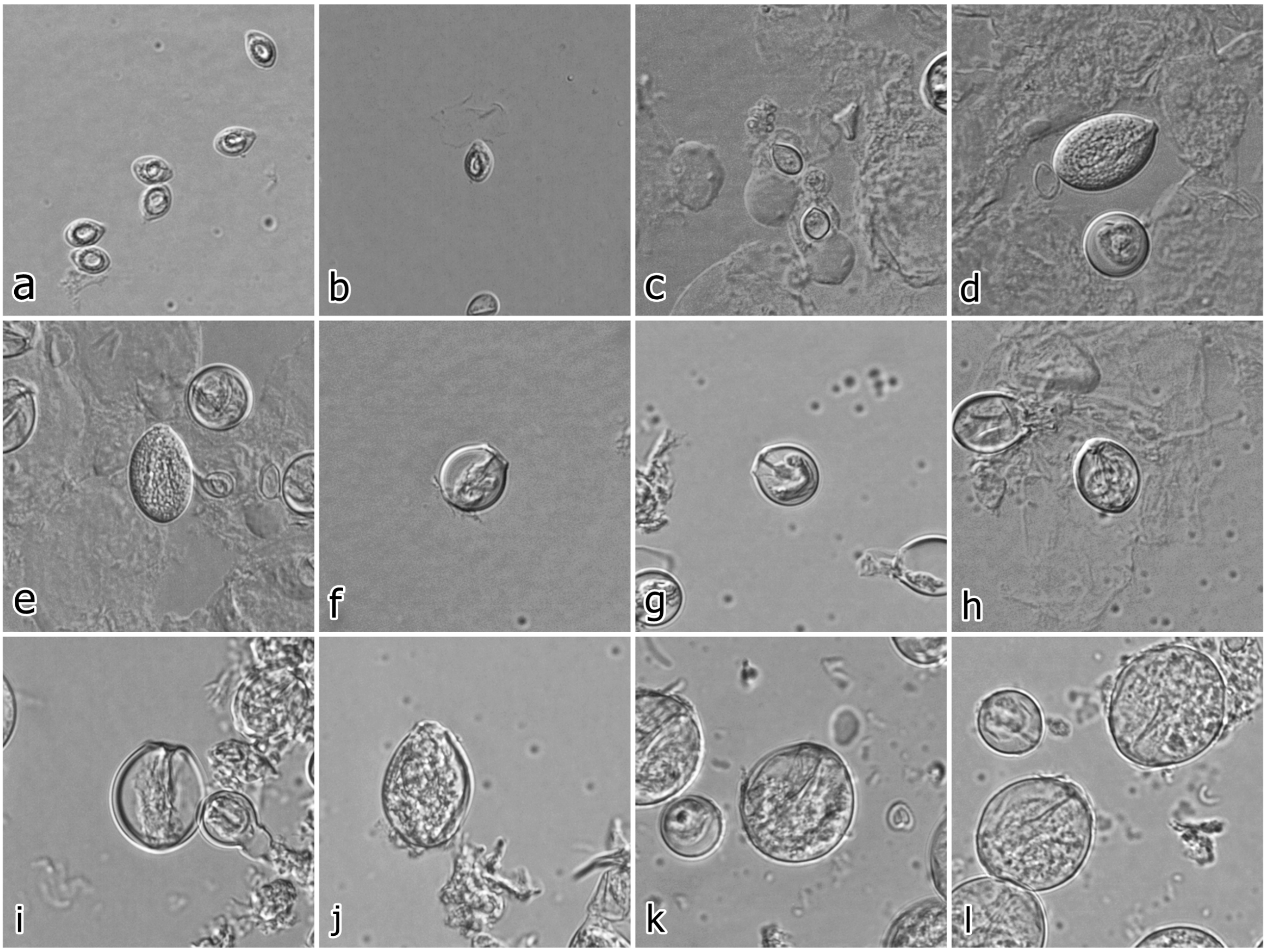

FIGURE 4. Anthoathecata: Tubulariidae, *Bouillonia* sp. (ROMIZ B5345), nematocysts. a, desmonemes, oral tentacle. **b,** desmoneme, aboral tentacle. **c,** desmonemes, discharged, aboral tentacle. **d,** microbasic mastigophore, aboral tentacle. **e,** microbasic mastigophore, aboral tentacle. **f,** small subspherical stenotele, aboral tentacle. **g,** small subspherical stenotele, oral tentacle. **h,** small oval stenotele, aboral tentacle. **i,** medium stenotele, oral tentacle. **j,** large oval stenotele, oral tentacle. **k,** large subspherical stenotele, oral tentacle. **l,** large subspherical stenoteles, oral tentacle.

Remarks. Hydroids of the deep-sea hydroid genus *Bouillonia* Petersen, 1990 have been reported infrequently and are inadequately known. Only two named species are currently assigned to the genus worldwide. *Bouillonia cornucopia* (Bonnevie, 1898), its type species, was originally described from the Greenland Sea west of Svalbard

(77°58'N, 05°10'E, 2438 m). It has subsequently been reported again from the Greenland Sea (72°42'N, 14°49'W, 2000 m, Jäderholm 1902) and the adjacent Fram Strait (79°4.55'N, 4°6.52'E, 2504 m, Bergmann *et al*. 2009). *Bouillonia denhartogi* Svoboda, Stepanjants & Ljubenkov, 2006, type locality in the eastern Weddell Sea (on a mooring at 69°23.79'S, 0°0.84'W, 2026 m), is now known to be circum-Antarctic in distribution (Peña Cantero 2012, 2019). Specimens assigned to a third putative species, identified only as *Bouillonia* sp. by Svoboda *et al*. (2006), were found in collections from the Norwegian Sea (69°04.8'–69°05.3'N, 04°41.6'–04°43.7'E, 3213 m and 69°21.9'–69°20.6'N, 10°25.2'–10°28'E, 2966 m), the Laptev Sea (78°16.22'N, 130°02.8'E, 2470 m), and possibly from the Mid-Atlantic Ridge off the Gulf of Guinea. Meanwhile, other unidentified species of *Bouillonia* have been reported from a deep-sea lander at 3690 m in the Charlie Gibbs fracture zone of the Mid-Atlantic Ridge (Blanco *et al*. 2013), and from photographs of benthic substrates in the Eurasian Central Arctic (Rybakova *et al*. 2019).

The single hydroid with a hydranth examined here from Nintoku Seamount shares characters with *B. cornucopia* and with the *Bouillonia* sp. of Svoboda *et al*. (2006). Numbers of tentacles correspond more closely with those of *B. cornucopia* (ca. 35–40 oral and 30 aboral tentacles) than with *Bouillonia* sp. (ca. 100 oral and 40–50 aboral tentacles). When not broken off at the base, the stems of our specimens appeared to arise from short hydrorhizal processes, as in *B. cornucopia*, rather than from a basal disk, as in both *Bouillonia* sp. and *B. denhartogi*. Conversely, the number of longitudinal canals in the hydrocaulus conformed more closely with *Bouillonia* sp. (ca. 10–12) than with *B. cornucopia* (ca. 40 near the top of the hydrocaulus). Geographically closest to specimens examined here are hydroids, identified by Svoboda *et al*. as *Bouillonia* sp., from the Laptev Sea. Those Arctic specimens lacked hydranths, but their perisarc tubes and cnidomes were reported to be of the types found in the genus. The Antarctic *B. denhartogi* is said by Svoboda *et al*. to differ from the other two in having ca. 200 or more oral tentacles that are arranged in irregular rows, rather than 100 or fewer in regular whorls. However, the three putative taxa are morphologically similar and difficult to distinguish. Molecular investigations of this group of solitary or mostly solitary hydroid polyps are clearly warranted.

Given the likelihood that at least some of the characters noted above vary with the age and size of the polyps, we have not assigned our specimens to any of the supposed species recognized by Svoboda *et al*. Instead, they have been identified simply as *Bouillonia* sp. (not *Bouillonia* sp. *sensu* Svoboda *et al*.).

Specimens examined here were also observed on video during their collection from Nintoku Seamount. Another specimen presumed to be the same species, from the same seamount, was noticed on a lost or discarded gillnet, found on bottom at 1326 m.

With only a single hydranth available, limited analysis of the nematocyst complement was possible. Examination was limited to nematocysts on a few oral and aboral tentacles. Categories observed were identified as desmonemes, microbasic mastigophores, and stenoteles (Figs. 4a–l).

Stenoteles varied considerably in shape and size (Figs. 4f–l), with those near the tips of the oral tentacles being of a large variety (Fig. 4l).

This is the first record of a species of *Bouillonia* in the North Pacific Ocean.

Tubulariidae (undetermined)

Fig. 2d

Material examined. Annei Seamount, Sta. ANN217-1, 36°38'35.0256"N, 171°36'22.4484"E, 17 August 2019, 1236 m, 2.9°C, 34.4 psu, on hexactinellid sponge, one fragmentary stem with a badly damaged hydranth, 7 mm high, with gonophores, ROMIZ B5346.

Observed on video. Annei Seamount, Sta. ANN217-1, 36°38'35.0256"N, 171°36'22.4484"E, 17 August 2019, 1236 m, 2.9°C, 34.4 psu, on hexactinellid sponge, two colonies, with gonophores; specimen collected and listed above under "Material examined".

Remarks. The fragmentary hydroid from the study was in poor condition could not be reliably identified to species or even to genus. In a photograph of the species from the video (Fig 2d), only the left quarter of the sponge was collected, and the better hydroids visible on the right two-thirds of the hexactinellid were not taken.

Suborder Filifera Kühn, 1913

Family Hydractiniidae L. Agassiz, 1862

Genus *Hydractinia* Van Beneden, 1844

Hydractinia galeai, sp. nov.

Figs. 3b–f, 5a–f, 6a–l

Type locality. Emperor Seamounts: Jingū Seamount, 38°51’06.291”N, 171°13’45.909”E, 1396.41 m.

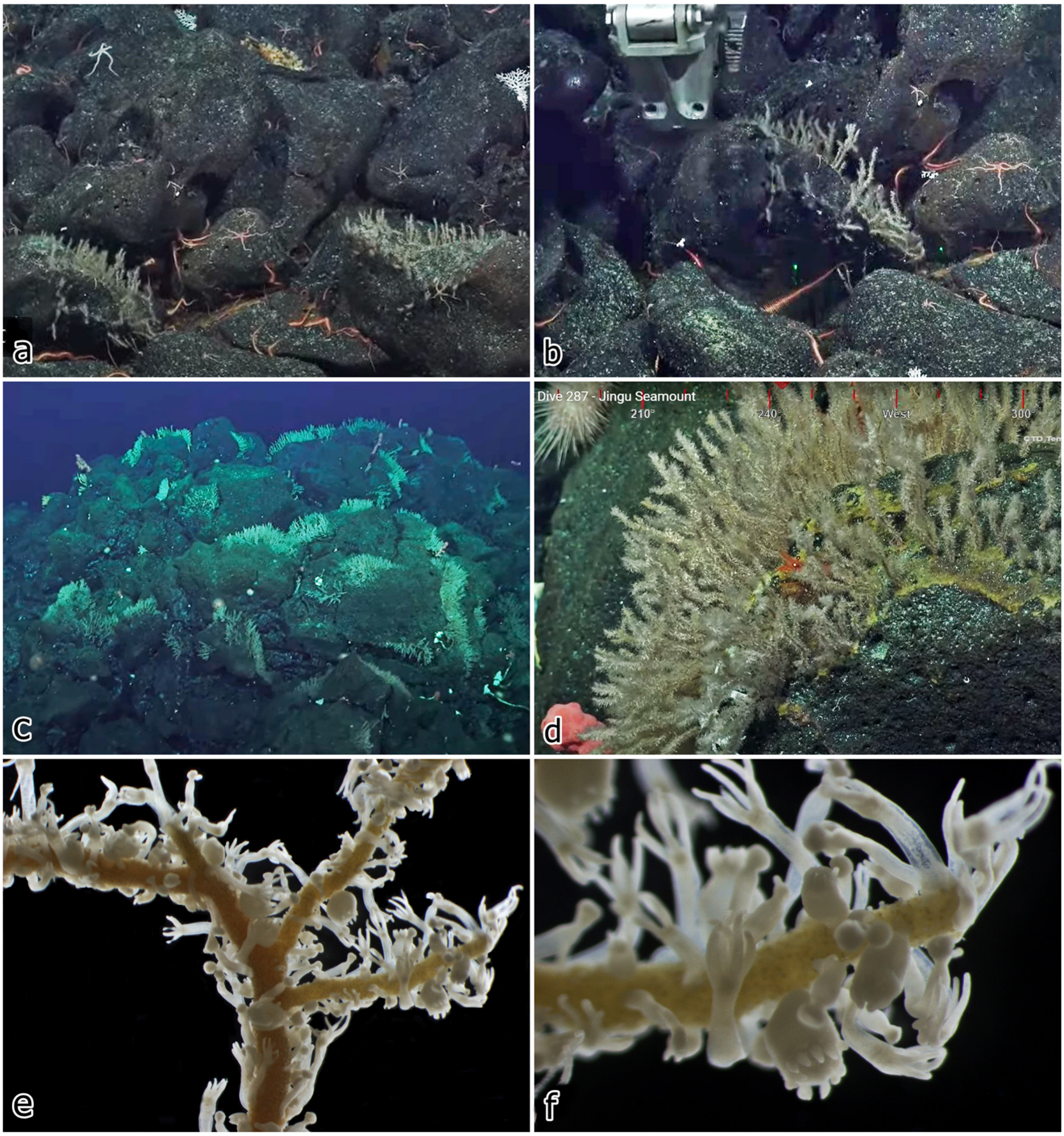

FIGURE 5. Anthoathecata: Hydractiniidae, *Hydractinia galeai*, sp. nov. a, two colonies on rocks, with holotype (ROMIZ B5347) on left prior to collection, Jingū Seamount, Sta. JIN 110-1**. b,** collection of the holotype (ROMIZ B5347), Jingū Seamount, Sta. JIN 110-1**. c,** multiple colonies on rocks, Jingū Seamount, near Sta. JIN 110-1. **d,** close-up of one colony, on rock, Jingū Seamount, near Sta. JIN 110. **e, f,** parts of holotype colony (ROMIZ B5347), Jingū Seamount, Sta. JIN 110-1.

Material examined. HOLOTYPE: Jingū Seamount, Sta. JIN110-1, 38°51’06.291”N, 171°13’45.909”E, 13 August 2019, 1396 m, 2.6°C, 34.4 psu, on rock, one colony, 3.1 cm high, with female gonophores, ROMIZ B5347.

PARATYPES: Jingū Seamount, Sta. JIN110-1, 38°51’06.291”N, 171°13’45.909”E, 13 August 2019, 1396 m, 2.6°C, 34.4 psu, on rock, two colonies, to 3.7 cm high, with female gonophores, ROMIZ B5348.—Jingū Seamount, Sta. JIN114-2, 38°50’46.0692”N, 171°13’39.144”E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, one colony, 9 mm high, with female gonophores, ROMIZ B5349.

Observed on video. HOLOTYPE, ROMIZ B5347 (Figs. 5a, b): Jingū Seamount, ROV *SuBastian* Dive 287, Sta. JIN 110-1, 38°51’06.291”N, 171°13’45.909”E, 13 August 2019, 1396 m, 2.6°C, 34.4 psu, on rock.

OTHERS: Jingū Seamount, ROV *SuBastian* Dive 287, 13 August 2019, no coordinates available, several colonies, on rocks, 1387 m (Fig. 5c); one colony, on rock, 1385 m (Fig. 5d).

Etymology. The specific name honours Dr. Horia R. Galea, distinguished student of hydrozoans, esteemed colleague, and friend.

Description. Hydractiniid hydroids with colonies erect, irregularly branched, somewhat arborescent, colonies planar. Shoots up to 3.7 cm high, 1.3 mm in diameter in present material, arising from an encrusting, broadened base attached to rock; calcification lacking. Upright stem and branches with a thick skeletal axis of intertwining and anastomosing chitinous fibers penetrated internally and invested externally by naked coenosarc; surface of stems and branches almost completely covered by coenosarc except in older, worn parts of colony, coenosarc surface dotted with large numbers of small (less than 0.1 mm diameter), whitish, spherical nodules bearing nematocysts; surface also with numerous minuscule spines, 0.1 mm or less high, formed by slight elevations of chitin. Skeletal stem and branches golden brown; polyps creamy white. Polyps polymorphic, occurring as four distinct, well represented morphs in a given colony, arising from all sides of stem and branches, all polyps sessile, naked, arising from coenosarc at surface of stem and branches, not embedded in skeleton, but with a very low perisarcal collar surrounding their bases. Gastrozooids uniformly short, rotund, about 1 mm high, 0.6 mm wide, strongly constricted at base, with a distal whorl of about 9–12 short, thick tentacles (Fig. 3e); hypostome slightly rounded, with a central mouth. Defensive zooids lacking tentacles but otherwise unlike the typically tentaculate dactylozooids of most other hydractiniids, these zooids long, up to ca. 3 mm high, slender, club-shaped, widening gradually from base to near distal end, about 0.3 mm at widest point, then constricted just below terminal knob, this knob bearing 3–4 bulbs, each with a dense aggregation of nematocysts (Fig. 3c). Fourth distinct zooid morph (Fig. 3b) of uncertain function but likely involved in capture and ingathering of prey, as well as defence (for convenience, here termed a sellectozooid, from the Greek word συλλέκτης, collector; gatherer); relatively slender and mostly cylindrical in shape, polyp trunk long, up to 3 mm or more high, appearing higher if measured from base to tips of extended tentacles, less than 0.5 mm wide, mostly directed upwards and gradually curved over colony; tentacles thick, somewhat tapered, about 4–7 in number, arranged in a single distal whorl; hypostome inconspicuous; no mouth could be located. Gonozooids in the form of blastostyles, lacking tentacles and mouth, about 1 mm high, mostly cylindrical but constricted distally just below a rounded, terminal knob, this knob covered over its top half or more by a dense aggregation of nematocysts (Fig. 3d).

