Zootaxa 5131 (1): 001–115
https://www.mapress.com/zt/
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Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
https://doi.org/10.11646/zootaxa.5131.1.1
http://zoobank.org/urn:lsid:zoobank.org:pub:CF550031-D6A9-48A3-A953-A1BD40C72F5E

ZOOTAXA

5131

Taxonomy, ecology and zoogeography of the Recent species of *Rhamphostomella* Lorenz, 1886 and *Mixtoscutella* n. gen. (Bryozoa, Cheilostomata)

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Magnolia Press
Auckland, New Zealand

Accepted by E. Di Martino: 14 Mar. 2022; published: 2 May 2022

ANDREI V. GRISCHENKO, DENNIS P. GORDON, PAUL D. TAYLOR, PIOTR KUKLINSKI, NINA V. DENISENKO, MARY E. SPENCER-JONES & ANDREW N. OSTROVSKY
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(*Zootaxa* 5131)

115 pp.; 30 cm.

2 May 2022

ISBN 978-1-77688-506-0 (paperback)

ISBN 978-1-77688-507-7 (Online edition)

FIRST PUBLISHED IN 2022 BY

Magnolia Press

P.O. Box 41-383

Auckland 1041

New Zealand

e-mail: magnolia@mapress.com

https://www.mapress.com/zt

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ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of Contents

Abstract

Twenty-four Recent species of the boreal-Arctic and Pacific cheilostome bryozoan genus *Rhamphostomella* are described. The species *R. tatarica* and *R. pacifica* are transferred to *Rhamphostomella* from *Posterula* and *Porella*, respectively. Eight species are new: *R. aleutica* **n. sp.**, *R. aspera* **n. sp.**, *R. commandorica* **n. sp.**, *R. echinata* **n. sp.**, *R. microavicularia* **n. sp.**, *R. morozovi* **n. sp.**, *R. multirostrata* **n. sp.** and *R. obliqua* **n. sp.** Neotypes are selected for six species, and lectotypes for eight species. *Mixtoscutella* **n. gen.** is established for several *Rhamphostomella*-like species, including *M. androsovae* [formerly *Smittina androsovae* Gontar], *M. cancellata* [formerly *Escharella porifera* forma *cancellata* Smitt], *M. harmsworthi* [formerly *Schizoporella harmsworthi* Waters], *M. ovata* [formerly *Cellepora ovata* (Smitt)], and *M. ussowi* [formerly *Schizoporella ussowi* (Kluge)]. In addition to taxonomic revision, the morphology (frontal shields, ovicells and multiporous septula), ecology and zoogeography of these cheilostomes are discussed, and identification keys are presented. Most species of *Rhamphostomella* have broad bathymetric distributions. Some have long protuberances on their basal walls that allow them to grow elevated above allelopathically active substrates such as sponges. The diversity of *Rhamphostomella* peaks in the northwestern Pacific.

Key words: *Rhamphostomella*, *Mixtoscutella*, taxonomy, ecology, zoogeography

Introduction

Rhamphostomella Lorenz, 1886 is a distinctive genus in Cheilostomata, with a boreal-Arctic distribution and a rich fossil record (Römer 1863; Waters 1891; Canu 1904, 1908, 1916, 1919; Canu & Bassler 1919, 1920, 1923; Kataoka 1957; Hayami 1975; Sakagami *et al*. 1980; Pouyet 1997; Li 1990; Martha *et al.* 2021; Taylor 2021). The geologically oldest species are known from the Eocene, in Ypresian (Labracherie & Sigal 1976) and Priabonian sediments (Waters 1891; Lagaaij 1952; Ghiurca & Mongereau 1981). Including more than 30 nominal species (of which about 10 are extinct), *Rhamphostomella* is among the most diverse bryozoan genera in Recent seas of the Northern Hemisphere.

Lorenz (1886) originally established *Rhamphostomella* for six species of Arctic cheilostomes from Jan Mayen Island in the Greenland Sea. After accounting for convoluted synonymies, 16 Recent species are currently recognized from various areas of the Arctic and North Pacific (Smitt 1868a; Lorenz 1886; Hincks 1877, 1889; Nordgaard 1906; O'Donoghue & O'Donoghue 1923; Kluge 1929; Osburn 1952; Gontar 1993a).

Species of *Rhamphostomella* are distinguished by their predominantly encrusting, sometimes erect-bilamellar, colonies closely or loosely overgrowing the substratum. Zooids have an umbonuloid frontal shield, and a suboral avicularium is always present. Orificial characters (presence/absence of a lyrula, condyles and oral spines) vary within the genus. Large adventitious avicularia can be present. Ovicells are initially hyperstomial but often become less prominent when the ooecium is covered by secondary calcification; the ectooecium is pseudoporous. Basal surfaces of zooids are fully calcified, with tubular protuberances in some species. The ancestrula is tatiform and becomes rapidly overgrown by surrounding zooids.

Historically, and in recent years, the taxonomic position of *Rhamphostomella* has been uncertain, reflected by the assignment of the genus to seven different ascophoran families: Celleporidae, Escharidae, Mucronellidae, Smittinidae, Rhamphostomellidae, Porellidae and Umbonulidae. The earliest workers included the type and related species either in *Cellepora* and the Celleporidae (Smitt 1868a; Verrill & Smitt 1873; Whiteaves 1874; Lütken 1877), or in *Mucronella* (Verrill 1879) and the Escharidae (Hincks 1889). Bassler (1953) and Mawatari (1963) included the genus in the Mucronellidae. Subsequently, *Rhamphostomella* was removed to the lepralioid-shielded family Smittinidae, remaining there for a long time principally because of the presence of a lyrula in many putative species (Levinsen 1909 [as *Discopora*]; Canu & Bassler 1917, 1929; Osburn 1932, 1936, 1952; Lagaaij 1952; Androsova 1958; Hansen 1962; Powell 1967, 1968a; Gordon 1984; Dick & Ross 1988). Vigneaux (1949) included *Rhamphostomella* in his new smittinid subfamily Porellinae. Kluge (1962) established the family Rhamphostomellidae for *Rhamphostomella* and *Escharopsis* (together with *Ragionula* including three genera after taxonomic splitting; see Ryland [1969] for discussion of nomenclatural problems), without stating specifically why, although he did supply a thorough family diagnosis. He was followed in this by Kubanin (1975), Gostilovskaya (1978) and Mawatari & Mawatari (1981). Hayward (1975) and Hayward & Thorpe (1988) described *Rhamphostomella* as a Northern Hemisphere genus with a circumpolar distribution, all species of which have an umbonuloid frontal shield, thereby justifying the introduction of a new genus *Rhamphosmittina* for *Rhamphostomella bassleri* Rogick, 1956 from Antarctica, which has an apparently lepralioid frontal shield. Gordon & Grischenko (1994) examined the type species of *Rhamphostomella* and *Rhamphosmittina*, placing them, together with *Porella*, in Porellidae, elevated from subfamily rank. Recently, Winston & Hayward (2012) included *Rhamphostomella* in the Umbonulidae.

Aside from the challenges of classification, some authors have pointed out that the genus is perhaps heterogeneous. Osburn (1952) noted that there are two morphological groups among eastern Pacific *Rhamphostomella*, differing especially in orificial characters (see Gordon & Grischenko 1994; Soule *et al*. 1995). He also stated that "Probably *R. ovata* (Smitt), which has a perforated frontal and an imperforate ovicell should be placed by itself…" (Osburn 1952, p. 425). Winston & Hayward (2012) suggested the new combination *Rhamphostomella ussowi* for *Schizoporella ussowi* Kluge, 1908a because of its striking similarity to *R. ovata*. Both taxa have a uniformly pseudoporous area of frontal shield bordering a central imperforate area, and these authors tentatively considered them to belong to *Rhamphostomella* pending a deeper investigation of their morphology.

The unpublished MSc Thesis of Grischenko (2003a), based on detailed examination of a large collection of *Rhamphostomella* specimens representing 18 species (including two undescribed) using a scanning electron microscope (SEM), indicated that the majority of species have an umbonuloid frontal shield, suggesting placement of the genus in the family Umbonulidae Canu, 1904. In addition, that study provided new data on heteromorphy within the genus, and recognized four morphological groups superficially distinguishable by key characters that included (1) obligatory adventitious avicularia (six species); (2) lack of adventitious avicularia (10 species); (3) obligatory articulated oral spines (two species); and (4) a mixed (umbonuloid/lepralioid) frontal shield (*R. ovata*). Whether these groups represent evolutionary lineages or clades, and determining the relationships among them, will require formal phylogenetic analysis based on both skeletal characters and molecular sequence data. Similar concern was recently expressed in a large revision of the genus *Exechonella*, which grouped species into five species complexes (Cáceres-Chamizo *et al.* 2017).

Given the continuing question concerning the phylogenetic relationships of *Rhamphostomella* and the taxonomically incomplete coverage of all cheilostome genera studied with SEM, restudy of this genus is clearly timely. This is especially so in view of the need for definitive data on genera and their type species for the forthcoming revision of the cheilostome bryozoan volume of the *Treatise on Invertebrate Paleontology*.

Study of newly collected material from the North Pacific, together with specimens, including types, from several Russian and international museums (see Materials and methods), has allowed us to undertake a thorough systematic revision of *Rhamphostomella*. Our study includes SEM data for a standard set of both external and internal characters, permitting a reliable comparison of all species examined.

Materials and methods

This study is based largely on specimens sorted from numerous benthic samples collected by various expeditions in poorly explored areas along the North Pacific Rim (Gulf of Alaska, the Commander-Aleutian Ridge, eastern and western coastal waters of the Kamchatka Peninsula, the Kuril Islands, Moneron Island in the northern part of the Sea of Japan, and Hokkaido) during the period 1931–2013. These include the collections of E.F. Guryanova (Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia [formerly Leningrad, USSR]) from Bering Island (1931); the A.V. Zhirmunsky National Scientific Center of Marine Biology, Vladivostok, Russia [formerly the Institute of Marine Biology (IMB)], from the Commander Islands (1972, 1973) and southern to middle Kuril Islands (2011); the Kamchatka Institute of Ecology and Nature Management (KIENM), Petropavlovsk-Kamchatsky, Russia, from the eastern Kamchatka Peninsula, Bering Sea (1988), the coastal waters of the Commander Islands (1990–1992), and upper slope of the western Kamchatka Peninsula, Sea of Okhotsk (2008); the Pacific Institute of Bioorganic Chemistry (PIBOC), Vladivostok, Russia, from the Gulf of Alaska, Commander Islands, and Lesser Kuril Ridge (1991); A.V. Grischenko (Perm State University, Perm, USSR/Russia) from the Commander Islands (1990–1992) and the coastal waters of western Kamchatka, Sea of Okhotsk (1992); M.H. Dick (Hokkaido University, Sapporo, Japan) from the Bering Sea slope off Amchitka Island, Rat Islands, western Aleutians Islands (2004); P. Kuklinski (initially based at the Natural History Museum, London, UK, and currently at the Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland) from the Pacific and Beringian coastal waters around Adak and Amchitka Islands, Aleutian Islands (2011), and from the Laptev Sea (1993); and the Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO), Petropavlovsk-Kamchatsky, Russia, from along the western Kamchatka shelf, Sea of Okhotsk (2013). Boat types employed for collecting are abbreviated as RV (Research Vessel), FV (Fishing Vessel), and MFRT (Middle Fishery Refrigerator Trawler).

In addition, we examined material loaned from the Zoological Institute of the Russian Academy of Sciences (abbreviated as ZIRAS), Saint Petersburg, Russia; the Natural History Museum (NHMUK), London, UK; the United States National Museum (USNM), Smithsonian Institution, Washington DC, USA; the Aquatic Collection, University of Alaska Museum of the North (UAM), Fairbanks, Alaska, USA; the Natural History Museum (NHMW), Vienna, Austria; the Swedish Museum of Natural History (SMNH), Stockholm, Sweden; and the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology (MIMB), Vladivostok, Russia. In all, we examined more than 1040 specimens. Station data are given in Appendix 1.

Taxonomic descriptions are based on the specimens mentioned in the text as Material examined. With the exception of a few historical type specimens, these were studied with SEM and measured. Sections headed “Additional material” include specimens identified with a stereomicroscope.

Specimens examined had initially been dried, or fixed in 70% ethanol or 4% formaldehyde. Colonies were cleaned in a sodium hypochlorite solution, rinsed with tap-water, and air-dried. Measurements of zooidal characters were made at 40 × magnification by using an ocular micrometer with a Nikon SNZ–10 or MBS–10 stereoscopic microscope. Measurements are given in millimeters and are presented in the text as the range, followed in parentheses by the mean and standard deviation; unless stated otherwise, the sample size for each measurement was $N = 30$ zooids or structures per colony or colony fragment. Depending of the size and preservation state, one to several colonies/fragments were used for measurements. Abbreviations used for measurements are as follows: ZL, zooid length; ZW, zooid width; ZD, zooid depth (height); OrL, orifice length; OrW, orifice width; OeL, ooecium length; OeW, ooecium width; Av(s)L, suboral avicularium length; Av(ad)L, adventitious avicularium length; Av(vic)L, vicarious avicularium length; P(m)N, number of marginal pores (areolae) around the entire frontal shield periphery, with the modal number in parenthesis; P(oe)N, number of ooecial pseudopores, with the modal number in parenthesis; P(f)N, number of frontal pseudopores, with the modal number in parenthesis; Sp(or)L, orificial (oral) spine lengths; AnL, ancestrula length; AnW, ancestrula width; AnOpL, ancestrular opesia length; AnOpW, ancestrular opesia width.

Some dried specimens were mounted with double-sided adhesive tape on aluminium SEM stubs, coated with Pd–Pt in an ion sputter coater (Hitachi E–1030), and examined with a Hitachi S–2380N scanning electron microscope at 10–20 kV accelerating voltage. Uncoated specimens were examined with an ISI ABT–55, low-vacuum instrument (LEO 1455-VP) and Hitachi TM3000 SEM using a BSE (back-scattered electrons) detector at 5–15 kV accelerating voltage. All images were stored electronically as TIFF files at a resolution of 600 pixels in^{-1}. The size and clarity of image files were adjusted and assembled into figures for publication by using Adobe Photoshop CC 2017 software.

The classification used herein follows Bock & Gordon (2013). The benthic depth zonation follows the usage of Watling *et al*. (2013). The biogeographical definitions follow Golikov (1982), Golikov *et al*. (1990) and Kussakin (1990). Type specimens for the new species described are deposited in ZIRAS and NHMUK.

Remark on terminology. The protective calcified capsule of the ovicell (ooecium) is formed within the proximal part of the frontal shield of the next-distal (daughter) autozooid. However, because the ooecium is closely associated with the orifice of the maternal (egg-producing) zooid, the latter (following traditional usage) is described herein as the ovicellate autozooid.

Systematics

Phylum Bryozoa Ehrenberg, 1831

Order Cheilostomata Busk, 1852

Suborder Flustrina Smitt, 1868

Superfamily Lepralielloidea Vigneaux, 1949

Family Umbonulidae Canu, 1904

Genus *Rhamphostomella* Lorenz, 1886

Type species: *Eschara scabra* Fabricius, 1824.
Rhamphostomella Lorenz 1886, p. 11; Osburn 1952, p. 424; Kluge 1962, p. 535; 1975, p. 650.

Revised diagnosis. Colony encrusting, multiserial, unilaminar, or erect-bilamellar with encrusting part attached to substratum. Frontal shield umbonuloid, with marginal areolae except around distal margin. Primary orifice with or without lyrula and condyles. Oral spines present or absent. Secondary orifice cormidial. Peristome present or absent. Suboral avicularium always present; additional adventitious and large vicarious avicularia present in some species. Ovicell hyperstomial; with age, ooecium becoming less prominent, being covered by secondary calcification in some species. Ooecium formed by distal autozooid, ectooecium pseudoporous. Multiporous septula present in transverse zooidal walls, mural pore chambers in lateral walls. Basal zooidal wall fully calcified, with or without protuberances. Ancestrula tatiform in species where it has been observed, its basal wall sometimes with non-calcified window.

Remarks. Many authors have described or mentioned species of *Rhamphostomella*, and it was practically impossible to trace all previously reported specimens and corroborate their identifications. We made the list of “Additional references” following each synonymy as complete as we could but stress that nominal records lacking a description and/or illustrations (as often happens, for example, in faunal lists) may have been misidentified, which could in turn affect to some extent inferences of geographical distribution.

Rhamphostomella scabra (Fabricius, 1824)

(Figs 1, 25A, 30A, 31A, B, E, F)

Eschara scabra Fabricius, 1824, pp. 29, 30, tab. 1, figs 1–3.
Cellepora scabra: Smitt 1868a, p. 30 (part), pl. 28, figs 183–185, (?)188; 1868b, pp. 484, 485.
Rhamphostomella scabra: Lorenz 1886, p. 11, 12; Nordgaard 1905, p. 171, pl. 5, figs 8–11; Kluge 1955, p. 108, tab. 23, fig. 5; 1962, p. 536, fig. 374; 1975, p. 653, fig. 374; Gostilovskaya 1978, p. 225, fig. 141; Gordon & Grischenko 1994, p. 64, figs 7–12.
Discopora scabra: Nordgaard 1918, p. 77.
Rhamphostomella sollers Canu & Bassler, 1929, p. 353, pl. 43, figs 4–10.

Additional references. *Rhamphostomella scabra*: Nordgaard 1906, p. 30, 41; Kluge 1907, p. 196; 1908b, p. 553; 1929, p. 21; 1953, p. 178; 1961, p. 141; Osburn 1936, p. 542; Gostilovskaya 1957, p. 455; 1964, p. 219; Androsova 1977, p. 202; Kluge *et al*. 1959, p. 213; Hansen 1962, p. 41; Powell 1968a, p. 2312; Gontar 1980, p. 13; 1990, p. 132; 1992, p. 194; 1993b, p. 202; 1994a, p. 145; 1996, p. 46; 2010, p. 153; 2013, p. 48; Mawatari & Mawatari 1981, p. 55; Tarasova 1983, p. 26; Denisenko 1988, p. 13; 1990, p. 39; 2008, p. 188; 2011, p. 14; 2013, p. 184; Gontar & Denisenko 1989, p. 354; Grishankov 1995, p. 48; Kubanin 1997, p. 123; Grischenko 1997, p. 174; 2002, p. 114; 2015, p. 40; Grischenko *et al*. 1999, p. 112; Gontar *et al*. 2001, p. 195; Shunatova & Ostrovsky 2001, p. 118; Kuklinski 2002a, p. 181; 2002b, p. 203; 2009, p. 228; Grischenko & Mawatari 2002, p. 129; Kuklinski & Bader 2007a, p. 713; 2007b, p. 840; Denisenko & Kuklinski 2008, p. 48.
Rhamphostomella sollers: Kataoka 1957, p. 146; Sakagami *et al*. 1980, p. 330.

Material examined. *Neotype*: SMNH-Type-9304, one colony fragment, 1837, Hammerfest, Norway, North Atlantic Ocean, depth 73–110 m, collector S. Lovén.

SMNH-127473, one colony fragment, Norway, North Atlantic Ocean, collector S. Lovén. SMNH-128630, one colony on polychaete tube, Jenissej Expedition, Marine Stn 37, 1876, Kara Sea, 74°30.0′ N, 65°35.0′ E, depth 64 m. ZIRAS 10, two colony fragments, RV *Sibiriakov*, Stn 34, 14 September 1933, in front of Maria Pronchishcheva Bay, east side of Taymyr Peninsula, Laptev Sea, 75°38.0′ N, 112°58.0′E , bottom trawl, collector G.I. Gorbunov. USNM 208837, two colony fragments detached from shell of bivalve mollusc, Arctic Research Laboratory Collection, ?August 1948, Point Barrow, Alaska, Beaufort Sea, collector G.E. MacGinitie. ZIRAS 93/50106, five colony fragments, KIENM Collection, Stn 215, 30 July 1991, profile: Cape Vkhodnoy Reef–Toporkov Island, coastal waters of Bering Island, Pacific Ocean, 55°11.9′ N, 165°56.9′ E, depth 15 m, SCUBA, collector D.D. Danilin. ZIRAS 94/50107, one colony fragment, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 89, 10 September 1991, coastal waters of the Lesser Kuril Ridge, Pacific Ocean, 43°40.5′ N, 146°45.2′ E, depth 102 m, Sigsbee trawl, collector A.V. Smirnov. ZIRAS 95/50108, two colony fragments detached from broken shells of bivalve mollusc *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko. MIMB 2/50395, three colony fragments, IMB Collection, RV *Atma*, Stn 232/646, 3 August 1976, south-eastern coastal waters off Moneron Island, Sea of Japan, depth 80 m, Sigsbee trawl, collector V.I. Lukin.

Additional material. 40 specimens. IMB Collection (1972) Stn 32/99; (1973) Stns 215/536, 224/582; KIENM Collection (1988) Stns 86, 182; (1991) Stns 215, 220; (1992) Stns 25, 30, 38, 54, 97, 128; PIBOC Collection (1991) Stn 91; A.V. Grischenko Collection (1991) Stn 10; KamchatNIRO Collection (2013) Stns 63, 82 (see Appendix 1 for details).

Measurements. USNM 208837, Beaufort Sea (Fig. 1H, J, L). ZL, 0.92–1.59 (1.15 ± 0.17). ZW, 0.55–0.90 (0.72 ± 0.09). ZD, 0.62–0.82 (n = 2). OrL, 0.25–0.35 (0.30 ± 0.03). OrW, 0.32–0.40 (0.37 ± 0.02). OeL, 0.32–0.37 (0.35 ± 0.03) (n = 4). OeW, 0.43–0.52 (0.48 ± 0.04) (n = 4). Av(s)L, 0.14–0.22 (0.18 ± 0.02). Av(ad)L, 0.20–0.35 (0.29 ± 0.04). P(m)N, 15–22 (17). P(oe)N, 9–18 (14) (n = 4).

ZIRAS 93/50106, Bering Island, Commander Islands, Pacific Ocean (Figs 1B, E–G, I, K, M, 30A). ZL, 0.68–1.15 (0.82 ± 0.09). ZW, 0.42–0.58 (0.49 ± 0.05). ZD, 0.60–0.67 (n = 2). OrL, 0.20–0.25 (0.23 ± 0.02). OrW, 0.20–0.30 (0.26 ± 0.03). OeL, 0.25–0.33 (0.28 ± 0.02) (n = 25). OeW, 0.35–0.48 (0.41 ± 0.03) (n = 25). Av(s)L, 0.10–0.18 (0.13 ± 0.02). Av(ad)L, 0.15–0.26 (0.20 ± 0.03). P(m)N, 8–17 (12). P(oe)N, 3–12 (6).

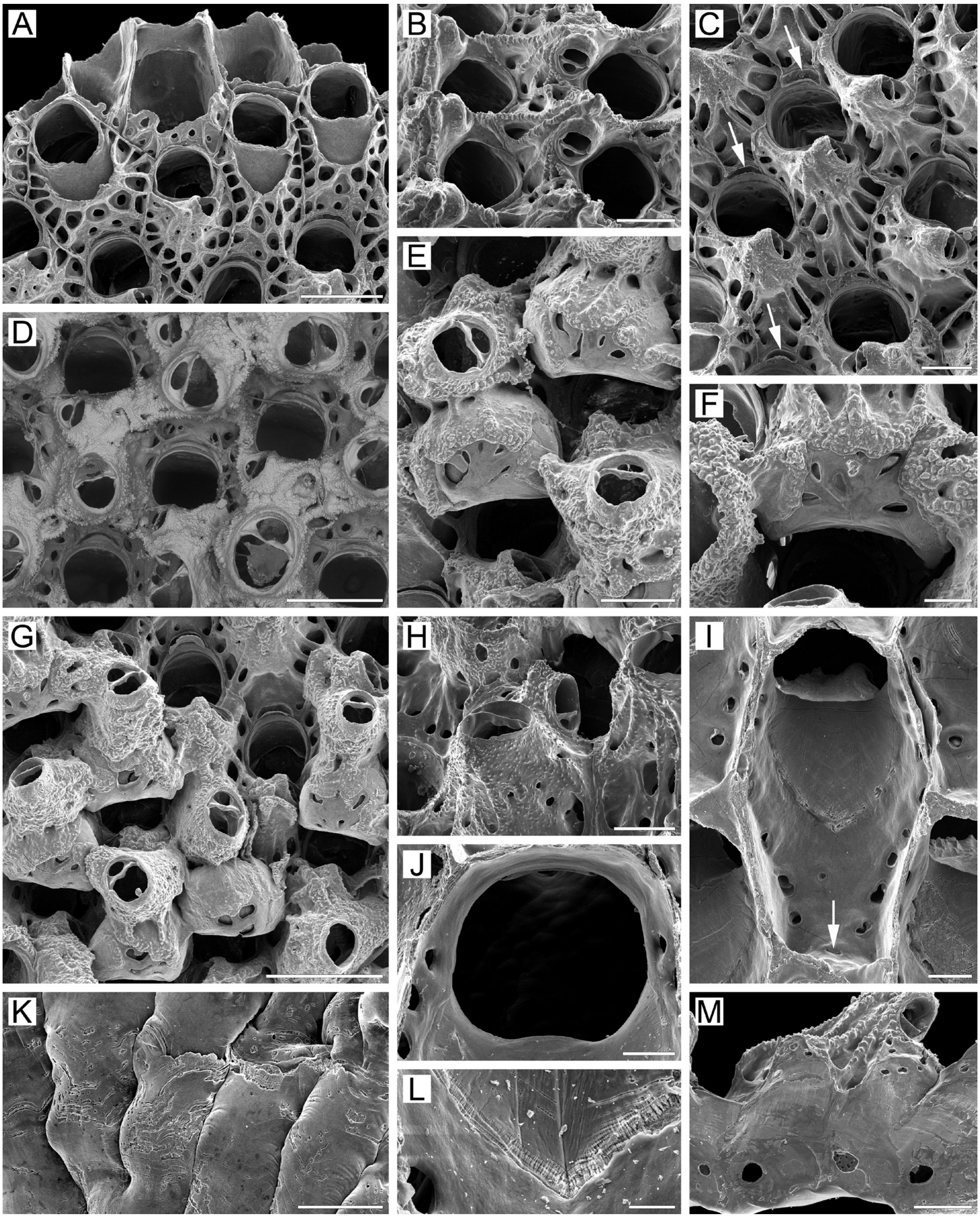

FIGURE 1. *Rhamphostomella scabra* (Fabricius, 1824). A. ZIRAS 94/50107 (Lesser Kuril Ridge, Pacific Ocean). B, E–G, I, K, M. ZIRAS 93/50106 (Bering Island, Commander Islands, Pacific Ocean). C. ZIRAS 95/50108 (western Kamchatka, Sea of Okhotsk). D. MIMB 2/50395 (Moneron Island, Sea of Japan). H, J, L. USNM 208837 (Beaufort Sea). A. Colony margin with developing zooids. B. Distolateral view of marginal zooids, showing form of orifice and suboral avicularia. C. Non-ovicellate zooids in young part of colony (arrows, early stages of ooecial development). D. Group of non-ovicellate zooids from older part of colony with suboral and adventitious avicularia. E. Old autozooids with ovicells and avicularia. F. Close-up of ooecium overgrown by secondary calcification. G. Group of ovicellate zooids in older part of colony. H. Proximolateral view of ovicellate zooid, showing position of suboral and adventitious avicularium. I. Interior of the frontal shield with ring scar, areolae, communication pore of adventitious avicularium and ooecial communication pore (arrow). J. Internal view of primary orifice. K. Basal surface of colony. L. Interior of frontal shield, showing ring scar and umbonuloid exterior wall microstructure. M. Lateral view of autozooid, showing suboral avicularium with communication pores and lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, E, H, M, 200 µm; C, 250 µm; F, I, J, 100 µm; L, 50 µm.

MIMB 2/50395, Moneron Island, Sea of Japan (Fig. 1D). ZL, 0.82–1.23 (1.05 ± 0.09). ZW, 0.60–0.93 (0.76 ± 0.08). ZD, 0.63–0.74 (n = 2). OrL, 0.27–0.34 (0.31 ± 0.02). OrW, 0.29–0.38 (0.35 ± 0.02). Av(s)L, 0.16–0.24 (0.20 ± 0.02). Av(ad)L, 0.25–0.37 (0.30 ± 0.03). P(m)N, 14–20 (17).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 1A), attaining up to 23 mm in any one direction, occasionally forming small erect bilamellar expansions and frills, orange to bright yellow when alive, light yellow when dry. Zooids large, broadly hexagonal to oval, arranged in regular rows in checkered pattern, demarcated by fine undulating sutures between vertical lateral walls in young parts of colony (Fig. 1A, C); these sutures occluded by secondary calcification in older parts of colony (Fig. 1D, G).

Frontal shield (Fig. 1A, C, I) umbonuloid, convex, with finely granulated surface in young zooids and with coarse granulation in older zooids; with numerous areolae separated by long, narrow, radially arranged interareolar ridges. In young zooids, deep pits around areolae irregularly oval to triangular, trapezoid or quadrate, occurring in one marginal row laterally and in 2–3 rows proximally (examination of underside of frontal shield showed that centrally placed "holes" are not pseudopores) (Fig. 1A). In older zooids, secondary calcification of frontal shield resulting in fusion of proximal pits around areolae in one proximal row; these pits also becoming elongate, as do interareolar ridges connected with cystid of suboral avicularium that sometimes continue to apex to form small, pointed bulge (Fig. 1B–D, G). Areolar pits surrounding areolar openings (for convenience, termed areolae throughout the text) reduced in size in oldest zooids owing to thickening of frontal shield by secondary calcification. Umbonuloid component occupying about 50% of length of frontal shield, with fine, parallel lineation and accretionary banding. Ring scar discrete (Fig. 1L), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 1A, J) roundly quadrate or bell-shaped to transversely oval; distal and lateral margins formed by upper terminal part of distal transverse wall, sometimes bearing narrow shelf distally and forming ill-defined condyles laterally (Fig. 1A, D); condyles not present in all zooids (Fig. 1A). Distal margin of orifice round, proximal margin straight or with very weak median prominence; proximolateral corners broadly rounded. Oral spines absent in "mature" zooids; two ephemeral spines can be seen at distal margin of primary orifice in some young zooids at colony periphery.

Secondary orifice (Fig. 1C, D, G) irregularly oval, cormidial, restricted proximally by distal area of frontal shield incorporating avicularian cystid. Distally and distolaterally, secondary orifice formed by elevated vertical walls of distal and lateral zooids.

Suboral avicularium with cystid not very large, occupying distal one-third to half of frontal shield, mostly situated centrally in respect to zooidal orifice (Fig. 1A–C); cystid conical, elevated (although less prominent in old zooids, Fig. 1D), with finely granulated surface; 2–5 small communication pores visible in wall of young avicularium (Fig. 1A, C). Frontal surface of avicularium (including rostral and postmandibular areas) situated on left or right slope of avicularian cystid, out of zooidal midline, facing distolaterally to laterally (Fig. 1A, C). Rostrum semioval, blunt (Fig. 1B–E), directed obliquely upwards. Palate short, semioval to semielliptical; in some zooids in same plane as postmandibular area (Fig. 1C–E, F, H), whereas in others there is right angle between them (Fig. 1A, D). Palatal foramen repeats shape of palate, semioval opesia (postmandibular area) oval or ellipsoidal. Crossbar complete, with small, low ligula.

Large adventitious avicularia of two size categories occupying proximal half of frontal shield in older zooids (Fig. 1D, E, G, H). Avicularian cystid broad, elevated, with finely granulated surface and 6–8 proximolateral communication pores (Fig. 1H). Avicularian frontal surface facing obliquely upwards. Rostrum broadly oval, blunt, directed medially upwards. Palate short, broadly semioval. Palatal foramen repeating shape of palate, semioval, opesia elliptical. Crossbar complete, often with low ligula. In older parts of colony, adventitious avicularia occupying most of frontal surface, rendering frontal shields scarcely visible (Fig. 1D, G).

Ovicell initially hyperstomial, but ooecium rapidly becoming covered by secondary calcification expanding from frontal shields of distal and distolateral zooids. Borders between calcification from different sources appearing as fine, meandering sutures (Fig. 1E–G). Secondary calcification granular, covering from half to two-thirds of ooecium, so ovicells becoming subimmersed and even appearing endozooidal (Fig. 1F). Ooecium formed by distal autozooid around shallow crescentic concavity with communication pore at bottom, situated in most proximal part of frontal shield just immediate to distal margin of maternal primary orifice (Fig. 1A, C, D, G). Pore leading to communication canal connecting ooecial and visceral coeloms and forming straight, slit-like ooecial communication pore on underside of frontal shield of distal zooid, very close to transverse wall (Fig. 1I). Ooecium spherical, broader than long, with wide, straight or slightly concave proximal margin (Fig. 1E–G). Ectooecium smooth, with oval, drop-like or slit-like pseudopores sometimes arranged in radial pattern. Ooecial base surrounded by round, oval or elongated areolae, separated by short, narrow ridges.

Zooids interconnected by one mural pore chamber in each distolateral wall (corresponding to large opening present in proximolateral wall) (Fig. 1M). Communication pores spread through basal half of transverse wall either as wide horizontal "band" or forming 1–4 groups (multiporous septula) of varying size, outline and pore density. Both patterns sometimes composed of random individual pores, and wide septula (pore "band") can be composed of small pore groups.

Basal surface of zooids (Fig. 1K) fully calcified, inflated. Numerous white spots (presumably lightly calcified areas) visible in semitransparent basal wall under light microscope. Numerous tubular protuberances (0.11–0.27 mm in diameter) present on basal surface of marginal colony area, beneath growing edge (Fig. 30A). Boundaries between zooids recognizable basally by deep meandering incisions.

Ancestrula (Fig. 25A) tatiform, basal outline irregularly circular; opesia circular, with nine basally jointed periopesial spines evenly distributed around opesial margin; budding triplet of periancestrular zooids distally and distolaterally; periancestrular zooids similar to but smaller than subsequent zooids, with three to six ephemeral oral spines around distal margin of orifice.

Remarks. There has been some confusion concerning the type species of *Rhamphostomella*. Following the suggestion of Smitt (1868a, b), the first information on this cheilostome was provided by Fabricius (1780, p. 433, No 437), who described a specimen from Greenland as *Millepora reticulata* Linnaeus. Fabricius himself, however, later admitted his mistake, realizing that his specimen belonged to "Coral-Barkene (Escharas)" (Fabricius 1824, pp. 29, 30). He named it *Eschara scabra* adding to his description three very schematic drawings all probably showing the same colony fragment under various low magnifications (tab. 1, figs 1–3). Smitt (1868a, p. 181), based on specimens collected during two different expeditions, redescribed this species as *Cellepora scabra*, indicating that this "form for the most part seems to have been the basis for Fabricius's description". This suggestion remains unconfirmed, since Fabricius's specimen was supposedly lost; although some of his specimens are kept in the collections of the Natural History Museum of Denmark, University of Copenhagen, Fabricius's specimen is not mentioned in the museum's catalogues for either the bryozoan or cnidarian collection (C. Nielsen, pers. comm., 2020).

In the same paper Smitt (1868a) described a new species, *C. plicata*, stressing that it is similar to *C. scabra*. He also mentioned both species *R. scabra* and *R. plicata* (as *Cellepora*) in his large taxonomic work published the same year (Smitt 1868b).

When Lorenz (1886) introduced the genus *Rhamphostomella*, he attributed six species to it, two of them new (see Remarks for *R. plicata* for details). Norman (1903, p. 125) chose "*Ramphostomella scabra* (Fabricius), Smitt", as the "Type", but uncertainty remains over the identity of Fabricius's species (see above), reflected in Lorenz's citation of the species in his synonymy as "*Eschara scabra* Fabricius, (teste Smitt)". Smitt (1868a, pl. 28, figs 183–185, ?188) presented some fairly good drawings of what he referred to as *Cellepora scabra*. Specimens illustrated in Smitt's figures 183–185 were interpreted by Lorenz on the basis of a range of specimens from Jan Mayen as depicting *R. scabra*, and figs 186–188 [?*Cellepora scabra* Fabricius: Smitt, ex parte] as depicting the new species *R. costata* Lorenz, 1886, distinguished especially by the shape of the avicularian mandibles and the generally lyrulate orifice. Levinsen (1909), taking into account the variation exhibited by these nominal species, saw no distinction between them. On the other hand, Hincks (1889), Whiteaves (1901), Norman (1903), Nordgaard (1905, 1906), Osburn (1952), Androsova (1958), Kluge (1962) and Powell (1968a) accepted two species, as we do here. Canu & Bassler (1917), evidently overlooking Norman's (1903) indication of the type species, selected *R. costata* as the type. While acknowledging Canu & Bassler's (1917) oversight, Harmer (1957) nevertheless argued that *R. costata* should stand in preference to *R. scabra*, "the trivial name of which belongs to a species insufficiently described by Fabricius." Harmer's argument must be rejected (Hayward 1975), but the conspecificity of Fabricius's and Smitt's material remained questionable until now.

Smitt's (1868a) figures 183–185 (and possibly 188) illustrate *R. scabra* as the species accepted by the most authors. To preclude further confusion, we have selected a neotype for this species from among specimens of Smitt collected in the North Atlantic (Norway), kept at the Swedish Museum of Natural History (for additional details and discussion, see Gordon & Grischenko 1994).

Kluge (1961) reported a new subspecies, *Rhamphostomella scabra orientalis*, from the intertidal zone of Bering Island, the Commander Islands, and Kronotsky Gulf, eastern Kamchatka. Although these records were not accompanied by a description or illustrations, Grischenko (1997, 2002) and Denisenko (2013) reported *R. scabra orientalis*. Our examination of the type material of *R. scabra orientalis* (ZIRAS 1/8801) showed that Kluge's (1961) subspecies was based on a misidentification of *Desmacystis sandalia* (Robertson, 1900), endemic to the North Pacific (Fig. 31C, D). *Rhamphostomella scabra orientalis* is thus a junior synonym of *D. sandalia*.

Canu & Bassler (1929) described a new species, *Rhamphostomella sollers*, based on material collected by the RV *Albatross* from Stn D. 4807 near Cape Tsiuka (41°36.1′ N, 140°36.0′ E), Sangar Strait, Sea of Japan. Our SEM examination of the syntype (USNM 8136) indicates that it is synonymous with *R. scabra* (Fig. 31E, F).

In several cases, *R. scabra* was apparently misidentified. For example, Androsova's (1958) material identified as *R. scabra* is very likely what we describe herein as *R. microavicularia* **n. sp.**. Records of *R. scabra* in particular regional studies in the Far East (Kluge *et al*. 1959; Kluge 1961; Gontar 1980, 1993b; Mawatari & Mawatari 1981; Denisenko 2013) might also need to be reexamined, since the material involved could have been confused with other, similar species (discussed in Remarks sections for particular species below).

Ecology. *Rhamphostomella scabra* has been reported from depths of 0–460 m on various bottom types/substrates, including boulders, pebbles, gravel, sand and silt. In addition to rocky surfaces, this species inhabits the shells of gastropod and bivalve molluscs, the tubes of serpulid and spirorbid polychaetes, and the surfaces of sponges and ascidians.

Distribution. *R. scabra* is a boreal-Arctic, circumpolar, sublittoral to upper bathyal species, widely distributed in the seas of the Northern Hemisphere. In the Arctic, it has been recorded from the Barents Sea (Smitt 1868a, 1878a, 1878b; Bidenkap 1900a; Andersson 1902; Nordgaard 1905; Kuznetsov 1941; Kluge 1962, 1975; Denisenko 1988, 1990), White Sea (Smitt 1878a; Kluge 1907, 1962, 1975; Gostilovskaya 1957, 1978; Grishankov 1995; Shunatova & Ostrovsky 2001), Kara Sea (Smitt 1878b; Levinsen 1887; Nordgaard 1912; Kluge 1929, 1962, 1975; Denisenko 2021), Laptev Sea (Kluge 1929, 1962, 1975; Gontar 1990, 1996), East-Siberian Sea (Kluge 1962, 1975; Gontar 1994a; Denisenko 2011), Chukchi Sea (Kluge 1962, 1975; Denisenko 2008; Gontar 2010), Point Barrow, Alaska, Beaufort Sea (MacGinitie 1955), Canadian Arctic Archipelago (Nordgaard 1906; Osburn 1936), Baffin Bay (Hansen 1962), Davis Strait (Hansen 1962; Kluge 1962, 1975), Labrador (Gontar & Denisenko 1989), western Greenland (Henning 1896; Norman 1906; Kluge 1908b; Levinsen 1914; Osburn 1919; Denisenko & Blicher 2021), eastern Greenland (Andersson 1902; Levinsen 1916; Kuklinski & Bader 2007a, 2007b), Jan Mayen Island (Lorenz 1886), Spitsbergen (Gontar *et al*. 2001; Kuklinski 2002a, 2002b, 2009; Kuklinski & Bader 2007b; Denisenko & Blicher 2021), Franz-Jozef Land (Denisenko 1990), Lofoten Islands (Nordgaard 1918), and northern Norway (Nordgaard 1905). In the northwestern Atlantic, *R. scabra* extends along the east coast of North America from the Gulf of St Lawrence to the Gulf of Maine (Whiteaves 1901). In the northwestern Pacific, it has been reported from the Bering Sea in Provideniya Bay, Kamchatskiy Gulf, Kronotsky Gulf and Avacha Gulf (Kluge 1961; Kubanin 1997; Grischenko 2002; Gontar 2013; our data), Commander Islands (Kluge 1961; Grischenko 1997, 2002; Kubanin 1997); Sea of Okhotsk, including western Kamchatka shelf and slope (Grischenko *et al*. 1999; Grischenko 2015; Grischenko & Mawatari 2002; our data), eastern coastal waters of southern Sakhalin Island (Kluge *et al*. 1959; Kubanin 1997), Shantar Archipelago (Kluge 1961; Kubanin 1997), along Kuril Islands, including Paramushir, Makanrushi, Onekotan, Raschua, Simushir, Urup, Kunashir, Shikotan (Kluge 1961; Gontar 1980, 1993b), and South Kuril Strait (Kluge *et al*. 1959; Gontar 1980); Sea of Japan, along the western shore of southern Sakhalin Island (Androsova 1958; Kluge 1961; Kluge *et al*. 1959), Primorye (Kluge 1961; Tarasova 1983), Moneron Island (our data), Hokkaido (Mawatari & Mawatari 1981) and Sangar Strait (Canu & Bassler 1929). We stress here that existing uncertainties in some records mentioned above as well as overlaps of distribution areas of similar species should be considered during future research.