Gonophores fixed sporosacs, borne on gonozooids; each gonozooid with a single oval gonophore arising on a lateral stalk; all observed gonophores female, each with numerous small, polygonal oocytes.

Nematocysts.

Gastrozooids:
desmonemes (n = 10): 4.6–6.2 µm long × 2.6–3.6 µm wide
heterotrichous microbasic euryteles (n = 10): 8.0–9.7 µm long × 2.8–3.3 µm wide
elongate heterotrichous microbasic euryteles (n = 10): 9.2–10.3 µm long × 2.5–2.9 µm wide

Gonozooids:
elongate heterotrichous microbasic euryteles (n = 10): 9.0–11.5 µm long × 2.4–2.9 µm wide

Defensive zooids:
elongate heterotrichous microbasic euryteles (n = 10): 10.0–11.9 µm long × 2.4–3.2 µm wide

Sellectozooids:
desmonemes (n = 10): 5.3–6.4 µm long × 2.9–3.6 µm wide
heterotrichous microbasic euryteles (n = 10): 8.7–10.1 µm long × 3.2–3.7 µm wide
elongate heterotrichous microbasic euryteles (n = 10): 11.0–12.2 µm long × 3.1–3.7 µm wide

Encrusting mat:
elongate heterotrichous microbasic euryteles (n = 10): 9.4–11.0 µm long × 2.6–3.7 µm wide
robust heterotrichous microbasic euryteles (n = 10): 8.6–11.6 µm long × 3.3–5.2 µm wide

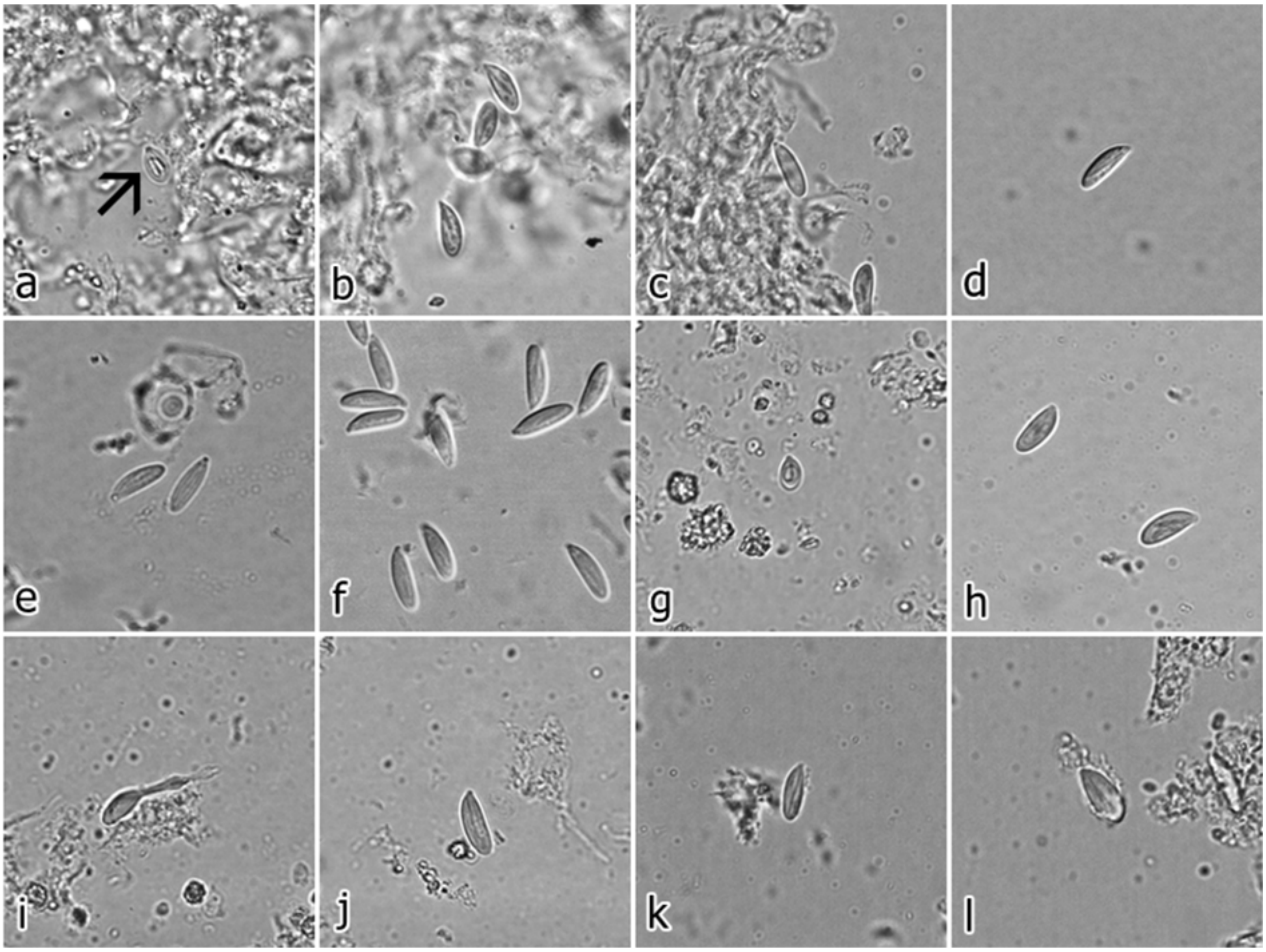

FIGURE 6. Anthoathecata: Hydractiniidae, *Hydractinia galeai*, sp. nov. (ROMIZ B5347), nematocysts. a, desmoneme, gastrozooid. **b,** microbasic euryteles, gastrozooid. **c,** elongate microbasic eurytele, gastrozooid. **d,** elongate microbasic eurytele, gonozooid. **e,** elongate microbasic euryteles, defensive zooid. **f,** cluster of elongate microbasic euryteles, defensive zooid. **g,** desmoneme, sellectozooid. **h,** microbasic euryteles, sellectozooid. **i,** discharged microbasic eurytele, sellectozooid. **j,** elongate microbasic eurytele, sellectozooid. **k,** microbasic eurytele, encrusting mat. **l,** robust microbasic eurytele, encrusting mat.

Remarks. Hydractiniid hydroids are most familiar as sessile epizoites forming a flat, encrusting mat or a network of stolons over the substrate. By contrast, colonies of *Hydractinia galeai*, sp. nov., form an upright, arborescent, chitinous skeleton invested with naked coenosarc. That character is nevertheless shared with several other hydractiniid species, including *Hydractinia arborescens* Carter, 1878, *H. angusta* Hartlaub, 1904, *H. rugosa* Fraser, 1938b, *H. prolifica* Fraser, 1948, *H. bayeri* Hirohito, 1984, *H. cryptogonia* Hirohito, 1988, *Hydrissa sodalis* (Stimpson, 1858), *Hydrodendrium gorgonoides* Nutting, 1905, and *Schuchertinia antonii* (Miglietta, 2006). Noteworthy differences between *H. galeai* and each of these species are summarized below. Erect colonies are also formed by the hydractiniids *Janaria mirabilis* Stechow, 1921a and *Hydrocorella africana* Stechow, 1921a, but their skeletons are formed of calcium carbonate rather than chitin. Apparently similar to these two is *Hydractinia calcarea* Carter, 1877 (see also Carter 1878), a largely overlooked species of obscure status, originally described from dry specimens lacking polyps.

Hydractinia arborescens, described from a dry specimen in poor condition, is considered here to be a *species inquirenda*. Although polyps were present in the type, its skeleton forms short, chitinous, spiny projections on a gastropod shell. That character is enough to distinguish it from *H. galeai*, with its erect and branched stems. Specimens thought similar to *H. arborescens* were briefly discussed and illustrated by Hirohito (1984, pl. 2, figs. 2, 3).

Hydractinia angusta forms both encrusting and erect colonies (Hartlaub 1904; Stepanjants 1979; Galea & Schories 2012; Peña Cantero *et al*. 2013). Its polyps are distinct from those of *H. galeai* in being dimorphic or trimorphic instead of quadrimorphic, with gastrozooids, gonozooids, and occasionally dactylozooids of a different shape from those studied here. Gastrozooids of the species are tall (as much as 5 mm high in preserved material, but higher in life), their hypostomes are large and dome-shaped, and tentacles are long and number about 6–16. Gonozooids are distinctive from those of *H. galeai* in being reduced (ca. 1 mm high) but tentaculate (1–6 tentacles), with gonophores arranged in a ring around the base. Spines are usually reported to be present.

Hydractinia rugosa and *H. prolifica* have been taken to be conspecific (Calder *et al*. 2009), but if not, they nevertheless resemble one another in overall colony form. They both differ significantly from *H. galeai* in being bimorphic rather than quadrimorphic, and they form erect, horn-like, chitinous spikes that provide a substrate for the zooids (Fraser 1938b, 1948; Calder *et al.* 2009). The upright spikes of the two are much shorter than the arborescent stems of specimens examined here, reaching only 1.8 cm high in the lectotype of *H. rugosa* and 2.5 cm high in that of *H. prolifica* (Calder *et al*. 2009). Spines are large and prominent in both species, rather than being inconspicuous. Gastrozooids of the species are taller and less rotund than those of *H. galeai*, and gonozooids are armed at the distal end with numerous small bulbs of nematocysts rather than only a few (3–4). Gastrozooid tentacles of *H. rugosa* were originally described by Fraser (1938b) as being of two sizes, with approximately half of them being longer than the others.

Hydractinia bayeri appears closest to *H. galeai* in overall colony form. However, it possesses only three zooid morphs rather than four, and its gonozooids and defensive zooids are distinctly different in morphology. Gonozooids of the species are capped with many knob-shaped nematocyst batteries rather than a single terminal nematocyst knob. Defensive zooids are whip-shaped rather than club shaped, their distal ends are only slightly rounded distally, and they apparently lack the terminal cap of knob-like nematocyst batteries present on those of *H. galeai*.

Hydractinia cryptogonia appears to be monomorphic, unlike the polymorphic *H. galeai*. The single female colony of the species described by Hirohito (1988) lacked gonozooids, dactylozooids, and spines. Its hydranths are small (reaching 0.3 mm high), sparsely distributed, and morphologically like those of *Hydrodendrium gorgonoides*, with about 10–12 filiform tentacles. Rather than arising from gonozooids, groups of 2–5 large eggs were located within the outer part of the coenosarc.

Hydrissa sodalis differs from *H. galeai* in forming short, chitinous, arborescent processes on gastropod shells rather than forming long, branched stems (Stimpson 1907; Stechow 1907). Zooids of the two species are also different in morphology. As described by Hirohito (1988), gastrozooids of *H. sodalis* are columnar, with numerous tentacles (up to 60). Tentaculozooids are mostly spiral zooids, with from 0–20 short, knob-shaped tentacles. Gonozooids of the species each give rise to several sporosacs, and a few short tentacles occur on them at the distal end.

Hydrodendrium gorgonoides is distinct in having colonies that appear to be monomorphic, like those of *Hydractinia cryptogonia*, rather than polymorphic, as in *H. galeai* (Nutting 1905; Hirohito 1988; Calder 2010). Gonophores arise as hernia-like projections from the gastric column of polyps that seem essentially identical to normal gastrozooids rather than typical gonozooids. Colonies of the species, reaching at least 21 cm high and superficially resembling those of certain octocorals, are much more massive than those of *H. galeai*.

Schuchertinia antonii is readily distinguished from *H. galeai* in having a heavily calcified base, as well as possessing zooids of three morphs instead of four (Miglietta 2006). These all differ in shape from zooids of the species studied here. Gastrozooids are small (1.2 mm high), with tentacles that are thick and few in number (2–5; usually 2). Gonozooids, of the same size as the gastrozooids, give rise to 1–3 eumedusoid gonophores with four radial canals. Tentaculozooids of varied shape, from long and thin to short and thick, are numerous and equally distributed throughout the colony.

Hydractinia dendritica Hickson & Gravely, 1907, also somewhat resembling *H. galeai*, was assigned by Stechow (1921b) to a new genus, *Hydronema*. That genus has seldom been adopted in hydrozoan literature, and the hydroid examined here is assigned instead to *Hydractinia* Van Beneden, 1844. Moreover, Stechow (1962) discovered that the name *Hydronema* was a homonym of *Hydronema* Martynov, 1914 (Trichoptera), and proposed *Halorhiza* as a replacement for it. Like *Hydronema*, *Halorhiza* too remains unused at present. As for *H. dendritica*, it is now taken to be conspecific with *Hydractinia angusta* Hartlaub, 1904 (Stepanjants 1979; Galea & Schories 2012).

Examined colonies of *H. galeai* from Jingū Seamount were in good condition for the most part, and fertile gonozooids were present. The species is unusual in having four kinds of polyps, namely gastrozooids, gonozooids, defensive zooids, and a morph of uncertain function termed here a sellectozooid. That polyp form resembles the gastrozooids of certain species of *Hydractinia*, but the true gastrozooids of *H. galeai* are much shorter and more rotund, with a significantly larger number of tentacles than in sellectozooids. It is suspected that these zooids are first and foremost food gatherers, securing and transporting prey to the short, rotund gastrozooids at the surface of the stems and branches. However, they may also join with defensive zooids in providing protection for the gastrozooids and gonozooids beneath a canopy of their tentacles.

The cnidome varied from one polyp type to another in colonies of *H. galeai*. Only microbasic euryteles of an elongate form were observed in defensive zooids (Figs. 6e, f) and gonozooids (Fig. 6d). Gastrozooids and sellectozooids had desmonemes (Figs. 6a, 6g) and microbasic euryteles of two forms (Figs. 6b, c, h, i, j), including the elongate form seen in defensive zooids and gonozooids. Two types of euryteles were also seen in the encrusting mat, the first of a typical form and the second a form with a thicker capsule (Figs. 6k, l).

On Jingū Seamount, *H. galeai* was observed over a depth range between 1410 m and the top of ROV *SuBastian* Dive 287 at 1283 m. It was one of the dominant epifaunal species, on rocks and occasionally on dead octocorals (Fig. 5c), at depths above 1400 m over the surveyed area of the seamount. Curiously, it was neither collected nor observed in videos from any of the other seamounts.

Reported distribution. Known only from the type locality.

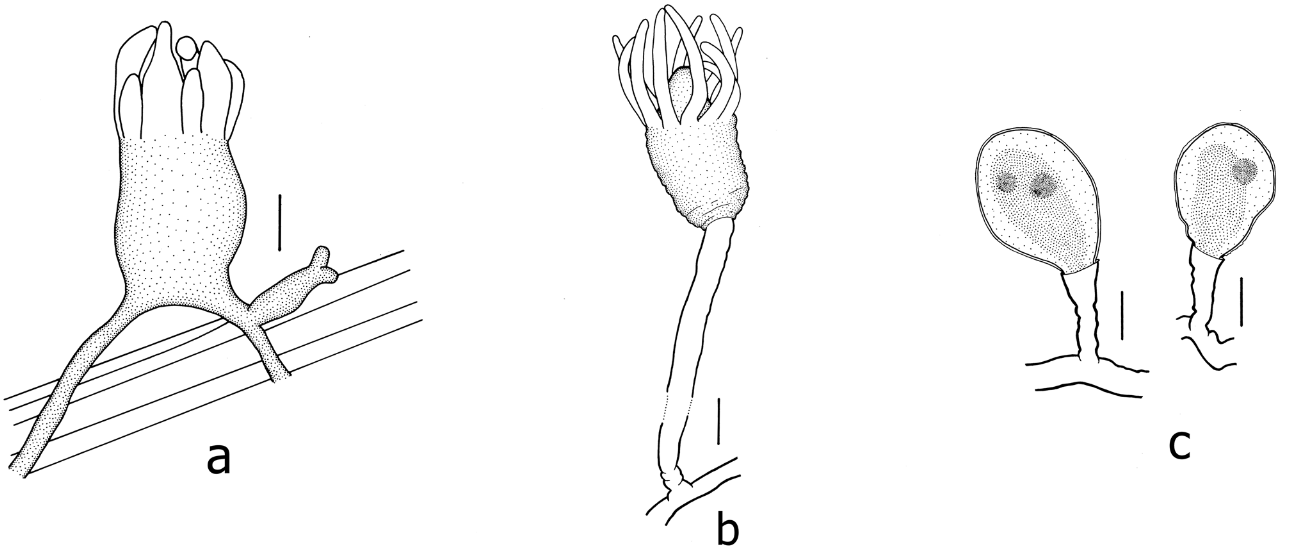

FIGURE 7. Hydractiniidae and Pandeidae. a, ***Latebrahydra schulzei***, gen. et sp. nov., Hess Rise, Sta. HES102-3A, polyps, one fully developed and one juvenile, dissected from the hexactinellid sponge *Walteria flemmingii,* ROMIZ B5350. Scale equals 0.2 mm. **b,** ***Rhizorhagium*** **cf.** ***roseum*****,** hydranth and pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5351. **Scale equals 0.2 mm. c,** ***Rhizorhagium*** **cf.** ***roseum*****,** two gonophores, Jingū Seamount, Sta. JIN114-2, ROMIZ B5351. **Scale equals 0.2 mm.**

Genus *Latebrahydra*, gen. nov.

Type species. *Latebrahydra schulzei*, sp. nov., designated herein.

Etymology. The name *Latebrahydra* is derived from the Latin "*latebros*", meaning "hiding" or "refuge", in reference to the obscure, sheltered habitation of this hydroid, and "*hydra*", referring only to a generalized hydrozoan polyp. The gender of the name is feminine.

Diagnosis. Filiferan hydroids endobiotic in hexactinellid sponges. Colonies stolonal, apparently monomorphic; hydranths somewhat reduced, interconnected basally by stolons, sessile, naked, hypostome slightly rounded, with a whorl of essentially filiform tentacles of two distinct sizes; cnidome comprising desmonemes and microbasic euryteles. Gonophores unknown.

Latebrahydra schulzei, sp. nov.

Figs. 7a, 8a, b, 9a, b

Commensal hydroid polypes.—Schulze, 1887: 98.
Two commensal hydroids.—Schulze, 1887: Pl. 11, fig. 4.

Type locality. Hess Rise, 34°08’43.97809”N, 176°22’32.36407”E, 1702 m, in the hexactinellid sponge *Walteria flemmingii* Schulze, 1886.

Material examined. HOLOTYPE: Hess Rise, Sta. HES102-3A, 34°08’43.97809”N, 176°22’32.36407”E, 31 July 2019, 1702 m, 2.2°C, 34.5 psu, in hexactinellid sponge *Walteria flemmingii*, one fragmentary colony, without gonophores, ROMIZ B5350.

Observed on video. Annei Seamount, Sta. ANN217-1, 36°38’35.0256”N, 171°36’22.4484”E, 17 August 2019, 1236 m, 2.9°C, 34.4 psu, on hexactinellid sponge.

Etymology. The specific name honours German zoologist, anatomist, and hexactinellid sponge specialist Dr. Franz Eilhard Schulze (1840–1921), who first observed and illustrated the species but did not name it.

Description. Filiferan hydroid colonies living as endobionts in lateralia of the deep-sea hexactinellid *Walteria flemmingii*; polyps interconnected by a stolon network, apparently of naked coenosarc, extending through syncytial mass of sponge host. Sterile colony with typical hydranths only, these being sessile, naked, stout, moderately spaced, embedded within partially elevated special chambers in sponge wall; these hydranth-bearing polyp chambers nearly cylindrical internally, apparently formed by sponge host in response to presence of hydroid symbiont and reinforced with siliceous spicules, chambers oblique or perpendicular to sponge axis. Hydranths cylindrical to elliptical, fully developed ones about 0.4–0.9 mm high excluding tentacles, 0.8–1.3 high including tentacles, 0.4–0.5 mm wide, tapered at base and there connected to stolons; distal end with a whorl of about 12 essentially filiform tentacles of two distinct forms, these two forms alternating and occurring in about equal numbers, all heavily armed with desmonemes and microbasic euryteles; large tentacles exceptionally thick proximally, tapering near tip, extending above hydranth, partially blocking polyp chamber at or below its orifice and sheltering hydranth when retracted; smaller tentacles oblong, interposed between larger ones; hypostome low, slightly rounded, with a central mouth. Juvenile hydranths arising as buds from stolons. Polyps cream coloured in ethanol, appearing white in videos.

Gonophores not seen.

Nematocysts.

Hydranths:
desmonemes (n = 10): 5.9–7.0 µm long × 3.8–4.4 µm wide
heterotrichous microbasic euryteles (n = 10): 9.0–10.9 µm long × 2.7–3.4 µm wide

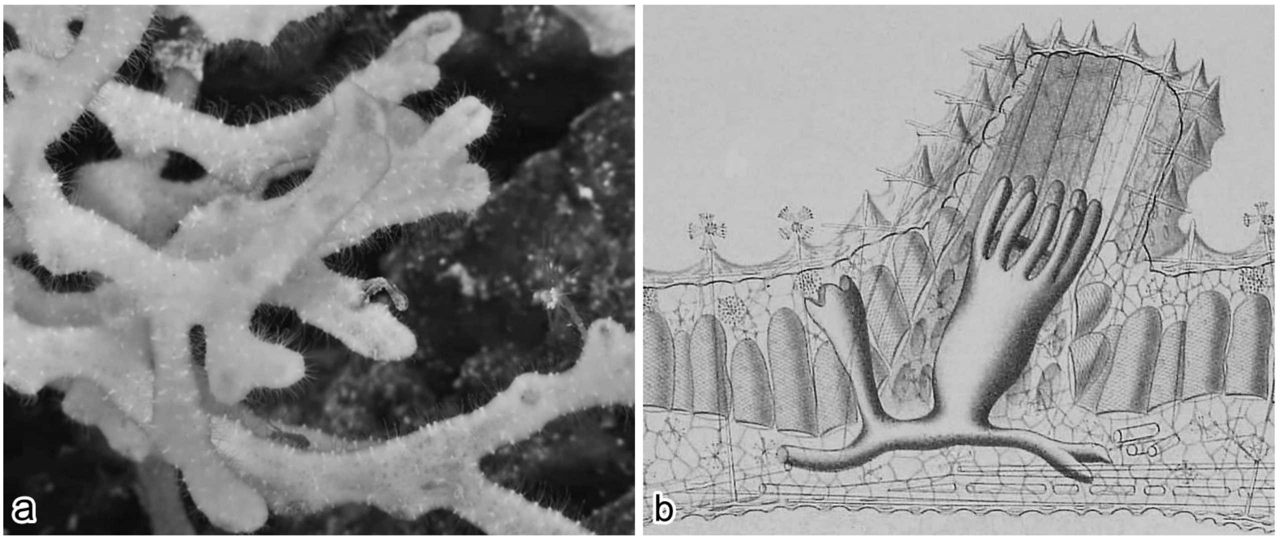

FIGURE 8. Anthoathecata: Hydractiniidae, *Latebrahydra schulzei*, gen. et sp. nov. a, polyps appearing as white spots embedded in hexactinellid sponge, Annei Seamount, Sta. ANN217-1. **b,** two hydranths of an unnamed hydroid in the hexactinellid sponge *Walteria flemmingii*, H.M.S. *Challenger* Sta. 170A (from Schulze 1887: Pl. 11, fig. 4).

Remarks. Hydroids frequently occur as epizoites on hexactinellid sponges, particularly on the stalks of deep-sea species (Calder 1996; Beaulieu 2001), but few have been reported to live as endobionts of these poriferans (Puce *et al*. 2005). During this study, colonies of *Latebrahydra schulzei*, gen. et sp. nov., were found within specially modified spaces, here termed polyp chambers, on lateralia of the hexactinellid sponge *Walteria flemmingii* Schulze, 1886 (the specific name of this species is sometimes spelled *flemmingi*, but its original and correct spelling is *flemmingii*; ICZN Art. 32.3). The overall morphology of this hydroid has been modulated by the symbiotic interaction with its sponge host, and affinities of the species have thereby been obscured. The cnidome of *L. schulzei*, comprising desmonemes and microbasic euryteles, and lacking stenoteles, affirms that it is a filiferan. The familial affinities of the species are much less certain. While it could be a cytaeidid, it has been provisionally assigned here instead to Hydractiniidae L. Agassiz, 1862 based on the resemblance of its hydranths to gastrozooids in species of the family.

Latebrahydra schulzei is believed to be conspecific with an unnamed hydroid, occurring in association with the same sponge host, illustrated and briefly described by Schulze (1887). The specimens studied by Schulze were collected near the Kermadec Islands, in the western South Pacific, during the voyage of H.M.S. *Challenger*. The polyps that he illustrated, and those from Hess Rise examined here, both inhabit cylindrical chambers in their host sponge. The orientation of these polyp chambers is either perpendicular or oblique to the axis of sponge lateralia (Fig. 8b). Schulze (1887) believed that the structures are produced in response to the presence of hydroids, which thereby modify the shape of the body wall of the sponge. Rather than being solitary, the polyps are interconnected by strands of naked coenosarc, resembling stolons, that extend through the inner syncytial mass of the sponge. In their account of *W. flemmingii*, Reiswig & Kelly (2018) noted that stolons of these hydroids branch throughout the tissue of this euplectellid.

In examined material, polyps of *L. schulzei* were immersed within the polyp chambers of their host. However, they are capable of extending beyond the openings of these chambers in life (Fig. 8a). Tentacles of all polyps examined here were arranged such that they essentially blocked the orifice, and their function appears to be protection of the hydranths as well as prey capture. The tentacles bore dense aggregations of the two nematocyst categories.

The exact nature of the symbiosis between *L. schulzei* and its basibiont *W. flemmingii* is presently unclear. The interaction is considered obligate for the hydroid, as it is unlikely to survive without the sponge. Both a suitable substrate and protection of its entire colony are gained from the host. For the sponge, the association is facultative in that specimens without the hydroid have been observed (Schulze 1887). It is presently unclear whether the sponge is significantly harmed by its endobiotic associate and the modifications in morphology that it induces, or helped, perhaps by some added defence that the hydroid might provide. For now, *L. schulzei* is considered a commensal rather than a parasite in *W. flemmingii*. It remains to be established whether it is identical with a hydroid occurring in *W. leuckarti* Ijima, 1896 (see Ijima 1896; Puce *et al*. 2006; Reiswig & Kelly 2018).

Other hydroids known to live within hexactinellids include *Bibrachium euplectellae* (Schulze, 1880) and *Brinckmannia hexactinellidophila* Schuchert & Reiswig, 2006. Hydranths of both species are much different in morphology from those of *L. schulzei*, as outlined below. Nomenclaturally, the genus *Bibrachium* Stechow, 1919 is a replacement name for *Amphibrachium* Schulze, 1880, a junior homonym of *Amphibrachium* Hertwig, 1879 (Radiolaria). Although the name *Amphibrachium* Hertwig, 1879 was applied to a radiolarian, a group no longer included in the Animal Kingdom, homonymy nevertheless exists with *Amphibrachium* Schulze, 1880 under provisions of the code of zoological nomenclature (ICZN Art. 2.2).

The hydroid of *B. euplectellae* (Anthoathecata incertae sedis) was said to be abundant in specimens of the hexactinellid sponge *Euplectella aspergillum* Owen, 1841 from "Zebu" (=Cebu, Republic of the Philippines), collected during the *Challenger* Expedition (Schulze 1880). Hydranths of this endobiont are readily distinguished from those of *L. schulzei*. They were described by Schulze (1880) as club-shaped with a short, hemispherical hypostome, a terminal mouth, and two rather long, opposite tentacles. Each tentacle was rounded at the tip, and a subterminal adoral semicircular thickening was present, with both enlargements containing aggregations of nematocysts. Elsewhere, the tentacles were flattened. The hydranths projected into inhalant lacunae of the sponge, and were interconnected by a delicate, perisarc-covered stolon system extending through the sponge syncytium. No gonophores were observed.

Hydroids of *Brinckmannia hexactinellidophila* (family Bythotiaridae Maas, 1905) were found in the inhalant and exhalent canals of hexactinellids of the genus *Heterochone* Ijima, 1927 from the eastern North Pacific (British Columbia, Alaska, California, Washington) (Schuchert & Reiswig 2006). An intimate, obligate relationship was said by these authors to exist between the sponge and its endobiotic hydroid. The minute (0.1–0.3 mm high) and atentaculate polyps of *B. hexactinellidophila* are much more reduced than those of *L. schulzei*. Its hydranths are usually bulbous at the distal end, with a dense cap of nematocysts, and no mouth could be located. Polyps are either solitary or occur as small colonies, with hydranths of colonies being linked by basal connections of naked coenosarc. Rather than having gonophores, gametes of the species apparently arise at the tip of the hydranth, displacing the nematocyst cap.

The gonophores of *L. schulzei* have yet to be described. Only the trophosome was mentioned by Schulze (1887), and specimens from the present collection appear to have been sterile. Asexual reproduction occurs by the development of buds that arise from the internal tubes of coenosarc.

It seems probable that the geographic distribution of this hydroid will eventually be shown to approach that of its basibiont sponge.

Reported distribution. Kermadec Islands: 29°45'S, 178°11'W, 630 fm (1152 m) (Schulze 1887, unnamed hydroid in the hexactinellid sponge *Walteria flemmingii*); Hess Rise; Annei Seamount (this study).

Family Pandeidae Haeckel, 1879

Genus *Rhizorhagium* M. Sars, in G. O. Sars, 1874

Rhizorhagium cf. *roseum* M. Sars, in G. O. Sars, 1874

Figs. 7b, c, 9c–f

Rhizorhagium roseum M. Sars, in G.O. Sars, 1874: 129.—Brinckmann-Voss, 1996: 94–96.
Garveia groenlandica.—Fraser, 1914a: 117, pl. 4, figs. 8A–C; 1935a: 143; 1936: 123; 1937: 35, pl. 5, figs. 21a–c; 1948: 195.

Type locality. Norway: Mangerfjord, Bognestrømmen, 20 fm (37 m) (Rees 1956).

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, on a pedicel and stolons of *Bonneviella superba* Nutting, 1915, on stem of *Lafoea fruticosa* (M. Sars, 1850), and on an unidentified substrate, all removed from skeleton of octocoral *Primnoa* sp., four colonies or colony fragments, to 4 mm high, one colony with gonophores, ROMIZ B5351.

Description. Colonies all stolonal, with hydranth pedicels arising from a creeping hydrorhiza; stolons tubelike and branched. Hydranth pedicels unbranched, of varied length but mostly elongate, reaching 1 cm long, 0.09–0.12 mm in diameter, variably curved or twisted, of essentially uniform diameter throughout; perisarc of pedicel thickest basally, becoming thinner distally, predominantly smooth except for occasional constrictions and wrinkles, without regular annulations, sometimes wrinkled at insertion with hydrorhiza; perisarc extending as an ultra-thin, filmy covering over hydranth, this apparent only after maceration of hydranth in a solution of sodium hypochlorite, not forming a large, loose, goblet-shaped, rugose pseudohydrotheca, and not extending as tubes over tentacles or hypostome. Hydranths sac-shaped, relatively large, to 0.65 mm high from base to tip of hypostome, 0.37 mm wide; tentacles filiform, tapering gradually from broad base to slender tip, about 10 in number, arranged in a single whorl around distal end of hydranth; hypostome nipple-shaped, large relative to hydranth.

Gonophores fixed sporosacs. Female sporosacs borne on pedicels arising from hydrorhiza; pedicels short, 0.3–0.4 mm long, with wrinkled perisarc, slender at base, 0.08 mm wide, increasing quite rapidly in diameter towards base of gonophore, there reaching 0.14–0.15 mm wide; spadix enveloped within a balloon-shaped, transparent membrane of thin perisarc, this capsule 0.5–0.6 mm high and 0.40–0.45 mm wide; planulae developing from sides of spadix within cavity of gonophore capsule. Male gonophores not seen.

Nematocysts.

Hydranths (including tentacles):
desmonemes (n = 10): 4.5–5.0 μm long × 2.8–3.2 μm wide
microbasic euryteles (n = 10): 7.6–8.3 μm long × 3.4–3.7 μm wide
hooked microbasic euryteles (n = 10): 7.7–8.3 μm long × 3.1–3.6 μm wide

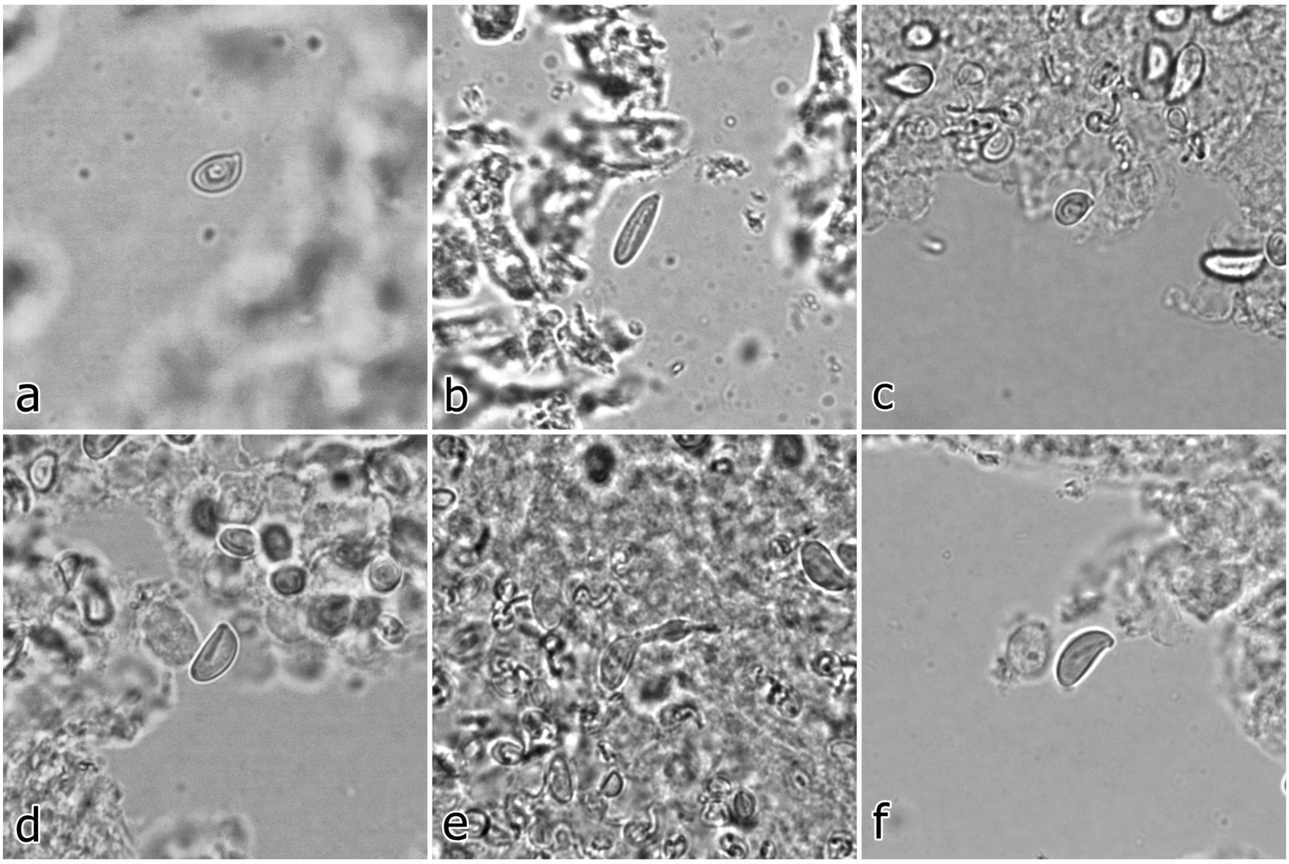

FIGURE 9. Anthoathecata: Hydractiniidae and Pandeidae, nematocysts. a, *Latebrahydra schulzei*, gen. et sp. nov. (ROMIZ B5350), desmoneme. **b, *Latebrahydra schulzei*, gen. et sp. nov. (ROMIZ B5350),** microbasic heterotrichous eurytele. **c, *Rhizorhagium* cf. *roseum* (ROMIZ 5351),** desmoneme. **d, *Rhizorhagium* cf. *roseum* (ROMIZ B5351),** microbasic heterotrichous eurytele. **e, *Rhizorhagium* cf. *roseum* (ROMIZ B5351),** microbasic heterotrichous eurytele, discharged. **f, *Rhizorhagium* cf. *roseum* (ROMIZ B5351),** microbasic heterotrichous eurytele, hooked at tip.