Rhamphostomella commandorica **n. sp.**
(Figs 2, 30B)

Diagnosis. Colony encrusting, multiserial. Zooids large, hexagonal to oval. Frontal shield convex, pustulose. Marginal areolae large, separated by high interareolar ridges connected with cystid of suboral avicularium. Umbonuloid component extensive. Primary orifice sunken, broadly semicircular to bell-shaped, with blunt condyles; proximal

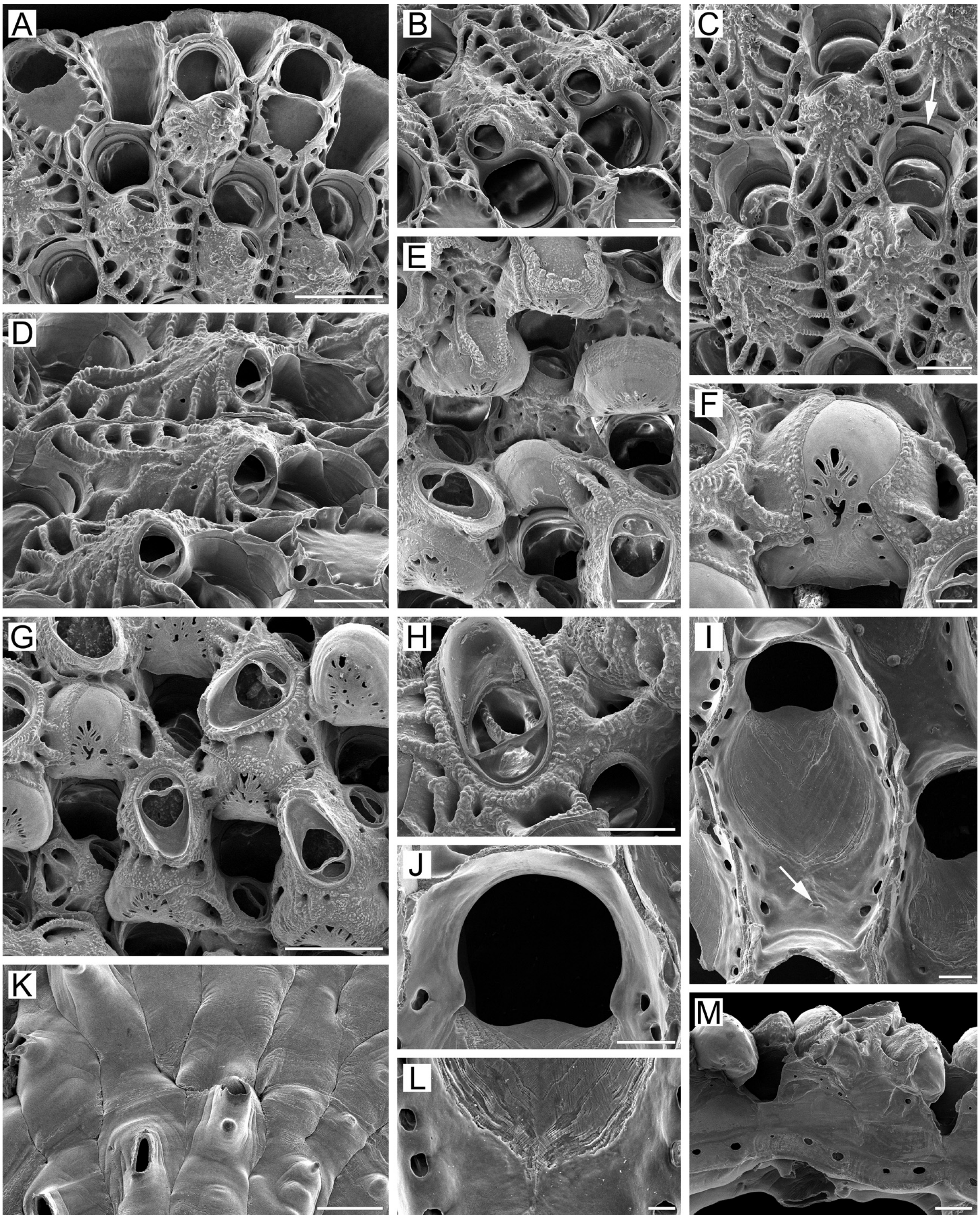

FIGURE 2. *Rhamphostomella commandorica* **n. sp.** *Holotype*, ZIRAS 1/50125 (Medny Island, Commander Islands, Pacific Ocean). A. Colony margin with developing zooids. B. Distolateral view of young zooids, showing details of primary orifice and suboral avicularium. C. Non-ovicellate zooids in young part of colony (arrow, communication pore of future ooecium). D. Lateral view of autozooids in young part of colony, showing details of suboral avicularia. E. Ovicellate zooids in older part of colony with suboral and adventitious avicularia. F. Ooecium overgrown by secondary calcification, showing arrangement of pseudopores. G. Group of ovicellate zooids in older part of colony. H. Distolateral view of frontal shield, showing comparative size and shape of suboral and adventitious avicularia. I. Interior of frontal shield, showing ring scar, areolae and ooecial communication pore (arrow). J. Internal view of primary orifice. K. Basal colony surface, showing small protuberances. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooidal row, showing ooecia (some covered by secondary calcification) and adventitious avicularia on frontal surface, tubular processes on basal surface, and lateral wall with mural pore chambers. Scale bars: A, G, K, 500 µm; B, H, M, 200 µm; C–E, 250 µm; F, I, J, 100 µm; L, 50 µm.

margin with low, wide median prominence. No oral spines. Secondary orifice irregularly oval, cormidial. Suboral avicularian cystid large, bulging, occupying most of frontal shield, finely granulated. Avicularian frontal surface situated asymmetrically in respect to zooidal orifice, crossing zooidal midline, facing distolaterally and slightly overhanging proximal margin of primary orifice. Rostrum semicircular, blunt. Palate short, broadly triangular to semiround. Crossbar complete. Large adventitious avicularia also present, often associated with ooecia. Rostrum elongate-oval or elongate-triangular, blunt. Palate elongate-triangular or spatulate. Palatal foramen heart-shaped. Crossbar complete, with small ligula. Ovicells hyperstomial, rapidly subimmersed by secondary calcification. Ectooecium smooth, with pseudopores arranged in arch around a few central pseudopores. Two mural pore chambers in distolateral wall, and 1–3 multiporous septula in transverse walls. Basal surface of zooids fully calcified with some tubular protuberances.

Material examined. *Holotype*: ZIRAS 1/50125, single colony fragment, IMB Collection, Stn 224/582, 2 October 1973, Poludennaya Bight, coastal waters of Medny Island, Commander Islands, Pacific Ocean, 54°36.8′ N, 167°21.5′ E, depth 130–250 m, rock dredge, collector S.D. Vavilin. *Paratype*: NHMUK 2013.10.21.1, one colony, RV *Norseman*, Stn AS–1, 17 July 2011, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°46.2′ N, 176°25.6′ W, depth 10 m, SCUBA, collector P. Kuklinski.

Etymology. The species name alludes to the type locality in the Commander Islands (in Russian, "Komandorskie ostrova").

Type locality. Poludennaya Bight, coastal waters of Medny Island, Commander Islands, Pacific Ocean, 54°36.8′ N, 167°21.5′ E, depth 130–250 m.

Measurements. ZIRAS 1/50125, Medny Island, Commander Islands, Pacific Ocean (Figs 2A–M, 30B). ZL, 0.77–1.28 (1.03 ± 0.12). ZW, 0.47–0.75 (0.59 ± 0.07). ZD, 0.62–0.67 (*n* = 2). OrL, 0.22–0.30 (0.26 ± 0.02). OrW, 0.22–0.35 (0.28 ± 0.03). OeL, 0.32–0.45 (0.39 ± 0.03). OeW, 0.42–0.58 (0.51 ± 0.04). Av(s)L, 0.15–0.28 (0.20 ± 0.03). Av(ad)L, 0.37–0.53 (0.44 ± 0.04). P(m)N, 12–18 (14). P(oe)N, 11–16 (15) (*n* = 10).

NHMUK 2013.10.21.1, Adak Island, Aleutian Islands, Pacific Ocean. ZL, 0.59–1.08 (0.85 ± 0.09). ZW, 0.34–0.57 (0.45 ± 0.06). ZD, 0.55–0.61 (*n* = 2). OrL, 0.16–0.24 (0.20 ± 0.02) (*n* = 25). OrW, 0.18–0.28 (0.23 ± 0.02) (*n* = 25). Av(s)L, 0.12–0.17 (0.14 ± 0.01) (*n* = 14). P(m)N, 14–24 (19) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 2A), more or less circular, attaining 12 × 15 mm in size, pink when dry. Zooids large, hexagonal to oval, arranged in regular rows in checkered pattern, demarcated by fine sutures between lateral and transverse walls (Fig. 2A–D); sutures occluded by secondary calcification in older parts of colony.

Frontal shield umbonuloid (Fig. 2A–D, I), thick, convex, pustulose, with numerous, large, elongate areolae along zooidal margins, separated by narrow, high interareolar ridges connected with cystid of suboral avicularium. Some proximal ridges fusing with each other. Thickening of frontal shield resulting in smaller areolae. Umbonuloid component extensive, occupying about 70% of length of frontal shield (72% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 2I, L). Ring scar forming boundary between umbonuloid exterior wall microstructure and extra-umbonuloid calcification clearly visible but not as single discrete line (Fig. 2L).

Primary orifice (Fig. 2A, B, J) broadly semicircular to bell-shaped or oval; its distal and lateral margins formed by upper terminal part of distal transverse wall (Fig. 2A, B, E) and bearing low blunt condyles proximolaterally (Fig. 2J). Distal margin of orifice round, proximal margin with low, wide median prominence and broadly rounded proximolateral corners. No oral spines.

Secondary orifice (Fig. 2A–E, G) irregularly oval, cormidial, formed proximally by avicularian cystid connected with thin vertical wall surrounding primary orifice (Fig. 2A–D). Distally and distolaterally, secondary orifice restricted by vertical walls of distal and lateral zooids. With increasing secondary calcification, outline of secondary orifice often changing, acquiring trapezoidal shape (Fig. 2E, G) in ovicellate zooids.

Suboral avicularium with cystid large, bulging, broad, occupying most of frontal shield, with 6–9 communication pores connecting avicularian and hypostegal coelomic cavities (Fig. 2A, C, D); surface finely granulated when young, pustulose in older zooids. Avicularian frontal surface (rostral/postmandibular areas) situated asymmetrically with respect to zooidal orifice, on right or left slope of avicularian cystid, normally crossed by zooidal midline, facing distolaterally or laterally, tilted frontodistally at angle of 60–90°. Rostrum semicircular, blunt, directed proximomedially upwards. Palate short, semicircular to rounded-triangular. Palatal foramen repeating shape of palate, opesia oval or semielliptical, surrounded by cryptocystal shelf. Crossbar complete.

Large adventitious avicularia developing by frontal budding in older parts of colony, often associated with ooecia. Zooidal orifices deeply immersed in areas where avicularia are numerous. Avicularian cystid broad, with finely granulated surface (Fig. 2E, G, H). Frontal surface of avicularium facing obliquely upwards. Rostrum elongate-oval or elongate-triangular, blunt, oriented distolaterally to proximolaterally. Palate elongate-triangular or spatulate. Palatal foramen heart-shaped, with extensive distal cryptocystal shelf. Opesia oval or semielliptical, cryptocyst narrow. Crossbar complete, with small ligula. In older parts of colony, adventitious avicularia cover most of free space, together with thick secondary calcification, strongly changing appearance of colony (compare Fig. 2A, C, D with Fig. 2E, G).

Ovicells initially hyperstomial, rapidly becoming subimmersed as ooecium is covered by thick secondary calcification proceeding from daughter and neighbouring zooids; surface finely granular, often with 1–2 sutures demarcating calcification (often bearing interareolar ridges) from different zooids (Fig. 2E, F, G). In older parts of colony, secondary calcification covering half to two-thirds of ooecium; ovicell appearing endozooidal when only proximal triangular or semicircular area of ectooecium with pseudopores is visible (Fig. 2G). Ooecium formed by distal autozooid around distinctive curved slit (Fig. 2A, C, D) in slope of proximal vertical wall of distal zooid contributing to secondary orifice, immediately distal to margin of primary orifice of maternal zooid; this slit leading to communication canal connecting ooecial and visceral coeloms, opening on underside of frontal shield of distal zooid as small, straight, slit-like communication pore at mid-distance between transverse wall and ring-scar (Fig. 2I). Ooecium spherical, with straight or slightly concave proximal margin often bearing very low, central convexity (Fig. 2F). Ectooecium smooth, with oval, irregular or often slit-like pseudopores arranged in compressed arch around one large or several small central pseudopores, oval or irregular. Ooecial base surrounded by oval to elongate areolae separated by short, narrow ridges (Fig. 2F, G).

Zooids interconnected by two mural pore chambers (Fig. 2M) in each distolateral wall, and by one wide, horizontal or 2–3 (usually 2) compact multiporous septula in basal half of transverse wall. Distally transverse wall can bear up to three buttressed recesses (each with multiporous septula) resembling basal pore chambers (Fig. 2A).

Basal surface of zooids (Figs 2K, M, 30B) fully calcified, convex, smooth, with numerous tubular protuberances (0.04–0.27 mm in diameter) having fine parallel folds on surface. Boundaries between zooids recognizable basally by deep undulating incisions. Sparse white spots (presumably weakly calcified areas) visible in semitransparent basal wall under light microscope.

Ancestrula and early astogeny not observed.

Remarks. In the general appearance of the zooids, as well as in having: 1) a bulging, broad oval suboral avicularium with semicircular palate, and 2) ooecia with a narrow arch of slit-like pseudopores, *R. commandorica* **n. sp.** resembles *R. pacifica* (see below), but differs from the latter as follows: 1) the primary orifice is submerged in zooids of *R. commandorica* **n. sp.** at all stages of zooidal development, whereas it is clearly visible in non-ovicellate zooids and surrounded by a tubular peristome in ovicellate zooids of *R. pacifica*; 2) the palatal foramen of the adventitious avicularia is heart-shaped in *R. commandorica* **n. sp.**, but Y-shaped in *R. pacifica*; 3) the two known colonies of *R. commandorica* **n. sp.** are both encrusting, whereas colonies of *R. pacifica* are encrusting only initially, but rapidly grow into erect bilamellar ruffled expansions.

Ecology. *Rhamphostomella commandorica* **n. sp.** has been found at depths of 10–250 m, on mixed bottoms (silt, pebbles, boulders). The original substrata for our specimens are unknown.

Distribution. Presently known only from Poludennaya Bight off Medny Island, Commander Islands, and Adak Island, Andreanof Islands, Aleutian Islands, *R. commandorica* **n. sp.** can be categorized as a Pacific high-boreal, sublittoral species.

Rhamphostomella costata **Lorenz, 1886**

(Figs 3, 31G–I)

Cellepora scabra: Smitt 1868a, p. 30 (part), pl. 28, figs 186, 187.

Rhamphostomella costata Lorenz, 1886, p. 12, pl. 7, fig. 11 (mentioned as fig. 12 in the text).

Rhamphostomella costata: Hincks 1889, p. 426, pl. 21, figs 7, 8; Nordgaard 1905, p. 171, pl. 5, figs 21, 22; Kluge 1962, p. 537, fig. 375; 1975, p. 654, fig. 375; Osburn 1912a, p. 244, pl. 26, figs 62a, b, pl. 31, fig. 100; 1952, p. 426, pl. 50, fig. 7; Gostilovskaya 1978, p. 226, fig. 142; Androsova 1958, p. 171, fig. 102; Mawatari 1965, p. 619, text-figs 126c, d; Tarasova 1983, p. 25, fig. 31; Dick & Ross 1988, p. 67, pl. 5a; Ryland & Hayward 1991, p. 39, fig. 59.

Rhamphostomella scabra var. *costata*: Nordgaard 1929, p. 7.
Rhamphostomella magnirostris Canu & Bassler, 1928, p. 120, pl. 19, figs 5–7, text-figs 22e, f.

Additional references. *Rhamphostomella costata*: Nordgaard 1906, p. 30, 41; Kluge 1908a, p. 533; 1908b, p. 553; 1928, p. 257; 1929, p. 21; 1952, p. 160; 1953, p. 178; 1961, p. 141; 1964, p. 190; Osburn 1936, p. 542; 1955, p. 38; O'Donoghue & O'Donoghue 1923, p. 44; 1925, p. 105; 1926, p. 72; Gostilovskaya 1957, p. 455; 1968, p. 70; Kluge *et al*. 1959, p. 213; Hansen 1962, p. 41; Powell 1968a, p. 2310; 1968b, p. 257; Gontar 1980, p. 13; 1990, p. 132; 1992, p. 195; 1994a, p. 144, 145; 1994b, p. 106; 2010, p. 153; Mawatari & Mawatari 1981, p. 55; Dick & Ross 1986, p. 89; Denisenko 1988, p. 13; 1990, p. 39; 2008, p. 187; 2011, p. 14; 2013, p. 184; Gontar & Denisenko 1989, p. 354; Grishankov 1995, p. 48; Grischenko 1997, p. 174; 2002, p. 115; 2015, p. 40; Gontar *et al*. 2001, p. 195; Kuklinski 2002b, p. 203; 2009, p. 228; Kuklinski & Bader 2007b, p. 840; Denisenko & Kuklinski 2008, p. 48; Kuklinski & Taylor 2009, p. 497; Ostrovsky 2009, p. 206, fig. 78c; 2013, p. 8, fig. 2.41c; Foster 2010, p. 57.

Material examined. *Lectotype*: NHMW 92531 (=1884.II.50), three fragments of one colony initially encrusting shell of *Chlamys islandica*, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 200–270 m, ollector F. Fischer. *Paralectotype* 1: NHMW 72990 (=1884.II.50), a few small fragments of one colony initially encrusting shell of *Chlamys islandica*, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 200–270 m, collector F. Fischer. *Paralectotype* 2: NHMW 92532 (=1884.II.92), colony encrusting gastropod shell, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 200–270 m, collector F. Fischer.

NHMUK 1911.10.1.1574A, colony encrusting bivalve shell, A.M. Norman Collection, HMS *Valorous*, 1875, Greenland, depth 104 m. NHMUK 1899.5.1.273, three colony fragments, locality not given, T. Hincks Collection. NHMUK 2010.2.9.6, one colony fragment, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 17, 12 August 1991, near Kodiak Island, Gulf of Alaska, Pacific Ocean, 57°58.2′ N, 151°07.5′ W, depth 83 m, Sigsbee trawl, collector A.V. Smirnov. P. Kuklinski Collection, two colony fragments, RV *Ivan Kireev*, Russian-German Expedition Transdrift 1, Stn 48, 18 August 1993, Laptev Sea, 74°30.0′ N, 137°05.0′ E, depth 22 m, rock dredge, collectors M.K. Schmid and D. Piepenburg. SMNH-1730, one colony fragment, Swedish Arctic Expedition, August 1861, Waygat Islands, Hinlopen Strait, Svalbard and Jan Mayen, 79°10.0′ N, 19°00.0′ E, depth 55 m, rocks. SMNH-126202, one colony, Egedesminde (Aasiaat), Disko Bay, Western Greenland, 68°42.0′ N, 52°45.0′ W, collector O. Torell. SMNH-126208, four fragments, Swedish Arctic Expedition, 1861, Treurenberg Bay, west Spitsbergen, Svalbard and Jan Mayen, depth 67 m. SMNH-126585, one colony, Swedish Arctic Expedition, 1861, Waygat Islands (Vaigattøyane), Hinlopen Strait, Svalbard and Jan Mayen, 79°10.0′ N, 19°00.0′ E, depth 55 m, stones. SMNH-132267, four fragments of a single colony, Spetsberg Expedition, June 1864, Safehaven, Isfjorden, Spitsbergen, depth 55 m. SMNH-178050, two colony fragments, Swedish Arctic Expedition, August 1861, Waygat Islands, Hinlopen Strait, Svalbard and Jan Mayen, 79°10.0′ N, 19°00.0′ E, depth 50 m, rocks. USNM 11115, nine colony fragments, Arctic Research Laboratory Collection, ?August 1948, Point Barrow, Alaska, Beaufort Sea, depth 99.9 m, collector G.E. MacGinitie. USNM 11148, six colony fragments, Arctic Research Laboratory Collection, ?August 1948, Point Barrow, Alaska, Beaufort Sea, depth 99.9 m, collector G.E. MacGinitie. ZIRAS 71/50109, large bifoliate colony, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 15, 12 August 1991, near Kodiak Island, Gulf of Alaska, Pacific Ocean, 58°22.4′ N, 150°56.8′ W, depth 61 m, Sigsbee trawl, collector A.V. Smirnov.

Additional material. 71 specimens. IMB Collection (1973) Stns 110/292, 150/385; KIENM Collection (1988) Stns 148, 182, 326, 348, 380, 406; (1991) Stns 219, 226; (1992) Stns 5, 38, 53, 54, 55, 89, 99, 113, 117, 118, 124, 125, 126, 129, 132, 137, 146; (2008) Stn 1–K–1; PIBOC Collection (1991) Stns 14, 16, 17, 58; A.V. Grischenko Collection (1991) Stn 17; KamchatNIRO Collection (2013) Stn 69 (see Appendix 1 for details).

Measurements. NHMUK 1899.5.1.273, locality unknown (Fig. 3B, C, I). ZL, 0.80–1.43 (1.03 ± 0.14). ZW, 0.42–0.70 (0.53 ± 0.06). ZD, 0.50–0.55 (n = 2). OrL, 0.22–0.30 (0.27 ± 0.03). OrW, 0.25–0.37 (0.30 ± 0.03). OeL, 0.27–0.40 (0.34 ± 0.03). OeW, 0.37–0.50 (0.44 ± 0.03). Av(s)L, 0.15–0.30 (0.21 ± 0.04). Av(ad)L, 0.32–0.67 (0.46 ± 0.09). P(m)N, 8–15 (10). P(oe)N, 9–14 (12).

ZIRAS 71/50109, Kodiak Island, Gulf of Alaska, Pacific Ocean (Fig. 3A, D–F, H, J–M). ZL, 0.71–1.08 (0.91 ± 0.10). ZW, 0.39–0.63 (0.50 ± 0.05). ZD, 0.47–0.51 (n = 2). OrL, 0.22–0.31 (0.26 ± 0.02). OrW, 0.22–0.30 (0.26 ± 0.02). OeL, 0.27–0.35 (0.32 ± 0.02). OeW, 0.33–0.50 (0.43 ± 0.04). Av(s)L, 0.14–0.25 (0.19 ± 0.03). Av(ad)L, 0.29–0.45 (0.37 ± 0.04). P(m)N, 8–13 (11). P(oe)N, 10–17 (15) (n = 20).

Description. Colonies initially encrusting, multiserial, unilaminar, but rapidly forming extensive bilamellar

(Fig. 3A, M) ruffled vertical structures attaining up to 70 × 52 mm in size; bright yellow when alive, light yellow when dried. Bilaminate parts of colony reaching thickness up to 1.15 mm. Colonies lacking complete accretion

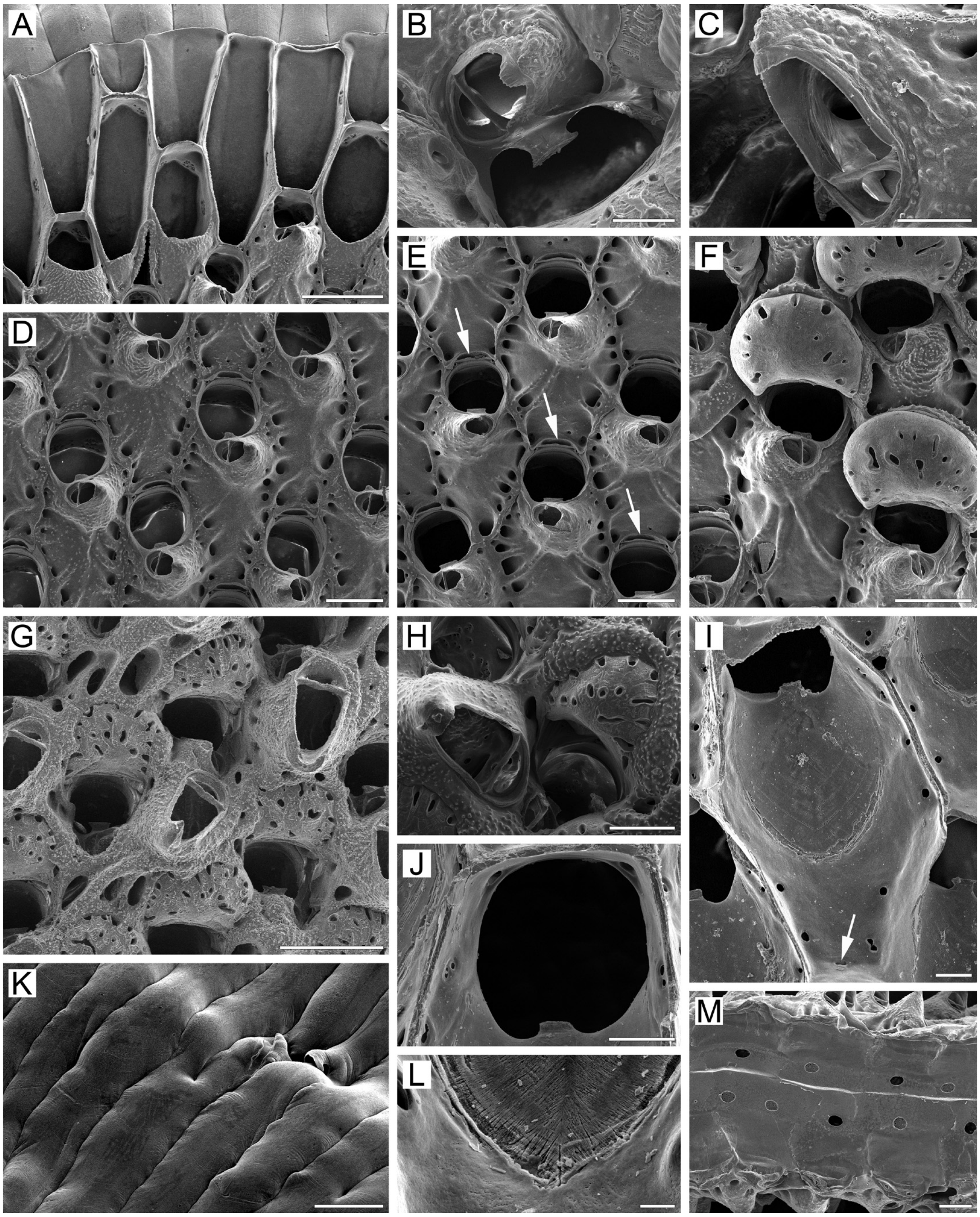

FIGURE 3. *Rhamphostomella costata* Lorenz, 1886. A, D–F, H, J–M. ZIRAS 71/50109 (Kodiak Island, Gulf of Alaska, Pacific Ocean). B, C, I. NHMUK 1899.5.1.273 (locality unknown). G. USNM 11148 (Point Barrow, Beaufort Sea). A. Growing margin of bilaminate erect part of colony, with one layer asynchronously encrusting opposite basal surface of another. B. Distal view of orifice of ovicellate zooid, showing lyrula and suboral avicularium. C. Suboral avicularium. D, E. Non-ovicellate zooids in young part of colony (in E, arrows indicate communication pores of future ooecia). F. Ovicellate zooids in young part of colony. G. Ovicellate zooids in older part of colony, showing ooecia overgrown by the secondary calcification and large adventitious avicularia. H. Oblique view of ovicellate zooid, showing ooecium embedded in the secondary calcification and size difference between suboral and adventitious avicularia. I. Interior of frontal shield, showing ring scar and areolae. J. Internal view of orifice, showing lyrula. K. Basal surface of one lamina of bilaminate colony. L. Close-up of frontal shield interior, showing ring scar, exterior wall microstructure of umbonuloid component and ooecial communication pore (arrow). M. Zooidal lateral walls in bilaminate colony, showing mural pore chambers. Scale bars: A, G, K, 500 µm; B, C, I, J, 100 µm; D–F, 250 µm; H, M, 200 µm; L, 50 µm.

of adjoining layers, with narrow slit-like spaces present between them. Orientation of zooidal rows in apposed layers (Fig. 3A) not entirely coinciding, with angles of 5–10° between them. Rates of development of zooids of apposed layers not fully synchronized, with one layer preceding another (Fig. 3A). Zooids large, hexagonal to oval, comprising regular straight rows, packed in quincunx; demarcated by lateral and transverse walls, sometimes with fine sutures. Boundaries between zooids clearly visible in young parts of colony but obscured by secondary calcification in older parts (Fig. 3D–G).

Frontal shield (Fig. 3A, D, E, I) thickened, convex, smooth or with sparse fine granulation in young zooids and densely granular in older parts of colony, with round to elongate-oval and angular areolae along zooidal margins, separated by relatively long, narrow radially arranged interareolar ridges, some of which (distal as well as proximal) connected with cystid of suboral avicularium (Fig. 3D–F). Umbonuloid component occupying about 60% of length of frontal shield (58% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 3I). Ring scar discrete (Fig. 3L), forming regular boundary between exterior-walled umbonuloid part with exterior-wall planar-spherulitic fabric and extra-umbonuloid part having interior wall microstructure.

Primary orifice (Fig. 3E, J) irregularly rounded to oval, often angular; distal and lateral margins formed by upper terminal part of distal transverse wall (Fig. 3A, D, E). Distal margin of orifice shallowly rounded, proximal margin concave with anvil-shaped or trapezoidal median lyrula. Condyles absent. Oral spines absent in majority of zooids, but two ephemeral oral spines occasionally evident in marginal zooids.

Secondary orifice (Fig. 3D–G) round to oval or irregularly triangular in outline, cormidial, formed proximally by smooth distal part of frontal shield incorporating avicularian cystid. Frontal shield later forming very low, vertical collar-like extension surrounding secondary orifice (Fig. 3D, E), especially evident in ovicellate zooids (Fig. 3F). Secondary orifice restricted distally and distolaterally by vertical walls of distal and lateral zooids. Outline of secondary orifice often changing during development of secondary calcification, acquiring an irregular oval (Fig. 3G) or even roughly triangular shape.

Suboral avicularian cystid relatively small, occupying one-third of zooidal frontal shield or less, conical, strongly elevated, abruptly narrowing terminally, with blunt tip, placed on left or on right side with respect to zooidal orifice; surface finely granular, with 3–5 communication pores (Fig. 3B–E); avicularian frontal surface (rostral/postmandibular areas) situated on left or right slope of cystid, usually crossed by zooidal midline, facing obliquely laterally. Rostrum elongate-triangular or oval-like, with blunt apex and small, finely denticulate hook at rostral tip (Fig. 3B, C), directed medially or proximomedially upwards. Palate elongate-triangular to semielliptical. Palatal foramen large, conforming to shape of both rostrum and palate, opesia more or less semicircular. Crossbar complete.

Large adventitious avicularium of similar form, developing on frontal shield of older zooids, occupying entire surface of zooid, sometimes extending to marginal area of neighbouring lateral zooid (Fig. 3G, H); cystid broad, strongly elevated, with finely granulated surface, frontal surface of avicularium facing distofrontally; rostrum elongate-triangular, blunt, with hooked tip, directed proximolaterally to proximally; palate and palatal foramen elongate-triangular to spatulate, with rounded distal end, opesia semicircular. Crossbar complete. In older parts of colony, adventitious avicularia and thick secondary calcification covering most of frontal surface, strongly changing appearance of zooids (compare Fig. 3D, E, F with Fig. 3G).

Ovicells cleithral, hyperstomial in young zooids (Fig. 3F), becoming subimmersed in older zooids due to secondary calcification arising from daughter and neighbouring zooids and covering ooecium. Further development of secondary calcification resulting in strong immersion, with brood chamber becoming similar to an endozooidal ovicell (Fig. 3G–H). Ooecium broader than long, proximal margin slightly concave. Ectooecium initially smooth, with scattered round, oval, or irregular pseudopores. In older zooids, sometimes slightly eroded and partly covered by finely granular secondary calcification, sometimes showing fine sutures demarcating calcification originating from different zooids; some peripheral pseudopores partly occluded by secondary calcification (Fig. 3G). Ooecium formed by distal autozooid from slit-like concavity with communication pore at bottom, situated in proximalmost part of frontal shield immediately distal to margin of maternal primary orifice (Fig. 3D, E); communication pore leading to canal connecting ooecial and visceral coeloms, opening on underside of frontal shield of distal zooid as straight, slit-like communication pore very close to transverse wall (Fig. 3I).

Zooids interconnected by one or two mural pore chambers in each distolateral wall (Fig. 3M). Usually, two multiporous septula in basal half of transverse walls (Fig. 3A), sometimes with additional individual/paired pores in between. Some transverse walls with one or three septula of various sizes.

Basal surface of zooids (Fig. 3K) fully calcified, inflated, with sparse white spots; rare tubular protuberances present (0.09–0.28 mm in diameter), narrowing terminally. Boundaries between zooids recognizable basally by deep, slightly meandering incisions.

Ancestrula and early astogeny not observed.

Remarks. Although Lorenz (1886) interpreted Smitt's (1868a, pl. 28) figures 186–188 as depicting his new species *R*. *costata*, and gave his own image (pl. 7, fig. 11), we doubt whether he correctly attributed the specimen for Smitt's fig. 188 to *R*. *costata*.

In the general appearance of zooids and the particular combination of 1) an elevated, conical suboral avicularium and 2) strongly protruding adventitious avicularia that occupy the entire surface of the frontal shield and have an elongate-triangular rostrum with a hooked tip, this species strongly resembles *R*. *cristata*; this resemblance has resulted in many instances of misidentification of both species (see the synonymy for *R*. *cristata* below). However, *R*. *costata* clearly differs from *R*. *cristata* as follows: 1) the proximal border of the primary orifice always has a central lyrula in *R*. *costata*, whereas there is only a small median prominence in *R*. *cristata* (if an equivalent process develops in the latter species, it is always broad and very shallow); 2) the lateral margins of the secondary orifice are even in *R*. *costata* but have tall, symmetrical triangular lappets in *R*. *cristata*; 3) the palate in adventitious avicularia is elongate-triangular to spatulate, with a rounded tip, in *R*. *costata*, whereas it is strictly elongate-triangular and acute in *R*. *cristata*; 4) the ridges separating areolae reach only the sides of the suboral avicularian cystid in *R*. *costata* but continue to the cystid apex in *R*. *cristata*, giving a very characteristic costate pattern to the frontal shield exterior; 5) ovicells are initially prominent, but the ooecium is rapidly overgrown by secondary calcification proceeding from surrounding zooids, leaving only the central area of ectooecium free in *R*. *costata*, whereas they remain exposed and not covered by calcification in *R*. *cristata*; 6) colonies of *R*. *costata* are initially encrusting, later producing erect parts, whereas those of *R*. *cristata* are solely encrusting; and 7) numerous protuberances develop on the basal surface of zooids in *R*. *costata*, wheras these protuberances are rare in *R*. *costata*.

Canu & Bassler (1928) described *Rhamphostomella magnirostris* from Cedar Keys, western Florida, Gulf of Mexico (about 29°05.0′ N, 83°04.0′ W), pointing out the obvious resemblance of their new species to *R*. *costata*. Our SEM examination of the syntype specimen of *R*. *magnirostris* (USNM 7579) clearly indicated that it is *R*. *costata* (Fig. 31H, I). One explanation for the presence of a boreal-Arctic species in the tropical Caribbean is that it was introduced, but it is more likely that the specimen was collected in the Arctic/boreal region of North America and subsequently mistakenly labeled.

The Canadian Museum of Nature contains a dried specimen of *R*. *costata* from British Columbia identified by O'Donoghue (Cat. No. – CMNI 1988-0286, False Narrows), but unfortunately, we were unable to examine the specimen or images of it.

Ecology. *Rhamphostomella costata* has been reported over a depth range of 0–308 m, predominantly on hard bottoms (including rocky plateaus, silty rocky platforms, crevices and vertical surfaces), inhabiting rocky substrates such as boulders, blocks, and pebbles). Colonies also encrust bivalve and gastropod mollusc shells, polychaete tubes, hydroids, barnacles and other bryozoans (e.g. *Dendrobeania fruticosa*, *Celleporina nordenskjoldi*) and are occasionally found on flexible substrates such as the thalli of laminarian and red algae. Large, erect parts of colonies of *R*. *costata* in turn provide a niche for a diverse epibiotic community, including hydrozoans, spirorbid polychaetes, other bryozoans, ascidians and amphipod and isopod crustaceans.

Distribution. This boreal-Arctic, circumpolar, sublittoral to upper bathyal species is widely distributed in the seas of the Northern Hemisphere. Arctic records include the Barents Sea (Nordgaard 1896, 1900, 1907a, 1912, 1918; Bidenkap 1900a, 1900b; Waters 1900; Andersson 1902; Norman 1903; Kluge 1906, 1915, 1962, 1975; Kuznetsov 1941; Denisenko 1988, 1990), White Sea (Kluge 1908a, 1928; Gostilovskaya 1957, 1978; Grishankov 1995; Ostrovsky 2009, 2013), Kara Sea (Levinsen 1887; Kluge 1962, 1975; Denisenko 2021), Laptev Sea (Kluge 1929, 1962, 1975; Gontar 1990), East Siberian Sea (Nordgaard 1929; Kluge 1929, 1962, 1975; Gontar 1994a, 1994b; Denisenko 2011), Chukchi Sea (Kluge 1929, 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), Point Barrow, Alaska, Beaufort Sea (Osburn 1955), Canadian Arctic Archipelago (Nordgaard 1906, 1929; Osburn 1932, 1936), Baffin Bay (Hansen 1962), Hudson Bay (Gontar & Denisenko 1989), Labrador (Osburn 1912b), Davis Strait (Kluge 1962, 1975; Hansen 1962), western Greenland (Smitt 1868a; Norman 1906; Kluge 1908b; Osburn 1919, 1936; Denisenko & Blicher 2021), eastern Greenland (Andersson 1902; Denisenko 2008; Denisenko & Kuklinski 2008; Denisenko & Blicher 2021), Jan Mayen Island (Lorenz 1886), Franz-Jozef Land (Denisenko 1990), Spitsbergen (Gontar *et al*. 2001; Kuklinski 2002b, 2009; Kuklinski & Bader 2007b; Kuklinski & Taylor 2009) and northern Norway (Nordgaard 1905, 1918). In the northwestern Atlantic, *R*. *costata* is known from the Gulf of St Lawrence (Hincks 1889; Whiteaves 1901) and the Gulf of Maine southwards to Cape Cod and Woods Hole (Osburn 1912a, 1933; Powell 1968b; Ryland & Hayward 1991). In the northwestern Pacific, it is known from the Bering Sea, including Chaplin Cape, Chukotsky Cape, St Lawrence Island, Anadyrsky Gulf, Navarin Cape (Kluge 1961; Grischenko 2002), Korfa Gulf (our data), Litke Strait (our data), Africa Cape, Avacha Gulf (Kluge 1961; Grischenko 2002; our data), Commander Islands (Grischenko 1997, 2002); Sea of Okhotsk along the western Kamchatka shelf and slope (Grischenko 2015; our data), eastern coast of southern Sakhalin Island (Kluge *et al*. 1959; Kluge 1961), Aniva Gulf (Kluge 1961), Shantar Archipelago (Kluge 1961), Kuril Islands, including Paramushir and Shikotan (Kluge 1961; Gontar 1980), and South Kuril Strait (Kluge *et al*. 1959); Sea of Japan, including Tatar Strait, western shore of the southern Sakhalin Island (Androsova 1958; Kluge *et al*. 1959; Kluge 1961), northern Primorje (Kluge 1961; Tarasova 1983), Hokkaido (Mawatari 1965; Mawatari & Mawatari 1981). In the northeastern Pacific this species is known from Cook Inlet (Kessler 1985; Foster 2010) and near Kodiak Island, Gulf of Alaska (Dick & Ross 1986, 1988; our data) south to Puget Sound (O'Donoghue & O'Donoghue 1925).

Rhamphostomella cristata **(Hincks, 1889)**

(Figs 4, 30C, 31J, K)

Rhamphostomella costata var. *cristata* Hincks, 1889, p. 426, pl. 21, fig. 6.
Rhamphostomella costata var. *cristata*: Osburn 1912b, p. 286; 1932, p. 14; Kluge 1962, p. 539, fig. 376; 1975, p. 656, fig. 376; Androsova 1977, p. 202; Denisenko 1988, p. 13; 1990, p. 39; Gontar & Denisenko 1989, p. 359.
Rhamphostomella costata cristata: Tarasova 1983, p. 25, fig. 32; Gontar 1994a, p. 146; 2010, p. 153; Grischenko 1997, p. 174; Gontar *et al*. 2001, p. 195.
Rhamphostomella cristata: Grischenko 2002, p. 115; 2003b, p. 237; Denisenko 2011, p. 14; 2013, p. 184.
Rhamphostomella fortissima Bidenkap, 1900a, p. 524, pl. 19, fig. 8.
Rhamphostomella fortissima: Osburn 1952, p. 427, pl. 50, figs 1, 2; 1955, p. 38; Gontar 2010, p. 153; Foster 2010, p. 57.
Discopora scabra var. *fortissima*: Nordgaard 1918, p. 78; 1929, p. 7.

Material examined. *Neotype*: NHMUK 1911.10.1.1576A, one colony fragment, A.M. Norman Collection, Gulf of St Lawrence, Atlantic Ocean, collector J. Whiteaves.

NHMUK 2013.10.21.7a, one colony encrusting oyster shell, RV *Norseman*, Stn AST–2, 16 July 2011, reef in middle of Boot Bay, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°44.4′ N, 176°30.3′ W, depth 10–12 m, SCUBA, collector P. Kuklinski. ZIRAS 2/50110, two colony fragments, KIENM Collection, Stn 142, 28 July 1992, Cape Lebyazhy, coastal waters of Medny Island, Commander Islands, Pacific Ocean, 54°35.9′ N, 167°52.1′ E, depth 30 m, SCUBA, collector V.V. Oshurkov.

Additional material. 64 specimens. IMB Collection (1972) Stns 6/16, 34/104; (1973) Stns 110/290, 110/292, 158/393, 233/591; KIENM Collection (1991) Stns 215, 221; (1992) Stns 4, 20, 28, 34, 38, 39, 99, 125, 128, 137, 142, 145, 146; KamchatNIRO Collection (2013) Stn 189 (see Appendix 1 for details).

Measurements. ZIRAS 2/50110, Medny Island, Commander Islands, Pacific Ocean (Figs 4A–M, 30C). ZL, 0.79–1.33 (1.01 ± 0.14). ZW, 0.47–0.65 (0.56 ± 0.04). ZD, 0.57–0.70 (n = 2). OrL, 0.25–0.33 (0.29 ± 0.02). OrW, 0.27–0.38 (0.31 ± 0.02). OeL, 0.30–0.40 (0.35 ± 0.03). OeW, 0.39–0.55 (0.48 ± 0.03). Av(s)L, 0.15–0.31 (0.24 ± 0.04). Av(ad)L, 0.17–0.33 (0.26 ± 0.04). P(m)N, 14–23 (18). P(oe)N, 11–32 (20) (n = 10).

NHMUK 2013.10.21.7a, Adak Island, Aleutian Islands, Pacific Ocean. ZL, 0.56–1.04 (0.83 ± 0.12). ZW, 0.32–0.53 (0.43 ± 0.05). ZD, 0.49–0.58 (n = 2). OrL, 0.19–0.27 (0.23 ± 0.01). OrW, 0.21–0.28 (0.24 ± 0.02). OeL, 0.28–0.36 (0.34 ± 0.02) (n = 10). OeW, 0.38–0.47 (0.43 ± 0.02) (n = 10). Av(s)L, 0.13–0.31 (0.21 ± 0.05) (n = 23). P(m)N, 6–16 (12) (n = 10). P(oe)N, 17–25 (20) (n = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 4A), more or less circular, attaining up to 51 mm in any one direction; bright red when alive, orange to light pink when dry. Zooids large, oval, hexagonal or pyriform, widest in distal half, arranged in regular rows with checkerboard pattern, demarcated by fine sutures between lateral and transverse walls, visible predominantly in young parts of colony.