Remarks. In having long, unbranched pedicels of nearly uniform diameter throughout, vasiform to sac-shaped hydranths with a large, nipple-shaped hypostome, and fixed gonophores that arise only from the hydrorhiza, hydroids examined here resemble certain species currently assigned to the pandeid genera *Rhizorhagium* M. Sars, in G. O. Sars, 1874 and *Garveia* Wright, 1859. While closely related, as reflected by the morphological resemblance and genetic affinities of their type species, *Garveia nutans* Wright, 1859 and *R. roseum* (Prudkovsky *et al*. 2016; Calder 2017), both genera currently include a polyphyletic assemblage of species, including some that are likely bougainvilliids rather than pandeids.

Specimens examined here were compared with accounts of all species currently assigned in WoRMS (Schuchert 2021) to the genera *Rhizorhagium* and *Garveia*, including *R. arenosum* (Alder, 1862), *R. roseum*, *R. formosum* (Fewkes, 1889), *R. antarcticum* (Hickson & Gravely, 1907), *R. palori* Mammen, 1963, and *R. sagamiense* Hirohito, 1988, together with *G. nutans*, *G. gracilis* (Clark, 1876), *G. annulata* Nutting, 1901, *G. grisea* (Motz-Kossowska, 1905), *G. arborea* (Browne, 1907), *G. crassa* (Stechow, 1923b), *G. clevelandensis* Pennycuik, 1959, and *G. belyaevi* Stepanjants & Chernyshev, 2015. The binomen *Garveia polarsterni*, currently included as valid in WoRMS (Schuchert 2021), is a *nomen nudum*. The name appeared in a species list, compiled by S.D. Stepanjants, in a publication by Sirenko (2001). It referred to a hydroid that remains neither described nor illustrated (Antsulevich 2015; Stepanjants & Chernyshev 2015).

Hydroids from Jingū Seamount more closely resemble *R. roseum* than *G. nutans*, and have been assigned to the genus *Rhizorhagium* rather than *Garveia*. Their identification to species rank was more uncertain. Although identical in most respects with *R. roseum*, pseudohydrothecae over hydranths of the specimens were scarcely discernable. With their identification therefore somewhat uncertain, we compared our material with each of the species listed above. Hypostomes were large and nipple-shaped, as in *R. roseum*, rather than conical or dome-shaped, as in *R.*

arenosum, *R. sagamiense*, *G. arborea*, *G. crassa*, *G. gracilis*, *G. grisea*, *G. clevelandensis*, and *G. belyaevi.* Colonies were strictly stolonal rather than having erect, branched colonies with polysiphonic stems as in *G. annulata*, *G. arborea*, *G. crassa*, *G. gracilis*, and *G. nutans*. Pedicels were long and of nearly equal diameter throughout rather than being short and tapering, as in *G. belyaevi* and *R. palori*. Hydroids of *G. grisea* and *R. sagamiense* differ in having distinct, two layered perisarc over pedicels and hydranth bases. Gonophores arose from the stolons, as in *R. roseum*, *R. formosum,* and *R. antarcticum*, rather than on stems or pedicels, as in all the others. Overall, our hydroids most closely resembled *R. roseum* and have been provisionally assigned to that species here. *Rhizorhagium roseum* is usually considered a shelf species, with a depth range extending from 10–200 m (Antsulevich 2015). If correctly identified, the lower range of the species is extended here to 1283 m.

Hydranths of examined specimens superficially resembled those of species of *Eudendrium* Ehrenberg, 1834, but unlike in that genus the hypostome is nipple-shaped and gonophores are located on the stolons rather than on hydranths or blastostyles. The cnidome also differs from that of eudendriids in having desmonemes, a category not known to occur in any species of *Eudendrium*, as well as microbasic euryteles. The nematocyst complement, and morphology of the three types present, are the same as in those of *R. roseum* from the Bay of Fundy (Calder 2017). However, desmonemes and microbasic euryteles were larger, and hooked microbasic euryteles (therein termed “large euryteles”) were smaller, than in material from Fundy.

Hydroids of *R. roseum* were found on the pedicel and stolons of the hydroid *Bonneviella superba* Nutting, 1915, on a fragment of *Lafoea fruticosa* (M. Sars, 1850), and on an unidentified substrate, all removed from the skeleton of a species of the octocoral genus *Primnoa* Lamouroux, 1812. The collection, from Jingū Seamount Station JIN114-2, included a total of seven hydroid species. The presence of gonophores on one of the colonies of *R. roseum* indicates that environmental conditions at the site were favourable for the species.

Reported distribution. *North Pacific*. Eastern North Pacific, from Alaska to Vancouver Island and questionably to San Pedro, California (Fraser 1914a, 1935a, 1936, 1937, 1948, all as *Garveia groenlandica*; Brinckmann-Voss 1996).

Elsewhere. Reaching into the Arctic from boreal waters of both eastern and western North Atlantic. Reported from Hudson Strait (Fraser 1931, as *G.groenlandica*) and Greenland (Schuchert 2001) to southern Massachusetts (Fraser, 1944, as *G. groenlandica*) in the west, and from Franz Josef Land (Antsulevich 2015) to western Scotland (Schuchert 2007) in the east.

Family Eudendriidae L. Agassiz, 1862

Genus *Eudendrium* Ehrenberg, 1834

Eudendrium sp.

Fig. 10

Observed on video. Nintoku Seamount, ROV *SuBastian* Dive 286, ca. 40.2°N, 170.3°E, 12 August 2019, 1118 m, 2.7°C, on sponge.

Remarks. No hydroids referable to *Eudendrium* Ehrenberg, 1834 were collected during the survey. However, colonies referable to the genus were observed in a video from ROV *SuBastian* Dive 286. These hydroids, bright red in colour (Fig. 10) and colonizing a large, white sponge, were present at 1118 m on Nintoku Seamount. Several Arctic to northern boreal species of *Eudendrium* possess red hydranths, including *E. caricum* Jäderholm, 1908 and *E. vaginatum* Allman, 1863. However, in the absence of specimens and knowledge of their cnidome, the identity of our species is uncertain. Moreover, gonophores in observed colonies, if present, were obscure. We therefore refer to these hydroids simply as *Eudendrium* sp.

FIGURE 10. Anthoathecata: Eudendriidae, *Eudendrium* sp. a, red colonies on a sponge, Nintoku Seamount, ca. 40.2°N, 170.3°E, 1118 m.

Order Leptothecata Cornelius, 1992

Family Tiarannidae Russell, 1940

Genus *Stegolaria* Stechow, 1913a

Stegolaria geniculata (Allman, 1888)

Figs. 11a, 12a

Cryptolaria geniculata Allman, 1888: 41, pl. 20, figs. 1, 1a, b.
Stegolaria geniculata.—Vervoort, 1946a: 299, figs. 2, 3a, b.—Stepanjants, 2013a: 232; 2013b: 40.

Type locality. Fiji: off Matuku, 315 fm (576 m) (Allman, 1888, as *Cryptolaria geniculata*).

Material examined. Koko Seamount, Sta. KOK108-1A, 35°33’17.4012”N, 171°57’39.1128”E, 17 August 2019, 2030 m, 2.0°C, 34.6 psu, on a dead bamboo coral stalk, ca. 30 colony fragments, to 5 cm high, no gonophores observed, ROMIZ B5352.

Observed on video. Koko Seamount, Sta. KOK108-1A, 35°33’17.4012”N, 171°57’39.1128”E, 17 July 2019, 2030 m, 2.0°C, 34.6 psu, on a dead bamboo coral stalk; specimens collected and listed above under “Material examined” (ROMIZ B5352).

Description. Hydroid colonies erect, up to 5 cm high and 1.5 mm in diameter at base, growing on the exposed skeleton of a bamboo coral, attached by a dense mat of stolons that radiate out in all directions on substrate. Hydrocaulus variably geniculate, less distinctly so at thickened base, strongly polysiphonic except at extreme distal end, there becoming monosiphonic; main tube overgrown by accessory tubules; nodes oblique, rather indistinct, being most apparent at monosiphonic tips of stem and branches. Branching mostly irregular, in one plane; branches resembling hydrocaulus in being polysiphonic except distally, unbranched or secondarily branched. Perisarc thickened basally, becoming thin at distal ends of colony. Hydrothecae alternately arranged, oriented in one plane on both hydrocaulus and branches, partly adnate to axial tube, immersed to a varying degree by accessory tubes over polysiphonic parts, curving outwards and becoming free distally; hydrothecae 0.08–0.15 mm in diameter at base, gradually increasing in diameter distally, measuring 0.22–0.37 mm in diameter at rim; hydrothecal walls smooth, with relatively thin perisarc, especially towards distal end; abaxial wall 0.92–1.50 mm long, nearly straight over proximal half, concave over distal half; adaxial wall adnate to axial tube for half or more of its length, length adnate 0.85–1.10 mm, length free 0.50–0.90 mm, facing outwards, convex to nearly straight; a ring of desmocytes and a diaphragm-like remnant of hydrothecal attachment occasionally detectable at base of empty hydrothecae; abcauline walls of axillary hydrothecae adnate to adjacent branches over much of their length. Operculum comprising a roof-shaped enclosure, with two longitudinally pleated valves seated within two broad, U-shaped embayments between two large, triangular cusps. Hydranths elongate, most in poor condition, with about 12 filiform tentacles.

Gonothecae not seen.

Remarks. Allman (1888) described this species, as *Cryptolaria geniculata*, from collections taken off Fiji during the *Challenger* Expedition. It was included in the new genus *Stegolaria* by Stechow (1913a), along with *Cryptolaria operculata* Nutting, 1905, and designated as type species of that genus in a later work (Stechow 1923c: 147). The validity of the genus has been reviewed by Edwards (1973).

Stegolaria geniculata is a species of the deep sea, with a reported bathymetric distribution of 252–4152 m (Millard 1977; Vervoort 1985). *Cryptolaria operculata*, originally described from Hawaii and now assigned to *Stegolaria* Stechow, 1913a, has been included in *S. geniculata* by some authors, including Millard (1977), Ramil & Vervoort (1992), and Calder & Vervoort (1998), but excluded by others (Vervoort 1985; Hirohito 1995; Vervoort & Watson 2003; Watson 2017). Vervoort (1985) noted that the two are similar in morphology, but reserved judgment on whether they were conspecific, not having compared their types. They have been treated as distinct species here, although they may eventually be found conspecific. We assigned material from Koko Seamount to *S. geniculata*. As for putative distinguishing characters, the ultimate branches are said to be geniculate in *S. geniculata* while those of *S. operculata* are more nearly straight (Ramil & Vervoort 1992), but that character seems to be a variable one (Millard 1977). Other species included in the genus include *S. irregularis* Totton, 1930 from New Zealand, and *S. laevigata* Watson, 2017 from Australia.

Nomenclaturally, the generic name *Stegolaria* was presented as new in two separate works by Stechow (1913a, b), and it is presently unclear which was published first. The paper cited here as Stechow (1913a) appeared in *Zoologischer Anzeiger*, Volume 43, No. 3, dated 02 December 1913 (see journal page 97). No date other than the year 1913 is given in the other work (Stechow, 1913b), and no greater detail was added about it in the leptolid bibliography of Vervoort (1995). The chronology adopted for them here, coinciding with that in Vervoort (1995) and Ruthensteiner *et al*. (2008), is based on both a provision of the International Code of Zoological Nomenclature (ICZN Art. 21.3) and the fact that Stechow (1913b: 162) fully cited Stechow (1913a) in his References section. Additional evidence is still needed, however, to settle the issue.

Hydroids of *S. geniculata* were present in a collection from Koko Seamount (Figs. 11a, 12a), but all of the specimens were in rather unsatisfactory condition. It was difficult to find a colony with a hydrotheca having an intact operculum, and no gonothecae were observed in any of them. Fertile, well-preserved specimens from Indonesia were described and illustrated by Vervoort (1946a).

Reported distribution. *North Pacific.* Indonesia: Kwandang Bay, 400–500 fm (732–914 m) (Vervoort 1946a).—Sea of Japan, 517–994 m (Stepanjants 2013a, b).

Elsewhere. Atlantic, Pacific, and Indian oceans, deep sea, in lower and middle latitudes (e.g., Millard 1977; Ramil & Vervoort 1992; Calder & Vervoort 1998; Watson & Vervoort 2001; Vervoort 2006; Peña Cantero & Horton 2017).

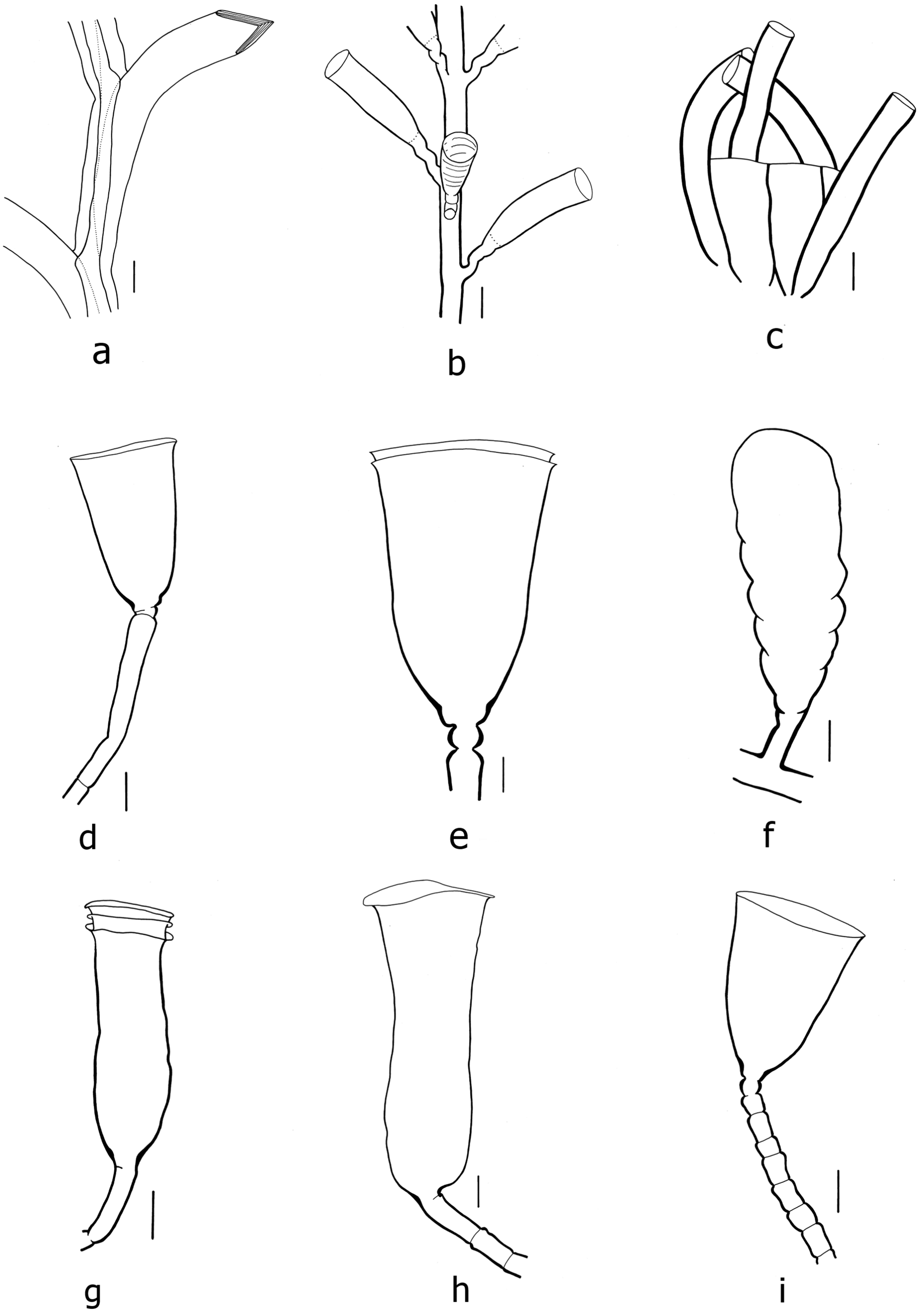

FIGURE 11. Leptothecata: Tiarannidae, Lafoeidae, and Campanulariidae. a, ***Stegolaria geniculata***, part of a colony with one complete hydrotheca, Koko Seamount, Sta. KOK108-1A, ROMIZ B5352. Scale equals 0.2 mm. **b,** ***Lafoea fruticosa***, distal end of hydrocaulus with three hydrothecae, Yomei Seamount, YOM103-1A, ROMIZ B5353. Scale equals 0.2 mm. **c,** ***Lafoea fruticosa***, fragment of a coppinia, with defensive tubes and two gonothecae, Yomei Seamount, YOM103-1A, ROMIZ B5353. Scale equals 0.1 mm. **d,** ***Bonneviella*** **cf.** ***gracilis,*** hydrotheca and pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5354. Scale equals 0.2 mm. **e,** ***Bonneviella*** **cf.** ***gracilis,*** hydrotheca and distal end of pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5354. Scale equals 0.1 mm. **f,** ***Bonneviella*** **cf.** ***gracilis,*** gonotheca, Jingū Seamount, Sta. JIN114-2, ROMIZ B5354. Scale equals 0.2 mm. **g,** ***Bonneviella regia,*** hydrotheca and distal portion of pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5355. Scale equals 0.5 mm. **h,** ***Bonneviella superba,*** hydrotheca and distal portion of pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5356. Scale equals 0.5 mm. **i,** ***Bonneviella*** **sp.**, hydrotheca and distal portion of pedicel, Jingū Seamount, Sta. JIN114-2, ROMIZ B5357. Scale equals 0.2 mm.

Family Lafoeidae A. Agassiz, 1865

Genus *Lafoea* Lamouroux, 1821

Lafoea fruticosa (M. Sars, 1850)

Figs. 11b, c, 12b

Campanularia fruticosa M. Sars, 1850: 138.

Lafoea fruticosa.—Clark, 1877: 216, pl. 12, fig. 22.—Inaba, 1890: 145, figs. 14–16; 1892: 351.—Nutting, 1901: 178; ?1905: 945.—von Marenzeller, 1902: 564.—Jäderholm, 1907: 3, pl. 1, figs. 1, 2; pl. 2, figs. 1, 2; 1919: 6, pl. 1, fig. 7.—Fraser, 1911: 53; 1914a: 175, pl. 24, fig. 87A–E; 1914b: 220; 1936: 125; 1937: 120, pl. 25, figs. 138a–d; 1948: 230.—Linko, 1911: 98, fig. 17.—Stechow, 1913b: 109, fig. 84.—Stechow & Uchida, 1931: 550, pl. 15, fig. 3.—Leloup, 1938: 10, fig. 7.—Yamada, 1955: 123, fig. 1C.—Naumov, 1960: 275, fig. 164 [part]; 1966: 78, pl. 9, fig. 1.—Pequegnat, 1964: 277.—McCormick, 1965: 141.—Rho & Chang, 1974: 138, pl. 3, figs. 1, 2.—Brinckmann-Voss, 1983: 8, 12, 14.—Antsulevich, 1987: 49, fig. 11A.—Park, 1990: 78; 1991: 545; 1993: 266.—Park & Song, 2000: 59.—Samyn, 2014: 24.

Lafoea grandis.—Fraser, 1911: 53 [not *Lafoea grandis* Hincks, 1874].

Type locality. Norway: west coast, between Havøysund and Bergen (M. Sars 1850).

Material examined. Yomei Seamount, Sta. YOM103-1A, 42°25’54.8694”N, 170°26’06.5424”E, 09 August 2019, 1472 m, 2.4°C, 34.5 psu, nine colony fragments, to 6 cm high, three with coppiniae, on sponge skeleton adjacent to a stoloniferous octocoral, ROMIZ B5353.

Observed on video. Yomei Seamount, ROV *SuBastian* Dive 283, Sta. YOM103-1A, 42°25’54.8694”N, 170°26’06.5424”E, 09 August 2019, 1472 m, 2.4°C, 34.5 psu, several colonies, on sponge skeleton adjacent to an octocoral, with coppiniae; specimen collected (Fig. 12b) and listed above under “Material examined” (ROMIZ B5353).—Jingū Seamount, ROV *SuBastian* Dive 287, Sta. JIN114-2, 38°50.76782’N, 171°13.6524’E, 1285 m, 2.8°C, 34.4 psu, on skeleton of *Primnoa* sp., 13 August 2019.

Description. Hydroid colonies erect, up to 6 cm high and 1.25 mm in diameter at base, most broken off near proximal end, but two of them intact and with remnants of hydrorhiza. Hydrocauli predominantly straight, alternately branched for the most part, although with branches arising from all sides, larger hydrocauli and branches strongly polysiphonic except at their extremities, becoming progressively more slender distally and monosiphonic at distal end; larger branches resembling hydrocauli and branched in like manner, polysiphonic along most of their length; smaller and younger branches monosiphonic throughout; perisarc of both hydrocaulus and branches thickest proximally, thinning out distally. Hydrothecal pedicels arising from both axial and secondary tubes, spirally twisted, quite long for species of the genus, 0.20–0.24 mm in length, 0.05–0.09 mm in diameter, nearly uniform in width beyond insertion with stem or branch, given off from all sides of hydrocaulus and branches, never adnate basally, forming an angle of 45 degrees or less with hydrocaulus and branches. Hydrothecae deeply conical with essentially smooth walls, although these appearing very faintly wavy in apical view, sometimes almost symmetrical but more often somewhat curved, with abaxial wall less convex than adaxial side, length abaxial wall from desmocyte ring to rim 0.61–0.68 mm, length adaxial wall across same distance 0.65–0.73 mm; base of hydrotheca with an irregular whorl of desmocytes, then merging almost imperceptibly with pedicel; diameter across desmocyte ring 0.10–0.16 mm; hydrothecal margin entire, slightly to moderately everted, occasionally renovated in older parts of colony; orifice round, 0.19–0.23 mm in diameter; operculum and diaphragm absent. Hydranths with about 10–12 filiform tentacles.

Gonophores enclosed within a coppinia borne on hydrocauli and larger branches. Gonothecae irregular in cross-section with a flattened top, very densely packed, forming a solid mass around entire circumference of stem or branch; numerous perisarcal tubes of modified polyps extending above gonothecae, these structures being long, slender, and straight or curved.

Remarks. Three species or putative species of *Lafoea* Lamouroux, 1821, namely *L. dumosa* (Fleming, 1820), *L. fruticosa* (M. Sars, 1850), and *L. gracillima* (Alder, 1856), are common in cold waters of the northern hemisphere. Hydroids of the three resemble one another, and intraspecific variation in each is such that their morphology has been said to overlap. Synonymy of the three was proposed by Cornelius (1975), who noted that *L. fruticosa* and *L. gracillima* had been considered conspecific by some even at the time of Hincks (1869). Over the last half-century, all three have usually been taken to be identical, with the binomen *L. dumosa* having nomenclatural priority. Recently, however, Moura *et al*. (2008, 2012) found considerable cryptic diversity in hydroids assigned to *L. dumosa*, Until the taxonomy of the group can be more definitively resolved, all are recognized as valid here, as defined in their original descriptions.

Following characters utilized in traditional works on hydroids, *L. fruticosa* is distinguished from *L. dumosa* in having pedicels that are distinct and spirally twisted rather than short or essentially non-existent, and hydrothecae that are more bilaterally than radially symmetrical. *Lafoea gracillima* differs from them both in the extreme slenderness of its hydrothecae. According to Broch (1928), hydrothecae of *L. fruticosa* usually differ from those of *L. gracillima* in having both a small bulge at the base of the abaxial wall and a slight flare at the hydrothecal margin.

Material from the Emperor Seamounts corresponded most closely with accounts of *L. fruticosa*, and is assigned to that species here. The specimens were in good condition, with coppiniae being present on three of them. Somewhat resembling *L. fruticosa* is *L. benthophila* Ritchie, 1909, reported elsewhere from deep waters of the NW Pacific (e.g., Antsulevich & Vervoort 1993; Hirohito 1995; Namikawa 2009). However, hydrothecae of the latter, originally described from deep waters (1775 fathoms, 3246 m) south of the South Orkney Islands, are much larger (to 1 mm long) than in specimens examined here (<0.7 mm).

Lafoea fruticosa, considered a cosmopolitan species (Vervoort 1972), is likely circumpolar. The species extends from Arctic and subarctic regions into boreal waters on both sides of the North Pacific (Broch 1910; Fraser 1937; Yamada 1959; Naumov 1960; 1966) and North Atlantic (Fraser 1944; Vervoort 1946b). Its reported depth range is from 7–2000 m, with most records at depths of 50–200 m (Naumov 1960, 1966). Records of this Arctic-boreal species from bathyal depths in Hawaii, by Nutting (1905), are regarded here as questionable.

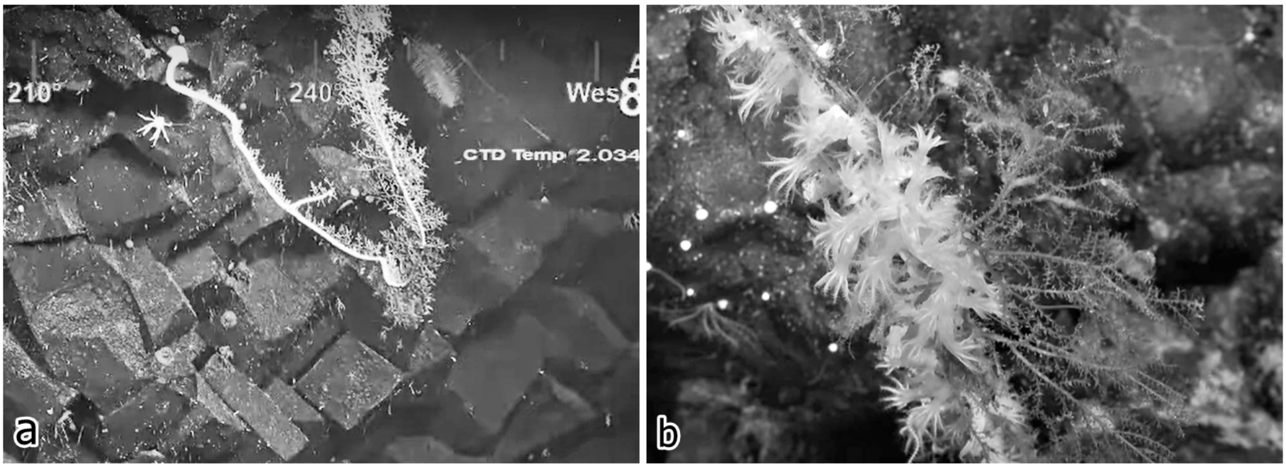

FIGURE 12. Leptothecata: Tiarannidae and Lafoeidae. a, *Stegolaria geniculata*, colony on a dead bamboo coral stalk, part of this colony examined and described herein (ROMIZ B5352), Koko Seamount, Sta. KOK108-1A. **b, *Lafoea fruticosa*,** colony on sponge skeleton to the right of polyps of a stolonal octocoral; part of this colony examined and described herein (ROMIZ B5353), Yomei Seamount, YOM103-1A.

Reported distribution. *North Pacific.* Alaska: Aleutian Islands, Kyska Harbor [=Kiska Harbor]; Shumagin Islands, Popoff Straits [=Popof Strait]; Shumagin Islands, Big Koniushi [=Yukon Harbor, Big Koniuji Island], Yukon Harbor (Clark 1877).—Alaska: Juneau; Berg Inlet; Kadiak [Kodiak Island] (Nutting 1901).—Washington state: Puget Sound (Nutting 1901).—Sea of Japan: 42°08’N, 130°39’E (von Marenzeller 1902).—?Hawaii: off Maui; NE of Island of Hawaii; between Hawaii and Maui (Nutting 1905).—Bering Sea: 55°24’N, 165°37’W (Jäderholm 1907).—Washington state: San Juan Archipelago (Fraser 1911, as *L. fruticosa* and *L. grandis*).—Sea of Japan (Linko 1911).—Japan: Sagami Bay (Stechow 1913b).—British Columbia: Queen Charlotte Islands [=Haida Gwaii], off Cape Edenshaw; W of Vancouver Island, Swiftsure Shoal [=Swiftsure Bank]; N of Gabriola Island; Gabriola Reefs (Fraser 1914a).—Alaska: Gulf of Alaska, SE of Trinity Islands (Fraser 1914b).—Japan: Sagami Bay, Misaki; Okinoshima; Goto Islands (Jäderholm 1919).—Japan: Mutsu Bay (Stechow & Uchida 1931).—British Columbia: Queen Charlotte Islands [=Haida Gwaii], N of Marble Island; Hope Island, off Cape James (Fraser 1936: 125).—California: lower San Francisco Bay, Shag Rock (Fraser 1937).—British Columbia: Queen Charlotte Islands [=Haida Gwaii], off Massett Sound [=Masset Sound]; Klashwan Point; Hope Island, off Cape James (Fraser 1937).—Alaska: Juneau, Mill Creek; Sumner Strait, off Shingle Island; Admiralty Island, off Gardiner buoy; Lynn Canal, Symonds Point (Fraser 1937).—Japan: Sagami Bay (Leloup 1938).—California: Santa Rosa Island, 2.4 km E of South Point + 4.8 km E of South Point + 20.9 km SSE of East Point; 17.3 km W of Point Dume; Santa

Catalina Island, 11.7 km SE of Seal Rocks + 4.0 km SE of Seal Rocks + 8.0 km E of Church Rock + 6.4 km SE of Church Rock + 11.3 km WSW of Church Rock; San Clemente Island, S of Pyramid Cove; 14.5 km off San Diego (Fraser 1948).—Alaska: Aleutian Islands, Agattu Island (Yamada 1955).—Russia: all far eastern seas of the country (Naumov 1960, 1966).—California: Corona del Mar, siltstone reef, shallow sublittoral (Pequegnat 1964).—Oregon: shelf and slope at depths from 64–1829 m (McCormick 1965).—South Korea: Jeju-do, Sup-do; Jeju-do, Seogwipo; Yeosu; Jeju-do, Wimiri (Rho & Chang 1974).—British Columbia: Quadra Island, Mudge Point; Dixon Entrance, 54°13'N, 132°09'W; off Flores Island (Brinckmann-Voss 1983).—Russia: Kuril Islands, everywhere on the Kuril shelf from 10 m to bathyal depths (Antsulevich 1987).—South Korea: Mip'o; Seogwipo; Ch'ongsando Island; Nohwado Island; Piyangdo Island; Kapado Island (Park, 1990).—South Korea: Seogwipo; Cheju Harbour; Ullungdo (Park 1991).—South Korea: Munsom (Park 1993).—South Korea: Dokdo Islands, Ji-nae Rock + Sujung Cave (Park & Song 2000).—Japan: Sagami Bay (Samyn 2014).

Elsewhere. Boreal NE Atlantic, including Greenland, Iceland, and the Faroes (Jäderholm 1909; Broch 1918; Vervoort 1946b), and southwards to the Bay of Biscay (Browne 1907; Vervoort 1985); boreal NW Atlantic southwards to Long Island, New York (Fraser 1944); all northern seas of Russia (Naumov 1960, 1966); eastern Canadian Arctic and subarctic (Calder 1970). *Lafoea fruticosa* has also been reported from the southern Hemisphere (e.g., Vervoort 1972). Records from warm temperate and tropical regions are considered doubtful herein.

Family Campanulariidae Johnston, 1837

Bonneviella Broch, 1909

Bonneviella cf. *gracilis* Fraser, 1939

Figs. 11d–f

Bonneviella gracilis Fraser, 1939: 59, figs. 1a–c.

Type locality. Canada: Nunavut, Dease Strait, 68°58'N, 106°20'W, 40 fm (73 m) (Fraser 1939).

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, on skeleton of *Primnoa* sp., three colonies or colony fragments, up to 7 mm high, with a gonotheca, ROMIZ B5354.

Description. Hydroid colonies stolonal, arising from stolons creeping over a skeleton of the octocoral *Primnoa* sp. Pedicels unbranched, very long relative to hydrothecae, reaching 6 mm in length, 0.08–0.13 mm in diameter, sometimes with slight wrinkles and an occasional constriction but lacking segments or regular annulations, smooth even at insertion with stolon but with a distinct subhydrothecal spherule at distal end; perisarc relatively thick basally, becoming thinner distally. Hydrothecae symmetrical, deeply campanulate, small for the genus, 0.74–0.85 mm from base to margin, hydrothecal walls constricted at base, convex over remaining basal half to two-thirds, straight to slightly concave below orifice; rim flaring, entire, occasionally renovated, diameter at margin 0.48–0.57 mm; perisarc fairly thin except for a distinct annular thickening at hydrothecal base; diaphragm absent. Hydranths with broad base attached to thickened basal wall of hydrotheca; tentacles filiform, in a single whorl, about 20–24 in number, inserting into gastric region of hydranth.