Frontal shield umbonuloid (Fig. 4A, E, I), thickened, convex, finely granulated, with numerous, comparatively small round to elongated areolae along zooidal margins, separated by long, narrow, prominent interareolar ridges, arranged centripetally and continuing to apex of suboral avicularium, giving very characteristic striated pattern to frontal shield (Fig. 4D, E). With age, size and number of areolae reduced as frontal-shield calcification thickens. Umbonuloid component extensive, occupying about 60% of length of frontal shield (63% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 4I, L). Ring scar discrete (Fig. 4L), forming regular boundary between exterior and interior wall microstructure.

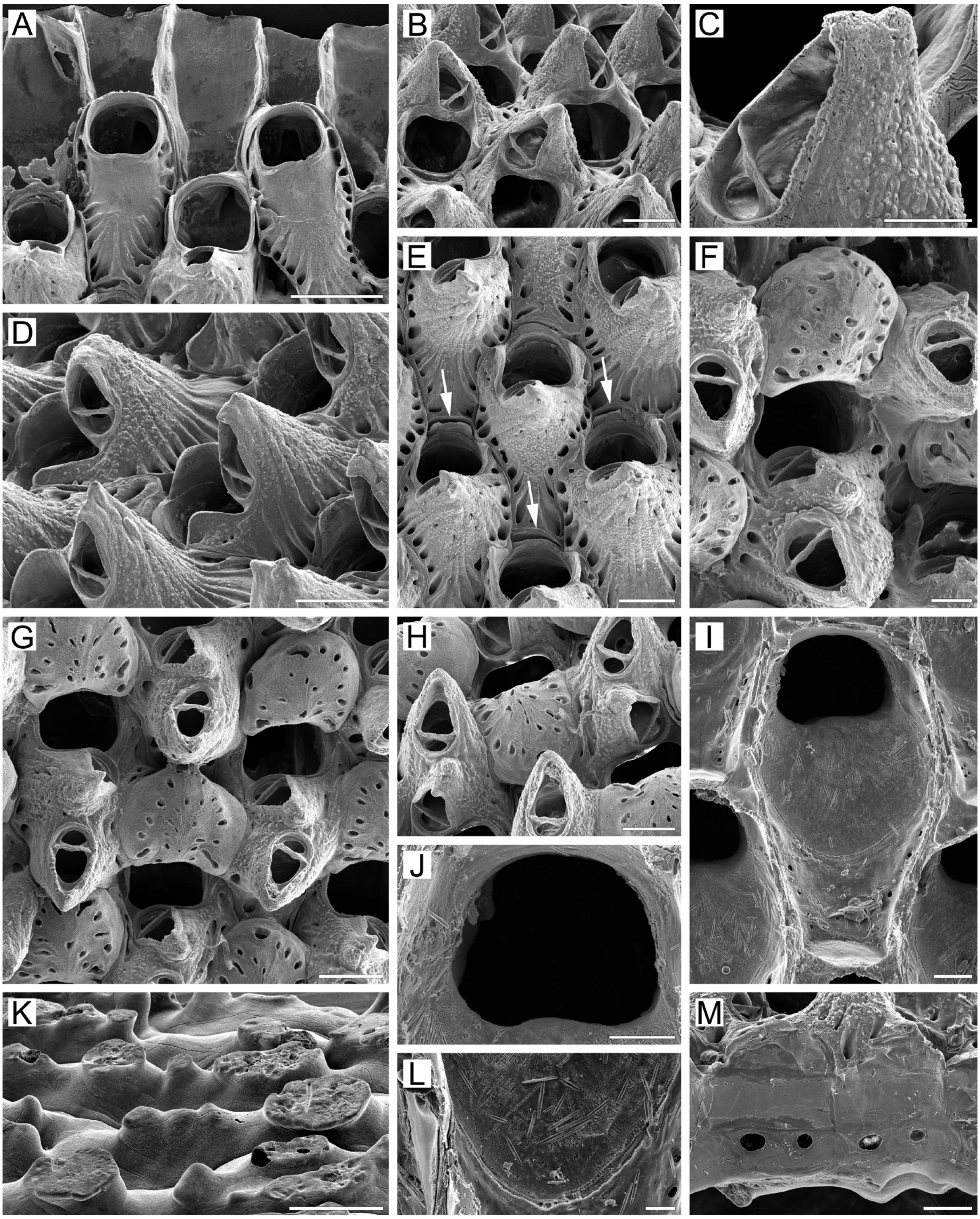

FIGURE 4. *Rhamphostomella cristata* (Hincks, 1889). ZIRAS 2/50110 (Medny Island, Commander Islands, Pacific Ocean). A. Colony margin with developing zooids. B. Distal view of non-ovicellate zooids, showing primary orifices and suboral avicularia. C. Suboral avicularium. D. Lateral view of non-ovicellate zooids, showing suboral avicularium and lobes of peristome. E. Group of non-ovicellate zooids in young part of colony (arrows, communication pores of future ooecia). F. Ovicellate zooid with ooecium, suboral and adventitious avicularia. G. Group of ovicellate zooids in older part of colony. H. Distal view of ovicellate zooids, showing suboral and adventitious avicularia. I. Interior of frontal shield, showing ring scar and areolae. J. Internal view of orifice, showing slightly curved proximal margin and hardly recognisible condyles. K. Lateral view of basal colony surface with numerous protuberances. L. Frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. M. Zooidal lateral wall with mural pore chambers. Scale bars: A, K, 500 µm; B, D, E, G, 250 µm; C, F, I, J, 100 µm; H, M, 200 µm; L, 50 µm.

Primary orifice (Fig. 4A, B, J) roundly quadrangular or bell-shaped; distal and lateral margins formed by upper terminal part of distal transverse wall sometimes forming narrow shelf (Fig. 4A). Distal margin of orifice round, proximal margin with broad, low median prominence and broadly rounded proximolateral corners. Condyles absent. Oral spines absent in majority of zooids, but two ephemeral oral spines occasionally evident at distal margin of orifice on marginal zooids.

Secondary orifice (Fig. 4E–G) round to semicircular and trapezoidal, cormidial, formed proximally by distal part of frontal shield incorporating avicularian cystid medially and having two tall, symmetrical, triangular lappets laterally. Secondary orifice distally and distolaterally restricted by elevated vertical walls of distal and lateral zooids. In ovicellate zooids, lateral lappets connecting to proximolateral corners of ooecium (Fig. 4F, G), conferring incomplete tubular peristomial form to secondary orifice.

Cystid of suboral avicularium large, broad, conical, strongly elevated, occupying most of frontal shield, with finely granulated surface and 4–7 communication pores (Fig. 4A, D, E). Frontal surface of avicularium (rostral/postmandibular areas) situated on left or right side of avicularian cystid, often out of zooidal midline, facing distolaterally. Rostrum elongate-triangular, pointed or sometimes blunt, directed proximomedially upwards, with short terminal hook. Palate elongate-triangular with pointed end. Palatal foramen triangular with rounded distal end, surrounded by very narrow cryptocystal shelf, opesia semicircular. Crossbar complete.

Adventitious avicularia developing in older parts of colony, occupying proximal half of frontal shield proximal to suboral avicularium. Avicularian cystid strongly elevated vertically, with finely granulated surface (Fig. 4F–H). Avicularian frontal surface facing obliquely frontodistally to distolaterally. Rostrum elongate-triangular, pointed, directed obliquely frontalwards, with a short terminal hook. Palatal foramen elongate-triangular or oval-triangular with narrow cryptocystal shelf distally, opesia rounded or elliptical, surrounded by narrow cryptocyst. Crossbar complete. In older parts of colony, adventitious avicularia and thick secondary calcification covering most of frontal shield, strongly changing appearance of zooids (compare Fig. 4E with Fig. 4G).

Ovicells hyperstomial. Ooecium formed by distal autozooid around slit-like concavity with communication pore at bottom, situated in proximalmost part of frontal shield just immediate to distal margin of maternal primary orifice (Fig. 4E). Ooecium broader than long (Fig. 4F–H), with straight or slightly concave proximal margin. Ectooecium smooth, with round, oval or slit-like pseudopores having radial arrangement. In most cases, ooecia not overgrown by secondary calcification, even in older zooids, or peripheral part surrounded by narrow rim (Fig. 4G). In older zooids, ovicells becoming less prominent relative to colony surface because of thickening of frontal shields in surrounding zooids and development of adventitious avicularia; ooecia mostly free of secondary calcification, however.

Zooids interconnected by two mural pore chambers in each distolateral wall (Fig. 4M) and usually two multiporous septula in basal half of transverse walls (corresponding to two recesses sometimes with medial buttress between them on distal side, Fig. 4A). Some such septula were complex, consisting of three to several small pore groups. Up to three "overlapping" septula of various sizes formed wide horizontal "band".

Basal surface of zooids (Figs 4K, 30C) fully calcified, convex, smooth, with numerous columnar protuberances (0.14–0.59 mm in diameter), flattened and broadened terminally. Boundaries between zooids clearly recognizable basally by deep, meandering incisions. Abundant white spots (presumably less-calcified areas) visible in semitransparent basal wall under light microscope.

Ancestrula and early astogeny not observed.

Remarks. According to Kluge (1962, 1975), zooids of *R. cristata* have a small oblique process or prominence on the proximal margin of the primary orifice, and our study confirms this (Fig. 4J). Some colonies have zooids with a broad, very low process along the proximal margin, in contrast to the central, clearly prominent and discrete process typical of *R. costata*.

Kluge (1962, 1975) mentioned a couple of ephemeral oral spines on the distal rim of the orifice in zooids at the colony margin. While most colonies we examined have a few marginal zooids with two oral spines, one colony (NHMUK 2013.10.21.7a) from the shallow waters of Adak Island, Aleutians, has a rather broad zone of marginal zooids, up to three generations deep, all of which have two or three short oral spines.

Some authors have considered *R. cristata* to be a subspecies or variety of *R. costata* (Hincks 1889; Osburn 1912b, 1932; Kluge 1962, 1975; Androsova 1977; Denisenko 1988, 1990; Gontar & Denisenko 1989; Gontar 1994a; Grischenko 1997). However, based on the set of characters described above (see Remarks for *R. costata*), *R. cristata* clearly differs from *R. costata* and we thus consider it to be a distinct species.

Because we could not locate Hincks's material, we have selected a neotype for this species based on a specimen collected by J. Whiteaves – similarly to Hincks (1889) – in the Gulf of St Lawrence, North Atlantic, and residing in the Natural History Museum, London.

Ecology. *Rhamphostomella cristata* has been recorded over a depth range of 10–197 m, mainly on hard bottoms and rock faces (including crevices), boulders, blocks and gravel, and sometimes on silty bottoms overlain with pebbles. In addition to rocky surfaces, colonies encrust serpulid tubes, hydroids, other bryozoans (e.g. *Dendrobeania murrayana*) and shells of bivalve molluscs. Some colonies were a component of the cryptic community inhabiting internal cavities formed by the crustose coralline alga *Clathromorphum nereostratum*.

Distribution. *R*. *cristata* is a high-boreal-Arctic, sublittoral species (Kluge 1962, 1975; Gontar & Denisenko 1989). Arctic records include the Barents Sea (Bidenkap 1900a; Kluge 1962, 1975; Denisenko 1988, 1990), Kara Sea (Gontar & Denisenko 1989; Denisenko 2021), East-Siberian Sea (Nordgaard 1929; Gontar 1994a; Denisenko 2011), Chukchi Sea (Gontar 2010), Point Barrow, Alaska, Beaufort Sea (Osburn 1952, 1955), Canadian Arctic Archipelago (Nordgaard 1929), Hudson Bay (Osburn 1932), Labrador (Osburn 1912b), eastern Greenland (Kluge 1962, 1975; Denisenko & Blicher 2021), Greenland Sea (Gontar & Denisenko 1989), Spitsbergen (Kluge 1962, 1975; Gontar *et al*. 2001), Franz-Josef Land (Kluge 1962, 1975; Denisenko 1990) and northern Norway (Nordgaard 1918). In the northwest Atlantic it has been reported from St Lawrence Gulf and Newfoundland (Hincks 1889; Whiteaves 1901; Gontar & Denisenko 1989). In the northwestern Pacific *R*. *cristata* is known from the Bering Sea near the Commander Islands (Grischenko 1997, 2002, 2003b), from the western Kamchatka shelf of the Sea of Okhotsk (our data) and along northern Primorye, Sea of Japan (Tarasova 1983). Northeastern Pacific localities include Cook Inlet, Gulf of Alaska (Foster 2010) and the coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean (our data).

Rhamphostomella gigantea Osburn, 1952

(Figs 5, 30D, 32A, B)

Rhamphostomella gigantea Osburn, 1952, p. 433, pl. 50, fig. 5.
Rhamphostomella scabra: Mawatari 1965, p. 619, text-figs 126a, b.
Petraliella sp.: Mawatari 1956, p. 123, figs 8a–c.

Additional references. *Rhamphostomella gigantea*: Osburn 1955, p. 38; MacGinitie 1955, p. 132; Foster 2010, p. 57; Gontar 2010, p. 153.

Material examined. *Holotype* (labeled as TYPE): USNM 11033, record name Che–982, one colony fragment, 9 August 1948, Point Barrow, Alaska, Beaufort Sea, depth 33.5 m, collector G.E. MacGinitie.

ZIRAS 1/50127, one colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 118, 28 May 1988, Avacha Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 52°53.0′ N, 160°08.0′ E, depth 176 m, rock dredge, collector A.V. Rzhavsky. ZIRAS 2/50128, one colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 119, 24 May 1988, Avacha Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 52°54.0′ N, 160°01.0′ E, depth 141 m, rock dredge, collector A.V. Rzhavsky. ZIRAS 3/50129, one colony fragment detached from broken shells of bivalve mollusc *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko. MIMB 3/50213 (recorded as *R*. *scabra*), five colony fragments. IMB Collection, RV *Atma*, Stn 248/697, 12 October 1976, coastal waters southwest of Moneron Island, Sea of Japan, 46°14.0′ N, 141°09.0′ E, depth 120 m, Sigsbee trawl, collector V.I. Lukin. NHMUK 2008.05.29.4, one colony fragment, Rusalca Expedition, RV *Professor Khromov*, Stn 62B, 22 August 2004, Chukchi Sea, 71°23.5′ N, 174°52.3′ W, depth 74.6 m, collector B. Bluhm. NHMUK 2010.2.9.3, one colony fragment detached from broken shell of bivalve *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko. UAM Bry–408, one colony fragment, Arctic Research Laboratory Collection, off Point Barrow, Beaufort Sea, 15 September 1948, depth 33.5 m, collector G.E. MacGinitie. UAM Bry 77–1, one colony fragment, RV *Surveyer*, 17 March 1977, northwest of Unimak Island, Aleutian Islands, Bering Sea, 54°40.3′ N, 165°09.1′ W, depth 82 m.

Additional material. Two specimens. KamchatNIRO Collection (2013) Stn 62 (see Appendix 1 for details).

Measurements. ZIRAS 1/50127, Avacha Gulf, eastern Kamchatka, Pacific Ocean (Fig. 5K–L). ZL, 1.05–2.31 (1.45 ± 0.33). ZW, 0.57–0.96 (0.75 ± 0.08). ZD, 0.55–0.80 (n = 2). OrL, 0.29–0.38 (0.33 ± 0.02). OrW, 0.30–0.38

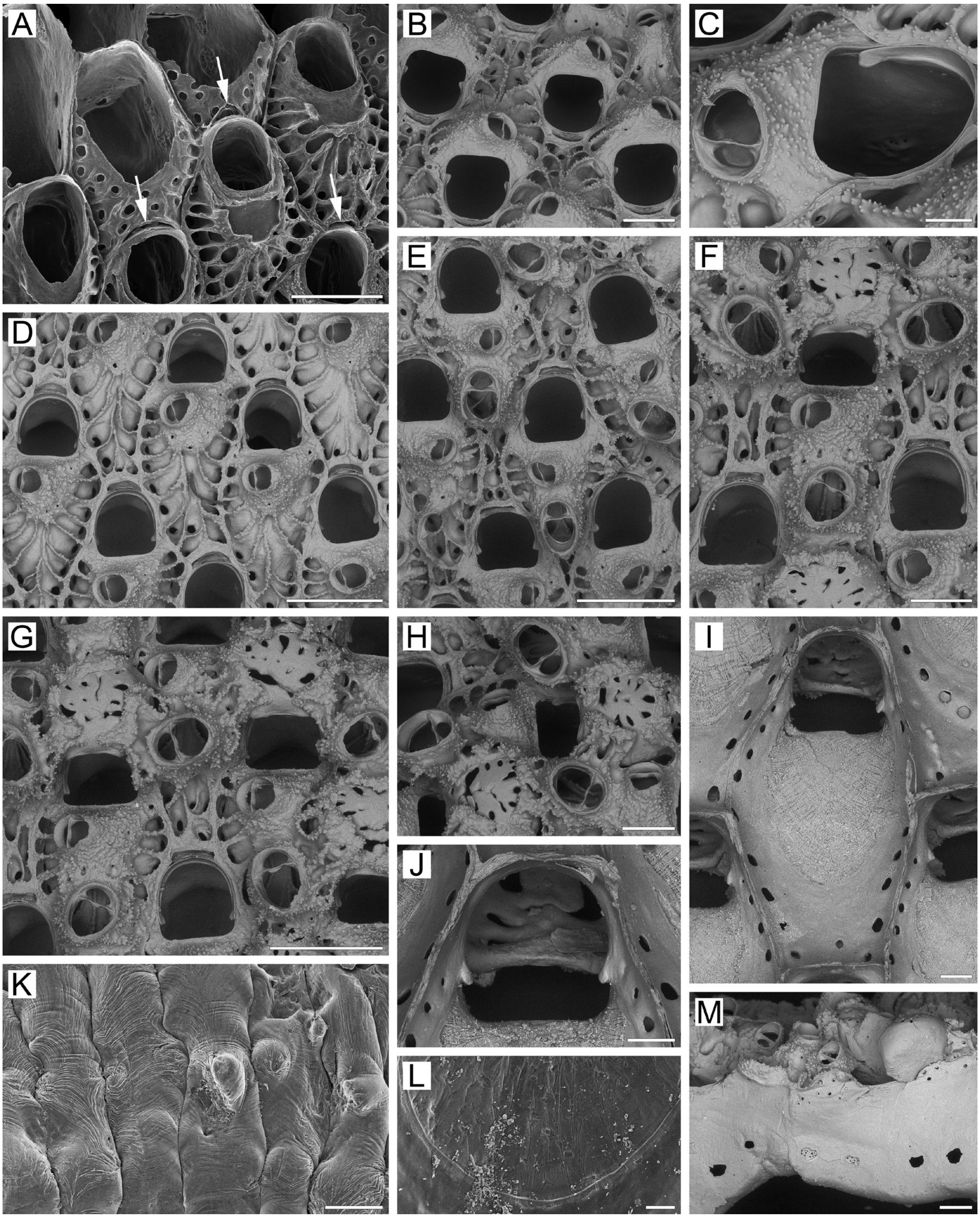

FIGURE 5. *Rhamphostomella gigantea* Osburn, 1952. A. ZIRAS 3/50129 (western Kamchatka, Sea of Okhotsk). B–J, M. MIMB 3/50213 (Moneron Island, Sea of Japan). K, L. ZIRAS 1/50127 (Avacha Gulf, eastern Kamchatka, Pacific Ocean). A. Colony margin with developing zooids (arrows, communication pores of future ooecia). B. Distal view of young part of colony with non-ovicellate zooids, showing details of the primary orifice and suboral avicularia. C. Lateral view of primary orifice with suboral avicularium. D. Non-ovicellate zooids with suboral avicularia in young part of colony. E. Group of non-ovicellate zooids with suboral and adventitious frontal avicularia in young part of colony. F, G. Ovicellate zooids with adventitious avicularia in older part of colony. H. Lateral view of ovicellate zooids in older part of colony. I. Interior of frontal shield, showing ring scar and areolae. J. Internal view of orifice, showing straight proximal margin and condyles. K. Basal colony surface. L. Frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of autozooids, showing suboral and adventitious avicularia, ooecium free of secondary calcification and lateral wall with mural pore chambers. Scale bars: A, D, E, G, K, 500 µm; B, F, H, 250 µm; C, I, J, 100 µm; L, 50 µm; M, 200 µm.

(0.34 ± 0.02). OeL, 0.35–0.46 (0.41 ± 0.03). OeW, 0.47–0.65 (0.58 ± 0.04). Av(s)L, 0.08–0.18 (0.13 ± 0.02). Av(ad)L, 0.17–0.28 (0.22 ± 0.02). P(m)N, 15–23 (17). P(oe)N, 5–13 (8) (*n* = 10).

ZIRAS 3/50129, western Kamchatka, Sea of Okhotsk (Figs 5A, 30D). ZL, 0.87–1.73 (1.18 ± 0.20). ZW, 0.49–0.90 (0.65 ± 0.09). ZD, 0.61–0.70 (*n* = 2). OrL, 0.31–0.38 (0.35 ± 0.02). OrW, 0.30–0.40 (0.33 ± 0.03). OeL, 0.37–0.48 (0.42 ± 0.03). OeW, 0.48–0.63 (0.53 ± 0.03). Av(s)L, 0.09–0.18 (0.13 ± 0.02). Av(ad)L, 0.12–0.28 (0.20 ± 0.04). P(m)N, 14–22 (17). P(oe)N, 7–24 (16) (*n* = 20).

MIMB 3/50213, Moneron Island, Sea of Japan (Fig. 5B–J, M). ZL, 1.03–1.48 (1.21 ± 0.11). ZW, 0.52–0.73 (0.62 ± 0.05). ZD, 0.54–0.73 (*n* = 2). OrL, 0.30–0.37 (0.34 ± 0.02). OrW, 0.27–0.34 (0.31 ± 0.02). OeL, 0.37–0.50 (0.45 ± 0.03). OeW, 0.42–0.58 (0.49 ± 0.04). Av(s)L, 0.15–0.24 (0.20 ± 0.03). Av(ad)L, 0.19–0.31 (0.25 ± 0.04). P(m)N, 13–20 (16). P(oe)N, 9–19 (14) (*n* = 12).

Description. Colonies initially encrusting, multiserial, unilaminar (Fig. 5A), giving rise to extensive erect, bilamellar, fan-like, ruffled expansions attaining up to 35 × 33 mm in size. Dried colonies pink to pale yellow. Bilaminate parts of colony up to 1.82 mm thick; adjoining layers incompletely adhering, with narrow spaces occurring between them. Growth directions of zooids in adjoining layers not coinciding, with angles of up to 15° between main axes in opposing layers. Zooids very large, hexagonal to irregularly oval, arranged in regular series in checkered pattern, delineated by fine sutures between lateral walls. Zooidal boundaries clearly visible in zooids of young parts of colony (Fig. 5A, B, G), but obscured by secondary calcification in older parts (Fig. 5E–G).

Frontal shield (Fig. 5A, B, D, E, I) umbonuloid, thickened, initially convex but becoming flatter with age, covered with sharp granules except in areolar depressions along zooidal margins. Areolae large, elongated, separated by narrow, long, radially arranged ridges approaching cystid of suboral avicularium. In some cases, proximalmost ridges fusing with each other along zooid midline (Fig. 5D). Young zooids usually have more than one row of areolae. With age, thickening of frontal shield reduces number of areolae and shortens interareolar ridges, causing a markedly changed appearance in the frontal shield (compare Fig. 5A, D with Fig. 5E–G). Umbonuloid component extensive, occupying about 60% of length of frontal shield (64% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 5I, L). Ring scar discrete (Fig. 5L), forming very regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 5B, D–G, I, J) bell-shaped, longer than wide; distal and lateral margins formed by upper terminal part of distal transverse wall bearing distinct shelf distally and forming condyles laterally; condyles conspicuous, with blunt, round or pointed tips (Fig. 5B–F, I). Distal margin of orifice round, proximal margin straight, devoid of lyrula or median prominence, with proximolateral corners gently rounded. No oral spines.

Secondary orifice (Fig. 5D–H) bell-shaped (longer than wide) to irregularly oval, cormidial, proximally coinciding with proximal margin of primary orifice. Distal and distolateral parts of secondary orifice restricted by vertical walls of distal and lateral zooids.

Suboral avicularium (Fig. 5B–D) with cystid occupying from one-quarter to one-third of frontal shield, inflated to moderately elevated as low cone, with finely granular surface and 2–6 communication pores connecting avicularian and hypostegal coelomic cavities. Frontal surface of suboral avicularium (rostral/postmandibular areas) situated on left or right slope of cystid, usually out of zooidal midline, facing laterally. Rostrum semioval or rounded- triangular, blunt, directed medially to distomedially. Palatal foramen occupying entire internal area of rostrum, opesia oval or semicircular. Crossbar complete.

Larger adventitious avicularium (Fig. 5E–H) oval, shallow, situated proximal to suboral avicularium in central to proximal area of frontal shield on most zooids in older parts of colony; cystid relatively narrow, only slightly elevated, with finely granulated surface. Frontal surface of larger avicularium facing obliquely frontalwards. Rostrum broadly oval, blunt, directed laterally to proximally; palatal foramen shorter than rostrum, with narrowly arcuate distal cryptocystal shelf, opesia semicircular. Crossbar complete. Avicularian cystid acquiring roughly tuberculate appearance with development of secondary calcification (Fig. 5G, H).

Ovicells prominent in young zooids, rapidly becoming subimmersed and even appearing endozooidal as secondary calcification spreads from distal and distolateral zooids to cover most of ooecium except central pseudoporous part (Fig. 5F–H). Secondary calcification finely granulated or pustulose, with sutures demarcating lobes formed by different zooids (Fig. 5H), additionally forming tongue-like lobes over proximal edge of ooecium to left and right and continuing around primary orifice. Ooecium formed by distal autozooid around narrow shallow concavity with communication pore at bottom, situated in proximalmost part of frontal shield just distal to distal margin of maternal primary orifice (Fig. 5A, B, D, E); communication pore leading to canal connecting ooecial and visceral coeloms, opening on underside of frontal shield of distal zooid as straight, slit-like communication pore very close to transverse wall. In bleached material, upper part of ectooecium formed by flat, coalesced costa-like projections (often with slightly elevated margins), with radially arranged or scattered irregular pseudopores of various sizes between them (Fig. 5F–J). Some pseudopores later occluded by secondary calcification. Each ooecium flanked by three larger avicularia.

Two mural pore chambers in each distolateral wall (Fig. 5M). Communication pores usually forming two multiporous septula in basal half of transverse walls. In some zooids septulum single, central, or as horizontal "band". Multiporous septula sometimes added by random individual pores.

Basal surface of zooids (Figs 5K, 30D) fully calcified, roughly lineated, with rare, small bulges (0.18–0.42 mm in diameter). Boundaries between zooids recognizable basally by deep meandering incisions. Basal areas of large, erect, bilamellar colonies often fully occupied with heavily calcified kenozooids; kenozooids large, rhomboidal to oval or irregular in form, positioned randomly, sometimes united in clusters with indistinguishable boundaries. Older regions of colony also frequently with numerous frontally budded zooids, orifices partly sealed by closure plates.

Ancestrula and early astogeny not observed.

Remarks. In the original description, Osburn (1952, p. 433) noted that "the primary aperture is only slightly asymmetrical on its proximal border, rounded distally and somewhat straighter on the sides, the length and breadth nearly equal" and "no cardelles". Osburn's illustration (1952, pl. 50, fig. 5) shows two zooids having primary orifices with a gently convex proximal margin. Our SEM examination of the unbleached holotype colony USNM 11033 (Fig. 32A, B) showed mostly a bell-shaped primary orifice, longer than wide (Fig. 32A), with a straight to insignificantly concave proximal margin and gently rounded proximolateral corners. Dry zooids have opercula with a flattened anter, with a distinctive inflexion of the poster down to the ascus (Fig. 32A) at about the proximal one-quarter to one-fifth of operculum length, indicating the presence of condyles, which are obscured by the opercum in the unbleached specimen. The bell-shaped form of the primary orifice with a straight proximal margin, and the inferred presence of condyles in the holotype specimen, is consistent with our material from the northwestern Pacific. Also, the non-ovicelled zooid in the illustration of Osburn (1952) shows an orifice with a shape (except for the proximal margin) generally corresponding to that in our material. We suggest that Osburn either overlooked the small condyles or was unable to see them because of the opercula.

Furthermore, Osburn (1952, p. 433) noticed that "the ovicells are … smooth and imperforate, prominent when young but with complete calcification almost entirely immersed". His illustration (pl. 50, fig. 5) shows a single ooecium with radially arranged slit-like pseudopores, giving a "costate" appearance to at least the distal part of the ectooecium. SEM images of the holotype colony (Fig. 32B) suggest that the ooecia have numerous, circular to (less frequently) slit-like pseudopores scattered over the entire surface of the ectooecium except in the most proximal region. Also, the secondary calcification surrounds only the distolateral periphery of ooecia, leaving most of the central and proximal parts not covered. Thus, the general structure of the ooecia and the variable form and arrangement of pseudopores in the holotype colony is identical to the condition in most of our specimens (see also below).

The position, orientation, and size of the suboral avicularium vary considerably in *R. gigantea*. Whereas the majority of specimens examined shows the palatal surface situated laterally on the avicularian cystid near the apex and tilted in the frontal direction (Fig. 5B, D), colonies collected on the western Kamchatka shelf, Sea of Okhotsk (ZIRAS 3/50129), have some zooids with the palatal surface situated on the distal slope of the cystid and facing strictly distally, or situated near the apex, facing frontally. In contrast, specimens from Avacha Gulf, eastern Kamchatka (ZIRAS 1/50127 and 2/50128), have zooids with the palatal face on the proximal slope of the cystid, facing proximolaterally to proximally. Occasionally, the suboral avicularium is entirely immersed in the frontal shield due to secondary calcification.

The form of the ooecial pseudopores, their pattern of distribution and the amount of secondary calcification on the ooecium are also highly variable in this species. Whereas specimens from the eastern Kamchatka shelf, Bering Sea (ZIRAS 1/50127 and 2/50128) and from Moneron Island, Sea of Japan (MIMB 3/50213), mostly have large, elongate, slit-like pseudopores with a random or radial arrangement, conferring a "costate" appearance to the ooecia, some colonies from the western Kamchatka shelf, Sea of Okhotsk (ZIRAS 3/50129), have ooecia with smaller, scattered, circular pseudopores. In addition, whereas most of the colonies studied have ovicells with the ooecium covered by secondary calcification only on the periphery (i.e. they have a large central pseudoporous area free of secondary calcification), colonies from the Alaska shelf, Bering Sea (UAM Bry 77–1, Bry–408) show heavily calcified ooecia almost entirely covered by secondary calcification except for a narrow, lunar proximal area.

In bleached material, the ooecial pseudopores look like slits or holes in the ooecial roof. Since the endooecium is not visible through them, we suggest that it was destroyed during bleaching, being either cuticular or very weakly calcified. Histological sectioning should help answer this question.

In general, *R*. *gigantea* resembles *R*. *scabra* in appearance, and this has resulted in misidentifications in the past. For example, some material that we examined (MIMB 3/50213) was previously identified by A.A. Kubanin as *R*. *scabra*. It is also obvious that the species identified and illustrated by Mawatari (1956) as *Petraliella* sp., based on material collected near Alaid Island, northern Kuril Islands, and afterwards cited and figured by Mawatari (1965) as *Rhamphostomella scabra*, is *R*. *gigantea*. In both papers, Mawatari noted a very distinctive "arch-shaped" primary orifice with straight lateral and proximal margins, and condyles. In the latter paper he also illustrated ovicells with the characteristic "radial" arrangement of slit-like pseudopores in *R*. *gigantea*. For these reasons we attribute Mawatari's (1956, 1965) specimens to *R*. *gigantea*.

Despite the overall similarity between *R*. *gigantea* and *R*. *scabra*, these two species differ in the following characters: 1) colonies only initially encrusting but rapidly forming extensive erect, bilamellar, fan-like expansions in *R*. *gigantea*, but nearly always encrusting and only occasionally forming small, erect bilamellar frills in *R*. *scabra*; 2) orifice bell-shaped with straight proximal margin in *R*. *gigantea*, but irregularly oval, with weak proximal median prominence in *R*. *scabra*; 3) condyles well developed in *R*. *gigantea*, but absent in *R*. *scabra*; 4) suboral avicularian cystid relatively low and inflated in *R*. *gigantea*, but cone-shaped and protruding in *R*. *scabra*; 5) frontal avicularia tending to be nearly the same size or slightly larger than suboral avicularia in *R*. *gigantea*, but these are consistently larger than the suboral avicularia in *R*. *scabra* (based on both our own measurements and published data, the ratio Av(ad)/Av(s) is 1.0–1.6 (usually 1.1–1.3) in *R*. *gigantea* vs 1.5–1.6 in *R*. *scabra*); 6) ooecial pseudopores in *R*. *gigantea* are mostly numerous, large, strongly elongate to slit-like, and arranged randomly or radially, giving an overall "costate" appearance to the ooecia, but less numerous and relatively small in *R*. *scabra*; 7) fully-formed ooecia leave more than half the primary orifice length uncovered in *R*. *gigantea* (Fig. 5F, G), but overhang half to two-thirds of the length in *R*. *scabra* (Fig. 1E–G); 8) mean zooid length is considerably larger in *R*. *gigantea* than in *R*. *scabra* (1.18–1.45 vs 0.82–1.15 mm, respectively).

Ecology. *Rhamphostomella gigantea* is known from a depth range of 33.5–176 m on hard and mixed bottoms, including rocks and gravel overlying sand and silt. Colonies have been found on pebbles, mollusc shells and polychaete tubes.

Distribution. *R*. *gigantea* is a rarely reported species, previously known from the Arctic at Point Barrow, Alaska, Beaufort Sea (Osburn 1952; MacGinitie 1955) and Chukchi Sea (Gontar 2010; our data); from the northwestern Pacific near Alaid Island, North Kuril Islands (Mawatari 1956, 1965), and from the northeastern Pacific at Cook Inlet, Gulf of Alaska (Foster 2010). The northern Pacific material described above was collected on the Alaska shelf, northwest of Unimak Island, Bering Sea; in Avacha Gulf, eastern Kamchatka Peninsula; near Cape Hayryuzova on western Kamchatka shelf, Sea of Okhotsk; and in the coastal waters off Moneron Island, Sea of Japan. Based on these records, *R*. *gigantea* is a Pacific boreal sublittoral species, extending to the Arctic.

***Rhamphostomella microavicularia* n. sp.**

(Fig. 6)

Diagnosis. Colony encrusting, multiserial. Zooids large, hexagonal. Frontal shield flattened, covered with fine pointed tubercles. Marginal areolae small, deeply submerged. Interareolar ridges short, mostly not reaching cystid of suboral avicularium. Umbonuloid component extensive. Primary orifice proportionally large, occupying over 30% of zooid length, roughly quadrangular, with large lateral condyles. No oral spines. Secondary orifice identical in form to primary orifice, cormidial. Suboral avicularian cystid small, slightly elevated, narrow, forming crescentic lip around proximolateral edge of primary orifice. Rostrum semioval, blunt. Crossbar complete, thickened in the middle or with very small ligula. Multiple adventitious frontal avicularia, 2–5 per zooid, of equal size and form, situated along lateral margins. Ovicells hyperstomial, rapidly subimmersed by peripheral secondary calcification. Ectooecium smooth, with scattered pseudopores. 3–5 pore chambers in distolateral wall and two multiporous septula in transverse walls. Basal wall of zooids fully calcified, with protuberances of irregular form.

?*Rhamphostomella scabra*: Androsova 1958, p. 169, fig. 100.

Material examined. *Holotype*: ZIRAS 1/50543, colony encrusting cirripede plate, IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 39/34, 19 July 2011, southeastward from Chiproy Island, middle Kuril Islands, Pacific Ocean, 46°20.7′ N, 150°58.7′ E – 46°21.3′ N, 150°58.8′ E, depth 436–480 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev. *Paratype*: ZIRAS 2/50544, two fragments of single colony originally growing on sponge, IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 63/53, 29 July 2011, northward from Iturup Island, South Kuril Islands, Sea of Okhotsk, 45°45.1′ N, 148°33.2′ E – 45°44.5′ N, 148°33.5′ E, depth 264–274 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev.

Etymology. The species name alludes to the numerous small adventitious avicularia developing along zooidal margins.

Type locality. Southeastward from Chiproy Islands, middle Kuril Islands, Northwestern Pacific, 46°20.7′ N, 150°58.7′ E – 46°21.3′ N, 150°58.8′ E, depth 436–480 m.

Measurements. ZIRAS 1/50543, Chiproy Island, Kuril Islands, Pacific Ocean (Fig. 6A–M). ZL, 1.07–1.68 (1.34 ± 0.17). ZW, 0.77–1.13 (0.96 ± 0.10). ZD, 0.77–0.87 (n = 2). OrL, 0.42–0.53 (0.46 ± 0.03). OrW, 0.36–0.45 (0.40 ± 0.02). OeL, 0.52–0.55 (n = 2). OeW, 0.55–0.58 (n = 2). Av(s)L, 0.10–0.17 (0.14 ± 0.02). Av(ad)L, 0.11–0.19 (0.15 ± 0.02). P(m)N, 15–26 (20). P(oe)N, 26 (n = 1).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 6A), irregular in outline, up to about 19 × 8 mm in size, light-yellow to beige when dry. Zooids large, hexagonal to irregularly oval, arranged in a checkered pattern, demarcated by fine undulating sutures between lateral and transverse walls (Fig. 6A, B, D–H).

Frontal shield umbonuloid (Fig. 6A, D, I), initially convex but becoming flattened with age, entirely covered with fine, pointed tubercles, with small, deeply submerged circular to oval areolae along zooidal margins, separated by narrow, short interareolar ridges, mostly not reaching cystid of suboral avicularium. Thickening of frontal shield in older parts of colony resulting in some reduction of areolae in size and number. While boundaries between zooids visible in all parts of colony, some sutures between vertical walls disappearing along with some interareolar ridges. Umbonuloid component extensive, occupying about 75% of length of frontal shield (77% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 6I). Ring scar discrete but fainter than typical (Fig. 6L), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 6A–C, I, J) quadrangular with broadly rounded angles to oval; distal and lateral margins formed by upper terminal part of distal transverse wall bearing distinct shelf distally and forming large condyles with blunt or pointed tips laterally (Fig. 6A–C, G, I, J). Distal margin of orifice round, proximal margin slightly concave or straight, with broadly rounded proximolateral corners. No oral spines.

Secondary orifice with the same outline as primary orifice; cormidial, formed proximally by finely granulated slope of avicularian cystid; distally and distolaterally restricted to vertical walls of distal and lateral zooids.

Suboral avicularium with cystid forming crescentic lip around proximolateral edge of primary orifice; relatively small, only slightly elevated above frontal shield, with finely granulated surface and 1–3 communication pores connecting avicularian and hypostegal coelomic cavities; frontal surface (rostral/postmandibular areas) normally crossed by zooidal midline and facing to right or left of it (Fig. 6A–H). Small rostral face of avicularium angled frontally at about 45° to frontal shield. Rostrum semioval, blunt, with serrated distal margin, directed medially upwards. Palate and palatal foramen conforming to shape of rostrum, opesia oval. Crossbar complete, thickened in middle or with very small ligula.

From one to five small adventitious avicularia of equal size and form present on lateral, proximolateral or proximal surface of zooidal frontal shield close to margins (Fig. 6A–H), more numerous in older parts of colony. Avicularian cystid low, with finely granulated surface, frontal surface (rostral/postmandibular areas) facing frontally. Rostrum semicircular to broadly oval, blunt, with serrated distal margin, directed outwards. Palate and palatal foramen conforming to shape of rostrum, short, semicircular to semioval, opesia oval or round, surrounded by cryptocyst. Crossbar complete, thickened in middle or with very small, low ligula. Orifices of non-ovicellate zooids surrounded by 3 adventitious avicularia (including suboral) in young areas of colony (Fig. 6B–D) and by 4–6 avicularia in older areas (Fig. 6E–H). Each ovicell surrounded by two to four avicularia (Fig. 6F–G).

Ovicells initially prominent, later becoming subimmersed due to peripheral overgrowth of ooecium by secondary calcification proceeding from daughter and neighbouring lateral zooids (Fig. 6F, G). Ooecium formed by distal autozooid around small, shallow concavity with communication pore at bottom, situated in proximalmost part of frontal shield just immediate to distal margin of maternal primary orifice (Fig. 6C, D). Ooecium with concave proximal margin, with smooth ectooecium and numerous rounded to elongate pseudopores.

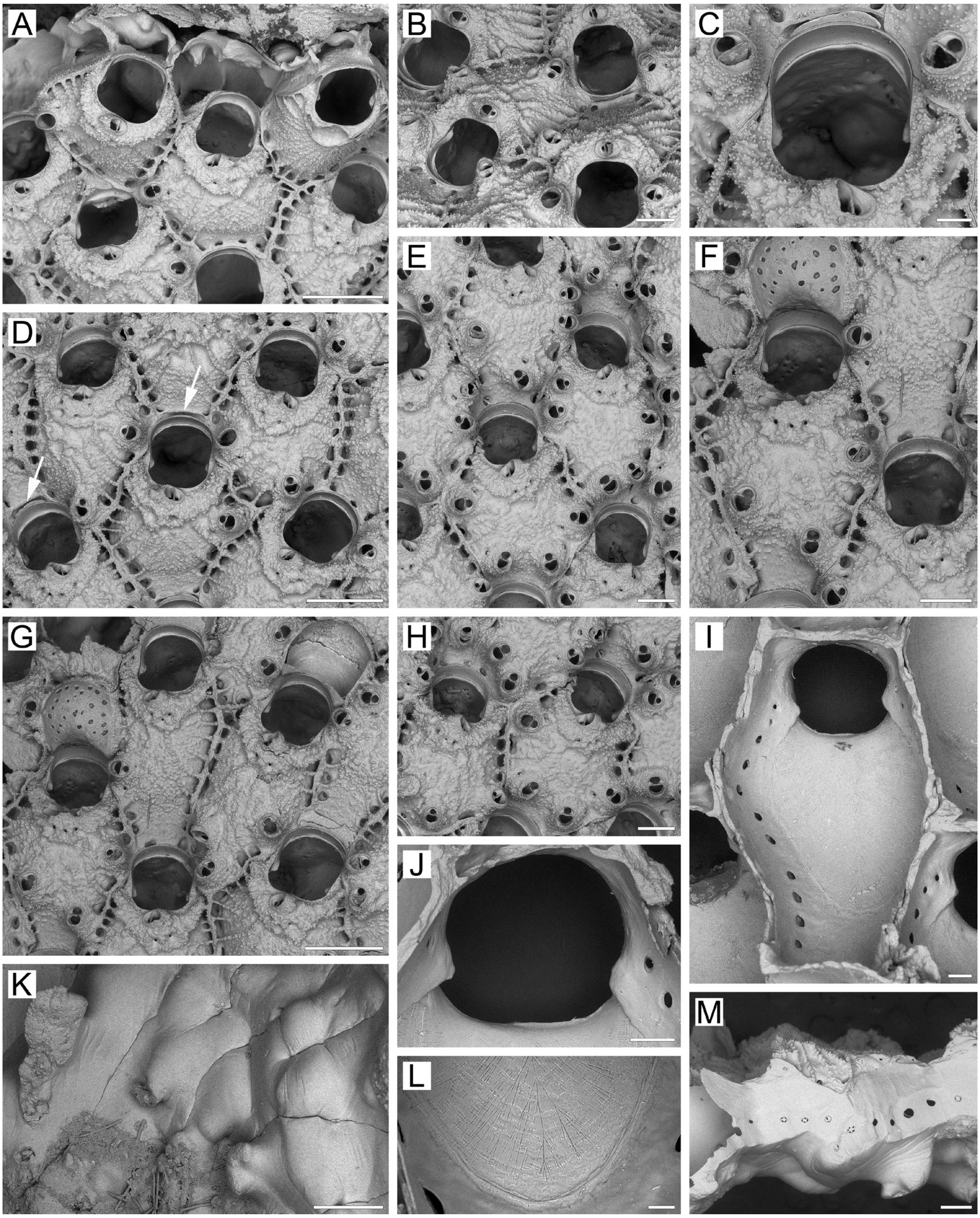

FIGURE 6. *Rhamphostomella microavicularia* **n. sp.** *Holotype*, ZIRAS 1/50543 (Chiproy Island, Kuril Islands, Pacific Ocean). A. Colony margin with developing zooids. B. Distal view of zooids from colony periphery, showing orifices with condyles and position of suboral and adjoining small adventitious avicularia. C. Orifice with suboral and adjoining adventitious avicularia (ooecial rudiment is visible near distal margin of orifice). D. Non-ovicellate zooids in young part of colony (arrows, communication pores of future ooecia). E. Zooids in older part of colony. F. Ovicellate zooid with ooecium, laterally surrounded by secondary calcification. G. Autozooids with complete and partially destroyed ooecia. H. Two zooids from old part of colony, showing numerous adventitious avicularia. I. Interior of frontal shield, showing umbonuloid component and areolae. J. Internal view of orifice, showing concave proximal margin and condyles. K. Basal colony surface. L. Frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. M. Zooidal lateral wall with mural pore chambers; protuberances on basal wall are clearly seen. Scale bars: A, D, G, K, 500 µm; B, E, F, H, 250 µm; C, I, J, 100 µm; L, 50 µm; M, 200 µm.