Gonophore a fixed sporosac, appearing to be male. Single confirmed gonotheca of species in collection solitary, borne on a short, smooth pedicel arising from hydrorhiza also bearing a hydrothecal pedicel and hydrotheca; pedicel 0.25 mm in length, 0.10–0.13 mm wide; gonotheca 1.45 mm long, 0.55 mm in maximum diameter, club-shaped, narrowest at base, rounded at apex but this part damaged and crushed flat, with a terminal orifice and possibly with a terminal collar when intact, gonothecal wall round in cross-section, with about five rounded ridges lacking keels. Perisarc moderately thick, being thickest on gonothecal pedicel.

Remarks. These hydroids closely resemble accounts of two little-known species, *Campanularia gracilis* Allman, 1876, from Japan, and *Bonneviella gracilis* Fraser, 1939, from Dease Strait, Canada. The specimens have been provisionally assigned to *B. gracilis*, and retained in *Bonneviella* Broch, 1909, based on the following evidence. A pre-oral chamber, diagnostic of *Bonneviella* and believed to be present in *B. gracilis*, appears to exist in better-preserved hydranths examined here. Hydrothecal pedicels conform with *B. gracilis* in lacking basal annulations, rather than having “one or two” of them as in *C. gracilis*. Fraser’s hydroids of *B. gracilis* were sterile; the single gonotheca examined here was club-shaped with about five rounded transverse ridges. By contrast, those of *C. gracilis* were more elongate and had about eight sharp ribs.

Hydroids of *B. gracilis* have not been reported since the original description of the species. While *C. gracilis* has been listed or briefly mentioned in several works (e.g., Marktanner-Turneretscher 1895; Bedot 1912, 1916, 1918, 1925; Stechow 1923a; Yamada 1959; Gili *et al*. 1989), it has been reported again only by Stechow (1925). Even that report, based on a sterile colony from South Africa, has been questioned, with Millard (1975) suspecting that it was based on *Orthopyxis integra* (Macgillivray, 1842). Of note, however, Stechow (1925: 424) also added a record of the species from St. Paul Island in the Bering Sea, based on material in the Zoologische Staatssammlung München. In that work, he included *Campanularia ritteri* Nutting, 1901, originally described from Juneau, Alaska, as a synonym of *C. gracilis*. However, hydrothecae of *C. ritteri* are described as cylindrical (Nutting, 1901) rather than deep bell-shaped as in *C. gracilis*. Both of them were included in the synonymy of *Orthopyxis integra* by Cornelius (1982).

In an earlier work, putative differences between Fraser’s (1939) *B. gracilis* and *Campanularia integra* (=*Orthopyxis integra*) were questioned (Calder 1970). As noted above, however, characters of *B. gracilis* appear to align it better with *Bonneviella* than with *Campanularia* Lamarck, 1816 or *Orthopyxis* L. Agassiz, 1862. While their colony habits and particularly their hydrothecae resemble one other, *B. gracilis* and *C. gracilis* are recognized as distinct here at the ranks of both genus and species. If taken to be conspecific and combined in the same genus, their binomena would become both synonyms and secondary homonyms, with the name of Allman’s hydroid having priority. Type material exists for both species, with that of *C. gracilis* at the Natural History Museum, London (BMNH 1877.4.12.5; Cornelius 1982: 66) and that of *B. gracilis* at the Royal British Columbia Museum (RBCM 976-00454-003; Calder & Choong 2018: 64).

Within the genus *Bonneviella*, *B. gracilis* most closely resembles *B. regia* (Nutting, 1901), *B. superba* Nutting, 1915, *B. enterovillosa* Naumov, 1951, and *B. uschakovi* Naumov, 1951. Nevertheless, it is distinguished from all currently recognized species of the genus by the following combination of characters: (1) colonies stolonal; (2) hydrorhiza a creeping stolon rather than a tangled mass of tubes; (3) hydrothecal pedicels long, unbranched, mostly unsegmented, and without annulations at the base; (4) subhydrothecal spherule separating pedicel and hydrotheca; (4) hydrothecae small (1 mm or less long), deep funnel-shaped, with a slight flare at the margin; (5) gonothecae with smooth, rounded ridges and without evidence of clustering.

Hydroids of *Bonneviella* are well represented in the North Pacific Ocean, with eight currently recognized species (Antsulevich 2015) in addition to *B. gracilis*. By contrast, only one species of the genus, *B. grandis* (Allman, 1876), has been reported in the North Atlantic (Broch 1918, 1948; Schuchert 2001). The group has therefore been considered native in the North Pacific, and *B. grandis* has been thought to be a likely invader of the Atlantic from there (Broch 1948). The genus *Bonneviella* is not known to occur in the southern Hemisphere. Fraser (1938a) described *B. minor* from the Galápagos Islands, Ecuador, but the species is now assigned to *Scandia* Fraser, 1912 (Calder *et al*. 2009).

Results from molecular and morphometric studies indicate that hydroids of the group, traditionally assigned to Bonneviellidae Broch, 1909 and distinguished primarily by the unusual internal morphology of the hydranth (Broch 1909, 1918; Nutting 1915; Bouillon *et al*. 2006), fall within Campanulariidae Johnston, 1837 (Govindarajan *et al*. 2006; Leclère *et al*. 2009; Maronna *et al*. 2016; Cunha *et al.* 2017, 2020). That evidence has been accepted here. The distinctive morphology of the hydranth thought characteristic of the family, namely the presence of a pregastric chamber, remains diagnostic of the genus *Bonneviella* (Cunha *et al.* 2017).

Bonneviella gracilis is a species of cold northern waters, with a reported depth range of 73–1283 m (Fraser 1939; this report).

Reported distribution. *North Pacific.* Emperor Seamounts (this study).

Elsewhere. Arctic Ocean: Dease Strait, Nunavut, Canada (Fraser 1939).

Bonneviella regia (Nutting, 1901)

Fig. 11g

Campanularia regia Nutting, 1901: 172, pl. 19, figs. 1, 2.—Fraser, 1914a: 138, pl. 12, figs. 34A–D.
Bonneviella regia.—Nutting, 1915: 95, pl. 26, figs. 2–5. Fraser, 1937: 56, pl. 12, figs. 47a–d.—Naumov, 1960: 292, figs. 15A,

184A, B.—Antsulevich, 1987: 62; 2009: 23; 2015: 678, figs. 331A, B.—Kussakin & Kostina, 1996: 220.—Govindarajan *et al*. 2006: 823.—Peña Cantero *et al*., 2010: 43.—Stepanjants, 2013b: 43.—Cunha *et al*., 2020: 9, fig. 2A.

Type locality. USA: Alaska, Prince William Sound, Orca Bay (Nutting 1901).

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, on pedicel of *Bonneviella superba* Nutting, 1915, one small hydroid, 4 mm high overall, without gonothecae, ROMIZ B5355.

Description. Hydroid stolonal, comprising a single, short, unbranched pedicel and its longer hydrotheca, arising from a stolon creeping over a pedicel of *Bonneviella superba* Nutting, 1915. Pedicel 0.9 mm high, 0.20–0.23 mm in diameter, lacking segments or annulations anywhere, smooth except for one slight constriction just above insertion with stolon and another just below hydrotheca, without a subhydrothecal spherule, diameter at juncture with hydrotheca 0.23 mm; perisarc of moderate thickness. Hydrotheca large, 2.50 mm from base to original margin, elongate-urceolate in shape, with bulbous base reaching 0.75 mm in diameter at widest point, narrowing gradually towards distal end, expanding again just below orifice; rim strongly flaring, entire, slightly sinuous, renovated twice, diameter at original margin opening 0.95 mm; perisarc moderately thick, with greatest thickening at base; diaphragm absent. Hydranth too deteriorated to describe.

Gonothecae absent.

Remarks. *Bonneviella regia* (Nutting, 1901) was originally described, as *Campanularia regia*, from a single, small, sterile colony collected in Prince William Sound, Alaska. That colony, the holotype by monotypy, is at the NMNH (USNM 71390; currently listed in the online database as a syntype). Other lots of the species at the NMNH (USNM 68848, USNM 70719, USNM 1106181), from different locations in the eastern North Pacific, comprise non-type material. Gonothecae of the species were first described by Fraser (1914a) in material from the San Juan Islands, Washington. The hydroid was reported by him to be plentiful in some collections from Friday Harbor, on San Juan Island.

Nutting (1901) recognized the similarity of *B. regia* to *B. grandis* (Allman, 1876), a species originally collected from an unstated location in Japan, but he considered it distinct based on the character of its pedicels, which lacked node-like enlargements below the hydrothecae. While their trophosomes are similar in shape, and distinguishing them can be difficult, the two species clearly differ in the shape of their gonothecae, which are cylindrical with annular ribs in *B. regia* and flask-shaped with longitudinal ridges in *B. grandis*.

Bonneviella regia is distinguished from other described species of the genus by a combination of morphological characters. Of note, its urceolate hydrothecae are deep and narrowest above the mid-region, with a length of less than 4 mm and a length to width ratio of approximately 2:1; the hydrothecal margin is distinctly flared; pedicels are unbranched and unsegmented, or mostly so, and arise from a creeping hydrorhiza rather than a polysiphonic stem; gonothecae occur in clusters and are tall and slender, with walls having about 7–8 annular ribs (Nutting 1915; Fraser 1937; Naumov 1960; Antsulevich 2015).

The material examined here comprised a single hydrotheca of less than 3 mm length, and a small, smooth pedicel arising from a rudimentary stolon. The specimen appeared to be only modestly developed, although the hydrothecal margin bore a couple of renovations. The only distinct nodes on the pedicel occurred at the base and again just above its insertion with the hydrotheca. In the absence of gonothecae, the hydroid was assigned to *B. regia* after comparing descriptions of species of *Bonneviella* Broch, 1909 in works by Nutting (1915), Fraser (1937), Naumov (1960), and Antsulevich (2015). In a group having generally similar trophosomes, its hydrothecae differed in being considerably smaller (< 3 mm high) than those of *B. grandis* (> 4 mm high), *B. superba* Nutting, 1915 (up to 17 mm long), and *B. uschakovi* Naumov, 1951 (10–11 mm high). Moreover, in being somewhat elongate-urceolate in shape, the hydrotheca examined here differed from the nearly cylindrical ones of *B. enterovillosa* Naumov, 1951, *B. laevigata* Naumov, 1960, and *B. extensa* Naumov, 1960.

Bonneviella regia is a boreal, amphi-Pacific species. Known distribution records, and the comments of Fraser (1914a; 1937) suggest that it may be relatively common in parts of its range. The species has been reported previously at depths from 23–303 m (Antsulevich 1987, 2015). Its lower limit has been extended here to 1283 m.

Reported distribution. *North Pacific.* Widely distributed across the northern North Pacific, from the San Juan Islands, Washington, to Haida Gwaii, the Aleutians, the Bering Sea, the Sea of Okhotsk, and the Sea of Japan (Nutting 1901, 1915; Fraser 1914a, 1937; Yamada 1959; Naumov 1960; Antsulevich 1987, 2015; Kussakin & Kostina, 1996; Govindarajan *et al*. 2006; Stepanjants 2013b; Cunha *et al*. 2020).

Elsewhere. Known only from the northern North Pacific.

Bonneviella superba Nutting, 1915

Figs. 11h, 15h

Bonneviella superba Nutting, 1915: 96, pl. 27, figs. 1–3.
? Not *Bonneviella superba*.—Cunha *et al*., 2020: 3, fig. 2B.

Type locality. USA: Alaska, Aleutian Islands, 52°06'N, 171°45'W, 283 fm (518 m) (Nutting 1915).

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, on skeleton of *Primnoa* sp., one fragmentary colony, 1.5 cm high, without gonothecae, ROMIZ B5356.

Observed on video. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, on skeleton of *Primnoa* sp., part of colony collected and listed above under "Material examined" (Fig. 15h).

Description. Hydroid colony arising from a hydrorhiza creeping over skeleton of the octocoral *Primnoa* sp., comprising erect, unbranched pedicels with terminal hydrothecae. Pedicels long, more or less straight, not annulated at insertion with hydrorhiza, either entirely smooth throughout or with 1–2 constrictions, widest just below hydrotheca, without a subhydrothecal spherule, 6.9–9.0 mm long, 0.32–0.47 mm in diameter, perisarc of moderate thickness. Hydrothecae immense, 4.6–6.2 mm in length from base to margin, deep goblet-shaped with a bulbous base, narrowing gradually in diameter towards mid-region, then progressively expanding in diameter to distal end, widest immediately below margin; rim entire, strongly flaring, with two low, rounded elevations and two shallow depressions, occasionally renovated, 1.7–2.3 mm in diameter; perisarc relatively thin except for a thickened annular ring at hydrothecal base; diaphragm absent. Hydranths large, with an expanded basal region attached to bottom of hydrotheca, a vase-shaped gastric region, and a broad, distally flattened pre-oral chamber; tentacles filiform, in a single whorl, about 20 in number, arising from gastric region.

Gonothecae absent.

Remarks. The hydroid of *Bonneviella superba* Nutting, 1915 is exceptional given the enormous size (originally reported to be up to 1.7 cm high) and striking shape of its hydrothecae. It is known previously only from the type locality, and from the original description. Although it was reported again from the Aleutian Islands by Cunha *et al.* (2020), their illustration (Fig. 2B) of it is not representative of the species. The hydrotheca in their photograph is of a much different shape than that of *B. superba*, and its hydrothecal pedicel appears to be regularly segmented. By contrast, pedicels in Nutting's (1915) type were described as strong, stiff, and "perfectly smooth" except for a constriction at each end. Naumov (1960) and Antsulevich (2015) included *B. superba* in their monographs on hydroids of Russian seas, but their records were based on the original account of Nutting (1915). Yamada (1969), too, mentioned the species in a paper on Japanese species of *Bonneviella* Broch, 1909, but only in reference to the original description. The present report of the species from Jingū Seamount thus appears to be the first since Nutting's original account. The material examined was in good condition, although no gonothecae were observed. From its distribution, *B. superba* is taken here to be a boreal species endemic to the northern North Pacific Ocean.

Bonneviella superba is distinguished from its congeners by a combination of characters in addition to hydrothecal size. Its hydrothecae are deep goblet-shaped, narrowest in the mid-region, and occasionally curved, with a length to width ratio approaching 3:1; hydrothecal margins have two slight elevations and two slight depressions; pedicels are unbranched and unsegmented or mostly so, and arise from a creeping hydrorhiza rather than a polysiphonic stem; gonothecae are clustered, tall and slender, with walls having about 6–8 rounded corrugations. Hydrothecae of the species most closely resemble those of *B. regia* (Nutting, 1901) in shape, but they are much larger (up to 17 mm vs. 3.5 mm long). Unlike in *B. regia*, its hydrothecal margin has two rounded elevations and two rounded depressions.

In describing *B. superba*, Nutting (1915) noted that "The type and only known specimen is from station 3480…". That colony (USNM 34528: R/V *Albatross* Sta. 3480, USA, Alaska, Andreanof Islands, Amukta Pass, SE of Seguam Island, 52°06'N, 171°45'W, 518 m, 08 July 1893, listed as a "syntype") is therefore the holotype by monotypy. Antsulevich (2015) included *B. enterovillosa* Naumov, 1951 as a questionable synonym *B. superba*, but the two species are recognized as distinct here.

Stechow (1921) established a new genus, *Caulitheca*, for *B. superba*, a species lacking a diaphragm. Also included by him in the same new genus was *B. grandis* (Allman, 1876). However, the generic name *Caulitheca* has not been adopted. In the same work, Stechow lowered Bonneviellidae Broch, 1909 in rank to a subfamily within the Lafoeidae A. Agassiz, 1865. Bonneviellidae continues to be recognized in some current classifications of hydroids as a distinct family, although evidence from molecular studies suggests that it falls within Campanulariidae Johnston, 1837, as noted above in remarks on *B. gracilis* (Allman, 1876).

Reported distribution. *North Pacific.* Aleutian Islands, Alaska, 518 m (Nutting 1915).—Jingū Seamount, 1283 m (this report).

Elsewhere. Known only from the northern North Pacific.

***Bonneviella* sp.**

Fig. 11i

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, unattached, one hydrotheca and fragmentary pedicel, <2 mm high, without gonothecae, ROMIZ B5357.

Description. Hydroid fragmentary, comprising a detached pedicel and its hydrotheca. Pedicel unbranched, almost as long as hydrotheca even though broken off at proximal end, 0.78 mm in length, 0.08–0.10 mm in diameter, divided throughout into oblong segments of various sizes by transverse constrictions, and with a distinct subhydrothecal spherule at distal end; perisarc of moderate thickness. Hydrotheca symmetrical, deeply campanulate, small for the genus, 0.80 mm from base to margin, hydrothecal walls constricted at base, convex over remaining basal half, concave below orifice; rim slightly flaring, entire, diameter at margin 0.64 mm; perisarc thin except for a distinct annular thickening at hydrothecal base; diaphragm absent. Hydranth essentially intact, large, filling much of hydrothecal cavity, with broad base attached to thickened basal wall of hydrotheca; tentacles filiform, in a single whorl, about 24 in number, inserting into gastric region of hydranth.

Gonothecae absent.

Remarks. The identity of this species could not be positively determined. The single hydrotheca in the collection was larger than those of *Bonneviella gracilis* Fraser, 1939, examined here, but it was otherwise similar in shape. Moreover, a subhydrothecal spherule was present at the base of the hydrotheca, as in that species, and the two were found together in a collection from Jingū Seamount. However, unlike in *B. gracilis*, the hydrothecal pedicel was repeatedly divided into oblong segments of varied lengths rather than being almost entirely smooth. Meanwhile, the funnel-shaped hydrothecae of the two morphotypes set them apart from other described species of the genus, with their deep and essentially cylindrical to urceolate hydrothecae. The specimen is likely a morphological variant of *B. gracilis*, but given its repeatedly segmented pedicel, it has been identified here simply as *Bonneviella* sp.

Family Clytiidae Cockerell, 1911

Genus *Clytia* Lamouroux, 1812

***Clytia* sp.**

Material examined. Annei Seamount, Sta. ANN217-1, 36°38'35.0256"N, 171°36'22.4484"E, 17 August 2019, 1236 m, 2.9°C, 34.4 psu, on hexactinellid sponge, two fragmentary stems, to 1.2 cm high, without gonothecae, ROMIZ B5358.

Remarks. No described species of *Clytia* Lamouroux, 1812 could be located that matched the morphology of this species, with its exceptionally deep hydrothecae. Specimens were damaged, no gonothecae were observed, and characters of the hydrothecal rim were difficult to discern, although rounded and quite deeply incised cusps appear to be present. No illustration of the species was attempted given the poor condition of examined material.

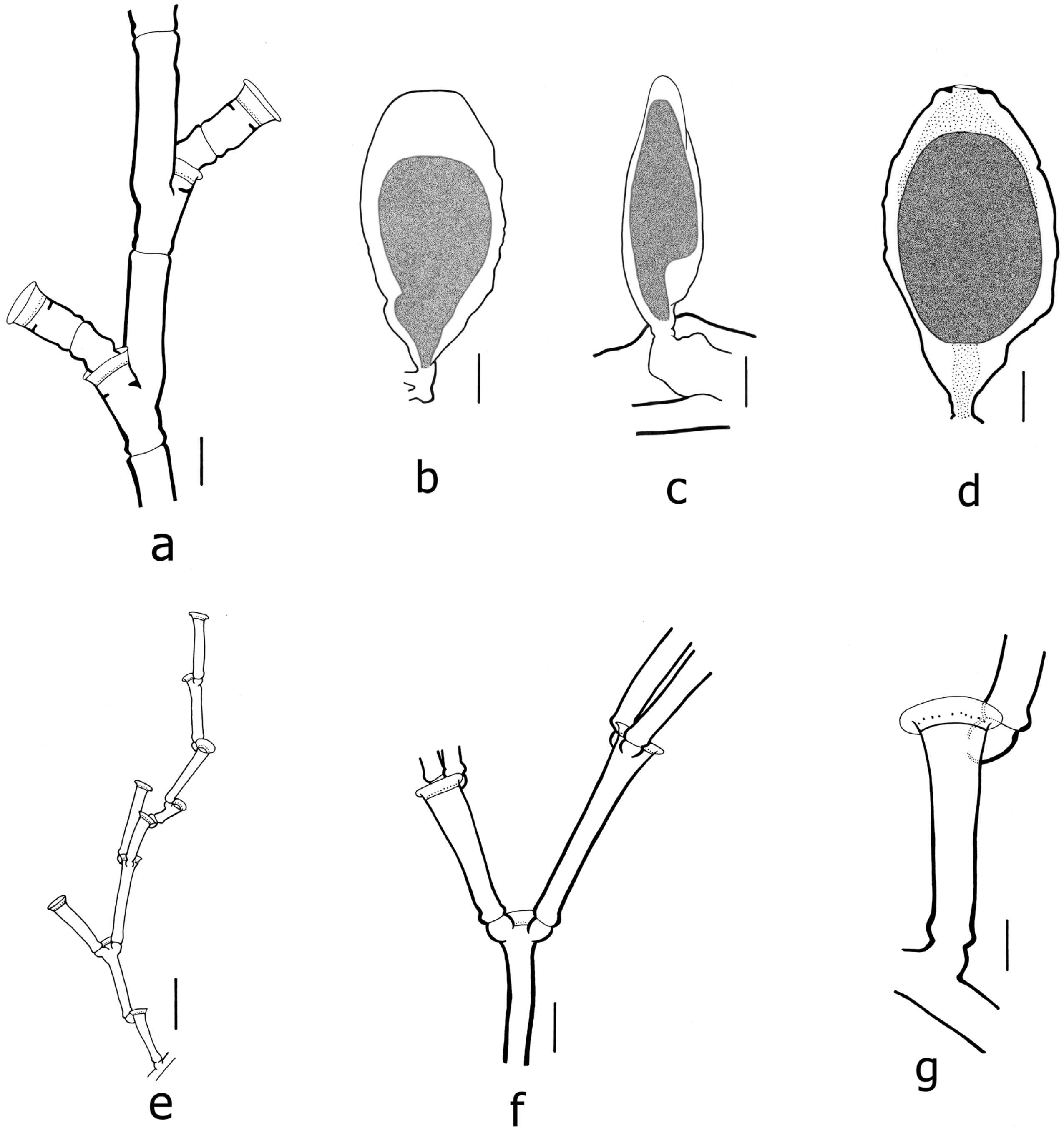

FIGURE 13. Leptothecata: Haleciidae. a, ***Halecium reversum,*** part of a branch, with hydrothecae, Jingū Seamount, Sta. JIN114-2, ROMIZ B5359. Scale equals 0.2 mm. **b,** ***Halecium reversum,*** juvenile male gonotheca, frontal view**,** Jingū Seamount, Sta. JIN114-2, ROMIZ B5359. Scale equals 0.2 mm. **c,** ***Halecium reversum,*** juvenile male gonotheca, side view, arising from a polysiphonic branch**,** Jingū Seamount, Sta. JIN114-2, ROMIZ B5359. Scale equals 0.2 mm. **d,** ***Halecium reversum***, mature male gonotheca, frontal view, Jingū Seamount, Sta. JIN114-2, ROMIZ B5359. Scale equals 0.2 mm. **e,** ***Halecium*** sp., part of a colony, Yomei Seamount, YOM103-1A, ROMIZ B5360. Scale equals 0.5 mm. **f,** ***Halecium*** sp., part of a colony, showing dichotomous branching, Yomei Seamount, YOM103-1A, ROMIZ B5360. Scale equals 0.2 mm. **g,** ***Halecium*** sp., part of a colony, with a hydrotheca, Yomei Seamount, YOM103-1A, ROMIZ B5360. Scale equals 0.1 mm.

Family Haleciidae Hincks, 1869

Genus *Halecium* Oken, 1815

Halecium reversum Nutting, 1901
Figs. 13a–d, 15h

Halecium reversum Nutting, 1901: 180, pl. 23, figs. 1, 2.—Linko, 1911: 68, figs. 13a–c.—Fraser, 1914a: 168, pl. 21, figs. 77A–C; 1937: 108, pl. 22, figs. 119a–c.—Feniuk, 1947: 3.—Naumov, 1960: 451, figs. 341A, B.
Halecium parvulum.—Linko, 1911: 42, figs. 9a–c [not *Halecium parvulum* Bale, 1888].

Type locality. USA: Alaska, Juneau, 20 fm (37 m) (Nutting 1901).

Material examined. Jingū Seamount, Sta. JIN114-2, 38°50'46.0692"N, 171°13'39.144"E, 13 August 2019, 1283 m, 2.8°C, 34.4 psu, three detached colonies or colony fragments, to 2.7 cm high, with male gonophores and gonothecae, ROMIZ B5359.

Observed on video. Jingū Seamount, ROV *SuBastian* Dive 287, Sta. JIN114-2, 38°50.76782'N, 171°13.6524'E, 1285 m, 2.8°C, 34.4 psu, on skeleton of *Primnoa* sp., 13 August 2019; specimens collected and listed above under "Material examined" (ROMIZ B5359) (Fig. 15h).

Description. Colonies erect, up to 2.7 cm high, arising from a mat of stolons. Hydrocaulus strongly polysiphonic, up to 0.8 mm in diameter at base, straight to slightly geniculate, with distal end monosiphonic, main tube divided into internodes, irregularly to somewhat regularly branched, branches mostly in one plane, with one or more branches nearly as large as main hydrocaulus; segmentation of internodes unusual, with nodes located just below hydrothecae, each hydrotheca thus located at proximal rather than distal end of an internode; perisarc of moderate thickness, minimal at distal ends of colony. Larger branches polysiphonic basally, unbranched or branched as in hydrocaulus; small branches monosiphonic, unbranched, straight to slightly geniculate, with internode segmentation as in hydrocaulus. Internodes moderately long and slender, 0.74–0.95 mm long, 0.14–0.18 mm wide, 0.13–0.175 mm wide at nodes, with slight bulges at proximal and distal ends, otherwise smooth; proximal end of each internode with a primary hydrotheca and, at that location, bent outwards and upwards, remainder of internode straight to slightly curved, directed upwards; branches, when present, mostly given off from the original location of a hydrotheca, much less often arising just beneath a hydrotheca that becomes axillary in position. Primary hydrothecae sessile, alternate, frequently regenerated; supplementary hydrothecae borne on hydrophores of varied length; hydrothecae of moderate depth, with a distinct diaphragm basally beneath a ring of desmocytes; pseudodiaphragm present; hydrothecae 0.05–0.10 mm deep from margin to diaphragm, widening from base to margin and with margin everted; diameter at diaphragm 0.14–0.18 mm, diameter at margin 0.19–0.23 mm. Hydranths relatively large, with a bulbous base, a dome-shaped hypostome, and a single whorl of about 20–22 tentacles; intertentacular web absent.

Gonophores fixed sporosacs. Gonothecae with only males observed, obovate, decidedly compressed, with sharp-edged sides, walls not ridged, ringed, or annulated, without spines, with a terminal opening when mature, flattened side two times wider than edge, length 1.18 mm, maximum width of flattened side 0.66 mm, maximum thickness in side view 0.33 mm, diameter at margin 0.20–0.22 mm, arising on short pedicels, less than 0.1 mm long, from accessory tubes on polysiphonic parts of hydrocaulus and larger branches, without any protruding hydranths; terminal aperture when present notch-shaped; perisarc thickened below aperture, thin elsewhere; gonangium enclosed within a thin capsule inside gonotheca.

Remarks. Nutting (1901) described *Halecium reversum* from a single colony collected off Juneau, Alaska, by the Harriman Alaska Expedition of 1899. A hydroid collected from the type locality, by the same expedition during the same year, exists in the Fraser Hydroid Collection at the Royal British Columbia Museum (RBCM976-00495-001; now dry). That specimen may be the holotype by monotypy. Material of the species at the National Museum of Natural History, Smithsonian Institution (USNM 100327), collected during the Harriman Alaska Expedition in nearby Berg Inlet, Glacier Bay, Alaska, appears not to be a type. A published report of the species from that location, taken at a depth of 50 fathoms (91 m), appeared later in Fraser (1937). No types or potential types of the species are listed in the online collection databases of the Museum of Comparative Zoology, Harvard University, or the American Museum of Natural History.

The original description of *H. reversum* by Nutting (1901) was brief and lacking in detail. However, specimens from Jingū Seamount agree with that account in essentially all characters including colony height, the presence of a polysiphonic stem, alternate (or mostly alternate) branching, everted hydrothecal margins, a distinct ring of desmocytes, hydranths with about 20 tentacles, and especially in the type of segmentation of the internodes. We have therefore assigned our specimens to Nutting's species. If not identical with *H. reversum*, they appear closely related to it.

Nutting (1901) considered the kind of internode segmentation in *H. reversum* to be unusual, with hydrothecae being located at the proximal rather than the distal end of segments composing stems and branches. As implied by the specific name, the nodes were thus reversed in location relative to most other species of the genus *Halecium* Oken, 1815. Others now known to have similar or somewhat similar internode segmentation include *Halecium minutum* Broch, 1903, *H. textum* Kramp, 1911, and *H. birulai* Spassky, 1929.

After its original description, *H. reversum* was reported again from north of Gabriola Island, British Columbia, by Fraser (1914a). His abbreviated account of its trophosome, and another later (Fraser 1937), provided little more to distinguish the species beyond the original description by Nutting (1901). Neither Nutting nor Fraser observed gonosomes of their specimens. Gonothecae of *H. reversum* appear to have been first described by Linko (1911) in a hydroid, from the Sea of Okhotsk, that he identified as *Halecium parvulum* Bale, 1888. Gonothecae of colonies examined here lacked the two distal spines described in Russian material by Linko (1911), Naumov (1960) and Antsulevich (2015), but our colonies were male and nearly all appear to be juveniles while theirs may have been female. If so, female gonothecal morphology in the species differs considerably from those of *H. halecinum* (Linnaeus, 1758), type species of the genus, in being compressed and elongate-oval in side view rather than mitten-shaped with a lateral aperture. The possible taxonomic significance of this, at the rank of genus, is as yet undetermined.

Antsulevich (2015) considered *H. reversum* to be a rare amphi-Pacific boreal species. It has been reported from Alaska and British Columbia in the eastern North Pacific (Nutting 1901; Fraser 1911, 1914a, 1937), and from the Sea of Okhotsk and the Bering Sea in the west (Linko 1911; Naumov 1960; Antsulevich 2015). Reports of the species from Russian waters were questioned by Ronowicz & Schuchert (2007), who suspected that they were based on hydroids of *H. labrosum* Alder, 1859. The trophosomes and gonosomes of *H. reversum* and *H. labrosum* are similar morphologically. However, the unusual internode segmentation considered distinctive of the species by Nutting, and dissimilar to that of *H. labrosum*, was constant in specimens examined here. The character is therefore taken to be taxonomically significant. An erroneous report of *H. reversum* from Japan by Fraser (1947) appears to have been based on the record of Linko (1911), in Stechow (1923a), from nearby Sakhalin, Sea of Okhotsk, Russia. The only report of the species from Japan and vicinity by Yamada (1959) is based on that same account.

Halecium reversum has previously been reported at depths from only 20–164 m (Naumov 1960). The record from Jingū Seamount extends its bathymetric range downwards for a considerable distance, to 1283 m, and colonies from the site were fertile and in good condition. This is perhaps not surprising, because bathymetric distributions of certain boreal and subarctic hydroid species from neritic waters of the North Atlantic are known to be quite extensive, reaching well into the bathyal zone (Calder 1997).

Specimens examined here (ROMIZ B5359) were recorded in the accompanying collection data as the "yellow hydroid". Yellowish hydroids in the upper left-center of Fig. 15h, from a video by ROV *SuBastian* at the same station (Sta. JIN114-2), are believed to be *H. reversum*.

Reported distribution. *North Pacific.* Alaska: Juneau (Nutting, 1901).—Russia: Sea of Okhotsk and Bering Sea (Linko 1911, in part as *Halecium parvulum* Bale, 1888).—British Columbia: north of Gabriola Island (Fraser 1914a).—British Columbia: Hope Island, off Cape James (Fraser 1937).—Alaska: Glacier Bay, Berg Inlet (Fraser 1937).—Russia: Sea of Okhotsk (Feniuk 1947).—Russia: Sea of Okhotsk and Bering Sea (Naumov 1960).

Elsewhere. Antsulevich (2015) considered records in Russian literature of *Halecium reversum* from the Laptev and East Siberian seas, as well as from the central part of the Polar Basin, to be doubtful.

***Halecium* sp.**

Figs. 13e–g

Material examined. Yomei Seamount, Sta. YOM103-1A, 42°25'54.8694"N, 170°26'06.5424"E, 09 August 2019, 1472 m, 2.4°C, 34.5 psu, one colony, 5 mm high, on *Lafoea fruticosa* (M. Sars, 1850), without gonothecae ROMIZ B5360.

Description. Colony fragments with erect hydrocauli reaching 5 mm high, arising from a stolonal hydrorhiza creeping over a colony of *Lafoea fruticosa* (M. Sars, 1850). Hydrocaulus monosiphonic, irregularly and sometimes dichotomously branched; perisarc relatively thick proximally, thinning out distally. Internodes 0.22–1.10 mm long from proximal end to base of hydrotheca, 0.07–0.14 mm wide at nodes, with a single bulge basally, smooth elsewhere, increasing gradually in diameter from proximal to distal end; diameter proximally 0.08–0.11 mm, diameter distally 0.13–0.15 mm; extreme distal end of each internode with a primary hydrotheca and an upwards-directed apophysis supporting internode above. Primary hydrothecae sessile, occasionally regenerated; supplementary hydrothecae pedicellate, with pedicels typically short. All hydrothecae shallow, with a distinct diaphragm basally just beneath a ring of desmocytes; depth from margin to diaphragm 0.03–0.05 mm; walls flaring; margin strongly everted; diameter at diaphragm 0.13–0.17 mm, diameter at margin 0.18–0.23 mm. Hydranths small, vase-shaped, with a disc-shaped proximal end anchored to base of hydrotheca and a whorl of tentacles at distal end; tentacles filiform, about 20 in number; hypostome dome-shaped; intertentacular web absent.

Gonophores not seen.