Zooids interconnected by 3–5 mural pore chambers in each distolateral wall (Fig. 6M). Two lateral or one central multiporous septula in basal half of transverse walls.

Basal wall of zooids (Fig. 6K, M) fully calcified, slightly convex, smooth, with some protuberances of irregular form (0.21–0.39 mm in diameter), and with fine, parallel folds on surface. Boundaries between zooids recognizable basally by deep undulating incisions. Numerous white spots (presumably less-calcified areas) visible in semitransparent basal wall under light microscope.

Ancestrula and early astogeny not observed.

Remarks. The following character combination clearly distinguishes *R. microavicularia* from congeners: 1) proportionally large orifice, occupying more than 30% of zooid length; 2) cystid of suboral avicularium around proximolateral edge of primary orifice narrow, crescentic; 3) interareolar ridges short, most not meeting suboral avicularian cystid except for those lateral to cystid; and 4) numerous, small, peripheral adventitious avicularia.

Androsova (1958) reported what might be this species as *R. scabra* from the northern part of the Sea of Japan, including Moneron Island (46°18.0′ N, 141°13.0′ E), and from three localities along the southwestern coast of Sakhalin Island, i.e., near the settlements of Kholmsk, Krasnogorsk and Uglegorsk (47°03.0′ N, 142°00.0′ E to 49°05.0′ N, 142°01.0′ E), at depths of 10–117 m on rocks and shells. She mentioned the unusually large orifice, comprising one-quarter to half of zooidal length, associated with numerous (3–5) adventitious avicularia arranged irregularly on the frontal shield. Hence, Androsova's material might have been *R. microavicularia* **n. sp.**. At the same time, she described and illustrated strongly enlarged marginal areolae separated by long interareolar ridges connected to a well-developed, elevated suboral avicularian cystid. It thus remains unclear whether our specimens and those of Androsova are conspecific.

Ecology. *Rhamphostomella microavicularia* **n. sp.** was found at 264–480 m depth on a barnacle shell plate and a sponge.

Distribution. Our two specimens were collected from two northwestern Pacific localities along the middle to southern Kuril Islands, including the Pacific slope between Urup and Chiproy Islands, and at one site northward of Iturup Island, Sea of Okhotsk. Accordingly, *R. microavicularia* **n. sp.** is a Pacific Asian high-boreal, sublittoral to upper-bathyal species.

***Rhamphostomella morozovi* n. sp.**

(Fig. 7)

Diagnosis. Colonies initially encrusting, multiserial, unilaminar, rapidly rising into bilamellar, fan-like expansions. Zooids very large, hexagonal. Frontal shield relatively flat, finely granulated. Marginal areolae initially large, reduced in size with age. Interareolar ridges short, not reaching cystid of suboral avicularium. Umbonuloid component medium-sized. Primary orifice wider than long, broadly semicircular, with small lateral condyles; proximal margin straight or with low median prominence. Oral spines lacking. Secondary orifice irregularly quadrangular to semicircular, cormidial, with lateral peristomial lappets in ovicellate zooids. Suboral avicularian cystid large, subconical, occupying one-third to half of frontal shield, less prominent in older zooids; frontal surface across zooidal axis, facing distolaterally. Rostrum broadly triangular or semielliptical, with blunt hooked tip. Crossbar complete. Adventitious avicularia small, central to proximal, facing frontalwards to slightly angled. Rostrum and palate broadly triangular to semielliptical, with a blunt hooked tip. Crossbar complete. Ovicells hyperstomial, rapidly subimmersed by secondary calcification. Ectooecium with few radially arranged slit-like proximal pseudopores. 1–3 pore chambers in distolateral wall and two multiporous septula in transverse walls. Basal surface of zooids fully calcified, with small prominences.

Material examined. *Holotype*: ZIRAS 1/50570, one colony fragment, KamchatNIRO Collection, RV *Professor Probatov*, Stn 62, 16 August 2013, coastal waters of western Kamchatka, Sea of Okhotsk, 57°14.9′ N, 155°37.7′ E, depth 116 m, bottom-grab "Ocean–50", collector T.B. Morozov. *Paratype*: ZIRAS 2/50571, two fragments from same colony, KamchatNIRO Collection, RV *Professor Probatov*, Stn 82, 11 August 2013, coastal waters of western Kamchatka, Sea of Okhotsk, 58°09.0′ N, 156°03.0′ E, depth 146 m, bottom-grab "Ocean–50", collector T.B. Morozov.

Etymology. The specific name honours Mr Taras B. Morozov (KamchatNIRO, Petropavlovsk-Kamchatsky, Russia), who collected and donated the type material.

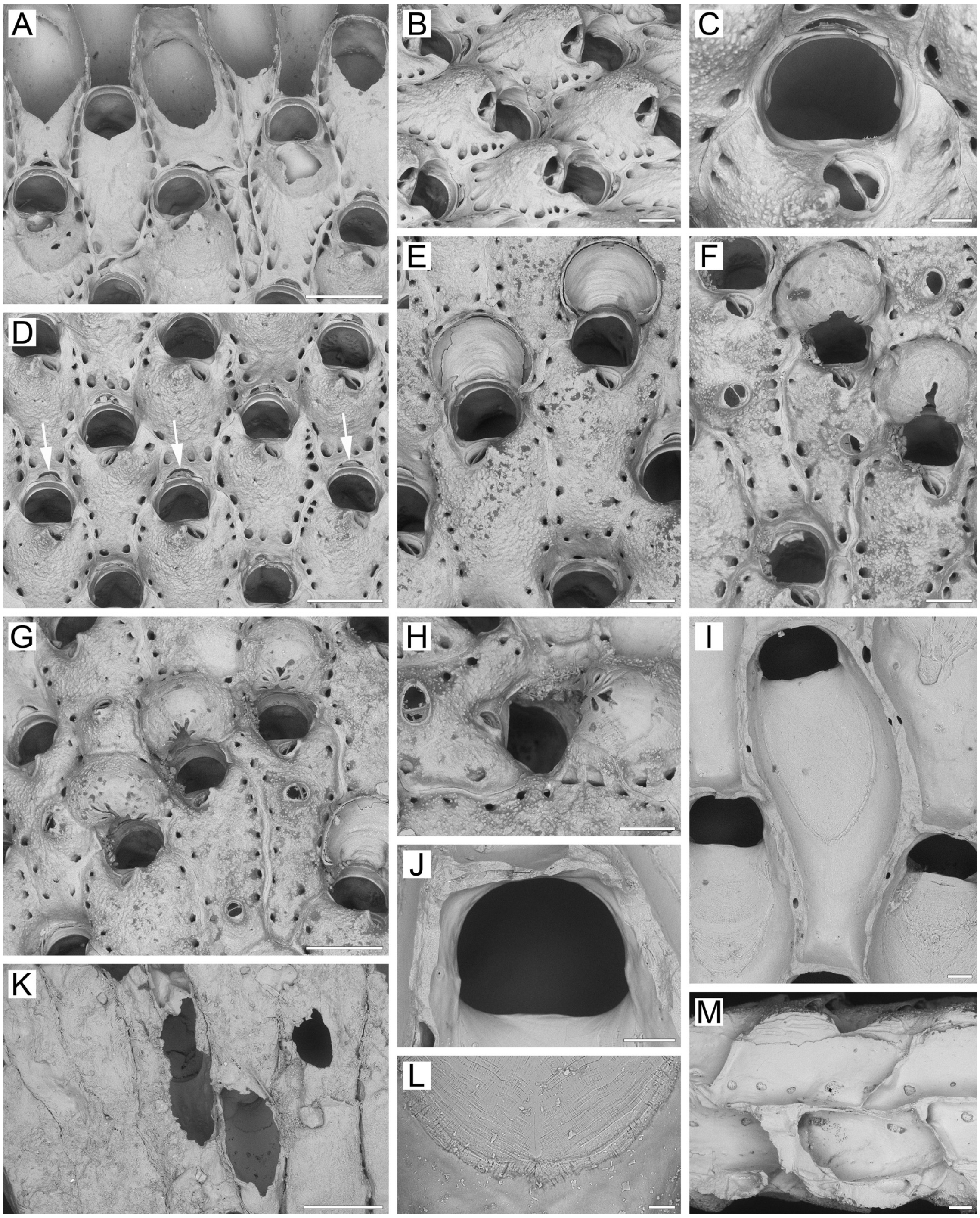

FIGURE 7. *Rhamphostomella morozovi* **n. sp.** *Holotype*, ZIRAS 1/50570 (western Kamchatka, Sea of Okhotsk). A. Growing margin of bilaminate colony, showing only one layer of developing zooids. B. Lateral view of zooids in young part of colony. C. Zooidal orifice with suboral avicularium (communication pore of future ooecium visible near distal margin of orifice). D. Group of non-ovicellate zooids in young part of colony (arrows, communication pores of future ooecia). E. Zooids with developing ooecia. F. Zooids with developing and nearly completed ooecia and small adventitious avicularia. G. Zooids with developing and nearly complete ooecia and small (central to proximal) adventitious avicularia. H. Lateral view of ovicellate zooid, showing ooecium embedded into secondary calcification and having slit-like proximal pseudopores; notice nearly identical size of suboral and adventitious avicularia. I. Interior of frontal shield showing ring-scar, areolae and communication pores of adventitious avicularium. J. Internal view of orifice, showing straight proximal margin and strongly reduced, pointed condyles. K. Basal surface of encrusting part of colony (some zooids damaged). L. Close-up of frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral walls of zooids in bilaminate colony, showing mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, E, F, H, 250 µm; C, I, J, 100 µm; L, 50 µm; M, 200 µm.

Type locality. Western Kamchatka shelf, Sea of Okhotsk, 57°14.9′ N, 155°37.7′ E, depth 116 m.

Measurements. ZIRAS 1/50570, western Kamchatka, Sea of Okhotsk (Fig. 7A–M). ZL, 1.11–2.03 (1.50 ± 0.26). ZW, 0.57–0.83 (0.68 ± 0.07). ZD, 0.90–1.03 (*n* = 2). OrL, 0.25–0.31 (0.28 ± 0.02). OrW, 0.30–0.38 (0.33 ± 0.02). OeL, 0.39–0.51 (0.45 ± 0.03). OeW, 0.46–0.60 (0.55 ± 0.03). Av(s)L, 0.15–0.31 (0.22 ± 0.04). Av(ad)L, 0.13–0.33 (0.21 ± 0.05). P(m)N, 11–18 (16). P(oe)N, 2–6 (5) (*n* = 10).

Description. Colonies initially encrusting, unilaminar (Fig. 7A), later rising into bilamellar (Fig. 7M), fan-like, ruffled expansions, about 80 × 50 mm in size. Dried colonies greyish to dark yellow. Bilaminate parts of colony up to 2.03 mm thick, adjoining layers of zooids closely adpressed (Fig. 7M). Directions of development of zooids in adjoining layers not fully coinciding, with angles of 5–10° between main axes of zooid rows in opposing layers. Zooids very large, hexagonal (Fig. 7D) to irregularly oval or tapering proximally (Fig. 7E–G), arranged in straight, regular rows in a checkered pattern in colony lobes, or arranged irregularly in older regions of colony. Autozooids demarcated by fine undulating sutures between lateral and transverse walls (Fig. 7A, F–H). Boundaries between zooids in older parts of colony often becoming occluded with increasing secondary calcification (Fig. 7E, G).

Frontal shield umbonuloid (Fig. 7A, B, D, I) initially relatively flat, gradually becoming more convex with age, finely granulated, granulation becoming coarser in older zooids. Relatively large oval to circular areolae along zooidal margins, separated by narrow short interareolar ridges not reaching cystid of suboral avicularium. With age, areolae reduced in size to small marginal holes separated by flat, broad areas of calcification (former interareolar ridges) (Fig. 7E, G, H). Umbonuloid component occupying about 50% of length of frontal shield (49% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 7I). Ring scar discrete (Fig. 7L), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 7A, C, J) broadly semicircular to bell-shaped (wider than long) and transversely oval; distal and lateral margins formed by upper terminal part of distal transverse wall bearing distinct shelf distally (Fig. 7A–E) and forming small, low triangular condyles with acute tips laterally (Fig. 7J). Distal margin of orifice round, proximal margin more or less straight or with low, ill-defined median prominence and broadly rounded proximolateral corners (Fig. 7C, J). Oral spines lacking.

Secondary orifice (Fig. 7B–H) irregularly quadrangular, oval to semicircular, cormidial, proximally formed by thickened frontal shield incorporating avicularian cystid medially, and laterally by two symmetrical, oblique, low triangular lappets that are outgrowths of frontal shield. Distally, distolaterally and sometimes laterally, secondary orifice restricted by vertical walls of distal and lateral zooids. In ovicellate (maternal) zooids, lateral outgrowths of frontal shields form peristomial lappets connecting with proximal corners of ooecium distally and with lappets formed by frontal shield of neighbouring zooid proximally (Fig. 7G, H).

Suboral avicularium with cystid large, broad, subconical, occupying from one-third to about half of frontal shield, strongly elevated in young zooids (Fig. 7A–D), becoming less prominent in older zooids (Fig. 7E–H) owing to immersion into thickening frontal shield; surface finely granulated, with 2–4 tiny communication pores on surface (Fig. 7A–D). Frontal surface of avicularium (rostral/postmandibular areas) situated on left or right slope of cystid, across zooidal axis, facing distolaterally. Rostrum broadly triangular or semielliptical, directed medially, laterally or proximolaterally upwards, blunt, with terminal hook. Palate and foramen conforming to shape of rostrum, with blunt distal end; opesia oval, surrounded by narrow cryptocyst. Crossbar complete.

Adventitious avicularia small, central to proximal on zooidal frontal shield in older parts of colony (Fig. 7F–H), with relatively narrow cystid, slightly elevated, with finely granulated surface; avicularian frontal surface facing frontally or slightly angled. Rostrum broadly triangular or semielliptical, directed laterally or proximally, with hooked tip, palate and palatal foramen conforming shape of rostrum, opesia oval or elliptical. Crossbar complete. Cystids of these avicularia frequently situated close to ooecia of neighbouring zooids (Fig. 7G).

Ovicells hyperstomial, rapidly becoming subimmersed, with ooecium peripherally overgrown by secondary calcification from neighbouring zooids in older parts of colony (Fig. 7F, G). In some ovicells, two-thirds of ooecium covered by secondary calcification (Fig. 7H). Ooecium formed by distal autozooid around small, shallow arch-like concavity with communication pore at bottom, situated in proximalmost part of frontal shield just immediate to distal margin of maternal primary orifice (Fig. 7B–D). Ectooecium with radial growth lines and a few radially arranged slit-like pseudopores near proximal margin. Finely granulated secondary calcification, produced by neighbouring zooids, overgrowing peripheral parts of ooecium, also forming two convex lateral lobes that fuse with lateral lappets of frontal shield to produce low peristome around orifice (Fig. 7F–H).

Zooids interconnected by 1–3 mural pore chambers in each distolateral wall (Fig. 7M). Communication pores usually form two multiporous septula in basal half of transverse walls. In some zooids, septulum single, as horizontal "band". (Fig 7A, D).

Basal surface of zooids (Fig. 7K) fully calcified, roughly lineated, with small prominences. Boundaries between zooids recognizable basally by deep, meandering incisions.

Ancestrula and early astogeny not observed.

Remarks. Apart from the striated appearance of young parts of the colony of *R. cristata*, *R. morozovi* **n. sp.** resembles this species in the following characters: 1) the elevated, conical suboral avicularian cystid with a hooked tip; 2) the primary orifice is commonly bell-shaped, occasionally with a weak median convexity in the proximal margin; and 3) the secondary orifice has two symmetrical, obliquely directed triangular lateral lappets. The quadrangular primary orifices that are rather common in *R. cristata* and the quadrangular secondary orifices in *R. morozovi* **n. sp.** add to this similarity. These two species differ, however, in the following characters: 1) the rostrum and palate of the suboral and adventitious avicularia in *R. morozovi* **n. sp.** are broadly triangular to semielliptical, with a blunt tip, but are elongate-triangular with an acute tip in *R. cristata*; 2) the suboral and adventitious avicularia are proportionally smaller relative to zooid size in *R. morozovi* **n. sp.** than in *R. cristata*; 3) fully formed ooecia of *R. cristata* have 11–32 circular to slit-like pseudopores scattered over the entire frontal surface (Fig. 4F–H), whereas ooecia have only 2–6 slit-like pseudopores near the proximal margin in *R. morozovi* **n. sp.** (Fig. 7G, H).

Ecology. *Rhamphostomella morozovi* **n. sp.** was recorded from a depth of 116–146 m on a mixed seafloor, including pebbles and gravel overlying sand and silt. Substrata unknown.

Distribution. Currently known from two nearby localities in the western Kamchatka shelf, Sea of Okhotsk, this is a Pacific Asian high-boreal, sublittoral species, possibly endemic to the Sea of Okhotsk.

***Rhamphostomella pacifica* (O'Donoghue, 1925)**
(Figs 8, 30E)

Porella pacifica O'Donoghue, 1925, p. 20, pl. 2, figs 7, 8.
Rhamphostomella n. sp. 2: Hirose 2010, p. 92, pl. 156a–d.

Material examined. *Neotype*: ZIRAS 1/50124, one colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 238, 11 June 1988, Kronotsky Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 54°53.0′ N, 162°15.0′ E, depth 122 m, rock dredge, collector A.V. Rzhavsky.

NHMUK 2010.2.9.4, one colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 119, 24 May 1988, Avacha Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 52°54.0′ N, 160°01.0′ E, depth 141 m, rock dredge, gravel, collector A.V. Rzhavsky. NHMUK 2010.2.9.7, one colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 170, 9 May 1988, Avacha Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 53°22.0′ N, 160°07.0′ E, depth 136 m, rock dredge, collector A.V. Rzhavsky.

Additional material. 30 specimens. KIENM Collection (1988) Stn 114; IMB Collection (2011) Stns 3/1, 16/12, 18/14, 20/16, 24/19, 42/37, 43/38, 48/42, 60/50 (see Appendix 1 for details).

Measurements. ZIRAS 1/50124, Kronotsky Gulf, eastern Kamchatka, Pacific Ocean (Figs 8A–M, 30E). ZL, 0.82–1.57 (1.14 ± 0.19). ZW, 0.42–0.75 (0.59 ± 0.10). ZD, 0.52–0.83 (*n* = 2). OrL, 0.17–0.22 (0.19 ± 0.01). OrW, 0.20–0.27 (0.24 ± 0.02). OeL, 0.32–0.43 (0.39 ± 0.03). OeW, 0.45–0.58 (0.51 ± 0.03). Av(s)L, 0.07–0.12 (0.10 ± 0.02). Av(ad)L, 0.20–0.90 (0.53 ± 0.18). Av(vic)L, 0.55–0.62 (*n* = 2). P(m)N, 13–21 (17). P(oe)N, 9–15 (12).

Description. Colonies initially encrusting, multiserial, unilaminar (Fig. 8A), giving rise to extensive, meandering, erect bilamellar expansions attaining 41 × 38 mm in size. Dry colonies pink to light yellow. Bilaminate parts of colony up to 1.55 mm thick, adjoining layers not fully adherent, sometimes with narrow slit-like spaces in between (Fig. 8M). Directions of growth of zooids in adjoining layers not wholly coinciding, with angles of up to 10° between main axes of opposing layers. Zooids large, elongate-hexagonal to oval, arranged in more or less regular straight, oblique rows, demarcated by fine undulating sutures between lateral and transverse walls. Boundaries between zooids clearly visible in young peripheral zooids (Fig. 8A–G), gradually becoming indistinct, completely obliterated in oldest parts of colony (Fig. 8H).

Frontal shield umbonuloid (Fig. 8A, I), initially convex, smooth in young zooids, becoming flatter with granulated surface (fine to coarse) in older zooids. Small, round or elongate areolae along margins, separated by narrow, elongate interareolar ridges; in distal third to half of frontal shield, these ridges connecting with avicularian cystid visible in young parts of colony (Fig. 8A, E); ridges sometimes fusing along zooidal midline in proximal part of frontal shield (Fig. 8D). Thickening of frontal shield in older parts of colony resulting in smaller areolae as well as broadening of interareolar ridges, with ridges becoming less distinct and often disappearing. Umbonuloid component extensive, occupying about 70% of length of frontal shield (68% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 8I, L). Ring scar discrete (Fig. 8F), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 8C, J) broadly semicircular to bell-shaped; distal and lateral margins formed by upper terminal part of distal transverse wall bearing ill-defined rim (Fig. 8A, C); rounded condyles laterally (Fig. 8C, J). Distal margin of orifice round, proximal margin more or less straight or with very weak median convexity, proximolateral corners gently rounded. No oral spines.

Secondary orifice (Fig. 8A–E) transversely elongate-semicircular to irregularly oval, cormidial, proximally and laterally restricted by frontal shield developing two low arch-like lobes that merge with distal part of avicularian cystid (Fig. 8B, E). In ovicellate (and older) zooids, two taller peristomial lappets fusing with two corresponding lobes of the secondary calcification overgrowing ooecium (Fig. 8F–H). Distolateral curvature of secondary orifice formed by vertical walls of distal and lateral zooids.

Suboral avicularium with cystid occupying one-quarter to about half of zooidal frontal shield (Fig. 8C, E), convex in young zooids, less prominent in older zooids, with finely granulated surface and 2–8 minute communication pores on surface. Frontal surface of avicularium (rostral/postmandibular areas) situated on left or right slope of cystid, overlapping or out of zooidal midline, facing distolaterally. Rostrum broadly semicircular, blunt, directed proximomedially and obliquely frontally. Palatal foramen semicircular, conforming to shape of rostrum, opesia small, oval, bordered by extensive cryptocyst. Crossbar complete, with prominent ligula.

Adventitious avicularia varying greatly in size, located centrally to proximally on frontal shield (Fig. 8F, G); cystid broad, inflated, oval to rounded, coarsely granulated. Avicularian frontal surface nearly parallel to frontal shield. Rostrum directed proximomedially to proximally, occasionally distally, spatulate or lingulate, blunt, palate of similar shape. Palatal foramen trifoliate, cryptocystal shelf extensive, opesia oval, bordered by well-developed cryptocyst. Crossbar complete, with conspicuous ligula.

Largest adventitious avicularia sometimes occupying significant area of frontal shield of adjacent zooids (Fig. 8G); in ovicellate parts of colony, ooecia often flanked by two or three adventitious avicularia (Fig. 8F, G).

Very large vicarious avicularia sometimes present near growing edge of colony (Fig. 8B). Avicularian frontal surface facing frontally. Rostrum spatulate, slightly broader distally, directed distally; palate of similar shape. Palatal foramen Y-shaped with extensive cryptocystal shelf, opesia roundly triangular. Crossbar complete, with large ligula.

Ovicells hyperstomial, with ooecium gradually becoming covered by secondary calcification encroaching from frontal shields of daughter and neighbouring zooids. Although secondary calcification sometimes covers most of the ooecium, ovicells remain prominent (Fig. 8F–H). Surface of secondary calcification finely granulated, with divergent sutures subdividing overgrowth originating from different zooids (Fig. 8I, L). Ooecium formed by distal autozooid around shallow, arch-like concavity with communication pore at bottom, situated in proximalmost part of its frontal shield just immediate to distal margin of maternal primary orifice (Fig. 8A, B, D, E). Ooecium with slightly concave proximal margin and smooth ectooecium bearing tiny slit-like pseudopores radially arranged in proximal half of ovicell roof (Fig. 8F–H). Most pseudopores in old ooecia occluded by secondary calcification (Fig. 8H). In ovicellate zooids, secondary calcification proceeding from frontal shields of neighbouring zooids forms bilaterally symmetrical peristome around zooidal orifice. Peristome consists of two lateral vertical lobes, connecting with proximal corners of ooecium (Fig. 8F–H).

Zooids interconnected by 2–3 mural pore chambers in each distolateral wall (Fig. 8M) and two multiporous septula in basal half of transverse wall, corresponding to two recesses with medial buttress (Fig. 8A).

Basal surface of zooids (Fig. 8K) fully calcified, with numerous irregular, sometimes bifurcate protuberances (0.12–0.39 mm in diameter) and transverse parallel folds on surface (Fig. 30E). Boundaries between zooids recognizable basally by deep sinuous incisions. Basal areas of massive erect colonies may contain only heavily calcified kenozooids, very irregular in form and arrangement; these occasionally united into large clusters with indistinguishable boundaries between. Frontally budded zooids, with normal or reversed polarity, also frequently present in older parts of colony, including some with orifices sealed by closure plates.

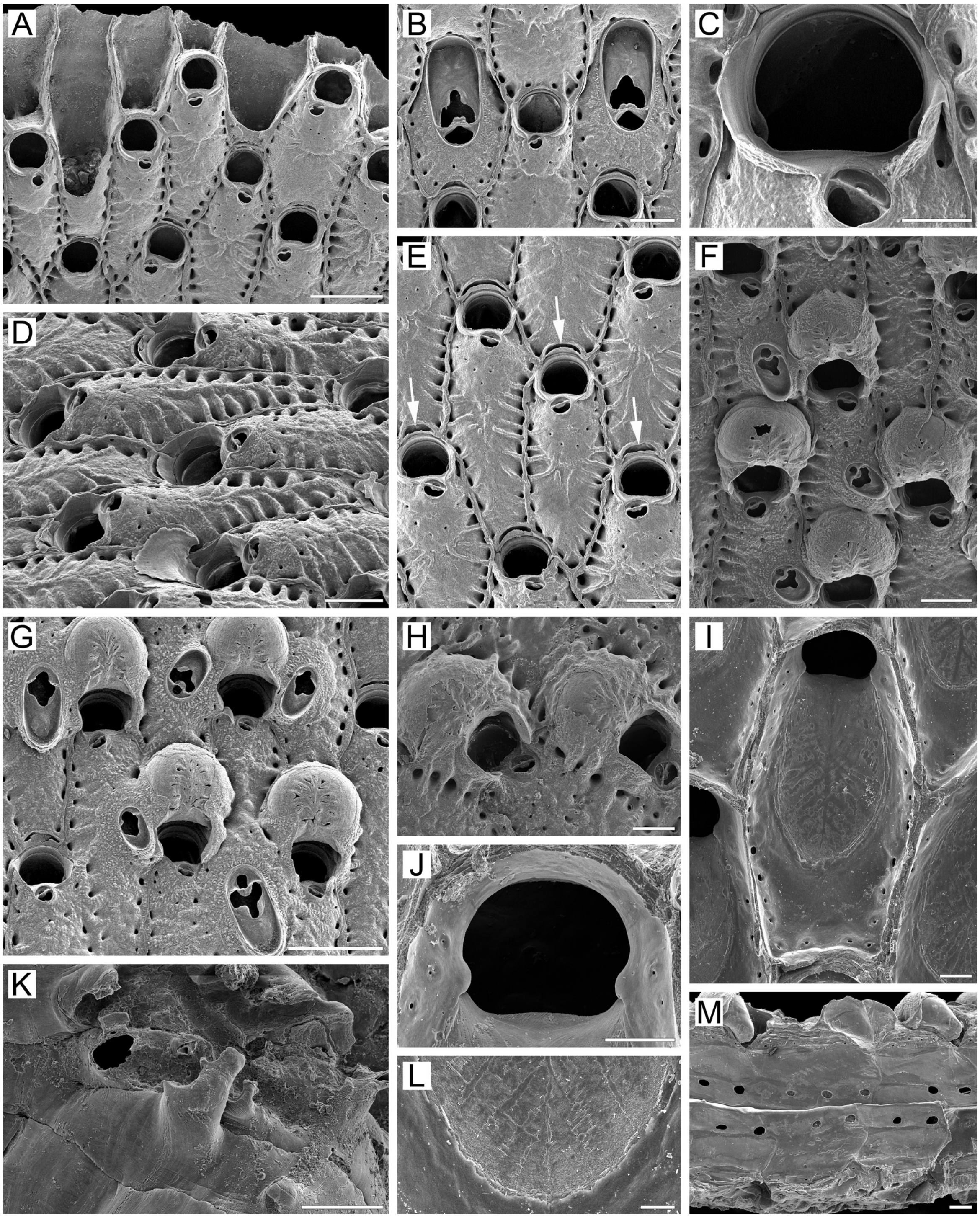

FIGURE 8. *Rhamphostomella pacifica* (O'Donoghue, 1925). *Neotype*, ZIRAS 1/50124 (Kronotsky Gulf, eastern Kamchatka, Pacific Ocean). A. Colony margin with developing zooids. B. Zooids and two vicarious avicularia near colony margin. C. Orifice with suboral avicularium. D. Lateral view of zooids in young part of colony, showing communication slits (sites of the future ooecial development), developing ooecium and position of suboral avicularium. E. Young autozooids, with communication slits (arrows) around which distal zooids will develop ooecia. F. Ovicellate zooids with suboral and adventitious avicularia in older part of colony. G. Ovicellate zooids, showing variation in size and position of adventitious avicularia. H. Oblique view of two ovicellate zooids in older part of colony, with ooecia covered by the secondary calcification. I. Interior of frontal shield, showing ring scar and areolae. J. Internal view of primary orifice. K. Basal colony surface, showing irregular protuberances. L. Frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of bilaminate part of colony, showing ooecia partially covered by secondary calcification and lateral walls with mural pore chambers. Scale bars: A, G, K, 500 μm; B, D–F, 250 μm; C, I, J, 100 μm; H, M, 200 μm; L, 50 μm.

Ancestrula and early astogeny not observed.

Remarks. O'Donoghue (1925) originally placed this species in *Porella* Gray, 1848, but noted the unusual combination of several characters: the stout bilamellar colony-form, the presence of adventitious avicularia, and the atypical position of the suboral avicularium. Concerning the last, he mentioned, "The avicularium is always situated nearer one side, never exactly median, and its semicircular mandible is directed postero-medially at angle of about 45–60 degrees to the hinder end of the aperture". Based on the generic diagnosis given by Hayward & Ryland (1979), *Porella* species lack adventitious and vicarious avicularia, and ooecia are imperforate or have a single central pseudopore. The combination of characters in *R. pacifica* that justify its inclusion in *Rhamphostomella* includes: 1) the oblique position of the suboral avicularium, situated asymmetrically nearer one side of the orifice, never exactly medially, with the rostrum at an angle of about 15–30° to the median line of the zooid; 2) ooecia with numerous slit-like pseudopores; and 3) the presence of adventitious and vicarious avicularia.

In some aspects, *R. pacifica* resembles *R. commandorica* **n. sp.**. However, it can be distinguished from the latter by the position of the primary orifice, and the form of the avicularian palatal foramen and overall colony morphology, as described above (see Remarks for *R. commandorica* **n. sp.**).

The characters of the two colonies from Sagami and Tokyo Bays, Honshu, Japan, described and illustrated by Hirose (2010) as *Rhamphostomella* n. sp. 2, fall within the range of morphological variation observed for *R. pacifica*.

Ecology. *Rhamphostomella pacifica* has been found at 97–490 m depth on mixed bottoms, including pebbles overlying silty sand. Substrata include pebbles and broken mollusc shells.

Distribution. In his original description, O'Donoghue (1925) stated: "These specimens are simply labelled *Albatross*. NW Pacific with no further data". Hirose (2010) reported the species from Hatsushima Island, western Sagami Bay and also Yokohama, western shore of Tokyo Bay, Honshu, Japan, at 150 m depth. Our material came from 122–176 m in Kronotsky and Avacha gulfs, eastern Kamchatka Peninsula, and along the Pacific and Sea of Okhotsk sides of the middle to southern Kuril Islands between Simushir and Kunashir at 97–490 m. Accordingly, *R. pacifica* is a Pacific Asian boreal, sublittoral to upper bathyal species, extending to the edge of the subtropics.

***Rhamphostomella aleutica* n. sp.**
(Fig. 9)

Diagnosis. Colony encrusting, multiserial. Zooids large, hexagonal. Frontal shield ventricose, finely tuberculated. Marginal areolae deep, separated by short interareolar ridges. Umbonuloid component extensive. Primary orifice submerged, irregularly circular, often with small median process. Condyles absent. No oral spines. Secondary orifice subcircular to irregularly oval, cormidial, defined by tubular peristome. Peristomial rim with acute or blunt-tipped spine-like tubular projections, 2–4 on each side, slightly tilted inwards. Suboral avicularian cystid asymmetrically situated proximolaterally to orifice, with coarsely granular surface. Rostrum elongate triangular with narrowing hooked tip. Crossbar complete. No adventitious avicularia. Ovicells hyperstomial. Ectooecium smooth, lacking secondary calcification, with small pseudopores. Two pore chambers in distolateral wall and 1–2 multiporous septula in transverse walls. Basal surface of zooids fully calcified, lacking protuberances.

Material examined. *Holotype*: NHMUK 2010.4.21.1, one colony encrusting a sponge, Alaska Fisheries Science Center and National Marine Fisheries Service Collection, FV *Sea Storm*, Haul 190, Stn 114–21, 23 July 2004, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°51.6′ N, 178°27.8′ E, depth 224–235 m, collector M.H. Dick.

Etymology. The species name alludes to the type locality in the Aleutian Islands.

Type locality. Coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°51.6′ N, 178°27.8′ E, depth 224–235 m.

Measurements. NHMUK 2010.4.21.1, Amchitka Island, Aleutian Islands, Bering Sea (Fig. 9A–L). ZL, 0.81–1.14 (0.93 ± 0.07). ZW, 0.54–0.87 (0.73 ± 0.08). ZD, 0.44–0.62 (n = 2). OrL, 0.27–0.40 (0.32 ± 0.03). OrW, 0.24–0.40 (0.33 ± 0.03). OeL, 0.34–0.37 (0.35 ± 0.01) (n = 3). OeW, 0.45–0.52 (0.48 ± 0.03) (n = 3). Av(s)L, 0.24–0.39 (0.32 ± 0.03). P(m)N, 15–20 (17) (n = 10). P(oe)N, 16–18 (17) (n = 4).

Description. Colony encrusting, multiserial, unilaminar (Fig. 9A), irregular in outline, about 8 × 7 mm in size, deep red when dry. Zooids large, hexagonal, broadly oval, pyriform or irregular (Fig. 9A, D–H), arranged in quincunx, demarcated by fine sutures between lateral and transverse walls; sutures visible in both young and old parts of colony.

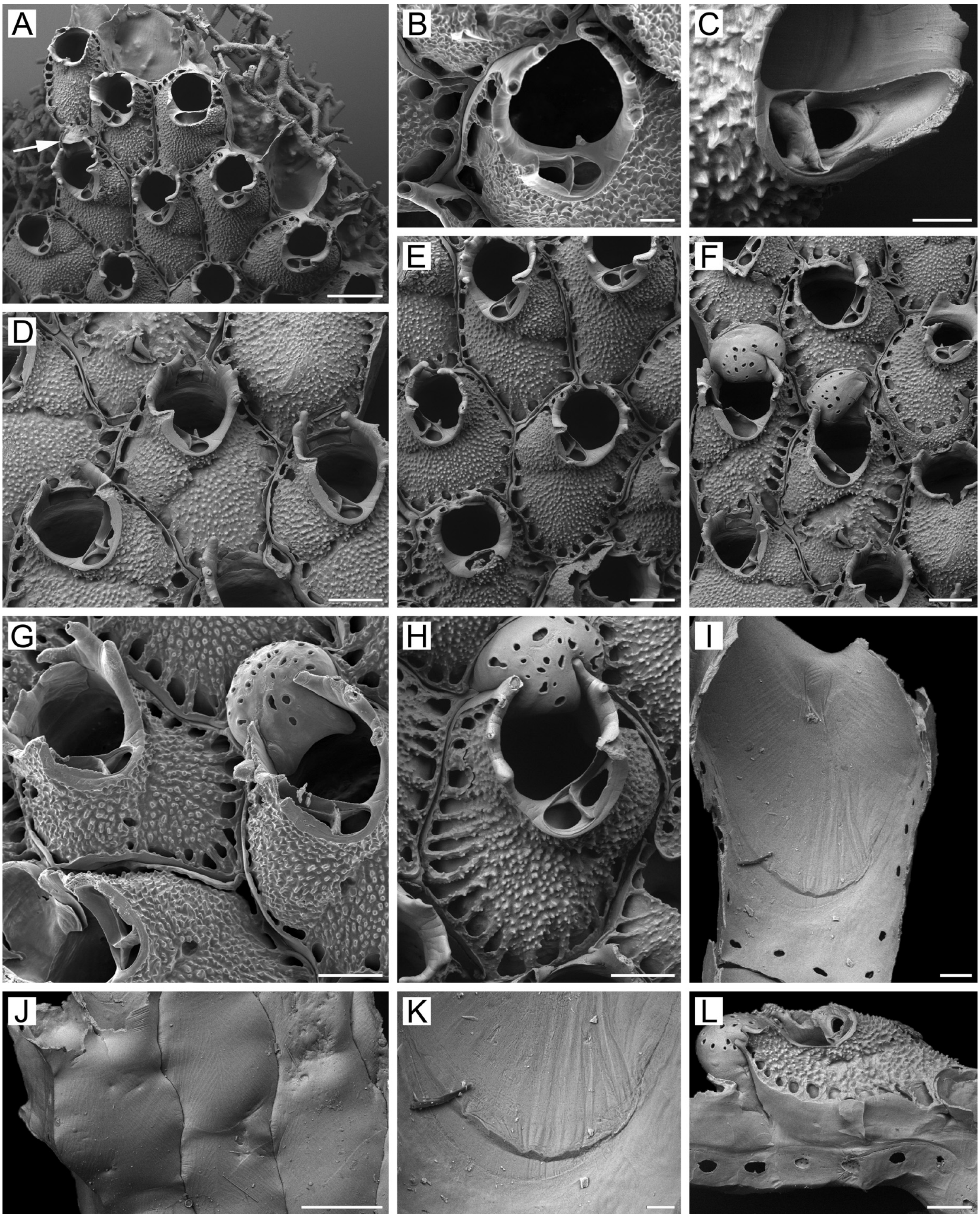

FIGURE 9. *Rhamphostomella aleutica* **n. sp.** *Holotype*, NHMUK 2010.4.21.1 (Amchitka Island, Aleutian Islands, Bering Sea). A. Colony margin with young, fully formed and developing autozooids (arrow, developing ooecium). B. Orifice with suboral avicularium. C. Suboral avicularium. D, E. Non-ovicellate zooids in young parts of colony, showing inflated cystids of suboral avicularia. F. Group of non-ovicellate and ovicellate zooids, showing traces of repair after damage. G. Close-up of autozooids in older part of colony, showing details of secondary orifice, suboral avicularia and ovicell. H. Frontal view of ovicellate zooid. I. Interior of frontal shield with ring scar and areolae. J. Basal colony surface. K. Close-up of frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. L. Lateral view of zooid, showing ooecium with peristome and suboral avicularium as well as lateral wall with mural pore chambers. Scale bars: A, J, 500 μm; B, C, I, 100 μm; D–F, 250 μm; G, H, L, 200 μm; K, 50 μm.

Frontal shield umbonuloid (Fig. 9A, I), moderately convex to strongly inflated, entirely covered by tiny pointed tubercles that enlarge in size and become coarse in older zooids (Fig. 9B–H). Frontal shield with deep areolae along margins (Fig. 9A, D–H), separated by short narrow interareolar ridges. Umbonuloid component extensive, occupying about 80% of length of frontal shield (77% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 9I, K). Ring scar discrete, forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 9A) submerged, irregularly circular, visible only in young zooids; distal and lateral margins formed by upper terminal part of distal transverse wall. Distal margin of orifice round, proximal margin shallowly concave, with small, narrow, pointed median process (Fig. 9B) that is barely evident or is absent in some zooids. Condyles absent. No oral spines.

Secondary orifice subcircular to irregularly oval, cormidial, defined by tubular peristome; distally formed by a slightly elevated proximal margin of daughter-zooid frontal shield (Fig. 9A–B, D); in older zooids becoming prominent vertical outgrowth (Fig. 9G). Laterally and proximally, secondary orifice comprising terminal part of flared peristome, incorporating avicularian cystid on one side. Peristomial rim with spine-like tubular projections, acute or blunt-tipped, 2–4 on each side (Fig. 9E–H), slightly tilted inwards. In ovicellate zooids, left and right sides of peristome encroaching onto surface of ooecium (Fig. 9F–H), occasionally pressing into it and causing partial ooecial deformation (Fig. 9F, H).

Cystid of suboral avicularium occupying one-quarter to one-third of frontal shield, asymmetrically situated proximolaterally to left or right of peristome, broad-based, bulging, with coarsely granulate surface, bearing 2–4 communication pores connecting avicularian and hypostegal coeloms; postmandibular area of frontal surface often crossing zooidal midline, facing obliquely in frontal direction (Fig. 9A–H). Rostrum elongate triangular, with narrowing hooked tip, incorporated into flared peristome, slightly curved distolaterally, directed distolaterally and frontally. Palatal foramen drop-shaped, cryptocystal shelf extensive distally, tapering proximally; opesia oval, surrounded by narrow cryptocyst. Crossbar complete, narrow, vertically deep (Fig. 9A–H).

No adventitious avicularia.

Ovicells hyperstomial (Fig. 9F–H). Ooecium formed by distal autozooid at colony periphery (Fig. 9A, L). Ectooecium smooth, free of secondary calcification, with numerous small, irregular, circular, oval to slit-like pseudopores; proximal margin of ooecium slightly concave, frontal area appressed to distalmost flanks of peristome (Fig. 9 F–H, L).

Zooids interconnected by two mural pore chambers in each distolateral wall (Fig. 9L) and 1–2 multiporous septula in basal half of transverse walls. In some zooids, transverse walls have two shallow recesses separated by medial buttress.