Remarks. The general colony form of this small hydroid somewhat resembles that of *H. curvicaule* Lorenz, 1886 (type locality: Jan Mayen), a species that has also been reported from the western North Pacific (Antsulevich 1987; Sheiko & Stepanjants 1997). However, its hydrothecal margins are much more flaring and sometimes recurved, as in *H. tenellum* Hincks, 1861 (type locality: Salcombe Bay, England) and the poorly known *H. ornatum* Nutting, 1901 (type locality: Glacier Bay, Alaska, USA). The species could not be confidently assigned to these or any other hydroids of the same genus having a generally similar colony form, including *H. dichotomum* Allman, 1888 (type locality: Cape of Good Hope, South Africa), *H. interpolatum* Ritchie, 1907 (type locality: Scotia Bay, South Orkney Islands), *H. pygmaeum* Fraser, 1911 (type locality: San Juan Islands, Washington, USA), *H. expansum* Trebilcock, 1928 (type locality: Dunedin, New Zealand), *H. scalariformis* Billard, 1929 (type locality: Indonesia), *H. cymosum* Fraser, 1935b (type locality: Sagami Bay, Japan), *H. vagans* Fraser, 1938a (type locality: La Plata Island, Ecuador), *Halecium fragile* Hodgson, 1950 (type locality: D'Entrecasteaux Channel, Australia), *H. linkoi* Antsulevich, 1980 (type locality: Kuril Islands, Russia), *H. tabulatum* Watson, 2005 (type locality: New Island, Western Australia), *H. interpolatum* Ritchie, 1907 (type locality: South Orkney Islands,) and *Halecium profundum* Calder & Vervoort 1998 (type locality: Mid-Atlantic Ridge, at 15°N). Identification of this hydroid colony was also hindered by its lack of gonosomes. It is nevertheless an unmistakable haleciid, identified here simply as *Halecium* sp.

FIGURE 14. Trachymedusae: Ptychogastriidae, *Ptychogastria polaris*. a, medusa on rock, Jingū Seamount, 1530 m**. b,** medusa on rock, Annei Seamount, 1457 m**. c,** medusa on rock, Annei Seamount, 1882 m**.**

Subclass Trachylinae Haeckel, 1879

Order Trachymedusae Haeckel, 1866

Family Ptychogastriidae Mayer, 1910

Genus *Ptychogastria* Allman, 1878

Ptychogastria polaris Allman, 1878
Figs. 14a–c

Ptychogastria polaris Allman, 1878: 290, figs. 1–3.—Bigelow, 1913 41.—Mackie, 1985: 760, fig. 14/20.—Stepanjants, 1989: 400, 402, 408, 416.—Larson *et al*., 1992: 282, fig. 2c.—Panteleeva *et al*., 1999: 373, figs. 1–10.—Miyake *et al*. 2004: 36, 40, fig. 10 (3 photographs).—Gasbarro *et al*. 2018: 51.

Type locality. Canada: Discovery Bay [an inlet of Lady Franklin Bay, Ellesmere Island, Nunavut], at 81°44'N (Allman 1878: 290, 292).

Observed on video. Nintoku Seamount, ROV *SuBastian* Dive 285, ca. 40°45'N, 171°E, 11 August 2020, one medusa each at 2423 m (near bottom, swimming; 1.7°C), 2421 m (near bottom, drifting; 1.7°C), 2418 m (near bottom, drifting; 1.7°C), 2324 m (near bottom, drifting; 1.8°C), 2310 m (near bottom, drifting; 1.8°C), and 2245 m (on rock; 1.8°C); all with gonads.—Jingū Seamount, ROV *SuBastian* Dive 287, ca. 38°51.2'N, 171°13'E, 13 August 2019, 1530 m, one medusa (on side of rock; 2.4°C), with gonads.—Annei Seamount, ROV *SuBastian* Dive 288, ca. 36.7°N, 171.6°E, 14 August 2019, one medusa each at 2021 m (on rock; 2.0°C), 1963 m (on rock; 2.0°C), and 1882 m (on rock; 2.1°C), all with gonads.—Annei Seamount, ROV *SuBastian* Dive 289, ca. 36.7°N, 171.6°E, one medusa each at 1457 m (on rock; 2.4°C) and 1422 m (on rock at first, then observed swimming upwards; 2.6°C), both with gonads.—Koko Seamount, ROV *SuBastian* Dive 290, ca. 35.5°N, 172°E, 17 August 2019, 2.0°–2.5°C, one medusa at 2033 m (near bottom, swimming; 2.0°C).

Remarks. While no specimens of *Ptychogastria polaris* (Allman, 1878) were collected during this study, medusae of the species were frequently seen on or near the sea floor in videos by ROV *SuBastian*. This unusual species, considered a "benthic medusa" (Larson *et al*. 1992), can swim but spends part of its existence directly on bottom. The species was observed either sedentary on rocks, or drifting or swimming near bottom at depths between 2423 m–2245 m on Nintoku Seamount, at 1530 m on Jingū Seamount, at 2021–1422 m on Annei Seamount, and at 2033 m on Koko Seamount. The reported bathymetric range of the species extends from 10 m to 2500 m (Galea *et al*. 2016). Always known as an inhabitant of cold waters, this medusa occurs in both the northern North Pacific and northern North Atlantic, and is known to be circumpolar in the Arctic Ocean. *Ptychogastria polaris* has also been regarded as a bipolar species (e.g., Stepanjants *et al*. 2006). In recent work, Grange *et al*. (2017) compared medusae from Japan and from the West Antarctic Peninsula, and provisionally concluded that they were conspecific.

A thorough account of *Ptychogastria polaris* has been given by Galea *et al*. (2016), together with a revision of the family Ptychogastriidae Mayer, 1910 and an overview of its currently included genera (*Ptychogastria* Allman, 1878, *Tesserogastria* Beyer, 1958, and *Glaciambulata* Galea, 2016). Their work included a detailed synonymy list and a comprehensive new description of the species, along with accounts of its taxonomy, morphology, ecology, and distribution. Exceptional photographs of the species, from Shiribeshi Seamount west of Hokkaido, Japan, appear in Miyake *et al*. (2004).

The type locality of *P. polaris* has been incorrectly cited in some works as "Greenland" or "East Greenland". The holotype (by monotypy) was collected in Discovery Bay, near the northeast tip of Ellesmere Island, Canada, at latitude 81°44'N (Allman 1878). It was found there by expedition naturalist Henry Wemyss Feilden (1838–1921) during the British Arctic Expedition of 1875–1876 with HMS *Alert* and HMS *Discovery*.

Ptychogastria polaris has been reported previously from cold waters of the northern North Pacific (e.g., Bigelow 1913; Mackie 1985; Stepanjants 1989; Larson *et al*. 1992; Panteleeva *et al*. 1999; Miyake *et al*. 2004; Gasbarro *et al*. 2018).

Reported distribution. *North Pacific*. Bering Sea (Bigelow 1913).—Jervis Inlet and Strait of Georgia, British Columbia, Canada (Mackie 1985).—Cobb and Brown Bear seamounts (Mackie 1985).—Bering Sea, Russia (Stepanjants 1989).—Monterey Canyon, California, USA (Larson *et al*. 1992).—Kuril Islands, Russia (Panteleeva *et al*. 1999).—Shiribeshi Seamount, west of Hokkaido, Japan (Miyake *et al*. 2004).—Douglas Channel fjord, British Columbia, Canada (Gasbarro *et al*. 2018).

Elsewhere. Arctic and northern North Atlantic oceans: Discovery Bay, Ellesmere Island, Canada (Allman 1878; Broch 1907).—Prøven, west Greenland, and off Halifax, Nova Scotia, Canada (Haeckel 1879, as *Pectyllis arctica*; 1882, as *Pectyllis arctica*).—Between Greenland and Iceland (Maas 1893, as *Pectyllis arctica*).—Ritenbenk, west Greenland (Levinsen 1893, as *Pectyllis arctica*; Aurivillius 1895, as *Pectyllis arctica*).—Spitzbergen (Grönberg 1898, as *Pectyllis arctica*).—West and east Greenland (Aurivillius 1899, as *Pectyllis arctica*).—Northern part of the Barents Sea (Linko 1904).—König Karls-Land, Svalbard (Maas 1906).—"Winterhafen 1900" (Ellesmere Island, Nunavut, Canada) (Broch 1907).—Labrador, Canada (Bigelow 1909).—West and east Greenland (Kramp 1914).—Jones Sound, between Ellesmere and Devon islands, Canada (Kramp 1942).—West coast of Greenland and Baffin Island, Canada (Kramp 1942; Dunbar 1942).—East Greenland (Kramp 1943).—West and east Greenland, south of Jan Mayen, north and southeast of Iceland, Kara Sea, Russia, and Norway (Kramp 1947).—Bays Fjord, Ellesmere Island, Canada (Vibe 1950).—Herdla, Norway (Rees 1953).—Prøven, west Greenland; re-examination of Haeckel's specimens (Kramp 1955).—Barents, Kara, and Laptev seas, Russia (Naumov 1960).—Spitzbergen; Norway; west and east Greenland; several records from the northeastern North Atlantic and Arctic in papers unavailable for this study

(Kramp 1961).—Barents Sea (Zelickman 1972).—Barents, Kara, and Laptev seas, Russia, considered circumpolar (Stepanjants 1989).—Laptev Sea, Russia (Sirenko *et al*. 1996).—Svalbard (Piepenburg *et al*. 1996).—Northeast Greenland (Starmans 1997).—Greenland, northern Barents Sea, including Svalbard (Stübing & Piepenburg 1998).—Svalbard (Palerud *et al*. 2004).—Barents Sea (Dvoretsky & Dvoretsky 2010, 2018).—Amundsen and Canada basins, Central Arctic Ocean (Kosobokova *et al*. 2011).—Greenland, Iceland, Jan Mayen Island, Norway south to Bergen, and north of Svalbard (Sswat *et al*. 2015).—Barents Sea and all other northern seas (Kara, Laptev, East Siberian, and Chukchi) of Russia (Antsulevich 2015).—Cambridge Bay, Nunavut, Canada (Heywood *et al*. 2018).—Kola region, Barents Sea, Russia (Prokopchuk & Trofimov 2019).—Newman Sound, Newfoundland, Canada (Proudfoot *et al*. 2020). Antarctic: Gauss Station (Vanhöffen 1912, as *Ptychogastria opposita*).—South Shetland Islands (Kramp 1957, 1961).—West Antarctic Peninsula (Grange & Smith 2013; Grange *et al*. 2017; Ziegler *et al*. 2017).

FIGURE 15. Some unidentified hydroids and a siphonophore in ROV *SuBastian* videos from six of the seven seamounts explored in the Emperor Seamounts chain. **a,** two tubulariids on an antipatharian, Suiko Seamount, 1360 m. **b,** hydroids growing on legs and carapace of a crab, Suiko Seamount, 1495 m. **c,** hydroids overgrowing rocks, Yomei Seamount, 1329 m. **d,** hydroids overgrowing a dead hexactinellid sponge, Yomei Seamount, 1544 m. **e,** Hydroid colony on rock surface, Godaigo Seamount, 2124 m. **f,** tubulariids on a rock, Nintoku Seamount, 2396 m. **g,** hydroids (including *Hydractinia galeai*, sp. nov., lower right) on a dead octocoral, Jingū Seamount, 1368 m. **h,** hydroids on a dead octocoral, Jingū Seamount, 1284 m. **i,** hydroid colony on a rock, Annei Seamount, 2055 m. **j,** hydroids fouling dead parts of a hexactinellid sponge, Annei Seamount, 1451 m. **k,** hydroids on and near a sponge, Annei Seamount, 2055 m. **l,** siphonophore near bottom, Nintoku Seamount, 2282 m.

Video surveys

With bathyal bottoms of the study area being predominantly rocky and free of heavy sedimentation, substrates appeared generally suitable for hydroid settlement, growth, diversity, and abundance. Hydrozoans were observed in videos from all of the seamounts explored during the study (Suiko, Yomei, Godaigo, Nintoku, Jingū, Annei, Koko, and an unnamed seamount on Hess Rise). However, most were considered unidentifiable from video images alone (Figs. 15a–l). On Yomei and especially on Jingū seamounts, hydroids were found to be an important and widespread component of the epibenthos. Colonies at these two were especially conspicuous on dead or dying octocorals and sponges, substrates providing elevation above the bottom (Figs. 15d, g, h). They were also observed on upper surfaces and edges of large, exposed rocks (Figs. 15c, e). At Jingū Seamount, the anthoathecate *Hydractinia galeai* comprised one of the dominant epifaunal species above 1400 m (Fig. 5c). By contrast, only occasional hydroids were seen on Suiko, Nintoku, Godaigo, Annei, and Koko seamounts, and on Hess Rise, most of them on rocks, stalks of dead sponges or octocorals, and living invertebrates (Figs. 15a, b, e, f, i, j, k).

In addition to hydroids, the trachymedusa *Ptychogastria polaris* Allman, 1878 was identified in videos by ROV *SuBastian* (Figs. 14a–c). Unidentifiable hydrozoan and scyphozoan medusae were frequent on Nintoku Seamount at depths between 2416–2050 m, but they were seldom seen above a depth of 2000 m. Also observed on Nintoku, just above bottom at 2282 m, was a species of siphonophore (Fig. 15l).

TABLE 1. Geographical distribution and depth of species collected or seen on seamounts in the Emperor Seamount Chain, and from Hess Rise. Province codes for other bathyal provinces (from Watling *et al.* 2013): BY1, Arctic; BY2, North Atlantic Boreal; BY3, North Pacific Boreal; BY4, North Atlantic; BY9, Antarctic; BY11, Indian; BY12, West Pacific; BY14, North Pacific.

Species	Emperor Seamount Location	Other Bathyal Provinces
	Jingū Seamount and North	
Candelabrum sp.	Yomei, 1472 m Nintoku, 1439 m	
Bouillonia sp.	Nintoku, 1326m; 1489 m; 1490 m	
Tubulariidae (undetermined)	Annei, 1236 m	
Hydractinia galeai, **sp. nov.**	Jingū, 1283 m; 1387 m; 1396 m	
?*Rhizorhagium* cf. *roseum*	Jingū, 1283 m	BY3, BY1, BY2, BY4
Eudendrium sp.	Nintoku, 1118 m	
Lafoea fruticosa	Yomei, 1492 m Jingū, 1285 m	BY3
Bonneviella cf. *gracilis*	Jingū, 1283 m	BY3, BY1
Bonneviella regia	Jingū, 1283 m	BY3
Bonneviella superba	Jingū, 1283 m	BY3
Bonneviella sp.	Jingū, 1283 m	
Halecium reversum	Jingū, 1283 m; 1285 m	BY3
Halecium sp.	Yomei, 1472 m	
Ptychogastria polaris	Jingū, 1530 m	
	Annei Seamount and South	
Latebrahydra schulzei, **gen. et sp. nov.**	Hess Rise, 1702 m Annei, 1236 m	
Stegolaria geniculata	Koko, 2030 m	BY14, BY11, BY12, BY4
Clytia sp.	Annei, 1236 m	
Ptychogastria polaris	Nintoku, 2245 m; 2310 m; 2324 m; 2418 m; 2421 m; 2423 m Annei,1882 m; 1963 m; 2021 m Koko, 2033 m	BY3, BY2, BY1, BY9

Biogeographical notes

The hydroid species documented here were collected as part of an expedition to discover a biogeographic boundary or transition area between two bathyal provinces in the North Pacific Ocean—the North Pacific Province (BY14) and the North Pacific Boreal Province (BY3), as proposed in Watling *et al*. (2013).

Distributions of species dealt with in this paper are given in Tables 1 and 2. Two distinct geographical groups of species were represented, with those found on Jingū, Nintoku, and Yomei seamounts constituting a "northern group" and those from Annei, Koko, and the unnamed seamount on Hess Rise a "southern group." Species in the northern group occurring elsewhere have been found in the more northern of the bathyal provinces of Watling *et al*. (2013), that is, the North Pacific Boreal (BY3), Arctic (BY1), North Atlantic Boreal (BY2), and North Atlantic (BY4) provinces. Only one species from the southern group has been reported elsewhere. *Stegolaria geniculata*, found in the deeper bathyal of Koko Seamount, is widely distributed across low and mid-latitudes of the Indian (BY11), West Pacific (BY12), and North Pacific (BY14) provinces, as well in the southern part of the North Atlantic Province (BY4). This pattern is also seen in some bathyal octocorals (e.g., Watling *et al*. 2011).

The only hydrozoan species represented in both northern and southern groups was the benthopelagic hydromedusa *Ptychogastria polaris* (Figs. 14a–c). Reports indicate that it is very widely distributed, with most records of it from the northern hemisphere (provinces BY3, BY2, BY1). However, the species has also been reported from the Antarctic Province (BY9). The conjectural disjunct distribution of this medusa may be due either to a lack of observations at suitable locations and depths or to the existence of cryptic species.

TABLE 2. Hydrozoans from seven seamounts in the Emperor Seamount Chain, and from Hess Rise, in the northwest Pacific Ocean. Under Biogeographic Province, BY3 = the North Pacific Boreal Bathyal Province and BY14 = the North Pacific Bathyal Province.

Seamount	Biogeographic Province	Species collected	Species seen from ROV
Yomei	BY3	*Lafoea fruticosa* *Halecium* sp.	*Candelabrum* sp. *Lafoea fruticosa* Other hydroids
Godaigo	BY3		Other hydroids
Nintoku	BY3	*Bouillonia* sp.	*Bouillonia* sp. *Candelabrum* sp. Tubulariids *Eudendrium* sp. *Ptychogastria polaris* Siphonophore
Jingū	BY3	*Rhizorhagium* cf. *roseum* *Hydractinia galeai* *Bonneviella* cf. *gracilis* *Bonneviella regia* *Bonneviella superba* *Bonneviella sp.* *Halecium reversum*	*Hydractinia galeai* *Bonneviella superba* *Halecium reversum* *Lafoea fruticosa* *Ptychogastria polaris*
Annei	BY14	Tubulariidae sp. *Clytia* sp.	Tubulariids *Latebrahydra schulzei* Other hydroids *Ptychogastria polaris*
Koko	BY14	*Stegolaria geniculata*	*Stegolaria geniculata* *Ptychogastria polaris*
Suiko	BY14		Tubulariids Other hydroids
Hess Rise	BY14	*Latebrahydra schulzei*	

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