Basal surface of zooids (Fig. 9J) fully calcified, smooth, thin. Numerous white spots (presumably weakly calcified areas) visible in semitransparent basal wall using light microscopy. Boundaries between zooids indicated basally by broadly sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. The elevated, subtubular peristome, with 2–4 spinous projections along each lateral margin, makes *R. aleutica* **n. sp.** unique in the genus, clearly distinguishable from congeners.

In the primary orifice with a pointed process, the shape and position of the suboral avicularium, and the umbonuloid shield, this species resembles species in *Drepanophora* (Lepraliellidae). Considering the pseudoporous ooecium in *R. aleutica* **n. sp.**, however, these are probably convergent similarities.

Ecology. The sole colony of *Rhamphostomella aleutica* **n. sp.** was found encrusting a sponge from 224–235 m depth.

Distribution. Currently known only from the type locality in the coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, *R. aleutica* **n. sp.** is a Pacific high-boreal, sublittoral species.

Rhamphostomella alutacea Gontar, 1993
(Figs 10, 32C–E)

Rhamphostomella alutacea Gontar, 1993a, p. 12, fig. 7.
Rhamphostomella alutacea: Denisenko 2013, p. 184.

Material examined. *Holotype*: ZIRAS 1/44569, colony encrusting skeleton of sea urchin, Kuril-Sakhalin Expedition of Zoological Institute (ZIRAS) and Pacific Institute of Fisheries and Oceanography (TINRO), 15 September 1949, Krabovaya Bight, Shikotan Island, Lesser Kuril Ridge, Pacific Ocean, depth 55 m, shell, rock dredge, collector E.F. Guryanova. *Paratype*: ZIRAS 2/50123, five fragments of single colony detached from broken shell of the bivalve *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko.

Measurements. ZIRAS 2/50123, western Kamchatka, Sea of Okhotsk (Fig. 10A–L). ZL, 0.60–0.93 (0.71 ± 0.09). ZW, 0.35–0.55 (0.44 ± 0.05). ZD, 0.59–0.65 (n = 2). OrL, 0.15–0.25 (0.19 ± 0.03). OrW, 0.20–0.27 (0.22 ± 0.02). OeL, 0.17–0.27 (0.24 ± 0.03). OeW, 0.24–0.35 (0.30 ± 0.03). Av(s)L, 0.07–0.14 (0.10 ± 0.01). P(m)N, 16–26 (19). P(oe)N, 1–10 (6).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 10A), irregular in form, attaining 33 mm in maximal dimension; bright red to orange when alive, dark red to pink when dry. Zooids of medium size, hexagonal, oval to pyriform or irregular, arranged in quincunx, demarcated by fine, meandering sutures between lateral and transverse walls (Fig. 10A, D–H); boundaries less distinct in older parts of colony.

Frontal shield umbonuloid (Fig. 10A, D, I), thickened, pustulose, convex in young zooids, flattened and smoother in older ones owing to its thickening. Large, deep, round to oval areolae along margins (Fig. 10D–H), separated by short narrow interareolar ridges that may reach suboral avicularian cystid in distal part of frontal shield, mainly in young zooids. Thickening of frontal shield in older parts of colony resulting in considerable change in appearance, with some areolae reduced in size and obliterated, and others partitioned, resulting in "migration" of openings toward central part of shield and possibly fusing (compare Fig. 10A, D, E with Fig. 10F–H). Umbonuloid component extensive, occupying about 60% of length of frontal shield (63% in one measured zooid). Ring scar discrete (Fig. 10I, K), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 10A, B) submerged, broadly circular or oval; distal and lateral margins formed by upper terminal part of distal transverse wall, with ill-defined rim (Fig. 10A, B, D, E). Distal margin of orifice rounded; proximal margin concave, with elongate to short, blunt or bifurcate median lyrula and two small acute or blunt processes situated proximolaterally. Sometimes one or both processes strongly reduced or absent (Fig. 10A, D–F). No condyles or oral spines.

Secondary orifice (Fig. 10E–H) round to oval, cormidial, formed distally by slightly elevated vertical walls of distal zooid and occasionally by lateral walls of neighbouring zooids (Fig. 10D, E, G); proximally restricted by thin walls of peristome, comprising two relatively tall, symmetrical lappets derived from frontal shield and incorporating avicularian cystid medially; lappets connecting to proximolateral corners of ooecium in ovicellate zooids (Fig. 10F, H).

Cystid of suboral avicularium small, occupying less than one-quarter of zooid frontal shield; low in young zooids (Fig. 10A, D, E), moderately to strongly elevated and conical in some older zooids; situated medially or (more often) lying transversely to left or right of median axis. Frontal surface (rostral/postmandibular areas) crossing zooidal midline. Rostral frontal surface at strong oblique angle to postmandibular area, overall facing laterally and obliquely frontally; this concave aspect of avicularium, as well as position in peristome, gives impression of pseudosinus in secondary orifice. Rostrum short, blunt, semioval, directed laterally to distolaterally and upwards (Fig. 10C); palatal foramen conforming to shape of rostrum, no cryptocystal shelf; opesia semicircular or lingulate, sometimes of same size as foramen. Crossbar complete.

No adventitious avicularia.

Ovicells initially hyperstomial, rapidly becoming subimmersed and even appearing endozooidal (Fig. 10F–H, L) through overgrowth by secondary calcification from adjoining daughter and neighbouring zooids that cover most of ooecium except for central pseudoporous part. Ooecium formed by distal autozooid. Ooecial and visceral coelomic cavities connected via communication canal opening on underside of frontal shield of distal zooid as large, angular communication slit near proximalmost areolae (Fig. 10I). Ooecium with straight or slightly concave proximal margin. Ectooecium smooth, with pseudopores varying markedly in number, size, form (round, oval, elongate, irregular) and pattern of arrangement.

Zooids interconnected by one mural pore chamber in each distolateral wall (Fig. 10L). Predominantly two (occasionally one) multiporous septula sometimes added by individual pores in basal half of transverse walls. In some zooids, transverse wall has two shallow recesses separated by medial buttress.

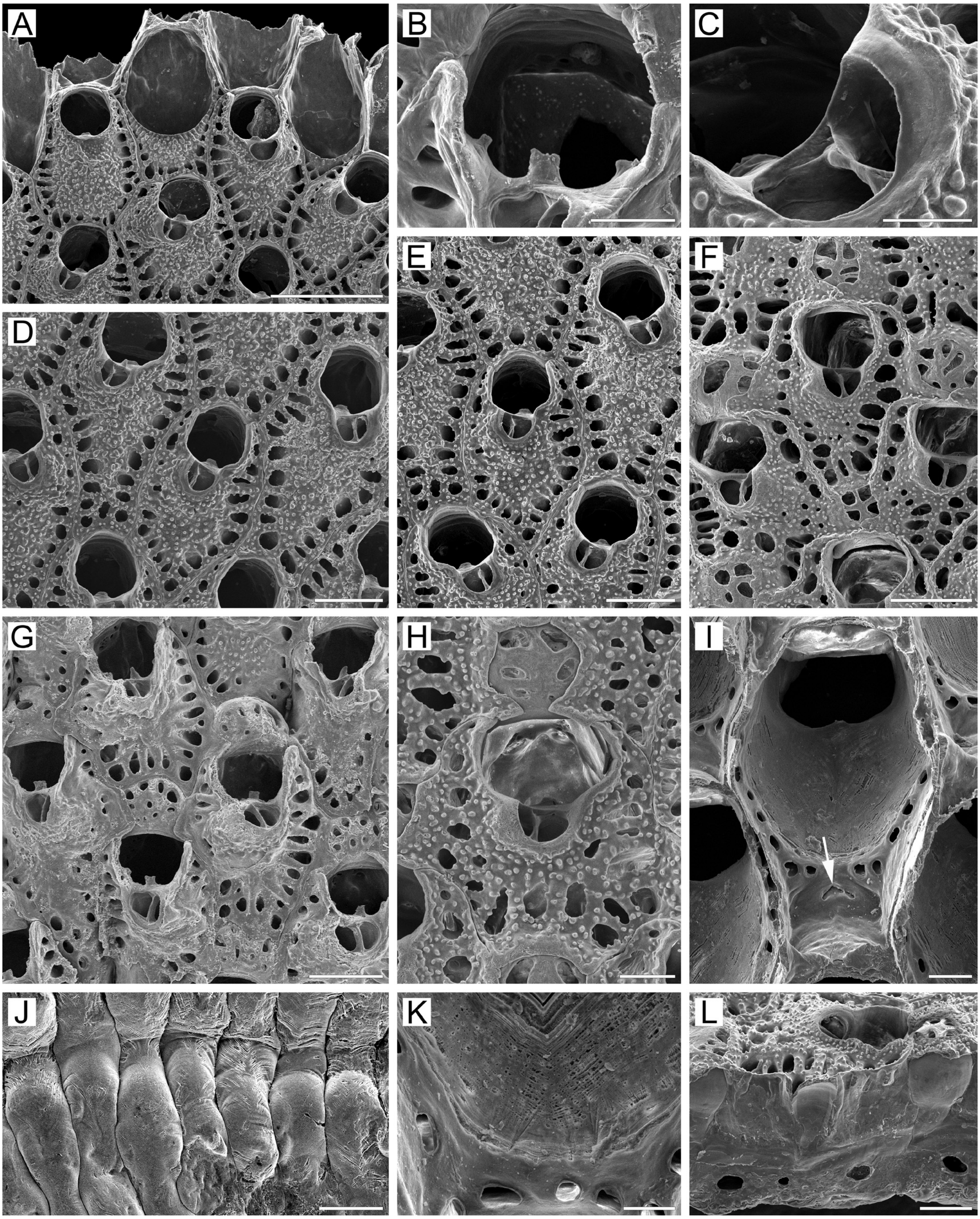

FIGURE 10. *Rhamphostomella alutacea* Gontar, 1993. ZIRAS 2/50123 (western Kamchatka, Sea of Okhotsk). A. Colony margin with developing zooids. B. Orifice, showing median lyrula and lateral denticles. C. Close-up of suboral avicularium. D, E. Group of non-ovicellate zooids in young part of colony. F, G. Ovicellate zooids in older part of colony, with ooecia embedded in secondary calcification arising from surrounding zooids. H. Close-up of ovicellate zooid, with coarsely granulate frontal shield and ooecium having pseudopores overlain with secondary calcification. I. Interior of the frontal shield, showing ring scar, areolae and proximal area with chevron-shaped communication slit of ooecium (arrow). J. Basal colony surface. K. Close-up of frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. L. Lateral view of zooidal lateral wall, showing mural pore chambers, and ooecium (to the right) embedded in secondary calcification. Scale bars: A, J, 500 µm; B, H, I, 100 µm; C, K, 50 µm; D–G, 250 µm; L, 200 µm.

Basal surface of zooids (Fig. 10J) fully calcified, convex, smooth or with coarse transverse lineation; without evident protuberances. Boundaries between zooids recognizable basally by deep, sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. *Rhamphostomella alutacea* differs from congeners in the strictly transverse position of the suboral avicularium, which is strongly angled upon itself to appear concave, with the rostrum facing obliquely frontally. The only congener with a similar transverse placement of the suboral avicularium, *R. radiatula*, has a narrow, U-shaped pseudosinus, with the avicularian rostrum often hidden or barely visible frontally (Fig. 18D–H).

In her original description, Gontar (1993a) mentioned and illustrated ovicells as having an ooecium with a single triangular or slit-like central pseudopore. In fact, the number, shape, and arrangement of the pseudopores can vary markedly (Fig. 10F–H). Contrary to the original description of the frontal shield as flattened, we observed that it can be convex in young zooids.

Ecology. *Rhamphostomella alutacea* was recorded from 55–81 m depth on sandy and silty bottoms overlain with gravel, where colonies encrust broken shells of the bivalve *Chlamys* sp. and sea urchin tests.

Distribution. This species was originally described from Krabovaya Bight, Shikotan Island, Lesser Kuril Ridge, northwestern Pacific; we report it also from the western Kamchatka shelf, Sea of Okhotsk. Thus, *R. alutacea* is a Pacific Asian boreal, sublittoral species.

***Rhamphostomella aspera* n. sp.**
(Fig. 11)

Diagnosis. Colony encrusting, multiserial. Zooids very large, broadly hexagonal. Frontal shield thickened, strongly convex, roughly granulated, with shaggy appearance. Marginal areolae separated by prominent radially arranged interareolar ridges continuing to apex of suboral avicularium, giving striated appearance to zooid. Umbonuloid component extensive. Primary orifice roughly quadrangular with round angles and ill-defined rounded lateral condyles. Proximal margin straight with broad low prominence. Pair of short, ephemeral, tubular oral spines often present. Secondary orifice oval or quadrangular, cormidial. Suboral avicularian cystid very large, occupying one-third to half of frontal shield, elevated, with acute conical apex, partially overhanging orifice, covered by interareolar ridges; frontal surface facing laterally to proximolaterally, occasionally proximally. Rostrum semioval, blunt. Crossbar complete, with small ligula. No adventitious avicularia. Ovicells hyperstomial, wider than long. Ectooecium smooth with sparse pseudopores; no secondary calcification. Pore chambers in distolateral wall and 1–2 multiporous septula in transverse walls. Basal surface of zooids fully calcified, tightly cemented to substratum.

Material examined. *Holotype*: ZIRAS 1/50542, colony encrusting sponge, IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 63/53, 29 July 2011, northward from Iturup Island, South Kuril Islands, Sea of Okhotsk, 45°45.1′ N, 148°33.2′ E – 45°44.5′ N, 148°33.5′ E, depth 264–274 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev.

Etymology. Latin, *asper*, rough, shaggy, alluding to the coarsely granular surface of the zooids that contrast strongly with the smooth spherical ooecia.

Type locality. Northward from Iturup Island, South Kuril Islands, Sea of Okhotsk, 45°45.1′ N, 148°33.2′ E – 45°44.5′ N, 148°33.5′ E, depth 264–274 m.

Measurements. ZIRAS 1/50542, Iturup Island, Kuril Islands, Sea of Okhotsk (Fig. 11A–M). ZL, 1.33–1.95 (1.58 ± 0.17). ZW, 0.85–1.30 (1.01 ± 0.09). ZD, 1.13–1.19 (*n* = 2). OrL, 0.40–0.51 (0.44 ± 0.03). OrW, 0.39–0.46 (0.43 ± 0.02). OeL, 0.42–0.55 (0.49 ± 0.04) (*n* = 10). OeW, 0.57–0.68 (0.62 ± 0.04) (*n* = 10). Av(s)L, 0.33–0.43 (0.38 ± 0.02). P(m)N, 19–31 (25). P(oe)N, 9–18 (12) (*n* = 10).

Description. Colony encrusting, multiserial, unilaminar (Fig. 11A), patch-like, about 11 × 16 mm in size, yellow when dry. Zooids very large, broadly hexagonal to oval, widest in midlength, arranged in checkered pattern, demarcated by fine sutures between lateral and transverse walls. Boundaries between zooids clearly visible in both young and old parts of colony.

Frontal shield umbonuloid (Fig. 11A, I), thickened, strongly convex, with rough surface composed of pointed granules conferring a shaggy appearance, with circular areolae along raised margins (sometimes forming double rows for a short distance) (Fig. 11B–F), separated by elongate, prominent, radially arranged interareolar ridges connected with cystid of suboral avicularium, frequently continuing to apex and thus giving a striated appearance to zooid. Areolae diminishing in size in older parts of colony. Umbonuloid component extensive, occupying about 80% of length of frontal shield (78% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 11I, L). Ring scar indistinct (Fig. 11I, L), nevertheless forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 11C, I, J) quadrangular with round angles to hoof-shaped, often longer than wide; distal and lateral margins formed by upper terminal part of distal transverse wall, with prominent shelf distally (Fig.11A, C); low, ill-defined rounded condyles laterally (Fig. 11C, I, J). Distal margin of orifice rounded, proximal margin straight with broad, low prominence having shallow median concavity and broadly rounded proximolateral corners. Pair of short, ephemeral, tubular oral spines (Fig. 11A, C, E, M) often present in marginal and non-ovicellate zooids and occasionally in some ovicellate zooids.

Secondary orifice (Fig. 11D, E) oval or quadrangular, cormidial, distolateral curvature formed by vertical walls of distal and lateral zooids, proximally restricted by thickened distal margin of frontal shield that medially incorporates cystid of suboral avicularium (Fig. 11B, D).

Suboral avicularian cystid very large, occupying distal one-third to half of frontal shield, bulbous to conical, strongly elevated, with roughly tuberculate surface, and with 3–7 minute frontal communication pores (Fig. 11A–H, M); gently tilted distally, partially overhanging orifice, covered by interareolar ridges that continue to acute conical projection on top, which is directed frontally or inclined laterally. Avicularian frontal surface (rostral/postmandibular areas) crossing zooidal midline or not, facing laterally to proximolaterally, occasionally proximally. Rostrum semioval, blunt, with acute projection at the apex of the cystid directed distolaterally upwards; palatal foramen semioval or rounded triangular, laterally bordered by narrow cryptocystal shelf, opesia oval, semiround or ellipsoid. Crossbar complete, with small ligula.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 11F–H). Ooecium wider than long, formed by distal autozooid around shallow, arch-like concavity with communication pore at bottom, situated in proximalmost part of frontal shield just distal to distal margin of maternal primary orifice (Fig. 11A, B, D, E). Ectooecium smooth, sharply contrasting with shaggy, coarsely granular surface of frontal shield, with circular to slit-like sparse pseudopores. Ovicells remain prominent, with ooecium uncovered by secondary calcification.

Zooids interconnected by four mural pore chambers in each distolateral wall of zooid (Fig. 11M) and 1–2 small multiporous septula in basal half of transverse walls, sometimes accompanied by individual pores.

Basal surface of zooids (Fig. 11A, K) fully calcified, inflated, tightly cemented to substratum.

Ancestrula and early astogeny not observed.

Remarks. The orientation of the frontal surface of the suboral avicularium varies greatly in this species. While in the majority of zooids it is situated on the lateral slope of the avicularian cystid and faces laterally, in others it is on the proximal slope, with corresponding orientation (Fig. 11D, lowest zooid), and occasionally faces frontally (Fig. 11A, central zooid).

Rhamphostomella aspera **n. sp.** most resembles *R. obliqua* **n. sp.** in the general appearance of zooids and in having: 1) a primary orifice of similar shape, 2) a bulbous to conical, strongly elevated suboral avicularian cystid tilted distally and overhanging the orifice, with a lingulate mandible; and 3) hyperstomial ovicells, with the ooecium free of secondary calcification. However, these species differ as follows: 1) the primary orifice has a broad, low, median prominence in *R. aspera* **n. sp.** and straight in *R. obliqua* **n. sp.**; 2) the suboral avicularian cystid has a pointed, conical apex that is sometimes tilted laterally in *R. aspera* **n. sp.**, but a blunt apex in *R. obliqua* **n. sp.**; 3) the opesial area of the suboral avicularium faces mostly laterally to proximolaterally or occasionally proximally in *R. aspera* **n. sp.**, but distolaterally to laterally in *R. obliqua* **n. sp.**; 4) the interareolar ridges are long, prominent and solid, and continue to the avicularian apex in *R. aspera* **n. sp.**, but are generally shorter and lower, reaching only the sides of the avicularian cystid in the distal half of zooids in *R. obliqua* **n. sp.**; 5) the entire frontal surface is evenly coarse, giving a shaggy appearance to *R. aspera* **n. sp.**, but smooth to finely granular in *R. obliqua* **n. sp.**, except for the coarsely granulated surface of the avicularian cystid; 6) colonies of *R. aspera* **n. sp.** are yellow, those *R. obliqua* **n. sp.** are either saturated-brown or light-brown; 7) the orifice in *R. aspera* **n. sp.** (0.40–0.51 × 0.39–0.46 mm) is larger than that in *R. obliqua* **n. sp.** (0.34–0.41 × 0.33–0.39 mm); 8) the ooecium in *R. aspera* **n. sp.** (0.42–0.55 × 0.57–0.68 mm) is larger than that in *R. obliqua* **n. sp.** (0.33–0.39 × 0.45–0.55 mm), with non-overlapping ranges.

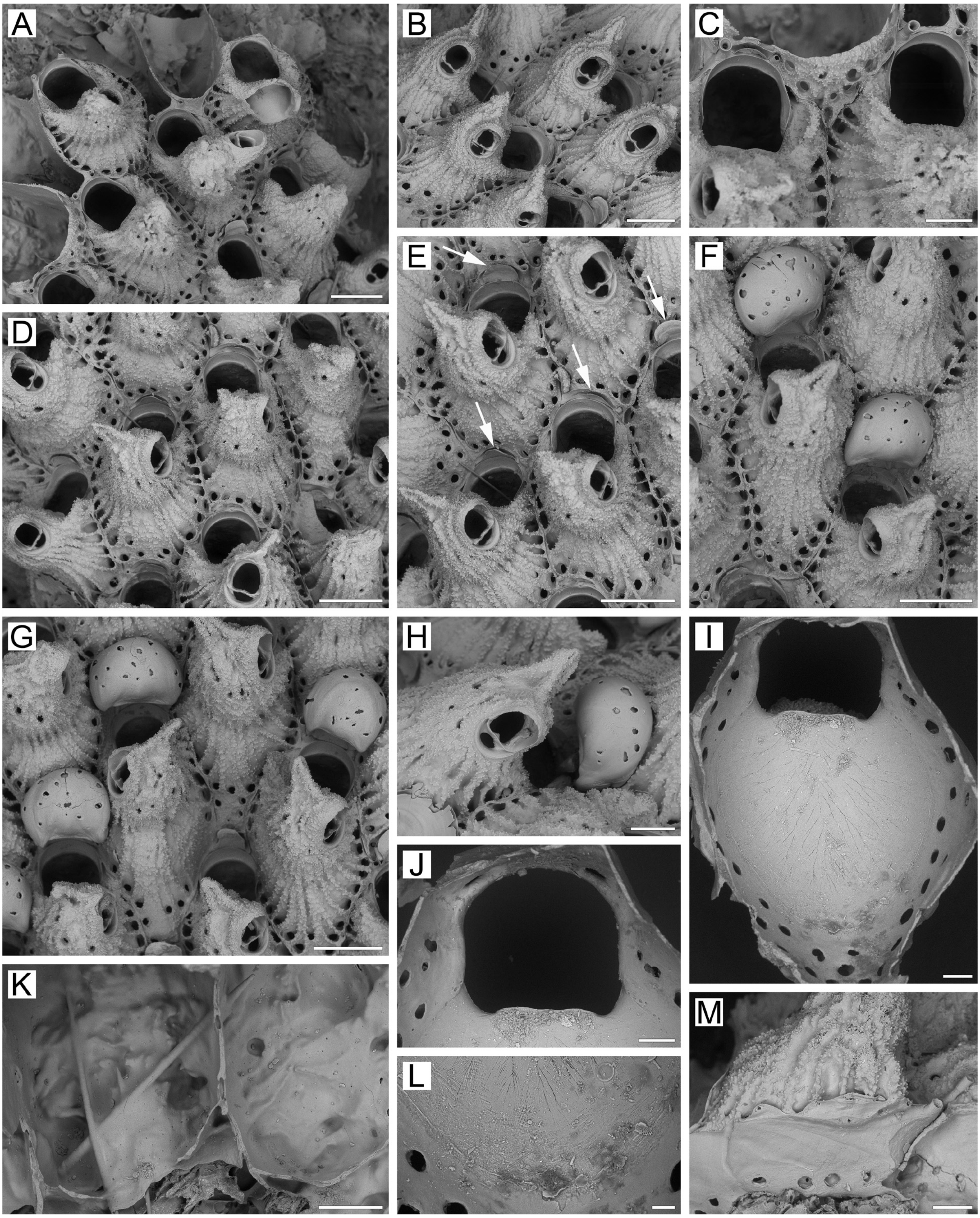

FIGURE 11. *Rhamphostomella aspera* **n. sp.** *Holotype*, ZIRAS 1/50542 (Iturup Island, Kuril Islands, Sea of Okhotsk). A. Colony margin with developing zooids. B. Lateral view of non-ovicellate zooids. C. Primary orifices of marginal zooids, showing the distal shelf, bases of oral spines and initial stage of ooecium formation (in left zooid). D. Group of non-ovicellate zooids, showing variability in opesial area of suboral avicularium. E. Zooids with early developing ooecia (arrows). F, G. Ovicellate zooids. H. Lateral view of ovicellate zooid. I. Interior of frontal shield, showing areolae and umbonuloid component. J. Internal view of orifice, showing broad proximal prominence and ill-defined condyles. K. Basal surface of colony. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing very large avicularian cystid, oral spines and zooid lateral wall with mural pore chambers. Scale bars: A, B, D–G, 500 µm; C, H, K, 250 µm; I, J, 100 µm; L, 50 µm; M, 200 µm.

Ecology. The only specimen of *Rhamphostomella aspera* **n. sp.** was encrusting a sponge from 264–274 m depth.

Distribution. This species is known from only a single locality north of Iturup Island, South Kuril Islands, Sea of Okhotsk, and can be categorized as a Pacific Asian high-boreal, sublittoral species.

Rhamphostomella bilaminata **(Hincks, 1877)**
(Figs 12, 32F, G)

?*Cellepora plicata*: Smitt 1868a, p. 30, 31 (part), pl. 28, fig. 191.
Cellepora bilaminata Hincks, 1877, p. 111, pl. 11, figs 6, 7.
Rhamphostomella bilaminata: Lorenz 1886, p. 13, pl. 7, fig. 10 (mentioned as fig. 11 in the text); Nordgaard 1906, p. 33, 41, pl. 4, fig. 57; Kluge 1962, p. 545, fig. 382; 1975, p. 663, fig. 382; Osburn 1912a, p. 244, pl. 26, fig. 61; 1952, p. 427, pl. 52, fig. 10; Gostilovskaya 1978, p. 231, fig. 147; Winston & Hayward 2012, p. 120, fig. 76.
Discopora bilaminata: Nordgaard 1918, p. 79.
Rhamphostomella porosa: O'Donoghue & O'Donoghue 1923, p. 45, pl. 4, fig. 35.

Additional references. *Rhamphostomella bilaminata*: Kluge 1908a, p. 533; 1928, p. 257; 1964, p. 190; Osburn 1936, p. 542; 1955, p. 38; MacGinitie 1955, p. 130; Gostilovskaya 1957, p. 454; 1968, p. 70; Hansen 1962, p. 39; Powell 1968a, p. 2311; 1968b, p. 257; Denisenko 1988, p. 13; 1990, p. 39; 2008, p. 187; 2011, p. 14; 2013, p. 184; Gontar 1989, p. 113; 1990, p. 133; 2010, p. 153; Gontar & Denisenko 1989, p. 359; Gontar *et al*. 2001, p. 194; Grishankov 1995, p. 48; Grischenko *et al*. 1999, p. 112; Grischenko 2001, p. 46; 2002, p. 115; 2014, p. 19; Shunatova & Ostrovsky 2001, p. 115, 118; Kuklinski 2002a, p. 181; 2002b, p. 203; 2009, p. 228; Shunatova & Nielsen 2002, p. 263, figs. 5a, c; Denisenko & Kuklinski 2008, p. 48; Ostrovsky 2009, p. 26; 2013, p. 8; Foster 2010, p. 57.

Material examined. *Neotype*: NHMUK 1911.10.1.1580A, one colony, A.M. Norman Collection, Gaspe, Gulf of St Lawrence, Atlantic Ocean, collector J. Whiteaves.

NHMW 92533 (=1884.II.49), one colony, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 20–130 m, collector F. Fischer. NHMW 72989, one colony fragment, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 20–130 m, collector F. Fischer. NHMUK 1911.10.1.1579A, five colony fragments encrusting hydroids, A.M. Norman Collection, Gaspe, Gulf of St Lawrence, Atlantic Ocean, collector J. Whiteaves. ZIRAS 23/50121, three colony fragments, detached from broken shells of bivalve mollusc *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko. ZIRAS 24/50122, one colony encrusting branch of bryozoan colony *Dendrobeania* sp., KIENM Collection, RV *Nazarovsk*, Stn 182, 11 May 1988, Avacha Gulf, eastern Kamchatka Peninsula, Pacific Ocean, 53°36.0′ N, 160°07.0′ E, depth 100 m, rock dredge, collector A.V. Rzhavsky. ZIRAS 32/50549, nineteen colonies encrusting a colony of the ctenostome bryozoan *Flustrellidra filispina*, 15 July 2003, Nakanoze Bank, Akkeshi Bay, Pacific coastal waters of Hokkaido Island, 43°00.4′ N, 144°46.6′ E, depth 4–6 m, rock dredge, collector A.V. Grischenko.

Additional material. Four specimens. PIBOC Collection (1991) Stn 19; IMB Collection (2011) Stns 3/1, 63/53, 64/54 (see Appendix 1 for details).

Measurements. NHMUK 1911.10.1.1579A, Gulf of St Lawrence, Atlantic Ocean (Fig. 12B–D, G–I). ZL, 0.47–0.75 (0.59 ± 0.07). ZW, 0.32–0.53 (0.43 ± 0.05). ZD, 0.43–0.49 (*n* = 2). OrL, 0.17–0.25 (0.22 ± 0.02). OrW, 0.20–0.30 (0.25 ± 0.02). OeL, 0.22–0.32 (0.27 ± 0.03). OeW, 0.27–0.43 (0.34 ± 0.03). Av(s)L, 0.12–0.20 (0.15 ± 0.02). P(m)N, 4–8 (6). P(oe)N, 5–11 (7).

ZIRAS 23/50121, western Kamchatka, Sea of Okhotsk (Fig. 12A, E, F). ZL, 0.50–0.93 (0.69 ± 0.10). ZW, 0.32–0.57 (0.45 ± 0.08). ZD, 0.40–0.48 (*n* = 2). OrL, 0.17–0.30 (0.25 ± 0.04). OrW, 0.20–0.31 (0.25 ± 0.04). OeL, 0.19–0.32 (0.27 ± 0.03). OeW, 0.30–0.45 (0.36 ± 0.04). Av(s)L, 0.11–0.27 (0.19 ± 0.04). P(m)N, 7–13 (9). P(oe)N, 12–23 (18) (*n* = 10).

ZIRAS 24/50122, Avacha Gulf, eastern Kamchatka, Pacific Ocean (Fig. 12 J–L). ZL, 0.47–0.68 (0.55 ± 0.05). ZW, 0.35–0.50 (0.42 ± 0.04). ZD, 0.48–0.53 (*n* = 2). OrL, 0.18–0.28 (0.22 ± 0.02). OrW, 0.18–0.25 (0.22 ± 0.02). OeL, 0.20–0.28 (0.24 ± 0.02). OeW, 0.27–0.38 (0.32 ± 0.03). Av(s)L, 0.13–0.24 (0.19 ± 0.03). P(m)N, 4–9 (6). P(oe)N, 7–13 (9).

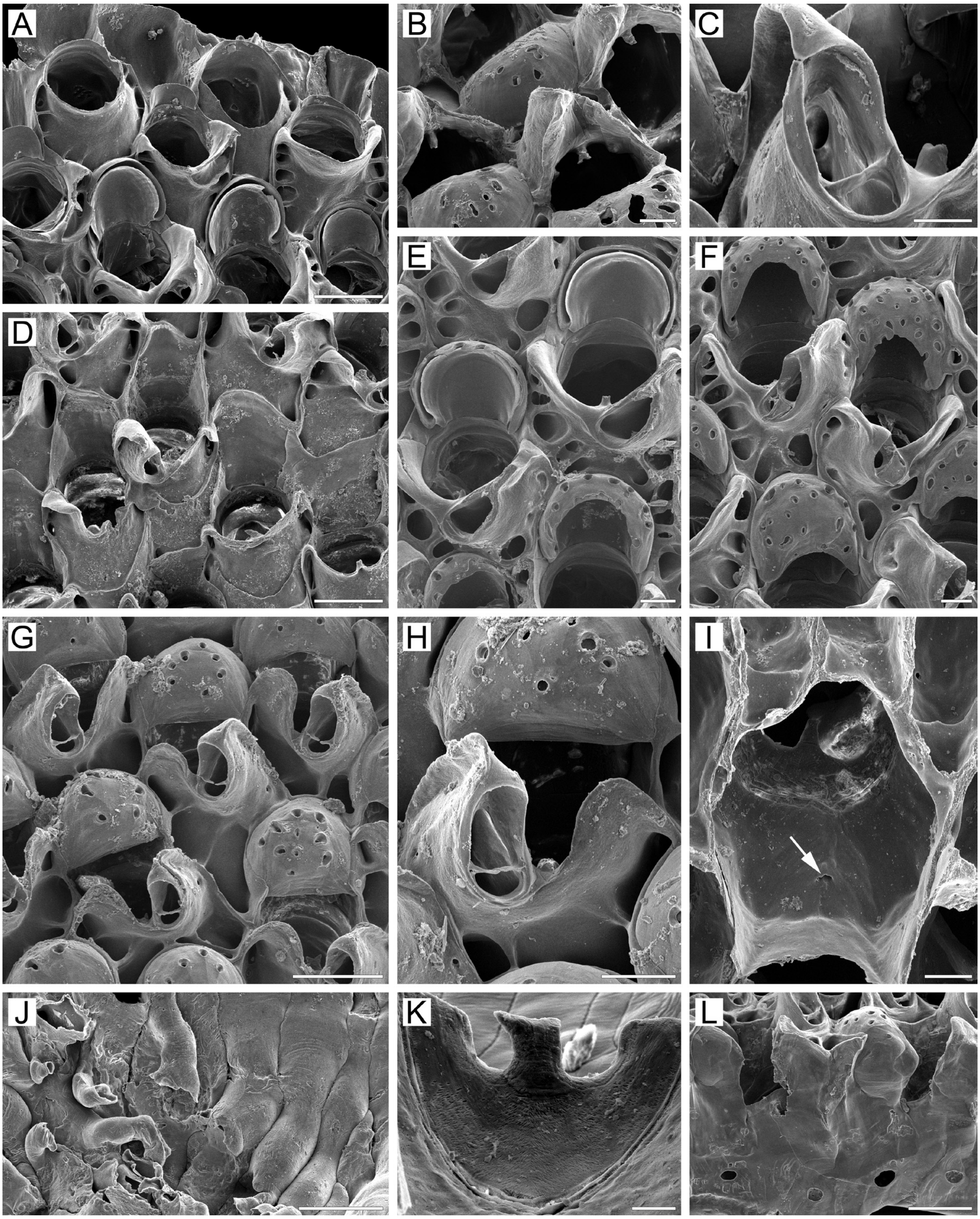

FIGURE 12. *Rhamphostomella bilaminata* (Hincks, 1877). A, E, F. ZIRAS 23/50121 (western Kamchatka, Sea of Okhotsk). B–D, G–I. NHMUK 1911.10.1.1579A (Gulf of St Lawrence, Atlantic Ocean). J–L. ZIRAS 24/50122 (Avacha Gulf, eastern Kamchatka, Pacific Ocean). A. Colony margin with developing zooids and ooecia. B. Distal view of ovicellate zooids, showing proximal margin of primary orifice with lyrula and denticles. C. Suboral avicularium. D. Non-ovicellate zooids with additional calcified layer expanding over frontal shield. E. Zooids with developing ooecia. F. Zooids with developing and one completed ooecia. G. Group of ovicellate zooids in older part of colony. H. Suboral avicularium in ovicellate zooid. I. Interior of frontal shield, showing umbonuloid component and ooecial communication pore (arrow). J. Basal surface of colony. K. Interior of frontal shield, showing ring scar and umbonuloid component, and median lyrula and two sinuses. L. Lateral view of zooid with a peristome, suboral avicularium, and ooecium; zooidal lateral wall shows mural pore chambers. Scale bars: A, D, G, 250 µm; B, E, F, H, I, 100 µm; C, K, 50 µm; J, 500 µm; L, 200 µm.

Description. Colonies encrusting, multiserial, unilaminar (Fig. 12A), more or less circular in outline, small, attaining 16 mm in maximal dimension; bright brown to orange when alive, light brown to pink when dry. Free-growing bilaminate folds can be present in some colonies. Zooids small, rectangular to hexagonal (Fig. 12A, D, H) or irregular in form, arranged in checkered pattern, demarcated by irregular sutures between lateral and transverse walls; boundaries indistinct at all parts of colony.

Frontal shield (Fig. 12A, D–F, I), thin, moderately to strongly convex, smooth, with deep areolae along strongly raised zooidal margins that occasionally expand above proximal half of frontal shield to form additional layer of calcification (Fig. 12D). Areolae separated by short, thin or thick interareolar ridges arranged radially and connected to lobe of peristomal lappet on one side and to avicularian cystid on the other (Fig. 12E–H). Umbonuloid component small, occupying about 35% of length of frontal shield, with fine parallel lineation and accretionary banding (Fig. 12I, L). Ring scar discrete, forming clear boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure (Fig. 12L).

Primary orifice submerged, circular; distal and lateral margins formed by upper terminal part of distal transverse wall (Fig.12A). Distal margin of orifice rounded, proximal margin bisinuate, with small trapezoidal or bifurcate lyrula in midline, lateral margins normally with short processes, blunt or pointed (Fig. 12B, C, I, K, L). Condyles absent. No oral spines.

Secondary orifice (Fig. 12D, G) rounded to asymmetrically oval or irregular, cormidial, distally and distolaterally restricted by strongly elevated vertical walls of distal and lateral zooids (Fig. 12D); laterally and proximally, formed by thin-walled and strongly elevated peristome, comprising two triangular or rounded flared lappets formed from frontal shield (one incorporating cystid of suboral avicularium and substituted by latter almost completely) with deep V- to U-shaped median pseudosinus between them (Fig. 12D–H). Peristomial lappets not fusing with proximolateral corners of ooecium in ovicellate zooids.

Cystid of suboral avicularium (Fig. 12A–H) not large but very distinct, elevated, situated asymmetrically with respect to zooidal orifice and associated with left or right peristomial lappet; surface smooth; one communication pore connecting avicularian and hypostegal coeloms. Frontal surface (rostral/postmandibular areas) of avicularium weakly concave, normally to one side of zooidal midline but sometimes crossing it, facing proximally to proximolaterally (Fig. 12C, F–H). Rostrum elongate oval, directed distolaterally, obliquely to vertically upwards, fusing with peristomial lappet distally. Shape of palate lingulate, palatal foramen elongate oval, with narrow cryptocystal shelf laterally, opesia semicircular. Crossbar complete. Avicularia lacking in some zooids, with paired peristomial lappets forming flared tubular peristome in this instance (Fig. 12D).

No adventitious avicularia.

Ovicells hyperstomial, cleithral (Fig. 12F–H). Ooecium formed by distal autozooid; ooecial fold forming at distal margin of primary orifice concurrently with formation of frontal shield of distal zooid (Fig. 12A). Ooecial and visceral coelomic cavities connected via communication canal opening on underside of frontal shield as small curved slit-like pore at some distance from transverse wall (Fig. 12I). Ectooecium smooth, with straight or slightly concave proximal margin and scattered circular to elongate pseudopores. Basal part of ooecium slightly overgrown by thin secondary calcification proceeding from frontal shields of neighbouring zooids (Fig. 12G, H); this calcification additionally forming thin vertical walls between distal margin of peristomial lappets and proximal corners of ooecia (Fig. 12G, H), adding to secondary orifice.

Zooids interconnected by one mural pore chamber in each distolateral wall (Fig. 12L) and two multiporous septula in basal half of transverse walls.

Basal walls of zooids fully calcified, smooth, inflated to moderately convex. Sparse white spots (presumably less-calcified areas) visible in semitransparent basal wall by light microscopy. Tubular protuberances of basal wall (0.06–0.19 mm in diameter) complex in shape, depending on substratum; textured by fine parallel lineation (Fig. 12J). Boundaries between zooids recognizable basally as slightly sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. Although Hincks (1877) described and illustrated *R. bilaminata* (as *Cellepora*) as distinct species, which was further confirmed by Lorenz (1886), it is still possible that it was first illustrated by Smitt (1868a) in his fig. 191 (pl. 28) under the name *Cellepora plicata*. Because we were unable to locate Hincks' (1877) specimen, we have selected as a neotype for this species a specimen from the Gulf of St Lawrence, North Atlantic, collected by J. Whiteaves and deposited in the Natural History Museum, London.

O'Donoghue & O'Donoghue (1923) described a new species, *Rhamphostomella porosa*, from British Columbia.

Osburn (1952, p. 427) synonymised *R*. *porosa* with *R*. *bilaminata*, arguing for the latter that "It has not been reported south of Alaska, except for O'Donoghue's record of *R*. *porosa* at Cape Ebenshaw, British Columbia. O'Donoghue recognized the similarity to *bilaminata*, but the distinguishing characters he indicates for *porosa* (viz., "the far larger size of the rostrum and peristome") are within the range of variation of *bilaminata*".

While most of the colonies examined were flat and encrusting, some from the shelf and slope of the southern Kuril Islands encircled hydroid stems, forming free-growing bilaminate folds and frills.

Ecology. *Rhamphostomella bilaminata* is known from 4–435 m depth, generally on mixed bottoms, including silt, sand, gravel and mollusc shells, encrusting hydroid stems, ascidians, molluscs and other bryozoans (*Alcyonidium* sp., *Flustrellidra filispina, Dendrobeania* sp.). Several colonies were detected on carapaces of the red king crab *Paralithodes camtshaticus*, caught at 78–81 m in the western Kamchatka shelf, Sea of Okhotsk (Grischenko 2001).

Distribution. This is a boreal-Arctic, circumpolar, sublittoral to upper bathyal species. Arctic records include Barents Sea (Bidenkap 1900a; Andersson 1902; Kluge 1915, 1962, 1975; Nordgaard 1918, 1923; Kuznetsov 1941; Denisenko 1988, 1990), White Sea (Kluge 1908a, 1928; Gostilovskaya 1957, 1978; Grishankov 1995; Shunatova & Ostrovsky 2001; Shunatova & Nielsen 2002; Ostrovsky 2009, 2013), Kara Sea (Nordgaard 1923; Kluge 1962, 1975), Laptev Sea (Kluge 1962, 1975; Gontar 1990), East Siberian Sea (Denisenko 2011); Chukchi Sea (Osburn 1923; Kluge 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), Point Barrow, Alaska, Beaufort Sea (Osburn 1955; MacGinitie 1955), Canadian Arctic Archipelago (Nordgaard 1906, 1929; Osburn 1936), Baffin Bay (Hansen 1962), Davis Strait (Kluge 1962, 1975; Hansen 1962), Hudson Bay (Osburn 1932), Labrador (Hincks 1877), western Greenland (Levinsen 1914; Osburn 1936; Denisenko & Blicher 2021), eastern Greenland (Gontar & Denisenko 1989; Denisenko & Blicher 2021), Greenland Sea (Gontar & Denisenko 1989), Spitsbergen (Gontar *et al*. 2001; Kuklinski 2002a, 2002b, 2009), Jan Mayen Island (Lorenz 1886; Nordgaard 1907b), northern Norway (Nordgaard 1918), Finmark (Smitt 1868a). In the northeastern Atlantic it has been reported from St Lawrence Gulf (Whiteaves 1901) southwards to Cape Cod (Osburn 1912b; Powell 1968b; Winston & Hayward 2012). In the northwestern Pacific it has been documented in Bering Strait (Gontar & Denisenko 1989), Avacha Gulf (our data) and Avacha Inlet off eastern Kamchatka Peninsula (Gontar 1989; Grischenko 2002); in the Sea of Okhotsk from Koni Peninsula, Tauyskaya Inlet (Grischenko 2014), along western Kamchatka (Grischenko *et al*. 1999; Grischenko 2001; our data), around Iturup and Kunashir Islands, south Kuril Islands (our data); in Japan it is known from Akkeshi Bay, Hokkaido, Japan (our data). In the northeastern Pacific it occurs in Cook Inlet (Foster 2010) and near Kodiak Island, Gulf of Alaska (our data) south to British Columbia (O'Donoghue & O'Donoghue 1923).

Rhamphostomella cellata (O'Donoghue & O'Donoghue, 1923)

(Fig. 13)

Smittina cellata O'Donoghue & O'Donoghue, 1923, p. 43, pl. 4, fig. 31.
Smittina cellata: O'Donoghue & O'Donoghue 1926, p. 68.
Rhamphostomella cellata: Osburn 1952, p. 431, pl. 52, fig. 9.
Not *Rhamphostomella cellata*: Hansen 1962, p. 39.
Smittina torquata O'Donoghue & O'Donoghue, 1923, p. 43, pl. 4, fig. 32.
Smittina torquata: O'Donoghue & O'Donoghue 1926, p. 68.

Material examined. *Lectotype*: NHMUK 1964.1.2.9, single colony detached from bivalve mollusc shell, fractured into nine fragments (mounted on seven SEM stubs), C.H. O'Donoghue Collection, Pacific coast of North America (presumably Vancouver Island, British Columbia).

Measurements. NHMUK 1964.1.2.9, Pacific coast of North America (Fig. 13A–L). ZL, 0.65–1.23 (0.89 ± 0.14). ZW, 0.32–0.55 (0.44 ± 0.06). ZD, 0.30–0.33 (*n* = 2). OrL, 0.15–0.25 (0.21 ± 0.02). OrW, 0.20–0.28 (0.23 ± 0.02). OeL, 0.25–0.33 (0.29 ± 0.02) (*n* = 22). OeW, 0.35–0.43 (0.38 ± 0.02) (*n* = 22). Av(s)L, 0.07–0.16 (0.11 ± 0.02). P(m)N, 17–27 (22).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 13A), more or less circular, attaining 22 mm in maximal dimension, light brown when dry. Zooids large, oblong-hexagonal to oval, or pyriform (Fig. 13A, D, F, G), arranged in checkered pattern, demarcated by fine sutures between lateral and transverse zooidal walls; sutures visible in both young and old parts of colony.

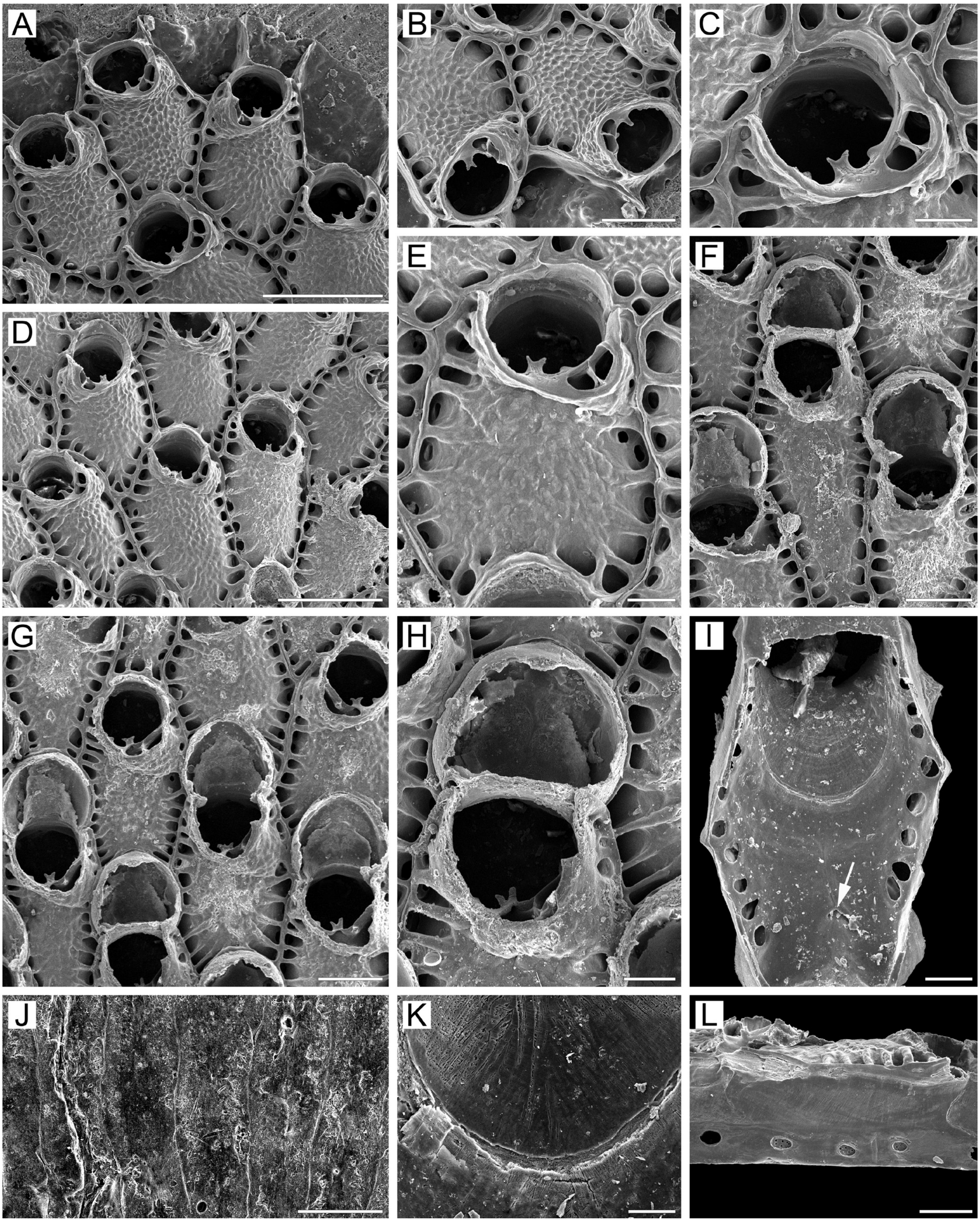

FIGURE 13. *Rhamphostomella cellata* (O'Donoghue & O'Donoghue, 1923). *Lectotype*, NHMUK 1964.1.2.9 (Pacific coast of North America, presumably Vancouver Island, British Columbia). A. Colony margin with developing zooids. B. Distolateral view of marginal zooids, showing shape of primary orifice and dimpled surface of frontal shield. C. Zooidal orifice with suboral avicularium. D. Group of non-ovicellate zooids in young part of colony. E. Single non-ovicellate zooid in older part of colony. F. Zooids with damaged ooecia in older part of colony. G. Zooids in older part of colony. H. Distal part of zooid with partially broken ooecium, showing form of secondary orifice and suboral avicularium. I. Interior of frontal shield, showing umbo, areolae and ooecial communication slit (arrow). J. Basal surface of colony, showing hardly recognizable boundaries between zooids. K. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. L. Lateral view of zooid, showing peristome, areolae and zooidal lateral wall with mural pore chambers. Scale bars: A, D, J, 500 µm; B, F, G, 250 µm; C, E, H, I, 100 µm; K, 50 µm; L, 200 µm.

Frontal shield umbonuloid (Fig. 13A, D, G, I), thin, inflated to slightly convex, smooth to dimpled, with reticulate appearance in young zooids (Fig. 13A, B, D) and smoothly tuberculate in older zooids (Fig. 13E–G); with numerous deep circular to oval areolae along margins, separated by short, narrow interareolar ridges. Umbonuloid component occupying about 40% of length of frontal shield, with parallel lineation and accretionary banding (Fig. 13I, K). Ring scar discrete (Fig. 13I, K), forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 13B, C, E) broadly circular to transversely oval; distal and lateral margins formed by upper terminal part of distal transverse wall incidentally bearing ill-defined rim (Fig. 13C). Distal margin of orifice rounded, proximal margin concave with median bifid lyrula having acute tips directed distolaterally, and distinct triangular process on each side with acute or round tip, occasionally strongly reduced. Condyles and oral spines absent.

Secondary orifice irregularly circular to oval, cormidial (Fig. 13C–H), distally and distolaterally restricted by elevated vertical walls of distal and lateral zooids; proximally formed by slightly elevated peristomial outgrowth of frontal shield, incorporating asymmetrically positioned cystid of suboral avicularium. In ovicellate zooids, lateral peristomial lappets connected to proximolateral corners of ooecium (Fig. 13F–H), conferring circular or sometimes irregularly triangular (because of avicularium) outline to secondary orifice.

Cystid of suboral avicularium small, low, asymmetrically situated proximolateral to zooidal orifice on left or right side, with dimpled surface and one small communication pore. Frontal surface (rostral/postmandibular areas) of avicularium concave, to one side of zooidal midline, facing obliquely frontally. Rostrum lodged within rim of peristome, slightly curving inward to conform to it, directed obliquely distolaterally and frontally (Fig. 13C, D, E, H). Palatal foramen lingulate to semioval and roundly triangular, conforming to shape of rostrum, opesia semioval to lingulate. Crossbar complete.

No adventitious avicularia.

Although all ooecia were broken in material studied, ovicells are clearly hyperstomial, with ooecia free of secondary calcification (Fig. 13F–H). Ooecium formed by distal autozooid, its coelomic cavity connected with visceral coelom via communication canal that opens on underside of proximal part of frontal shield of distal zooid as chevron-shaped communication slit about midway between transverse wall and ring scar (Fig. 13I). Remnants of ectooecium bear circular pseudopores in one specimen (Fig. 13F). Proximal margin of ooecium very weakly concave.

Zooids interconnected by three mural pore chambers in each distolateral wall (Fig. 13L) and two multiporous septula in basal half of transverse walls. In some zooids, transverse walls with two shallow recesses separated by medial buttress.

Basal walls of zooids entirely calcified (Fig. 13J), smooth, flat, without white spots or protuberances. Boundaries between zooids indicated basally by fine sutures.

Ancestrula and early astogeny not observed.

Remarks. The fragments examined have zooids with partially to fully damaged ovicells. One zooid shows the incomplete roof of an ovicell with two circular pseudopores and the remnants of a third laterally. In their original description, O'Donoghue & O'Donoghue (1923, p. 43) described the surface of ovicells as being "perforated by a series of large irregular pores" (their fig. 31 shows 10–12 oval to irregular pseudopores).

O'Donoghue & O'Donoghue (1923) described *Smittina cellata* and *S. torquata* from Vancouver Island. Osburn (1952, p. 431) synonymized these species, treating the former as the senior synonym of the latter and placing it in *Rhamphostomella*.

The surface of the frontal shield of *R. cellata* is dimpled, conferring a reticulate appearance similar to that in *R. curvirostrata* and *R. townsendi*. The former species clearly differs from the latter two in having the suboral avicularium located within the rim of peristome, slightly curving inwards to conform to it. While the suboral avicularium in the latter two species is connected with the peristome, both the rostrum and frontal surface differ from *R. cellata* in position, shape and orientation.

The Canadian Museum of Nature contains some material identified by O'Donoghue from British Columbia (24 items), including a dried specimen of *R. cellata* (Cat. No. – CMNI 1988-0135, Northumberland Channel). Unfortunately, there are no images, and the specimen is not mentioned as a type in the On-line Collection Data of the Museum. Accordingly, we selected a lectotype from C.H. O'Donoghue Collection deposited in the Natural History Museum, London. Although a precise locality was not written on the label, these specimens likely came from the waters around Vancouver Island, British Columbia.

Ecology. *Rhamphostomella cellata* is known only from the depth range 1.8–9.1 m. Colonies encrust mollusc shells.

Distribution. This little-known species was first described from Northumberland Channel and Gabriola Passage (about 49°52.0′ N, 123°72.0′ W), Vancouver Island, British Columbia (O'Donoghue & O'Donoghue 1923). O'Donoghue & O'Donoghue (1926) recorded it from numerous localities in British Columbia (Namu, Port Simpson, off Round Island, Houston Channel, Brotchie Ledge, Victoria, off Point Caution, off Breakwater Island, Cowichan Gap) and near the San Juan Islands in Puget Sound. The specimens examined by Osburn were collected from Middle Bank, Puget Sound (Osburn 1952). Records of the species from Baffin Bay and Davis Strait (Hansen 1962) are doubtful. From these distributional data, *R. cellata* is an Eastern Pacific boreal, sublittoral species.

Rhamphostomella curvirostrata O'Donoghue & O'Donoghue, 1923
(Figs 14, 30F)

Rhamphostomella curvirostrata O'Donoghue & O'Donoghue, 1923, p. 44, pl. 4, fig. 34.
Rhamphostomella curvirostrata: Osburn 1952, p. 430, pl. 50, fig. 4; Androsova 1958, p. 172, fig. 103; Hayami 1973, p. 51; 1975, p. 89, pl. 17, fig.4.

Additional references. *Rhamphostomella curvirostrata*: Kluge *et al*. 1959, p. 213; Kluge 1961, p. 141; Lukin 1979, p. 37; Gontar 1979, p. 246; 1980, p. 13; 1992, p. 197; 1993b, p. 202; Sakagami *et al*. 1980, p. 330; Grischenko 1997, p. 175; 2002, p. 115; Denisenko 2013, p. 184.

Material examined. *Lectotype*: NHMUK 1964.1.2.7, single colony detached from sponge, fractured into three fragments (mounted on two SEM stubs), C.H. O'Donoghue Collection, Pacific coast of North America (presumably Vancouver Island, British Columbia).

NHMUK 2010.2.9.5, one colony fragment, KIENM Collection, Stn 152, 10 August 1992, Cape Gladkiy, coastal waters of Medny Island, Commander Islands, Bering Sea, 54°44.8′ N, 167°45.3′ E, depth 46 m, SCUBA, collector V.V. Oshurkov. NHMUK 2013.10.21.8b, one colony, RV *Norseman*, Stn AS–1, 17 July 2011, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°46.2′ N, 176°25.6′ W, depth 10 m, SCUBA, collector P. Kuklinski. ZIRAS 1/50115, one colony fragment, KIENM Collection, Stn 152, 10 August 1992, Cape Gladkiy, coastal waters of Medny Island, Commander Islands, Bering Sea, 54°44.8′ N, 167°45.3′ E, depth 46 m, rock face, SCUBA, collector V.V. Oshurkov. ZIRAS 2/50116, one colony fragment, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 91, 10 September 1991, coastal waters of the Lesser Kuril Ridge, Pacific Ocean, 43°25.3′ N, 146°25.4′ E, depth 103 m, Sigsbee trawl, collector A.V. Smirnov. ZIRAS 4/50547, ten colony fragments, IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 55/47, 26 July 2011, westward from Iturup Island, South Kuril Islands, Sea of Okhotsk, 45°01.2′ N, 147°00.9′ E – 45°01.5′ N, 147°01.3′ E, depth 150–350 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev.

Additional material. 37 specimens. IMB Collection (1972) Stn 31/93; (1973) Stns 108/284, 173/408; (2011) Stns 11/7, 16/12, 18/14, 22/17, 29/24, 31/26, 37/32, 39/34, 43/38, 48/42, 55/47, 56/48; PIBOC Collection (1991) Stn 17; KIENM Collection (1992) Stns 127, 142, 150, 152 (see Appendix 1 for details).

Measurements. NHMUK 1964.1.2.7, Pacific coast of North America (Figs 14A, F, K, 30F). ZL, 0.64–0.95 (0.81 ± 0.08). ZW, 0.35–0.56 (0.44 ± 0.06). ZD, 0.34–0.37 (n = 2). OrL, 0.17–0.25 (0.22 ± 0.02). OrW, 0.20–0.28 (0.24 ± 0.02). OeL, 0.21–0.28 (0.24 ± 0.02). OeW, 0.30–0.40 (0.36 ± 0.03). Av(s)L, 0.17–0.36 (0.27 ± 0.05). P(m)N, 11–16 (14). P(oe)N, 11–17 (15).

ZIRAS 1/50115, Medny Island, Commander Islands, Bering Sea (Fig. 14D, E, I). ZL, 0.87–1.38 (1.11 ± 0.14). ZW, 0.37–0.63 (0.50 ± 0.07). ZD, 0.35–0.39 (n = 2). OrL, 0.18–0.32 (0.24 ± 0.05). OrW, 0.20–0.35 (0.27 ± 0.04). OeL, 0.23–0.32 (0.28 ± 0.03). OeW, 0.27–0.42 (0.33 ± 0.03). Av(s)L, 0.29–0.55 (0.43 ± 0.07). P(m)N, 12–20 (16). P(oe)N, 9–16 (15) (n = 10).

ZIRAS 4/50547, Iturup Island, Kuril Islands, Sea of Okhotsk (Fig. 14B, C, G, H, J, L, M). ZL, 1.05–1.58 (1.30 ± 0.15). ZW, 0.52–0.70 (0.60 ± 0.05). ZD, 0.46–0.52 (n = 2). OrL, 0.24–0.31 (0.27 ± 0.02) (n = 20). OrW, 0.24–0.29 (0.26 ± 0.01) (n = 20). OeL, 0.31–0.38 (0.35 ± 0.02). OeW, 0.35–0.44 (0.40 ± 0.02). Av(s)L, 0.39–0.53 (0.46 ± 0.03). P(m)N, 18–26 (22). P(oe), 13–20 (18) (n = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 14A), more or less circular, attaining 25 mm in maximal dimension; red, bright-orange to yellow when alive, light-orange or beige when dry. Zooids oblong,

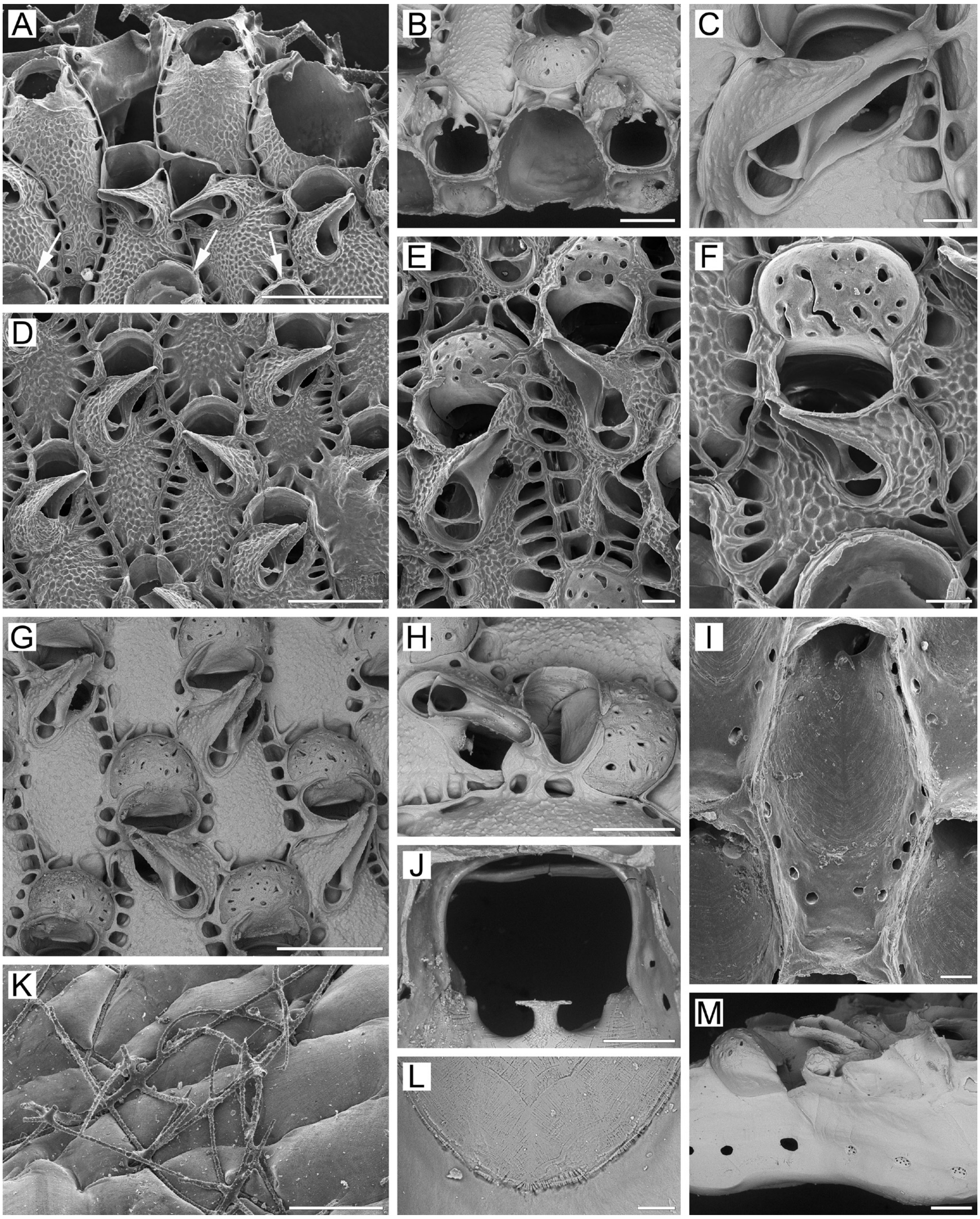

FIGURE 14. *Rhamphostomella curvirostrata* (O'Donoghue & O'Donoghue, 1923). A, F, K. *Lectotype*, NHMUK 1964.1.2.7 (Pacific coast of North America, presumably Vancouver Island, British Columbia). B, C, G, H, J, L, M. ZIRAS 4/50547 (Iturup Island, Kuril Islands, Sea of Okhotsk). D, E, I. ZIRAS 1/50115 (Medny Island, Commander Islands, Bering Sea). A. Colony margin with zooids developing above sponge spicules; developing ooecia visible near lower margin of image (arrows). B. Distal view of marginal zooids, showing primary orifices with median lyrula and lateral processes. C. Details of suboral avicularium. D. Non-ovicellate zooids close to colony periphery. E. Two zooids with ooecia embedded in secondary calcification, and enlarged, deep marginal areolae separated by strongly elongate interareolar ridges. F. Frontal view of ovicellate zooid. G. Group of ovicellate zooids in older part of colony. H. Lateral view of distal part of ovicellate zooid, showing details of ooecium and suboral avicularium. I. Interior of frontal shield, showing lyrula, ring scar, and areolae. J. Internal view of orifice, showing lyrula, lateral processes and condyles. K. Basal surface of colony growing over sponge (spicules are evident). L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing ooecium, suboral avicularium and zooidal lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 μm; B, H, 250 μm; C, E, F, I, J, 100 μm; L, 50 μm; M, 200 μm.

hexagonal to pyriform or irregular in shape, arranged in checkered pattern and demarcated by fine sutures between lateral walls in both young and old parts of colony.

Frontal shield umbonuloid (Fig. 14A, D, I), thin, slightly convex, with either dimpled (Fig. 14A, D, F) or finely granulated (Fig. 14B, C, G, H) surface and angular areolae along zooidal margins, separated by short and relatively narrow interareolar ridges. In older zooids, areolae can be very large with thick, elongate interareolar ridges that sometimes fuse along zooidal midline, giving a costate appearance to zooids (Fig. 14E). Umbonuloid component extensive, occupying about 70% of length of frontal shield (67% in one measured zooid), with distinct parallel lineation and accretionary banding (Fig. 14I, L). Ring scar (Fig. 14L) discrete, forming regular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure.

Primary orifice (Fig. 14A, B, J) submersed, quadrangular; distal and lateral margins formed by upper terminal part of distal transverse wall bearing prominent shelf (Fig. 14B–D) and forming very low, blunt condyles laterally (Fig. 14B, J). Distal margin of orifice shallowly rounded, proximal margin with central anvil-shaped lyrula with acute tips directed distolaterally, laterally or proximally, and distinct triangular, round-tipped process on each side (Fig. 14B, J, I). In some colonies, marginal zooids and those from the zone of astogenetic change bearing pair of short, hollow, ephemeral oral spines at distolateral corners of orifice.

Secondary orifice transversely oval to irregularly triangular, cormidial, distally and distolaterally restricted by arch-like extensions of vertical walls of distal and distolateral zooids forming subcircular or semioval "collar" (Fig. 14D); proximal part of secondary orifice formed by asymmetrically placed cystid of suboral avicularium and narrow lappet derived from frontal shield. In ovicellate zooids, extensions of lateral walls of distolateral zooids grow as narrow lobes towards each other over central part of ectooecium and above avicularian cystid, forming peristome of two symmetrical arches (Fig. 14E–H), conferring to secondary orifice a circular, transversely oval to irregularly triangular outline with large suboral slit between frontal shield and avicularian rostrum.

Cystid of suboral avicularium of moderate to large size, elevated, situated proximolateral to zooidal orifice on left or right side, with dimpled or granulated surface having gymnocystal rim and 1–2 communication pores (Fig. 14A–H). Rostrum long, curved or straight, elongate triangular, sometimes with short hooked tip (Fig. 14C), reaching or sometimes fusing with peristomial lappet on opposite side of peristome, directed distolaterally and angled so as to conceal most of palate. Avicularian frontal surface (rostral/postmandibular areas) crossing zooidal midline, facing obliquely proximally and frontally. Palate elongate triangular, with pointed distal end and rounded tip, foramen elongate oval, bordered by narrow cryptocystal shelf; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells initially prominent, later becoming subimmersed, with ooecium peripherally overgrown by secondary calcification proceeding from daughter and neighbouring lateral zooids (Fig. 14B, E, F, G, H, M). Ooecium formed by distal autozooid at colony periphery (Fig. 14A, B), its coelomic cavity connected with visceral coelom via communication canal that opens on underside of proximal part of frontal shield of distal zooid as straight slit-like communication pore about mid-distance between transverse wall and ring scar. Ooecium with straight or concave proximal margin and circular to oval or slit-like pseudopores, some occluded by secondary calcification.

Zooids interconnected by three mural pore chambers in each distolateral wall (Fig. 14M) and two multiporous septula (sometimes with individual pores inbetween) in basal half of transverse walls (Fig. 14B).

Basal wall of zooids (Figs 14K, 30F) fully calcified, smooth, slightly convex, often with elongate tubular protuberances (up to 0.65 mm long, 0.12–0.45 mm in diameter). Occasionally basal protuberances strongly elongate (up to 1.55 mm long), with multiply divaricated, terminal "rootlets". Boundaries between zooids indicated by sinuous sutures.

Ancestrula and early astogeny not observed.

Remarks. *Rhamphostomella curvirostrata* clearly differs from congeners in the large suboral avicularium with curved or straight rostrum overhanging the proximal half of the orifice. Osburn (1952, p. 430) mentioned that "occasionally the avicularium is wanting and two lateral lappets extend towards each other across the aperture".

A specimen from the South Kuril Islands (ZIRAS 4/50547), while similar in zooid morphology and size to the other colonies studied, differs in having a finely granulated surface of the frontal shield and avicularian cystid, and smaller and more rounded areolae with relatively short interareolar ridges. In this specimen, the avicularian rostrum is normally straight, differing from the more or less curved shape in other colonies examined. The proximal margin of the ooecium is also straight, with a slightly raised edge. The overgrowth and subsequent immersion of ooecia by secondary calcification are less prominent in this specimen. The proximal margin of the primary orifice is bisinuate, with a lyrula having the tips directed distolaterally or laterally. In contrast, they are directed proximally in a colony from the Commander Islands (ZIRAS 1/50115). These various differences may indicate either considerable phenotypic variability or a sibling species. More specimens need to be studied to determine which is the case.

The Canadian Museum of Nature contains a dried specimen of *R*. *curvirostrata* from British Columbia (Cat. No. – CMNI 1988-0131). Unfortunately, there are no images, and the specimen is not mentioned as a type in the On-line Collection Data of the Museum. Accordingly, we selected a lectotype from C.H. O'Donoghue Collection deposited in the Natural History Museum, London. This colony likely came from the waters around Vancouver Island, British Columbia.

Ecology. *Rhamphostomella curvirostrata* occurs predominantly on rocky bottoms at 10–566 m depth. Colonies encrust pebbles, polychaete tubes, shells of gastropod and bivalve molluscs and sponges.

Distribution. This is a Pacific boreal, sublittoral to upper bathyal species, widely distributed across the North Pacific Rim. In the western Pacific, it has been recorded from the Commander Islands in the Bering Sea (Grischenko 1997, 2002; our data); along the shelf and slope of the Kuril Islands, Sea of Okhotsk (Lukin 1979; Gontar 1979, 1980, 1993b; our data); Sea of Japan, including the western shore of southern Sakhalin Island (Androsova 1958; Kluge *et al*. 1959) and Moneron Island (Kluge 1961); along the Pacific side of northern Honshu Island, Japan (Sakagami *et al*. 1980). In the eastern Pacific it has been documented from the coastal waters of Adak Island, Andreanof Islands, Aleutian Islands (our data), and the Gulf of Alaska near Kodiak Island (our data), and Northumberland Channel, Vancouver Island, British Columbia (O'Donoghue & O'Donoghue 1923), and southwards to southern California (Osburn 1952).

Hayami (1973, 1975) reported *R*. *curvirostrata* from Neogene deposits in northern Japan.

Rhamphostomella hincksi Nordgaard, 1906
(Figs 15, 30G, 32H, I)

?*Cellepora plicata* Smitt, 1868a, p. 30, 31 (part), pl. 28, figs 195, 196.
Cellepora plicata: Hincks 1877, p. 106, pl. 11, figs 3, 4.
Ramphostomella [sic] *hincksi* Nordgaard, 1906, p. 31, 41, pl. 4, fig. 51.
Rhamphostomella hincksi: Kluge 1962, p. 541, fig. 378; 1975, p. 658, fig. 378; Powell 1968a, p. 2311, fig. 10, pl. 13a; Hayami 1970, p. 332, pl. 36, fig. 1.

Additional references. *Rhamphostomella hincksi*: Osburn 1955, p. 38; Hansen 1962, p. 40; Hayami 1975, p. 89; Sakagami *et al*. 1980, p. 330; Gontar 1980, p. 18; 1990, p. 133; 2010, p. 153; 2013, p. 184; Gontar & Denisenko 1989, p. 357; Denisenko 1990, p. 39; 2008, p. 187; Kuklinski 2002b, p. 203; Denisenko & Kuklinski 2008, p. 48; Foster 2010, p. 57.

Material examined. *Neotype*: NHMUK 1976.8.6.39pt, three fragments from one colony, RV *Ernest Holt*, Stn 41, 74°25.0′ N, 18°02.0′ E (about 22 km westwards from Medvezhii Island, western Barents Sea), depth 128 m.

NHMUK 68.3.13.46, one colony, 1858, Spitsbergen, collectors O. Sorella and N. Nordenskjold. NHMUK 1877.11.28.112, two colonies encrusting pieces of the same bivalve shell, A.M. Norman Collection, HMS *Valorous*, 1875, Davis Strait. NHMUK 1899.5.1.876, two colony fragments, T. Hincks Collection, Labrador. NHMUK 1963.2.12.244, three colony fragments, no locality given, Dundee Collection. NHMW 72986, one colony, 1884, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 160–180 m, collector F. Fischer. NHMW 92534 (=1884.II.48), one colony fragment, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 160–180 m, collector F. Fischer. USNM 11130, nine colony fragments, Arctic Research Laboratory Collection, ?August 1948, Point Barrow, Alaska, Beaufort Sea, depth 55.5 m, collector G.E. MacGinitie. ZIRAS 7/50119, two colony fragments detached from broken shells of bivalve mollusc *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko.

Measurements. ZIRAS 7/50119, western Kamchatka, Sea of Okhotsk (Fig. 15A–G, I, K). ZL, 0.77–1.35 (1.00 ± 0.14). ZW, 0.37–0.60 (0.50 ± 0.06). ZD, 0.43–0.55 (*n* = 2). OrL, 0.15–0.28 (0.22 ± 0.03). OrW, 0.22–0.35 (0.29 ± 0.04). OeL, 0.28–0.32 (0.31 ± 0.01). OeW, 0.33–0.40 (0.37 ± 0.02). Av(s)L, 0.15–0.27 (0.20 ± 0.03). P(m)N, 7–13 (10). P(oe)N, 18–26 (25) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 15A), more or less circular, attaining 16 mm in maximal dimension, reddish or burgundy when alive, pink when dry. Zooids large, hexagonal (Fig. 15D), widest at midlength, arranged in regular, straight rows, packed in quincunx; demarcated by fine, undulating sutures between lateral and transverse walls; sutures visible in both young and old parts of colony.

Frontal shield umbonuloid (Fig. 15D, E, I), inflated or moderately convex, smooth to weakly dimpled centrally, with series of deep areolae along zooidal margins (Fig. 15D–G) separated by radially arranged interareolar ridges; in younger zooids, ridges relatively short, low, some connecting with cystid of suboral avicularium (Fig. 15A, D, E). In older zooids, ridges tall, thickened, elongate, often joining along zooid midline and connecting to peristomial lappet and avicularian cystid, giving strongly costate appearance to frontal shield (Fig. 15F, G). Interior of frontal shield (Fig. 15I) with discrete ring scar (Fig. 15K). Umbonuloid component occupying about 40% of length of frontal shield (44% in one measured zooid), with fine parallel lineation and accretionary banding.

Primary orifice submerged, irregularly round; rounded distally, sinuate or bisinuate (Fig. 15B) proximally (Fig. 15A, B, I); if bisinuate, with small process (Fig. 15B). Distal and lateral margins of primary orifice formed by upper terminal part of distal transverse wall.

Secondary orifice (Fig. 15C–E) broadly triangular in outline, cormidial, distally and distolaterally restricted by thickening of vertical walls of distal and distolateral zooids, laterally and proximally formed by avicularian cystid (often with small distal lappet on its rostrum) on one side and high lappet of frontal shield on opposite side; lappet triangular, straight, slightly concave or sinuous in profile, together with avicularium forming proximally broad deep V-shaped pseudosinus in secondary orifice (Fig. 15C–H). Distally, lappets connect with lateral walls of distolateral zooids; in ovicellate zooids, lappets not fused with proximolateral corners of ooecium. No oral spines.

Cystid of suboral avicularium (Fig. 15A–H) relatively small but distinct, bulbous, strongly elevated, with coarsely dimpled surface, and 1–3 (normally 2) communication pores connecting avicularian and hypostegal coeloms, asymmetrically placed to left or right side of proximal peristomial rim. Inclined frontal surface (rostral/postmandibular areas) of avicularium converging toward or crossing zooidal midline, facing obliquely frontally. Rostrum oblong-oval, weakly curving inward, with small, hooked tip directed laterally to distolaterally and upwards, extending somewhat over orifice (Fig. 15C, H). Palate semielliptical to triangular, with rounded distal end; palatal foramen elongate-oval or triangular, with rounded angles; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells initially hyperstomial (Fig. 15H), but ooecia rapidly becoming subimmersed by peripheral overgrowth of secondarily thickened lateral and proximal walls of distolateral and daughter zooids (Fig. 15F, G); thickened lateral walls plugging gaps between distal margins of peristomial lappets and proximal corners of ooecium, thus completing secondary orifice in ovicellate zooids (Fig. 15F, G). Ooecium formed by distal autozooid; ooecial fold arises on colony periphery concurrently with frontal shield of distal zooid. Ooecial coelomic cavity connected with visceral coelom via communication canal opening on underside of proximal part of frontal shield as small, curved slit-like communication pore close to transverse wall (Fig. 15I). Ooecium with slightly concave proximal margin and numerous small, scattered circular and oval (sometimes irregular) pseudopores.

Zooids interconnecting by two mural pore chambers in each distolateral wall (Fig. 15L). Communication pores in basal part of transverse walls arranged either as horizontal "band" or forming two multiporous septula.

Basal wall of zooids (Figs 15J, 30G) fully calcified, smooth, slightly convex, with tubular protuberances (up to 0.47 mm long, up to 0.28 mm in diameter). Boundaries between zooids indicated basally by gently sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. Described and illustrated by Hincks (1877) as *Cellepora plicata* from Iceland, *R. hincksi* was recognized and redescribed as a separate species by Nordgaard (1906) based on specimen from the Barents Sea. Still, it is rather possible that figures 195 and 196 of Smitt (1868a, pl. 28) show the same species. Regrettably, only a tiny, poorly preserved fragment of the presumed *R. hincksi* survived in Nordgaard's collection in the Natural History Museum, University of Oslo (E. Di Martino, pers. comm., 2020). To correct this situation, we have selected a neotype for this species based on a specimen collected in the Barents Sea from the RV *Ernest Holt*. Three fragments of one colony are deposited at the Natural History Museum, London.

In having a sinuate, elevated secondary orifice formed by an asymmetrically set avicularian cystid on one side and a high triangular lappet on the opposite side, and spherical ooecia with small, evenly distributed pseudopores, *R. hincksi* strongly resembles *R. plicata* (Smitt, 1868). Historically, this resemblance led to some misidentifications.

The differences between these species are as follows: 1) the frontal shield has a series of deep marginal areolae separated by tall, radially arranged ridges along the entire lateral wall in *R. hincksi*, but only a few areolae separated

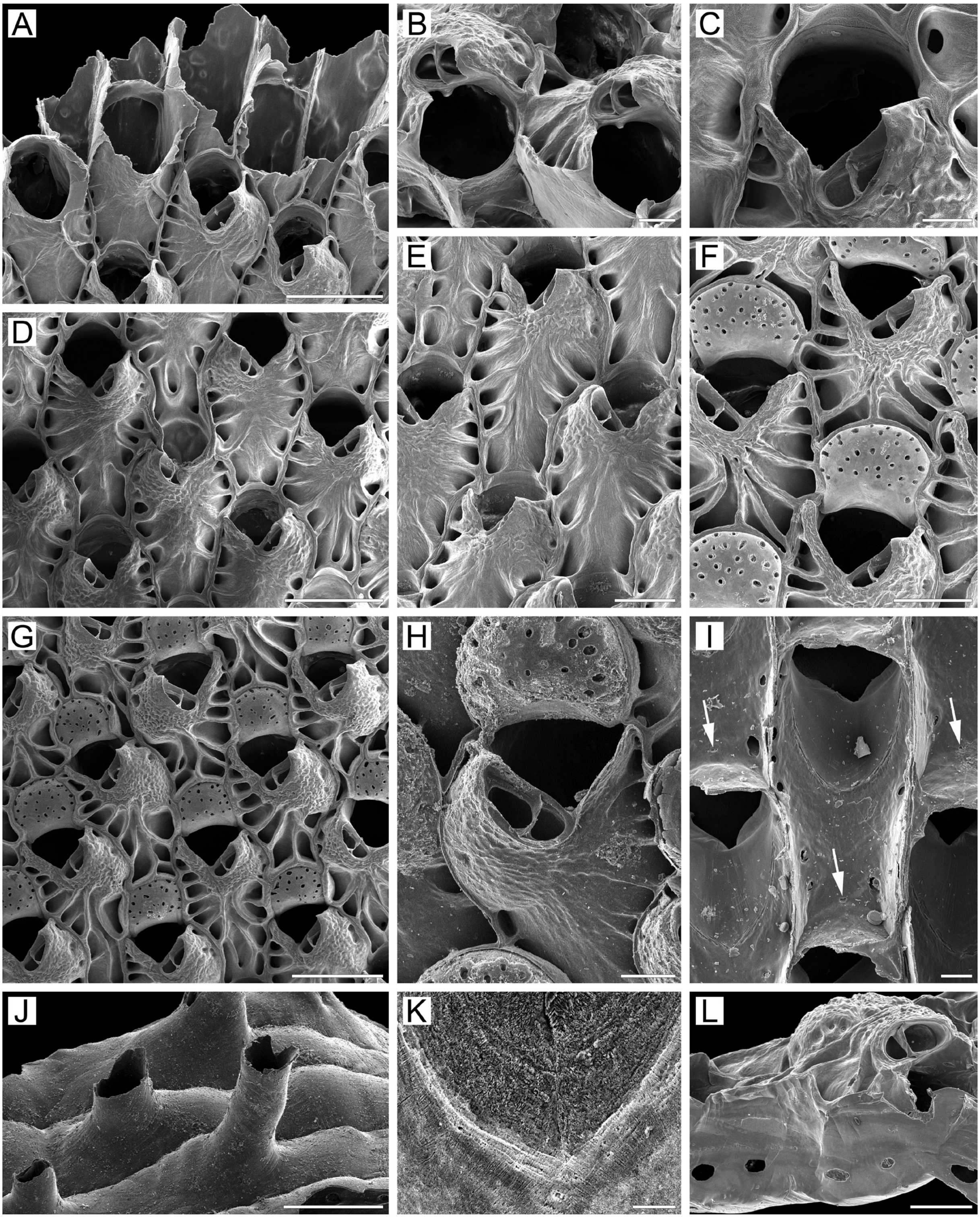

FIGURE 15. *Rhamphostomella hincksi* Nordgaard, 1906. A–G, I, K. ZIRAS 7/50119 (western Kamchatka, Sea of Okhotsk). H, J, L. USNM 11130 (Point Barrow, Beaufort Sea). A. Colony margin with developing zooids. B. Distal view of marginal zooids, showing primary orifices with small, slender median tooth. C. Orifice with suboral avicularium. D, E. Groups of non-ovicellate zooids in young parts of colony. F. Ovicellate zooids with strongly developed interareolar ridges of frontal shield in older part of colony. G. Ovicellate zooids in older part of colony. H. Ovicellate zooid with suboral avicularium. I. Interior of frontal shield in three zooids, showing ring scars, areolae and ooecial communication slits (arrows). J. Basal colony surface with numerous broken tubular protuberances. K. Frontal shield interior, showing ring scar and exterior wall microstructure of umbonuloid component. L. Lateral view of zooid, showing suboral avicularium and zooidal lateral wall with mural pore chambers. Scale bars: A, D, G, J, 500 µm; B, C, H, I, 100 µm; E, F, 250 µm; K, 50 µm; L, 200 µm.

by short ridges along the distal half of the zooid in *R*. *plicata*; 2) the palatal foramen of the suboral avicularium is gently curved in *R*. *hincksi* but straight in *R*. *plicata*; 3) ooecia are rapidly surrounded by growing and thickening vertical walls of neighbouring zooids in *R*. *hincksi*, but not in *R*. *plicata*; 4) the primary orifice lacks a lyrula in *R*. *hincksi* but may occasionally bear a very small denticle (Fig. 15B) (see also Nordgaard 1906; Osburn 1952; Kluge 1962, 1975), whereas a distinct lyrula is always present in *R*. *plicata*.

Ecology. *Rhamphostomella hincksi* has been recorded from depts of 10–270 m, predominantly on mixed bottoms, including silt, sand and gravel overlain with broken mollusc shells. Colonies encrust mollusc shells and colonies of other bryozoans.

Distribution. This is a boreal-Arctic, circumpolar, sublittoral species. In the Arctic *R*. *hincksi* has been recorded in the Barents Sea (?Smitt 1868a; Nordgaard 1896; Bidenkap 1900a; Waters 1900; Andersson 1902; Norman 1903; Kluge 1962, 1975; Denisenko 1990), Kara Sea (Kluge 1962, 1975; Denisenko 2021), Laptev Sea (Kluge 1962, 1975; Gontar 1990), Chukchi Sea (Kluge 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), Point Barrow, Alaska, Beaufort Sea (Osburn 1955), Canadian Arctic Archipelago (Nordgaard 1906), Baffin Bay (Hansen 1962), Davis Strait (Hansen 1962; Kluge 1962, 1975), Hudson Bay (Gontar & Denisenko 1989), western Greenland (Norman 1876; Kluge 1908b; Levinsen 1914; Osburn 1919, 1936; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1916; Denisenko & Blicher 2021), Iceland (Hincks 1877; Gontar & Denisenko 1989), Jan Mayen Island (Lorenz 1886), Franz Josef Land (Denisenko 1990), and Spitsbergen (Kuklinski 2002b). In the northern Atlantic, it is known from St Lawrence Gulf (Whiteaves 1901). Northwestern Pacific records are from the Sea of Okhotsk, including the eastern shore of southern Sakhalin Island (Kluge 1961; Kluge *et al*. 1959), the western Kamchatka shelf (our data), coastal waters of Iturup and Shikotan Islands and south Kuril Islands (Kluge 1961; Kluge *et al*. 1959; Gontar 1980). The only known locality in the northeastern Pacific is Cook Inlet, Gulf of Alaska (Foster 2010).

R. *hincksi* has also been reported from Miocene and Neogene deposits in northern Japan (Hayami 1970, 1975).

***Rhamphostomella obliqua* n. sp.**
(Fig. 16)

Diagnosis. Colony encrusting, multiserial. Zooids very large, broadly hexagonal. Frontal shield thin-walled, moderately convex, finely granular. Interareolar ridges low, short, reaching sides of suboral avicularian cystid in distal half of zooid. Umbonuloid component large. Primary orifice bell-shaped, slightly longer than wide, with blunt, ill-defined, lateral condyles; proximal margin straight. Secondary orifice conforming to shape of primary orifice, cormidial, with low, thin-walled proximal peristome. No oral spines. Suboral avicularian cystid strongly elevated, with blunt apex, occupying one-quarter to one-third of frontal shield symmetrically, bulbous to conical, coarsely granular, strongly tilted distally, overhanging orifice, facing distolaterally to laterally. Rostrum elongate oval. Crossbar complete. No adventitious avicularia. Ovicells hyperstomial. Ectooecium smooth with sparse circular to slit-like pseudopores, no secondary calcification. Two mural pore chambers in distolateral wall and two multiporous septula in transverse walls. Basal surface of zooids fully calcified, flat, smooth.

Material examined. *Holotype*: ZIRAS 1/50541, colony encrusting internal surface of broken shell of *Chlamys* sp., IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 31/26, 17 July 2011, eastward from Simushir Island, middle Kuril Islands, Pacific Ocean, 47°02.9′ N, 152°13.6′ E – 47°03.4′ N, 152°14.7′ E, depth 82–115 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev.

NHMUK 2013.10.21.2, one colony, RV *Norseman*, Stn AS–1, 17 July 2011, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°46.2′ N, 176°25.6′ W, depth 10 m, SCUBA, collector P. Kuklinski. NHMUK 2013.10.21.8a, one colony, RV *Norseman*, Stn AS–1, 17 July 2011, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°46.2′ N, 176°25.6′ W, depth 10 m, SCUBA, collector P. Kuklinski.

Additional material. Three specimens. IMB Collection (2011) Stns 31/26, 64/54 (see Appendix 1 for details).

Etymology. The species name refers to the oblique position of the large subavicularian cystid, which is strongly angled over the orifice.

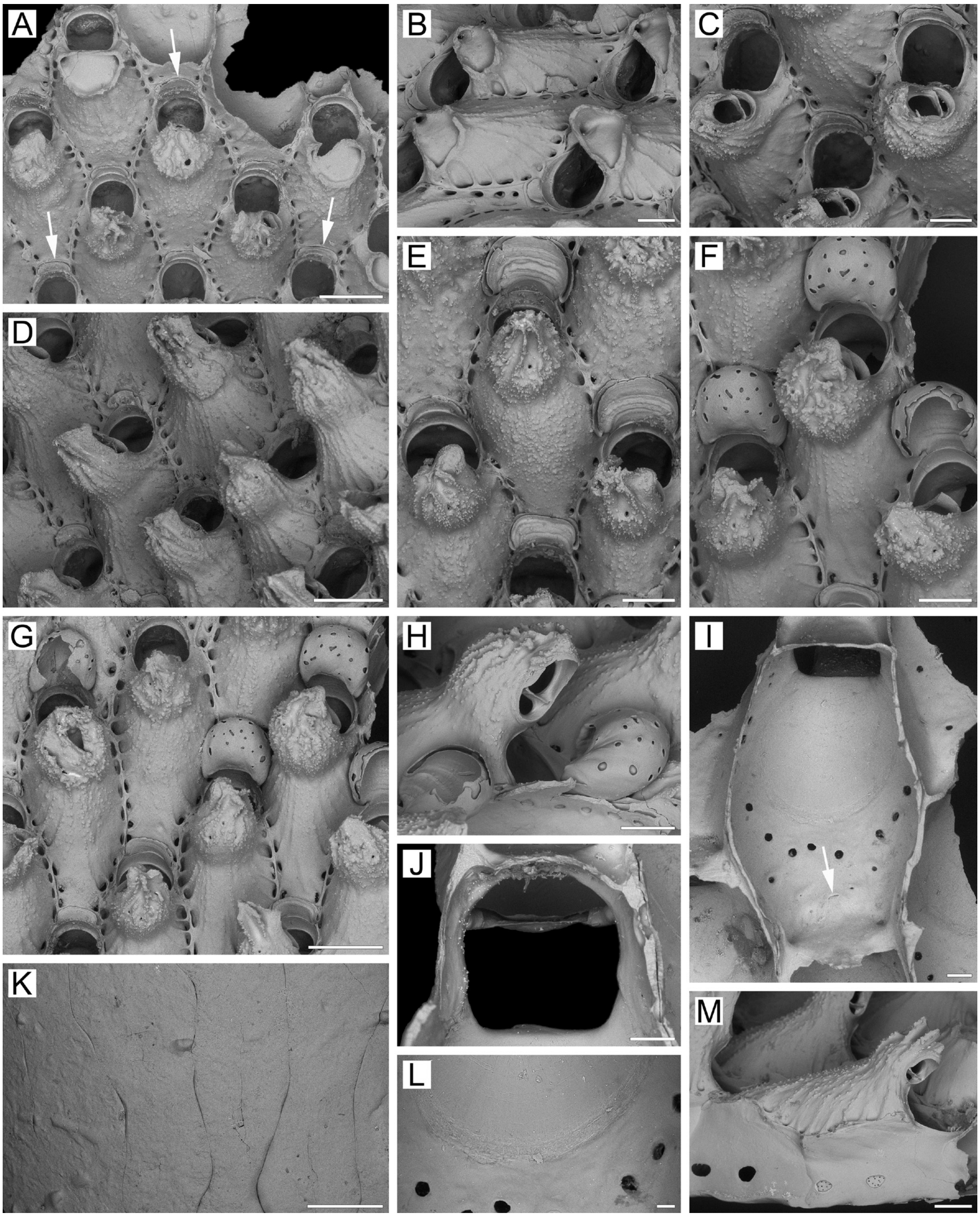

FIGURE 16. *Rhamphostomella obliqua* **n. sp.** *Holotype*, ZIRAS 1/50541 (Simushir Island, Kuril Islands, Pacific Ocean). A. Colony margin, showing young zooids with developing ooecia (arrows). B. Oblique view of young zooids, showing early stages of developing ooecia and avicularian cystids (interareolar ridges on the frontal shields are well evident). C. Zooids with fully developed suboral avicularia and early developmental stages of ooecia. D. Oblique view of zooids with fully-developed avicularia (some also with ooecia in early stage of development). E. Autozooids with developing ooecia in young part of colony (interareolar ridges on frontal shield have not yet developed). F. Ovicellate zooids in older part of colony (interareolar ridges on frontal shield weakly developed). G. Group of ovicellate zooids in older part of colony (interareolar ridges on frontal shield weakly developed). H. Lateral view of distal half of ovicellate zooid. I. Interior of frontal shield, showing ring scar, areolae and ooecial communication slit (arrow) (openings surrounding ring scar are not pseudopores, but lower openings of areolae). J. Internal view of orifice, showing straight proximal margin and minute condyles. K. Basal surface of colony. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing suboral avicularium and zooidal lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, C, E, F, H, 250 µm; I, J, 100 µm; L, 50 µm; M, 200 µm.

Type locality. Eastward from Simushir Island, middle Kuril Islands, Pacific Ocean, 47°02.9′ N, 152°13.6′ E – 47°03.4′ N, 152°14.7′ E, depth 82–115 m.

Measurements. ZIRAS 1/50541, Simushir Island, Kuril Islands, Pacific Ocean (Fig. 16A–M). ZL, 1.15–1.92 (1.50 ± 0.15). ZW, 0.65–0.95 (0.81 ± 0.08). ZD, 0.73–0.81 (*n* = 2). OrL, 0.34–0.41 (0.38 ± 0.02). OrW, 0.33–0.39 (0.35 ± 0.02). OeL, 0.38–0.48 (0.43 ± 0.03) (*n* = 15). OeW, 0.45–0.55 (0.48 ± 0.03) (*n* = 15). Av(s)L, 0.21–0.43 (0.33 ± 0.05). P(m)N, 17–27 (22). P(oe)N, 13–21 (18) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 16A), subcircular, deep brown to light brown when dry; maximal size observed 18 × 20 mm. Zooids very large, broadly hexagonal, widest in midline, rarely elongate oval and tapering proximally, arranged in checkered pattern, demarcated by fine sutures between lateral and transverse zooidal walls; sutures less visible in older parts of colony.

Frontal shield umbonuloid (Fig. 16A, I), thin-walled, fragile, moderately convex, finely granulated, with single row of mostly elongate areolae along raised margins, separated by low, interareolar ridges; ridges normally less prominent in young zooids (Fig. 16A), though sometimes evident in them too (Fig. 16B). In older parts of colony, these ridges, when developed, often connecting to cystid of suboral avicularium and continuing to its apex (Fig. 16D, M), but in some instances not very prominent on avicularium (Fig. 16E–G). Interior of frontal shield (Fig. 16I) with very fine ring scar (Fig. 16I, L). Umbonuloid component occupying about 70% of length of frontal shield (68% in one measured zooid), with fine parallel lineation and accretionary banding. In cleaned specimens, semicircle of large pores (lower openings of areolar canals) evident proximal to ring scar.

Primary orifice (Fig. 16C, J) bell-shaped, sometimes semioval, slightly longer than wide; distal and lateral margins formed by upper terminal part of distal transverse wall bearing prominent shelf distally (Fig. 16A–C, E, F) and forming blunt, ill-defined condyles laterally (Fig. 16J). Distal margin of orifice rounded, proximal margin straight, with broadly rounded proximolateral corners.

Secondary orifice (Fig. 16A–E) conforming to shape of primary orifice, cormidial; distolateral curvature restricted by thickening of proximal and lateral vertical walls of daughter and neighbouring zooids; proximally bounded by low, thin-walled peristome formed by frontal shield and centrally incorporating cystid of suboral avicularium (Fig. 16D, F, H). In ovicellate zooids, peristome usually reaching proximolateral corners of ooecium. No oral spines.

Cystid of suboral avicularium occupying distal one-quarter to one-third of zooidal frontal shield, situated mostly symmetrically relative to orifice, bulbous to conical, strongly elevated, coarsely and irregularly thickened on top; surface coarsely granulated, many granules look like sharp spinules, thus contrasting with rest of frontal shield, with 1–5 minute communication pores (Fig. 16A–H, M). Avicularian cystid strongly angled distally, overhanging orifice in older parts of colony (Fig. 16H), gradually tapering terminally, with raised vertical ridges uniting into conical tip. Avicularian frontal surface (rostral/postmandibular areas) situated on distolateral slope of cystid, usually crossing zooidal midline, sometimes to one side of it, facing distolaterally to laterally. Rostrum elongate oval, directed proximomedially to proximolaterally and frontally; palate lingulate, foramen elongate oval, bordered by narrow cryptocystal shelf; opesia more or less semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells hyperstomial in all parts of colony, ooecium never overgrown by secondary calcification. Ooecium formed by distal autozooid around crescentic slit with communication pore at bottom, situated in proximalmost part of frontal shield very close to distal margin of maternal primary orifice. Ooecial coelomic cavity connected to visceral coelom via communication canal opening on underside of proximal part of frontal shield of distal zooid as small, straight, slit-like communication pore situated halfway between transverse wall and ring scar (Fig. 16I). Ooecium with concave proximal margin. Ectooecium smooth, with sparse, circular to slit-like pseudopores.

Zooids interconnected by two mural pore chambers (Fig. 16M) in each distolateral wall. Communication pores spread across basal part of transverse walls either as horizontal "band" or forming two multiporous septula. In some zooids, transverse walls distally with two shallow recesses separated by median buttress.

Basal surface of zooids (Fig. 16K) fully calcified, flat, smooth. Boundaries between some zooids recognizable by intermittent fine incisions.

Ancestrula and early astogeny not observed.

Remarks. *R. obliqua* **n. sp.** is similar to *R. aspera* **n. sp.**, but differs from the latter in at least seven characters, described above (see Remarks for *R. aspera* **n. sp.**). This species also superficially resembles *R. scabra* in the conical, prominent suboral avicularian mucro, laterally facing palatal foramen, and lingulate mandible, but differs from the latter in lacking additional adventitious avicularia.

Ecology. *Rhamphostomella obliqua* **n. sp.** is known from depths of 10–435 m on pebbles and broken shells of the bivalve mollusc *Chlamys* sp.

Distribution. The known distribution is based on three records, including one from the Sea of Okhotsk side of the middle to southern Kuril Islands, another from their Pacific side, and the third from the Pacific side of Adak Island, Andreanof Islands, Aleutian Islands. *Rhamphostomella obliqua* **n. sp.** is thus a Pacific high-boreal, sublittoral to upper bathyal species.

Rhamphostomella plicata **(Smitt, 1868)**

(Figs 17, 32J, K)

Cellepora plicata Smitt, 1868a, p. 30, 31 (part), pl. 28, figs 189, 190 (?).
Cellepora plicata: Smitt 1868b, p. 484, 485.
Discopora plicata: ?Smitt 1878a, p. 31; ?1878b, p. 24; Nordgaard 1918, p. 78.
Rhamphostomella plicata: Lorenz 1886, p. 12, 13; Nordgaard 1905, p. 171, pl. 5, figs 14, 15; 1906, p. 30, 41, pl. 4, figs 49, 50; Gostilovskaya 1978, p. 230, fig. 146; Kluge 1962, p. 544, fig. 381; 1975, p. 662, fig. 381; Powell 1968a, p. 2312, fig. 10, pl. 13b; Winston & Hayward 2012, p. 121, fig. 78.
Rhamphostomella lorenzi Kluge, 1907, p. 188.
Rhamphostomella lorenzi: Kluge 1915, p. 386.

Additional references. *Rhamphostomella plicata*: Osburn 1936, p. 542; Gostilovskaya 1957, p. 456; 1964, p. 220; Kluge 1961, p. 142; Denisenko 1984, p. 76; 1988, p. 13; 1990, p. 39; 2008, p. 188; 2013, p. 184; Gontar & Denisenko 1989, p. 357; Gontar *et al*. 2001, p. 195; Grischenko 2002, p. 115; Kuklinski 2002b, p. 203; Denisenko & Kuklinski 2008, p. 48; Kuklinski & Taylor 2009, p. 497; Gontar 2010, p. 153; Denisenko *et al*. 2016, p. 366.

Material examined. *Lectotype*: SMNH-Type-1696, two fragments of one colony, Swedish Arctic Expedition, August 1861, Waygat Islands, Hinlopen Strait, Svalbard and Jan Mayen, 79°10.0′ N, 19°00.0′ E, depth 110–146 m, mud.

SMNH-132277, colony on bivalve shell, Sandeberg Expedition, Stn 28, 1877, off Waideguba, Kola Peninsula, Barents Sea, Russia, depth 73–100 m, gravel and shells. NHMUK 1911.10.1.1590, five colonies encrusting hydroid stolons and spirorbid tubes, ex Copenhagen Museum Collection, from G.M.R. Levinsen, A.M. Norman Collection, Greenland. USNM (no inventory number), two colony fragments, Thacher Island, Gulf of Maine, Massachusetts, USA, northwestern Atlantic Ocean.

Measurements. NHMUK 1911.10.1.1590, Greenland (Fig. 17A, D–G, I–J, L–M). ZL, 0.82–1.20 (0.99 ± 0.11). ZW, 0.37–0.60 (0.47 ± 0.05). ZD, 0.35–0.41 (*n* = 2). OrL, 0.21–0.28 (0.24 ± 0.03). OrW, 0.25–0.33 (0.31 ± 0.02). OeL, 0.25–0.38 (0.33 ± 0.03). OeW, 0.32–0.45 (0.39 ± 0.03). Av(s)L, 0.15–0.28 (0.23 ± 0.04). P(m)N, 5–10 (7). P(oe)N, 11–19 (16) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 17A), small, irregular in form, attaining about 14 mm in maximal size, beige to greyish when dry. Zooids large, oblong-rectangular to oval, or trapezoidal and irregular, in shape, often swollen and broadened distally, flattened and tapering proximally, arranged in quincunx, demarcated by fine sutures between lateral and transverse walls; sutures less visible in older parts of colony.

Frontal shield umbonuloid (Fig. 17A, I), thin, moderately convex, lower towards proximal margin, smooth in developing zooids (Fig. 17A), finely dimpled to wrinkled or reticulated in fully-formed zooids (Fig. 17D–H). Areolae sparse, elongate to triangular, separated by short interareolar ridges; ridges generally developed in distal half of zooid (Fig. 17D–G), may be strongly reduced or absent in young zooids (Fig. 17A, D, E). Interior of frontal shield (Fig. 17I, L) showing distinct or indistinct ring scar (Fig. 17I, L). Umbonuloid component occupying about 40% of length of frontal shield (38% in one measured zooid), with fine parallel lineation and accretionary banding.

Primary orifice (Fig. 17B, J) submerged, inversely pyriform, subcircular to oval; distal and lateral margins formed by upper terminal part of distal transverse wall. Distal margin of orifice rounded, proximal margin concave, tapering, with small median lyrula having straight, bifurcate or alate apex, and two small, short processes lateroproximally with rounded or pointed tips; processes sometimes ill-defined (Fig. 17F) or lacking (Fig. 17I). No condyles.

Secondary orifice (Fig. 17D–H) circular or broadly triangular in outline, cormidial; in contrast with most species studied, distally and distolaterally restricted by flared, thickened upper part of transverse wall of maternal zooid. Proximal and lateral walls of daughter and distolateral zooids adjoining this wall (Fig. 17D, E). Secondary orifice formed laterally and proximally by thin-walled, flared peristome of two triangular lappets from frontal

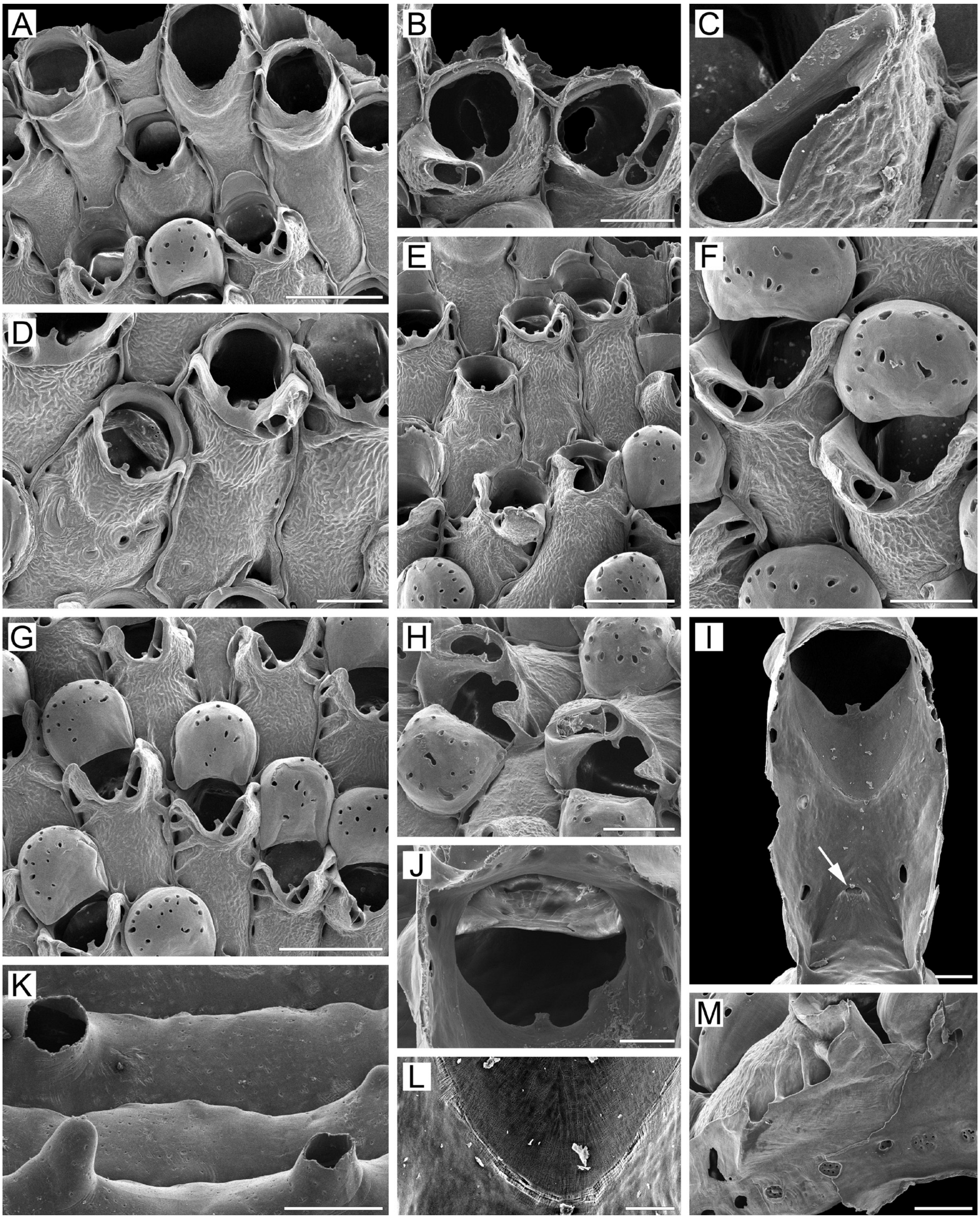

FIGURE 17. *Rhamphostomella plicata* (Smitt, 1868). A, D–G, I–J, L–M. NHMUK 1911.10.1.1590 (Greenland). B–C, H, K. USNM (without inventory number) (Thacher Island, Gulf of Maine, Atlantic Ocean). A. Colony margin with developing zooids and ooecia. B. Oblique view of two zooids from colony margin, showing details of primary orifice with median lyrula and lateral denticles. C. Suboral avicularium. D. Non-ovicellate zooids with finely dimpled frontal shields. E. Ovicellate and non-ovicellate autozooids with and without suboral avicularia. F. Ovicellate zooids. G. Group of ovicellate zooids showing details of peristome and ooecia. H. Distolateral view of ovicellate zooids, showing details of avicularium and bilobed peristome. I. Interior of frontal shield, showing lyrula, areolae and ooecial communication pore (arrow) in apex of ovicell floor. J. Internal view of orifice, showing lyrula and denticles. K. Basal colony surface with tubular protuberances. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing peristome, areolae, interareolar ridges and zooidal lateral wall with mural pore chambers. Scale bars: A, E, G, K, 500 μm; B, D, F, H, 250 μm; C, L, 50 μm; I, J, 100 μm; M, 200 μm.

shield, one lappet incorporating or virtually replaced by cystid of suboral avicularium; flared lappet on opposite side of peristome, plus avicularian cystid, defining broad, deep V- to U-shaped pseudosinus in secondary orifice (Fig. 17D–G). Distally, lappets inclining to vertical walls of distolateral zooids, abutting to proximolateral corners of ooecia in ovicellate zooids. No oral spines.

Cystid of suboral avicularium small, quite elevated, with dimpled surface and one communication pore, asymmetrically placed proximal to orifice on left or right (Fig. 17A–H). Avicularian frontal surface (rostral/postmandibular areas) to one side of midline, but sometimes crossing it, facing obliquely frontally. Rostrum elongate-lingulate, narrowing, with blunt tip, extending somewhat over orifice, directed distolaterally and frontally. Palate elongate, triangular, with rounded distal end; foramen elongate triangular or elongate oval, with cryptocystal shelf distally; opesia round triangular (Fig. 17A–C, F–H). Crossbar complete. Suboral avicularia lacking in some zooids.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 17F–H), ooecium free of secondary calcification except for very narrow basal rim visible in some ooecia (Fig. 17G, H). Ooecium formed by distal autozooid close to colony periphery. Ooecial coelomic cavity connecting to visceral coelom via communication canal opening on underside of proximal part of frontal shield as oval slit-like communication pore situated at apex of triangular area (ovicell floor) or halfway between transverse wall and ring scar (Fig. 17I). Ooecium smooth, with straight or insignificantly concave proximal margin and small, scattered, circular or irregular pseudopores.

Zooids interconnected by two mural pore chambers in each distolateral wall (Fig. 17M). In transverse walls, communication pores as horizontal "band" or two multiporous septula.

Basal wall of zooids fully calcified, smooth, flattened or slightly convex, with tubular protuberances (up to 0.60 mm long, 0.20–0.33 mm in diameter), textured by fine parallel lineation on surface (Fig. 17K). Numerous white spots (presumably less-calcified areas) visible in semitransparent basal wall by light microscopy. Boundaries between zooids recognizable basally by sinuous sutures.

Ancestrula and early astogeny not observed.

Remarks. In describing the new species *Cellepora plicata*, Smitt (1868a) indicated figures 189–196 (pl. 28) as illustrations. Comparing them with his own specimens, Lorenz (1886) distinguished three species (*Rhamphostomella spinigera*, *R. radiatula* and *R. plicata*) and indicated that only figures 189–191 and 195 of Smitt represent *R. plicata*. Nonetheless, only figure 189 unambiguously illustrates this species (figure 190 shows the colony basal surface). As to the other illustrations, figure 191 presumably shows *R. bilaminata*; figure 192, *R. spinigera*; figure 193, *R. radiatula*; and figures 195, 196, *R. hincksi* (see additional discussion in the Remarks elsewhere in the text).

Nordgaard (1906, p. 31) wrote of *R. plicata*, "This species is distinguishable from the next one (*R. hincksi*) by the circumstance that the proximal margin of the oral aperture is more rounded, the aperture has not so marked a triangular shape as is the case with *hincksi*. The most conspicuous difference, however, is that *plicata* has a distinct median denticle [lyrula] that is absent in *hincksi*". We can also add the strong difference in the frontal shield relief in these species.

Ecology. *Rhamphostomella plicata* is known from 12–146 m depth on mixed bottoms (sand, shell, gravel), where colonies encrust mollusk shells, ascidians and colonies of other bryozoans.

Distribution. This is a boreal-Arctic, circumpolar, sublittoral species. Arctic records include the Barents Sea (Smitt 1868a, 1868b, 1879b; Bidenkap 1900a; Nordgaard 1905; Kuznetsov 1941; Kluge 1962, 1975; Denisenko 1984, 1988, 1990), White Sea (Kluge 1907; Gostilovskaya 1957, 1978), Kara Sea (Nordgaard 1912; Kluge, 1962, 1975), Laptev Sea (Gontar & Denisenko 1989), Chukchi Sea (Kluge 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), Canadian Arctic Archipelago (Nordgaard 1906; Osburn 1936), Baffin Bay (Gontar & Denisenko 1989), Davis Strait (Kluge 1962, 1975), western Greenland (Norman 1906; Levinsen 1914; Osburn 1919, 1936; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1916; Denisenko & Blicher 2021) [Smitt (1868b) just mentioned Greenland], Iceland (Nordgaard 1924), Franz Josef Land (Denisenko 1990), Spitsbergen (Smitt 1868b; Gontar *et al*. 2001; Kuklinski 2002b; Kuklinski & Taylor 2009) and northern Norway (Nordgaard 1905, 1918). In the northwestern Atlantic, *R. plicata* has been reported from St Lawrence Gulf (Whiteaves 1901) and in the Gulf of Maine near Thacher Island (Winston & Hayward 2012; our data). The only record from the northeastern Atlantic is from the Faroe Islands (Denisenko *et al*. 2016). In the northwestern Pacific, it is documented in the Bering Sea between St Lawrence Island and Chukotskiy Cape (Kluge 1961; Grischenko 2002), and along the eastern coastal waters of Sakhalin Island, Sea of Okhotsk (Kluge *et al*. 1959; Kluge 1961).

Rhamphostomella radiatula (Hincks, 1877)

(Figs 18, 32L, M)

Cellepora plicata: Smitt 1868a, p. 30, 31 (part), pl. 28, fig. 193.
Lepralia radiatula Hincks, 1877, p. 104, pl. 10, figs 9–14.
Rhamphostomella radiatula: Lorenz 1886, p. 13, pl. 7, fig. 9 (mentioned as fig. 10 in the text); Nordgaard 1905, p. 172, pl. 5, figs. 16, 17; Kluge 1962, p. 543, fig. 380; 1975, p. 660, fig. 380; Gostilovskaya 1978, p. 229, fig. 145; Androsova 1958, p. 173, fig. 104; Winston & Hayward 2012, p. 124, fig. 79; Taylor 2021, p. 76, fig. 5a–e.
Discopora radiatula: Nordgaard 1918, p. 78.

Additional references. *Rhamphostomella radiatula*: Nordgaard 1906, p. 32, 41; 1924, p. 9; Kluge 1907, p. 196; 1908a, p. 534; 1928, p. 257; 1961, p. 142; 1964, p. 190; Gostilovskaya 1957, p. 455; Kluge *et al*. 1959, p. 213; Hansen 1962, p. 40; Gontar 1980, p. 13; 1992, p. 198; 1993b, p. 202; Mawatari & Mawatari 1981, p. 56; Denisenko 1988, p. 13; 1990, p. 39; 2013, p. 184; Gontar & Denisenko 1989, p. 354; Bennike *et al*. 1994, p. 199; Grishankov 1995, p. 48; Grischenko 1997, p. 175; 2002, p. 115; 2003b, p. 237; Gontar *et al*. 2001, p. 195; Kuklinski 2002b, p. 203; Ostrovsky 2009, p. 206, fig. 78b; 2013, p. 8, fig. 2.41b.

Material examined. *Neotype*: NHMUK 1911.10.1.1592, two fragments from one colony, ex Copenhagen Museum Collection, from G.M.R. Levinsen, A.M. Norman Collection, Iceland.

NHMW 72987, one colony fragment, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 20–130 m, collector F. Fischer. NHMUK 1899.5.1.878, six colony fragments, no locality given, T. Hincks Collection. ZIRAS 19/50114, two colony fragments, KIENM Collection, Stn 132, 23 July 1992, Rock Sivuchy Kamen, coastal waters of Medny Island, Commander Islands, Bering Sea, 54°47.4′ N, 167°39.3′ E, depth 10 m, SCUBA, collector V.I. Shalukhanov.

Additional material. 157 colonies and colony fragments. IMB Collection (1973) Stns 149/384, 229/587; (2011) Stn 27/22; PIBOC Collection (1991) Stns 14, 17, 18, 19, 20, 41; KIENM Collection (1992) Stns 3, 5, 7, 20, 27, 28, 29, 30, 32, 34, 38, 43, 44, 46, 56, 58, 61, 63, 65, 66, 67, 68, 69, 70, 72, 75, 79, 81, 88, 94, 96, 97, 99, 110, 111, 116, 119, 121, 128, 129, 130, 132, 136, 144, 145, 146, 147, 148; A.V. Grischenko Collection (1992) Stns 7, 8 (see Appendix 1 for details).

Measurements. ZIRAS 19/50114, Medny Island, Commander Islands, Bering Sea (Fig. 18A–M). ZL, 0.48–0.77 (0.61 ± 0.07). ZW, 0.35–0.53 (0.41 ± 0.05). ZD, 0.41–0.58 (n = 2). OrL, 0.15–0.27 (0.21 ± 0.03). OrW, 0.18–0.28 (0.22 ± 0.02). OeL, 0.20–0.25 (0.22 ± 0.01). OeW, 0.22–0.35 (0.28 ± 0.04). Av(s)L, 0.05–0.09 (0.07 ± 0.01) (n = 10). P(m)N, 12–19 (17) (n = 20). P(oe)N, 4–10 (8) (n = 20).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 18A), more or less circular, attaining 14 mm in maximal dimension, bright pink-reddish to brown-yellow when alive, light brown to pink when dry. Zooids small, hexagonal, trapezoid, oval to pyriform, arranged in checkered pattern, demarcated by fine sinuous sutures between lateral and transverse walls; sutures less visible in older parts of colony.

Frontal shield umbonuloid (Fig. 18A, D–G, I), strongly thickened, convex, smooth in youngest zooids, normally with numerous tubercles of differing form and size, concentrated around secondary orifice and also distributed over entire frontal surface (Fig. 18D–H). Large, deep circular areolae along zooidal margins, separated by short, narrow (in young zooids) to thick (in older zooids) interareolar ridges. Secondary calcification may be strongly developed, resulting in general thickening of frontal shield and enlargement of tubercles (Fig. 18E). Umbonuloid component occupying about 60% of length of frontal shield (62% in one measured zooid), with accretionary banding (Fig. 18I, J, L). Ring scar discrete (Fig. 18I, L).

Primary orifice (Fig. 18B, I) deeply submerged, circular to oval; distal and lateral margins formed by upper, terminal part of distal transverse wall (Fig. 18A). Distal margin of orifice rounded, proximal margin concave, tapering, with prominent, conical, acute median lyrula, curving in frontal direction (Fig. 18A, B, G, I, J). Condyles absent.

Secondary orifice (Fig. 18D, G) irregularly oval or broadly triangular in outline, with narrowly sinuate, U-shaped proximal margin, cormidial; distally restricted by vertical thickening of proximal wall of daughter zooid (Fig. 18D, E); proximally formed by thin-walled, low peristome of two lappets from frontal shield, one of which incorporates cystid of suboral avicularium (on left or right side). In ovicellate zooids, peristomial lappets connecting with ooecium, overgrowing its proximal surface toward each other and forming incomplete circle (Fig. 18F–H). No oral spines.

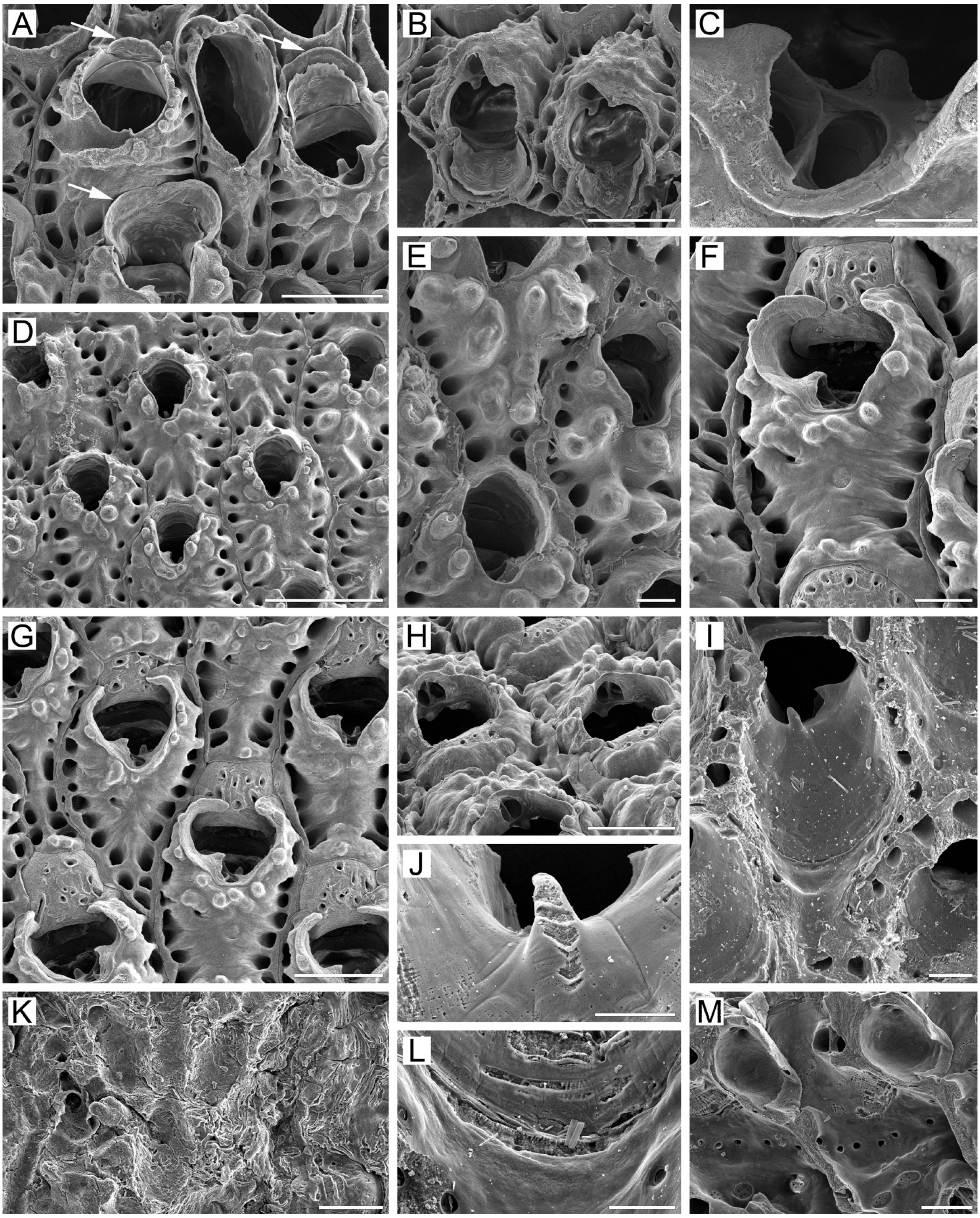

FIGURE 18. *Rhamphostomella radiatula* (Hincks, 1877). ZIRAS 19/50114 (Medny Island, Commander Islands, Bering Sea). A. Developing zooids with forming ooecia near colony margin. B. Distal view of marginal zooids with developing ooecia (arrows). C. Suboral avicularium. D. Non-ovicellate zooids in relatively young part of colony. E. Ovicellate (to the right) and non-ovicellate zooids with well-developed, bulge-like coarse tubercles of secondary calcification in older part of colony. F. Single ovicellate zooid, showing form of secondary orifice and ooecium in relatively young part of colony. G. Group of ovicellate zooids with ooecia overgrown by secondary calcification in relatively young part of colony. H. Distal view of ovicellate zooids, showing suboral avicularium and median process in older part of colony. I. Interior of frontal shield, showing lyrula, ring scar and areolae. J. Close-up of frontal-shield interior, showing median lyrula. K. Basal surface of colony that was overgrowing another bryozoan colony, *Celleporella hyalina*. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral section of zooids showing two ooecia, suboral avicularium, areolae (upper row) and zooidal lateral walls with mural pore chambers. Scale bars: A, B, G, H, 250 μm; C, J, L, 50 μm; D, K, 500 μm; E, F, I, 100 μm; M, 200 μm.

Cystid of suboral avicularium small, with tubercular surface and one communication pore (Fig. 18D, F), situated medially and transversely relative to zooidal midline, within pseudosinus of secondary orifice. Avicularian frontal surface (rostral/postmandibular areas) concave, crossing zooidal midline, facing obliquely distally. Rostrum short, curved, with tip hooked in profile, directed laterally to distolaterally and upwards (Fig. 18C, D, F–I), sometimes concealed within peristome and barely visible frontally. Palate short, lingulate to broadly triangular, foramen elongate oval; palatal face at right angle to postmandibular area, with semicircular opesia. Crossbar complete.

No adventitious avicularia.

Ovicells cleithral, initially hyperstomial, soon becoming subimmersed and later appearing endozooidal when only frontal area of ooecium remains visible (Fig. 18F, G, M), being sunken in secondary calcification originating from frontal shields of distal and distolateral zooids. Ooecium formed by distal autozooid, ooecial fold arising on colony periphery concurrently with formation of frontal shield of distal zooid (Fig. 18A). Ooecium with straight proximal margin and scattered circular, oval to slit-like pseudopores, some occluded by secondary calcification.

Zooids interconnected by three mural pore chambers (Fig. 18M) in each distolateral wall and multiporous septula in transverse walls, sometimes with buttressed recesses.

Basal surface of zooids (Fig. 18K) fully calcified, inflated, rough, textured by irregular lineation, without protuberances. Boundaries between zooids unrecognizable basally.

Ancestrula and early astogeny not observed.

Remarks. Smitt (1868a, pl. 28, fig. 193) initially illustrated *R*. *radiatula* under the name *Cellepora plicata*, together with three other species. Hincks (1877) described *R*. *radiatula* as a separate species (in *Lepralia*) from Iceland and Labrador, and Lorenz (1886) moved it to *Rhamphostomella*. Although we found six fragments of this species on a slide in the T. Hincks Collection housed in the Natural History Museum, London (NHMUK 1899.5.1.878, with the inscription "? Part of type material"), they are in poor condition and cannot be used for identification or comparison. Accordingly, we selected a neotype from Iceland from the A.M. Norman Collection, also in Natural History Museum, London.

The following combination of characters distinguishes *R*. *radiatula* from congeners: 1) suboral and frontal tubercles present, 2) small zooidal size, and 3) the right-angled aspect of the avicularian frontal surface. As discussed above, the only congener having a similarly right-angled frontal face to the suboral avicularium is *R*. *alutacea*. That species has a broad pseudosinus in the secondary orifice, in contrast to the narrow pseudosinus in *R*. *radiatula*, and the frontal surface of the avicularium is well visible in frontal view compared to *R*. *radiatula*, in which the avicularian frontal surface is barely visible frontally.

Kluge (1962, 1975) described the primary orifice of Arctic *R*. *radiatula* as having a pair of small triangular points on the median lyrula. We did not observe these in our material.

Kluge (1962, 1975) indicated that colonies of *R*. *radiatula* loosely overgrow the substratum. In contrast, our observations of a large number of specimens show that colonies are tightly cemented to a variety of hard substrata (barnacles, shells of molluscs, stones, etc.). In most cases, the basal wall of colonies conforms to irregularities in the substratum microtopography, resulting in very uneven patterning of the basal surface (Fig. 18K).

Ecology. *Rhamphostomella radiatula* has been found at depths of 2–280 m, predominantly on hard bottoms—rocks (including vertical surfaces and crevices), boulders, blocks, and gravel—and scattered on mixed seabeds with sand or silt overlain with broken shells. In addition to rocky surfaces, colonies encrust bivalve mollusc shells, ascidians, colonies of other bryozoans (*Flustrellidra gigantea*, *Tricellaria beringia*, *Celleporina robertsoniae*), polychaete tubes, sponges, barnacles and occasionally holdfasts of brown and red algae, and exists as a part of cryptic community inhabiting the cavities formed by the crustose coralline alga *Clathromorphum nereostratum*.

Distribution. This is a boreal-Arctic, circumpolar, sublittoral species. In the Arctic *R*. *radiatula* has been reported from the Barents Sea (Nordgaard 1896, 1918; Bidenkap 1900a, 1900b; Kluge 1906, 1915, 1962, 1975; Denisenko 1988, 1990), White Sea (Gostilovskaya 1957, 1978; Grishankov 1995; Ostrovsky 2009, 2013), Kara Sea (Nordgaard 1912; Kluge 1962, 1975; Denisenko 2021), Canadian Arctic Archipelago (Nordgaard 1906; Osburn 1932), Baffin Bay (Hansen 1962), Davis Strait (Hansen 1962; Kluge 1962, 1975), Labrador (Hincks 1877; Gontar & Denisenko 1989), western Greenland (Levinsen 1914; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1914, 1916; Denisenko & Blicher 2021), Jan Mayen Island (Lorenz 1886; Nordgaard 1907a), Iceland (Hincks 1877; Nordgaard 1924), Franz Josef Land (Denisenko 1990), Spitsbergen (Gontar *et al*. 2001; Kuklinski 2002b) and northern Norway (Smitt 1868a; Nordgaard 1905, 1918). In the northwestern Atlantic it has been reported from St Lawrence Gulf (Kluge 1962, 1975) and in the Gulf of Maine (Winston & Hayward 2012). In the northwestern

Pacific there are records from Africa Cape, eastern Kamchatka (Kluge 1961; Grischenko 2002), Commander Islands, Bering Sea (Kluge 1961; Grischenko 1997, 2002, 2003b; our data); Urup, Chiproy and Simushir Islands of the middle Kuril Islands, Sea of Okhotsk (Gontar 1980, 1993b; our data); western coastal waters of southern Sakhalin Island (Androsova 1958; Kluge *et al*. 1959) and Moneron Island in the Sea of Japan (Kluge 1961), and the Pacific coast of Hokkaido (Mawatari & Mawatari 1981). In the northeastern Pacific it occurs in the Gulf of Alaska near Kodiak Island (our data).

Bennike *et al*. (1994) documented *R*. *radiatula* from middle Pleistocene deposits in central western Greenland. Taylor (2021) reported this species from Pleistocene deposits of Scotland.

Rhamphostomella sibirica **(Kluge, 1929)**

(Figs 19, 25B, 30H, 33A, B)

Rhamphostomella bilaminata var. *sibirica* Kluge, 1929, p. 21.

Rhamphostomella bilaminata var. *sibirica*: Kluge 1952, p. 160; 1953, p. 178; 1955, p. 108, tab. 23, fig. 6; 1961, p. 142; 1962, p. 546, fig. 383; 1964, p. 190; 1975, p. 664, fig. 383; Gostilovskaya 1957, p. 455; 1978, p. 232, fig. 148; Kluge *et al*. 1959, p. 213; Kubanin 1976, p. 34; Androsova 1977, p. 202; Gontar 1980, p. 13; 1990, p. 133; Denisenko 1988, p. 13; 1990, p. 39; 2008, p. 187; Gontar & Denisenko 1989, p. 358.

Rhamphostomella sibirica: Kubanin 1997, p. 123; Grischenko 2002, p. 115; 2003b, p. 237; Grischenko & Ivanyushina 2002, p. 33; Denisenko & Kuklinski 2008, p. 48; Kuklinski 2009, p. 228; Denisenko 2011, p. 14; 2013, p. 184.

Rhamphostomella bilaminata: Levinsen 1916, p. 461; Nordgaard 1929, p. 7; Osburn 1933, p. 55, pl. 10, fig. 8.

Rhamphostomella bilaminata sibirica: Lukin 1979, p. 37; Gontar 1979, p. 246; 1992, p. 197; 1993b, p. 202; 1994a, p. 146; 1996, p. 46; 2010, p. 153; 2013, p. 48; Grischenko 1997, p. 175; Gontar *et al*. 2001, p. 194.

Rhamphostomella curvirostrata: Kubanin 1997, p. 123.

Rhamphostomella sp.: Kubanin 1997, p. 123.

Material examined. *Lectotype*: ZIRAS 1/50730, two fragments from one colony, RV *Vega*, Stn 71, 23 August 1878, Laptev Sea, 76°40.0′ N, 115°30.0′ E, depth 10.9 m, clay. *Paralectotype*: ZIRAS 2/50731, single colony, RV *Vega*, Stn 71, 23 August 1878, Laptev Sea, 76°40.0′ N, 115°30.0′ E, depth 10.9 m, clay.

P. Kuklinski Collection, one colony encrusting rock, Russian-German Expedition Transdrift 1, RV *Ivan Kireev*, Stn 48, 18 August 1993, Laptev Sea, 74°30.0′ N, 137°05.0′ E, depth 22 m, rock dredge, collectors M.K. Schmid and D. Piepenburg. ZIRAS 2/155–134, single colony fragment, Russian Polar Expedition, RV *Zarya*, St 46, 28 August (3 September) 1901, Laptev Sea, depth 60 m, silt with stones, otter trawl. ZIRAS 6/155–134, single colony fragment, Russian Polar Expedition, RV *Zarya*, Stn 15, 18(31) August 1901, Middendorff Bay, eastern side of Zarya Peninsula, Taymyr Peninsula, Kara Sea, 75°54.0′ N, 92°59.0′ E, depth 7.9–10.7 m, silted sand, dredge. ZIRAS 34/50113, nine colony fragments, KIENM Collection, Stn 133, 23 July 1992, Rock Sivuchy Kamen, coastal waters of Medny Island, Commander Islands, Bering Sea, 54°47.4′ N, 167°39.3′ E, depth 10 m, SCUBA, collector V.I. Shalukhanov. NHMUK 2013.10.21.5, one colony encrusting oyster shell, RV *Norseman*, Stn LT–2, 3 July 2011, Longshot, East of Square Bay, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°26.6′ N, 179°12.2′ E, depth 10 m, SCUBA, collector P. Kuklinski. NHMUK 2013.10.21.6, one colony encrusting oyster shell, RV *Norseman*, Stn CT–1, 8 July 2011, Cannikin, White Alice Creek, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Pacific Ocean, 51°28.6′ N, 179°07.3′ E, depth 10–15 m, SCUBA, collector P. Kuklinski.

Additional material. 310 specimens. E.F. Guryanova Collection (1931) Stn 223; IMB Collection (1972) Stns 5/12, 59/167; (1973) Stns 113/302, 113/305, 113/306, 217/558; KIENM Collection (1988) Stn 326; (1991) Stns 196, 197, 198, 199, 203, 208, 215, 217, 225, 227, 228, 229, 230, 236; (1992) Stns 19, 20, 25, 27, 32, 34, 57, 63, 66, 68, 69, 70, 71, 72, 75, 76, 77, 79, 87, 97, 99, 100, 105, 118, 120, 124, 128, 130, 133, 144, 148; A.V. Grischenko Collection (1990) Stns 5, 15; (1992) Stns 1, 7, 8 (see Appendix 1 for details).

Measurements. ZIRAS 34/50113, Medny Island, Commander Islands, Bering Sea (Figs 19A–L, 30H). ZL, 0.68–1.03 (0.80 ± 0.09). ZW, 0.36–0.51 (0.44 ± 0.04). ZD, 0.49–0.65 (n = 2). OrL, 0.22–0.36 (0.28 ± 0.03). OrW, 0.24–0.35 (0.29 ± 0.03). OeL, 0.20–0.30 (0.26 ± 0.03). OeW, 0.30–0.38 (0.36 ± 0.02). Av(s)L, 0.15–0.31 (0.22 ± 0.04). P(m)N, 7–15 (12). P(oe)N, 0–9 (6).

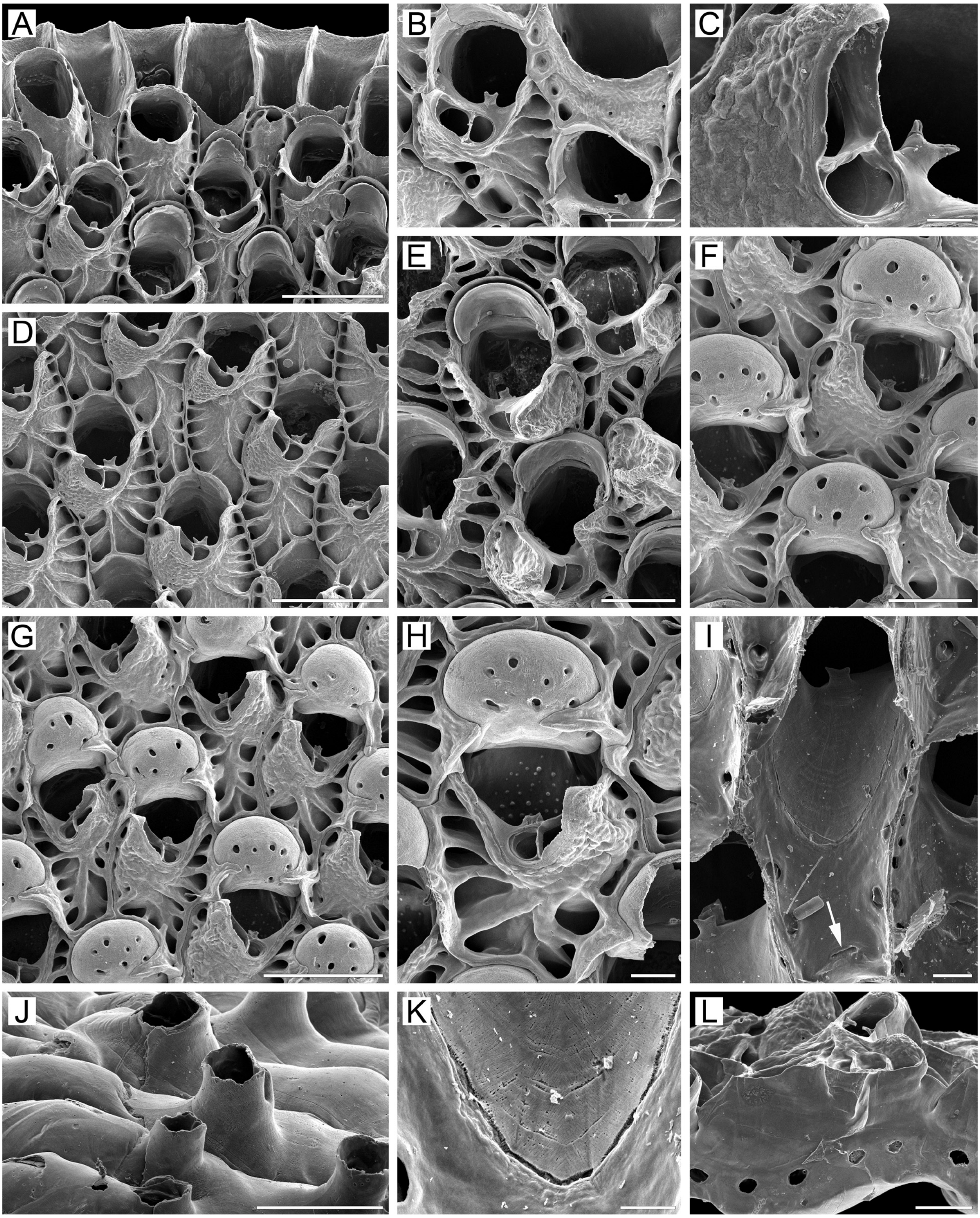

FIGURE 19. *Rhamphostomella sibirica* (Kluge, 1929). ZIRAS 34/50113 (Medny Island, Commander Islands, Bering Sea). A. Colony margin with developing zooids and ooecia. B. Zooids near colony margin showing form of primary orifice with lyrula. C. Suboral avicularium and lyrula. D. Group of non-ovicellate zooids in young part of colony. E. Zooids with developing ooecia. F, G. Ovicellate zooids in older parts of colony. H. Ovicellate zooid in older part of colony. I. Interior of frontal shield, showing lyrula, umbo, ring scar, areolae and ooecial communication pore (arrow). J. Basal surface of colony with tubular protuberances. K. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. L. Lateral view of zooid, showing suboral avicularium and zooidal lateral wall with mural pore chambers. Scale bars: A, D, G, J, 500 µm; B, E, F, 250 µm; C, K, 50 µm; H, I, 100 µm; L, 200 µm.

NHMUK 2013.10.21.5, Amchitka Island, Aleutian Islands, Bering Sea. ZL, 0.43–0.88 (0.64 ± 0.07). ZW, 0.28–0.49 (0.38 ± 0.05). ZD, 0.45–0.54 (*n* = 2). OrL, 0.21–0.30 (0.25 ± 0.02) (*n* = 21). OrW, 0.23–0.30 (0.27 ± 0.02) (*n* = 22). OeL, 0.21–0.31 (0.26 ± 0.02) (*n* = 20). OeW, 0.25–0.39 (0.33 ± 0.02) (*n* = 23). Av(s)L, 0.18–0.50 (0.28 ± 0.10). P(m)N, 6–12 (10) (*n* = 10). P(oe)N, 5–9 (7) (*n* = 20).

P. Kuklinski Collection, Amchitka Island, Aleutian Islands, Bering Sea (Fig. 25B). AnL, 0.36 (*n* = 1). AnW, 0.26 (*n* = 1). AnOpL, 0.16 (*n* = 1). AnOpW, 0.15 (*n* = 1).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 19A), more or less circular, attaining 22 mm in any one direction, bright-orange or red-brown when alive, light-orange to yellowish when dry. Free-growing bilaminate folds or occasionally multilayered zooidal aggregations with free spaces between adjoining zooidal layers developing in some colonies. Zooids of moderate size, irregularly hexagonal, oval or irregular in shape, tapering proximally, packed in quincunx, demarcated by fine sutures between lateral and transverse walls in all parts of colony, young and old.

Frontal shield umbonuloid (Fig. 19A, I), thin, moderately convex, smooth to gently dimpled on avicularian cystid, with large areolae along zooidal lateral walls, separated by interareolar ridges (Fig. 19A, D–H); ridges elongate, relatively low and thin in young zooids (Fig. 19A, D), tall and thick in older zooids, conferring to frontal shield a strongly costate appearance (Fig. 19E–H). As calcification progresses, ridges join along zooidal midline; some ridges connected to peristomial lappets and cystid of suboral avicularium. Umbonuloid component extensive, occupying about 60% of length of frontal shield (57% in one measured zooid), with parallel lineation and accretionary banding (Fig. 19I). Ring scar discrete (Fig. 19L).

Primary orifice (Fig. 19A, B) submerged, subcircular or sometimes oval; distal and lateral rim formed by upper terminal part of distal transverse wall. Distal margin of orifice rounded, proximal margin concave, with median, bifurcate or, sometimes, alate lyrula (Fig. 19B, C, I). Condyles absent.

Secondary orifice (Fig. 19D–H) asymmetrically oval to broadly triangular, cormidial, distolateral curvature formed by extensions of proximal and lateral walls of distal and distolateral zooids (Fig. 19D); proximally with deep, V-shaped pseudosinus defined by flared lappets from frontal shield, one of them concurrently fusing with cystid of suboral avicularium (Fig. 19D–H). In ovicellate zooids, lappets not fused with proximolateral corners of ooecia; instead, opposing lobes of secondary calcification growing from lateral walls of neighbouring zooids towards each other over proximal part of ectooecium (Fig. 19F–H). These lobes together with peristomial lappets and avicularian cystid forming incomplete circle giving tubular, transversely oval to irregularly triangular outline to secondary orifice. No oral spines.

Cystid of suboral avicularium occupying from one-fifth to one-third of frontal zooidal wall, elevated, broad, with dimpled surface and 2–3 communication pores, asymmetrically situated on the left or right side proximal to orifice (Fig. 19A–H). Frontal surface (rostral/postmandibular areas) of avicularium slightly concave, crossing zooidal midline, facing distally or obliquely frontally. Rostrum elongate-triangular, slightly curved laterally, occasionally with hooked tip, directed distolaterally and upwards (Fig. 19C). Palate elongate-triangular, with rounded distal end, insignificantly curved laterally, foramen elongate-oval, with distal cryptocystal shelf; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells initially hyperstomial, becoming subimmersed in older parts of colony by overgrowth of ooecium by secondary calcification (Fig. 19F–H). Ooecium formed by distal autozooid; ooecial fold developing concurrently with frontal shield of distal autozooid at colony periphery. Ooecial coelomic cavity connecting to visceral coelom via communication canal opening on underside of proximal part of frontal shield of distal zooid as straight slit-like communication pore situated near transverse wall (Fig. 19I). Ooecium hemispherical, smooth, with weakly concave proximal margin and 4–8 circular to oval pseudopores, sometimes occluded by secondary calcification.

Zooids interconnected by 2–3 mural pore chambers in each distolateral wall (Fig. 19L). Communication pores spread through basal part of transverse walls either as wide horizontal "band" or forming two multiporous septula.

Basal surface of zooids (Fig. 19J, 30H) fully calcified, smooth, thin, with numerous tubular protuberances (0.08–0.28 mm in diameter) and occasional fine transverse lineation on surface. Numerous white spots (presumably less-calcified areas) visible in semitransparent basal wall by light microscopy. Boundaries between zooids indicated basally by sinuous incisions.

Ancestrula modified tatiform (Fig. 25B), oval, basal wall with central uncalcified window; ancestrular opesia longitudinally oval, occupying distal half of cystid; eight spines evenly distributed around opesial margin. Ancestrula budding triplet of periancestrular zooids distally and distolaterally (left distolateral zooid not developed in Fig. 25B); periancestrular zooids similar to but smaller than subsequent zooids, with distal zooid bearing two hollow, ephemeral oral spines incorporated in lateral peristomial lappets.

Remarks. In contrast with early descriptions of an exclusively encrusting colony form in this species, some specimens we examined had erect, free-growing bilaminate folds or occasionally formed a multilayered compound aggregation of zooids.

Although Kluge (1962, 1975) mentioned the presence of tiny condyles, we did not observe them, although their presence/absence possibly falls into the range of variation for orificial characters in this species.

Rhamphostomella sibirica strongly resembles *R. bilaminata*, and the species was long considered to be a variety or subspecies of *R. bilaminata* (Kluge 1929, 1952, 1953, 1955, 1961, 1962, 1964, 1975; Gostilovskaya 1957, 1978; Kluge *et al*. 1959; Kubanin 1976; Androsova 1977; Gontar 1979, 1980, 1990, 1993b, 1994a, 1996; Denisenko 1988, 1990; Gontar & Denisenko 1989; Grischenko 1997). However, *R. sibirica* differs from *R. bilaminata* in the following characters: 1) zooids are longer in *R. sibirica*, with the mean length of zooids only just overlapping (0.64–0.80 mm in *R. sibirica* vs 0.55–0.69 mm in *R. bilaminata*); 2) the frontal shield is flattened to moderately convex in *R. sibirica*, whereas most zooids are swollen in the distal half in *R. bilaminata*; 3) interareolar ridges are numerous, prominent and long in *R. sibirica* (Fig. 19D–H) but very short, sparse or occasionally lacking in *R. bilaminata* (Fig. 12D); 4) the avicularian cystid has a neatly dimpled surface in *R. sibirica* but is entirely smooth in *R. bilaminata*; 5) the suboral avicularia have an elongate triangular rostrum with a slightly curved distal end in *R. sibirica*, whereas they are broadly lingulate in *R. bilaminata*; 6) the opposing peristomial lappets are generally convergent in *R. bilaminata*, defining a narrow U-shaped pseudosinus in the secondary orifice (Fig. 12G, H), but these are separated and the pseudosinus is V-shaped in *R. sibirica* (Fig. 19F–H). Based on these differences, we consider *R. sibirica* to represent a distinct species.

Ecology. *Rhamphostomella sibirica* has been recorded at depths of 0–170 m on various bottom types (including silty plateaux, vertical rocky surfaces and crevices) and substrates (boulders, blocks, pebbles, gravel, sand and silt). Colonies encrust holdfasts of brown algae (*Alaria fistulosa*, *Laminaria dentigera*, etc.), red algae (*Constantinea rosa-marina*, etc.), and the species also occurs as a component of the crytic communities in the cavities formed by the coralline red alga *Clathromorphum nereostratum*. Other substrata include sponges, hydroids, bivalve shells, ascidians and other bryozoans (*Tegella aquilirostris*, *Scrupocellaria elongata*, *Myriapora orientalis*, *Phidolopora elongata*, *Celleporina nordenskjoldi*).

Distribution. This is a boreal-Arctic, circumpolar, sublittoral species. Numerous Arctic records include the Barents Sea (Smitt 1868a; Kluge 1962, 1975; Denisenko 1988, 1990), White Sea (Gostilovskaya 1957, 1978), Kara Sea (Kluge 1929, 1962, 1975; Denisenko 2021), Laptev Sea (Kluge 1929, 1962, 1975; Gontar 1990, 1996), East Siberian Sea (Nordgaard 1929; Kluge 1929, 1962, 1975; Gontar 1994a; Denisenko 2011), Chukchi Sea (Kluge 1929, 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), western Greenland (Kluge 1962, 1975; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1916; Denisenko & Blicher 2021), Spitsbergen (Gontar *et al*. 2001; Kuklinski 2009), and Franz Josef Land (Denisenko 1990). In the northwestern Atlantic, *R. sibirica* has been reported from St Lawrence Gulf (Kluge 1962, 1975) and Gulf of Maine (Osburn 1933). In the northwestern Pacific, it has been documented in the northern part of the Bering Sea from St Lawrence Island, Provideniya Bay, Anadyr Gulf, Navarin Cape (Kluge 1961; Grischenko 2002; Gontar 2013), along eastern Kamchatka in the Litke Strait (our data), Africa Cape, Avacha Gulf (Kluge 1961; Grischenko 2002), and around the Commander Islands (Kubanin 1997; Grischenko 1997, 2002, 2003b; Grischenko & Ivanyushina 2002); in the Sea of Okhotsk at Zavjalov Island (Kubanin 1976), southwestern Kamchatka, Penzhinskaya, Gizhiginskaya, Yamskaya and Tauyskaya Inlets, Okhotsk, Ayan (Kubanin 1997); eastern coast of southern Sakhalin Island (Kluge 1961; Kluge *et al*. 1959), Sakhalin Gulf, Shantar Archipelago (Kluge 1961), Kuril Islands (Kluge *et al*. 1959; Kluge 1961; Lukin 1979; Gontar 1979, 1980, 1993b), and in the Sea of Japan from Tatar Strait (Kluge 1961). The only northeastern Pacific record is from Beringian coastal waters of Amchitka Island, Rat Islands, western Aleutians (our data).

Rhamphostomella tatarica (Androsova, 1958)

(Figs 20, 33C, D)

Escharopsis tatarica Androsova, 1958, p. 168, fig. 98.
Escharopsis tatarica: Kluge *et al*. 1959, p. 213; Kluge 1961, p. 141.

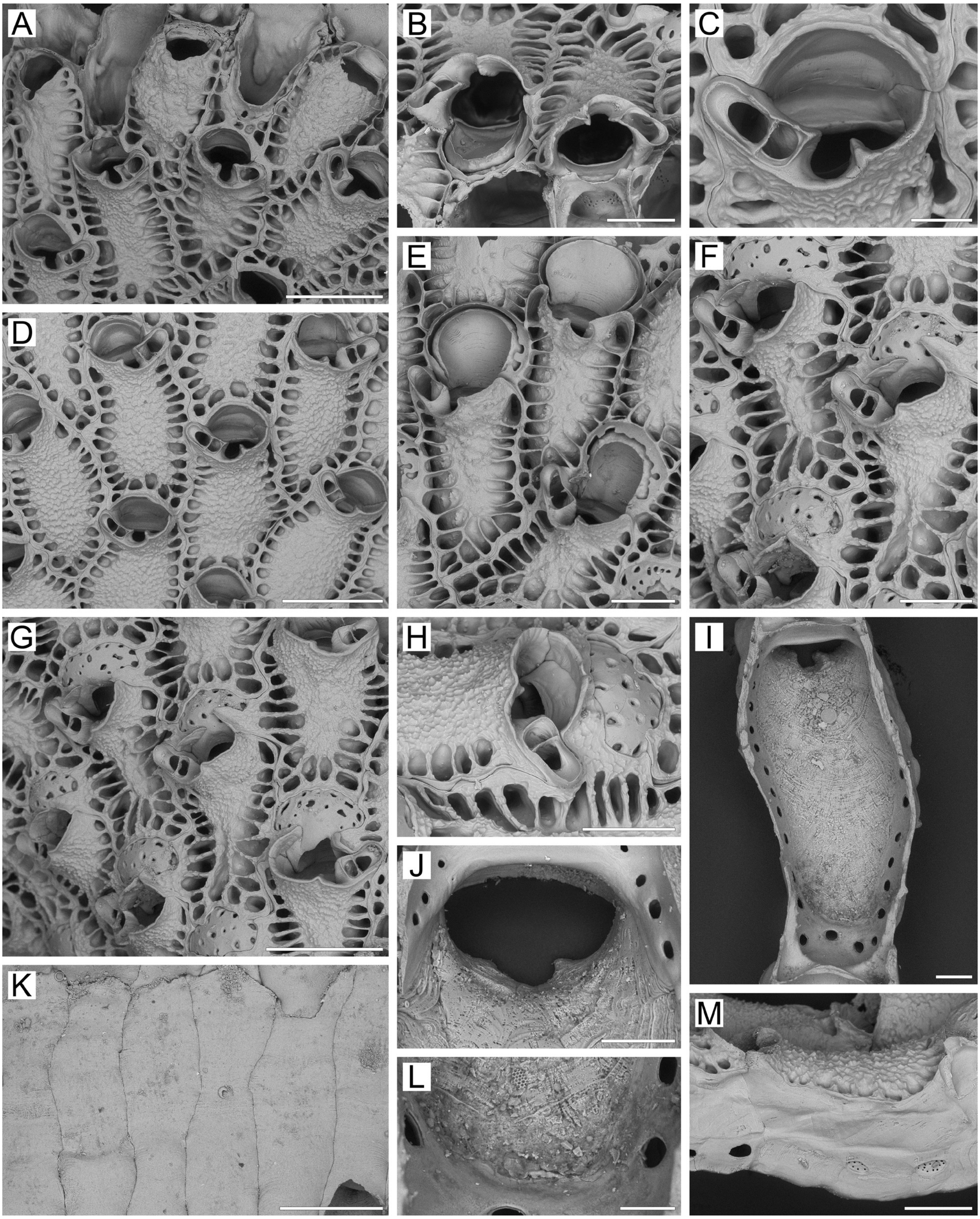

FIGURE 20. *Rhamphostomella tatarica* (Androsova, 1958). ZIRAS 7/50548 (western Kamchatka, Sea of Okhotsk). A. Colony margin with young and developing zooids. B. Distal view of marginal zooids, showing developing ooecia, details of orifice and multiporous septula in distal transverse wall. C. Orifice with suboral avicularium. D. Non-ovicellate zooids in young part of colony. E. Zooids with developing ooecia in young part of colony. F, G. Ovicellate zooids in older part of colony. H. Lateral view of distal half of ovicellate zooid. I. Interior of frontal shield, showing umbo, ring scar and areolae. J. Internal view of primary orifice. K. Basal surface of colony. L. Interior of frontal shield, showing ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing frontal shield and lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, E, F, H, 250 µm; C, I, J, 100 µm; L, 50 µm; M, 200 µm.

Posterula tatarica: Denisenko 2013, p. 185.

Material examined. *Holotype*: ZIRAS 1/3701, single colony, RV *Toporok*, Stn 12, 6 July 1947, eastern Tatar Strait, coastal waters of southern Sakhalin Island, Sea of Japan, depth 117 m, boulders, beam-trawl, collector Z.I. Kobjakova. *Paratype*: ZIRAS 2/3852, single colony, RV *Toporok*, Stn 29, 21 August 1949, Tatar Strait, Sea of Japan, depth 43 m, silted sand with shells, dredge, collector Z.I. Kobjakova.

ZIRAS 7/50548, two colony fragments, MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko.

Measurements. ZIRAS 7/50548, western Kamchatka, Sea of Okhotsk (Fig. 20A–M). ZL, 0.82–1.20 (1.01 ± 0.10). ZW, 0.37–0.78 (0.53 ± 0.07). ZD, 0.43–0.54 (*n* = 2). OrL, 0.21–0.29 (0.25 ± 0.02). OrW, 0.24–0.31 (0.28 ± 0.02). OeL, 0.29–0.36 (0.31 ± 0.02) (*n* = 10). OeW, 0.39–0.45 (0.42 ± 0.02) (*n* = 10). Av(s)L, 0.13–0.20 (0.16 ± 0.02). P(m)N, 19–30 (25). P(oe)N, 9–18 (15) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 20A), irregular in form; largest among our fragments was about 13 × 7 mm; bright brown when alive, light brown when dry. Zooids large, oblong hexagonal, pyriform, rectangular or irregular in shape (Fig. 20A, D–G), arranged in checkered pattern, demarcated by fine sinuous sutures between lateral and transverse walls recognizable in all colony parts.

Frontal shield umbonuloid (Fig. 20A), thin, dimpled with reticulate appearance, flat or moderately convex in young zooids (Fig. 20A, D), becoming more convex in older zooids (Fig. 20E–G). Frontal shield with angular marginal areolae (Fig. 20A, B, D–H), separated by short narrow interareolar ridges in young zooids (Fig. 20A, D), becoming more elongate and distinctly larger with age and, thus occupying noticeably larger area on frontal shield (Fig. 20F–H). Umbonuloid component very extensive, occupying about 90% of length of frontal shield (89% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 20I). Ring scar indistinct (Fig. 20I, L).

Primary orifice (Fig. 20A, B, J) submerged, transversely oval; distal and lateral margins formed by upper terminal part of distal transverse wall, bearing wide, flared shelf distally (Fig. 20A–C). Distal margin of orifice shallowly rounded, proximal margin with median oval sinus flanked by blunt or acute projection on each side (Fig. 20A–C, J). Condyles absent.

Secondary orifice (Fig. 20C) transversely oval, with deep, median U-shaped sinus in proximal margin, cormidial; sinus formed by ridges flanking primary orifice that continue into peristome, forming prominent peristomial "denticle" on one side and another "denticle" from proximo-interior corner of suboral avicularian cystid on other. Secondary orifice distally formed by vertical concave thickening of proximal shield of daughter zooid (Fig. 20B–D), proximally restricted by thin-walled peristome incorporating cystid of suboral avicularium on one side and high lappet with terminal denticle on opposite side. In ovicellate zooids, avicularian cystid and lappet both connecting to proximolateral corners of ooecium (Fig. 20E). Extensions of lateral walls of contiguous distolateral zooids growing as secondary calcification over ooecium, as two converging lobes that sometimes meet. Together with peristomial lappet and avicularian cystid, these lobes forming complete or incomplete circle (Fig. 20F–H), conferring tubular, transversely oval to irregular outline to peristomial orifice. No oral spines.

Cystid of suboral avicularium small, slightly elevated, with dimpled surface and one communication pore (Fig. 20A–H), asymmetrically placed proximally on left or right of orificial margin and slightly overhanging it. Frontal surface (rostral/postmandibular areas) of avicularium to one side of zooidal midline, facing distally or obliquely upwards. Rostrum lingulate, with slightly curved distal end, directed distolaterally (Fig. 20B–H), extending over surface of neighbouring zooid (Fig. 20D–G). Palate lingulate, foramen elongate oval with distal cryptocystal shelf; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells initially hyperstomial, rapidly becoming subimmersed and sometimes appearing endozooidal through overgrowth of ooecium by secondary calcification encroaching from walls of surrounding lateral and daughter zooids (Fig. 20F–H). Ooecium formed by distal autozooid, ooecial fold developing at colony periphery concurrently with formation of frontal shield of distal zooid. Ooecium smooth (Fig. 20F–H), with scattered circular or oval pseudopores, some occluded by secondary calcification; proximal margin arched.

Zooids interconnected by 2–3 mural pore chambers in each distolateral wall (Fig. 20M) and two multiporous septula (sometimes with individual pores in between) in basal half of transverse walls (Fig. 20B).

Basal wall of zooids fully calcified, smooth, flattened, with fine transverse parallel lineation in places (Fig. 20K). Boundaries between zooids visible basally as fine, sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. Androsova (1958) attributed her new species to *Escharopsis* Verrill, 1880 based solely on the absence of a lyrula in the primary orifice. At the same time, *Escharopsis* lacks evenly pseudoporous ooecia; instead, there are either no pseudopores or just a single central pseudopore. Denisenko (2013) placed this species in *Posterula* Jullien, 1903, but the peristomial secondary orifice with an asymmetrically set suboral avicularium and ovicells with numerous pseudopores warrant placement of this species in *Rhamphostomella*.

Ecology. *Rhamphostomella tatarica* has been recorded from depths of 30–117 m, on gravel and mollusc shells.

Distribution. The species was originally described from the northern part of the Sea of Japan, including off Kholms, Tomari, Ilyinskoye and Belinskoye along the southwestern coast of Sakhalin Island (47°03.0′ N, 142°00.0′ E to 48°15.0′ N, 142°08.0′ E) and from Primorye near capes Zolotoy (47°18.0′ N, 139°00.0′ E) and Syurkum (50°05.0′ N, 140°41.0′ E). It was subsequently reported by Kluge *et al*. (1959) and Kluge (1961) from the western part of southern Sakhalin and at Primorye. We obtained specimens from the western Kamchatka shelf of the Sea of Okhotsk. Based on these records, *R*. *tatarica* is a Pacific Asian high-boreal, sublittoral species.

***Rhamphostomella townsendi* Osburn, 1952**
(Fig. 21)

Rhamphostomella townsendi Osburn, 1952, p. 430, pl. 51, figs 2, 3.

Material examined. *Holotype*: USNM 11032, record name Che981–2, colony encrusting sponge, US Fish Commission Collection, RV *Albatross*, Stn 5695, 26 April 1911, Santa Rosa Island, SW of Channel Islands, Southern California, Pacific Ocean, 33°33.0′ N, 120°17.0′ W, depth 977 m.

ZIRAS 1/50117, colony encrusting branch of erect bryozoan *Microporina okadai*, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 5, 2 August 1991, southeast off Medny Island, Commander Islands, Bering Sea, 54°12.0′ N, 168°37.3′ E, depth 569 m, Sigsbee trawl, collector A.V. Smirnov. ZIRAS 2/50118, one colony encrusting sponge, PIBOC Collection, RV *Akademik Oparin*, 14th Expedition, Stn 5, 2 August 1991, southeast off Medny Island, Commander Islands, Bering Sea, 54°12.0′ N, 168°37.3′ E, depth 569 m, Sigsbee trawl, collector A.V. Smirnov. Specimen AL–WP–0019–0022, M.H. Dick Collection, one colony, Alaska Fisheries Science Center and National Marine Fisheries Service Collection, FV *Sea Storm*, Haul 190, Stn 114–21, 23 July 2004, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°51.6′ N, 178°27.8′ E, depth 224–235 m, collector M.H. Dick.

Measurements. ZIRAS 1/50117, Medny Island, Commander Islands, Bering Sea (Fig. 21C, F, H, I, K). ZL, 0.63–0.98 (0.76 ± 0.07) (*n* = 20). ZW, 0.45–0.65 (0.53 ± 0.06) (*n* = 20). ZD, 0.35–0.38 (*n* = 2). OrL, 0.18–0.22 (0.20 ± 0.02) (*n* = 10). OrW, 0.20–0.25 (0.22 ± 0.02) (*n* = 10). OeL, 0.22–0.30 (0.26 ± 0.02) (*n* = 10). OeW, 0.35–0.40 (0.37 ± 0.02) (*n* = 10). Av(s)L, 0.12–0.17 (0.14 ± 0.02) (*n* = 10). P(m)N, 12–19 (16) (*n* = 10). P(oe)N, 24–41 (34) (*n* = 6).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 21A), small, irregular in form, attaining about 5 mm in maximal dimension, light-brown to beige when dry. Zooids of medium size, rhombic, hexagonal to oval, sometimes tapering proximally (Fig. 21D, G, J), arranged in quincunx, demarcated by fine interzooidal sutures recognisable in all parts of colony.

Frontal shield umbonuloid (Fig. 21A, D–K), thin, strongly convex, tessellated, with oval and circular areolae along margins (Fig. 21D–H). Interareolar ridges lacking or indistinct in young zooids (Fig. 21D, J), short ridges appearing in zooids and areolae becoming angular in older parts of colony (Fig. 21F–H); reticulate pattern of frontal shield becoming coarser with age. Umbonuloid component occupying about 60% of length of frontal shield (61% in one measured zooid), with fine parallel lineation and accretionary banding (Fig. 21I, K). Ring scar indistinct (Fig. 21K), with uneven boundary between exterior-wall microstructure and extra-umbonuloid calcification.

Primary orifice (Fig. 21A, B) slightly submerged, transversely oval or trapezoidal; distal and lateral margins formed by upper part of distal transverse wall. Distal margin of orifice more or less straight; proximal margin bisinuate, with median bifurcate lyrula and pair of triangular lateral processes with rounded tip (Fig. 21B). Condyles absent. Pair of articulated oral spines sometimes present in distolateral corners of orifice in young, non-ovicellate zooids (Fig. 21B, D, J); oral spines absent in ovicellate zooids (Fig. 21A, H).

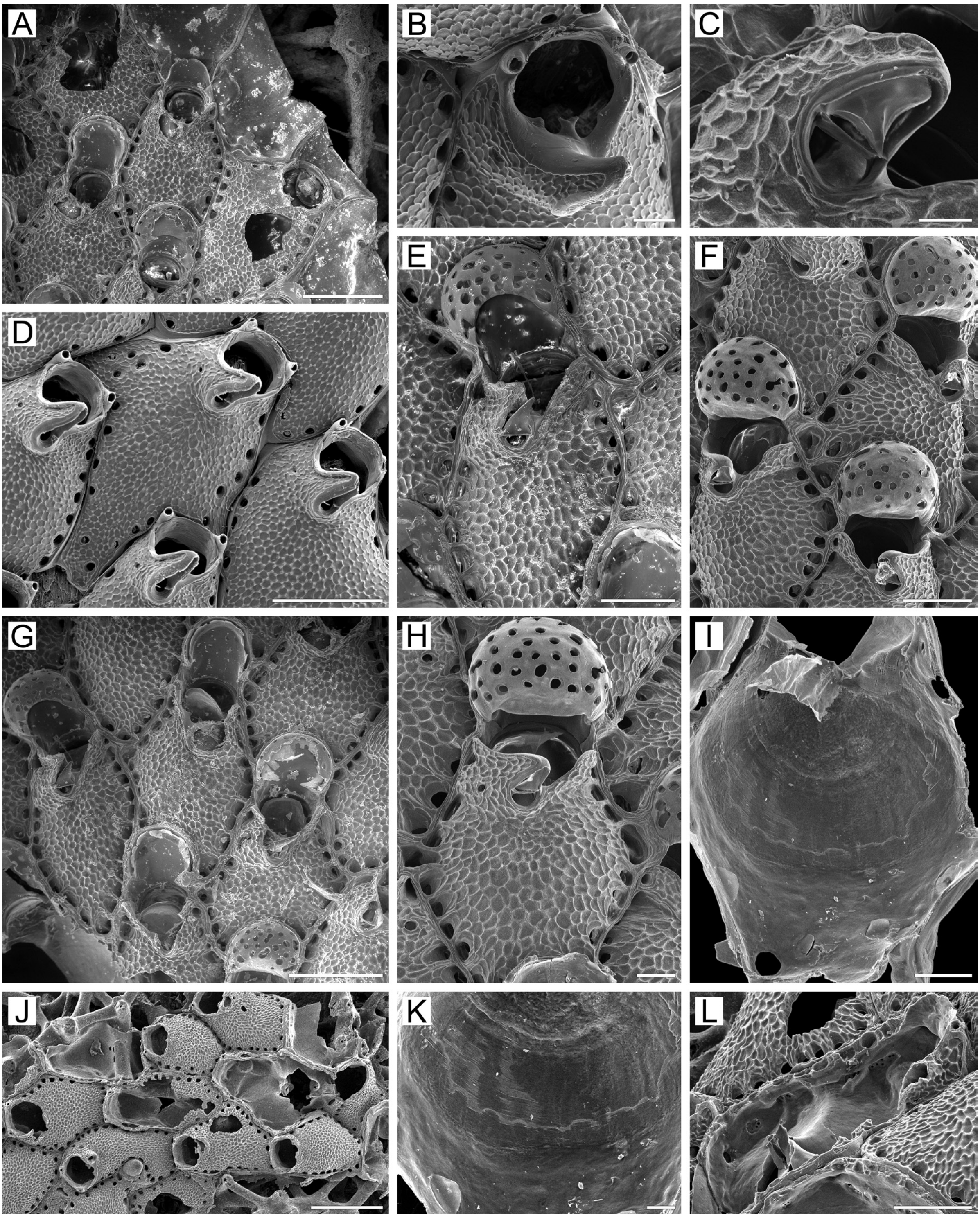

FIGURE 21. *Rhamphostomella townsendi* Osburn, 1952. A, E, G. *Holotype*, USNM 11032 (Santa Rosa Island, Pacific Ocean). B, D. Specimen AL–WP–0019–0022, M.H. Dick Collection (Amchitka Island, Aleutian Islands, Bering Sea). C, F, H, I, K. ZIRAS 1/50117, J, L. ZIRAS 2/50118 (Medny Island, Commander Islands, Bering Sea). A. Colony margin with developing zooids and ooecia. B. Orifice of non-ovicellate zooid, showing lyrula, lateral denticles and bases of oral spines. C. Suboral avicularium. D. Non-ovicellate zooids in young part of colony. E. Zooid with developing ovicell. F, H. Ovicellate zooids in older parts of colony. G. Zooids with developing and broken ooecia. I. Interior of frontal shield, showing blurred ring scar around umbonuloid component. J. General view of colony encrusting a sponge. K. Interior of frontal shield, showing blurred undulating ring scar and exterior wall microstructure of umbonuloid component. L. Zooid with broken frontal shield, showing areolae and lateral zooidal wall with mural pore chambers. Scale bars: A, D, G, J, 500 μm; B, H, I, 100 μm; C, K, 50 μm; E, F, 250 μm; L, 200 μm.

Secondary orifice (Fig. 21D–H) trapezoidal to irregularly oval and triangular, entirely formed by low tubular peristome; distal curvature formed by vertical extension of distal zooidal wall (Fig. 21D). Laterally and proximally restricted by two lappets of slightly elevated peristome, one incorporating cystid of suboral avicularium on left or right side; lappets low in non-ovicellate zooids, angular in ovicellate zooids. In ovicellate zooids, lappets defining U- to V-shaped, slightly asymmetrical pseudosinus (Fig. 21E–H) but not fusing with proximolateral corners of ooecium; extensions of lateral walls of contiguous distolateral zooids connecting proximolateral corners of ooecia with corresponding peristomial lappet, conferring irregular outline to secondary orifice (Fig. 21E–H).

Cystid of suboral avicularium relatively small, with tessellated surface and one or two minute communication pores, asymmetrically situated proximal to orifice (Fig. 21B–D, F–H). Frontal surface (rostral/postmandibular areas) of avicularium gently concave, normally crossing zooidal midline, facing obliquely proximally to proximolaterally. Rostrum elongate triangular, pointed, extending slightly across and overhanging proximal margin of orifice, gently curved, directed obliquely medially to laterally and upwards (Fig. 21B–D, F–H). Mandible elongate triangular, with rounded or pointed tip (Fig. 21C, E, G). Palate and palatal foramen triangular, with rounded distal end; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 21E–H). Ooecium formed by distal autozooid; ooecial fold developing at colony periphery concurrently with frontal shield of distal zooid. Ooecium with straight proximal margin and smooth ectooecium with numerous circular and oval pseudopores. Fully formed ovicells remaining prominent, with ooecia not embedded in secondary calcification.

Zooids interconnected by two mural pore chambers in each distolateral wall (Fig. 21L) and multiporous septula in basal half of transverse walls.

Basal wall of zooids fully calcified (Fig. 21A, J, L), smooth. Sparse white spots (presumably less-calcified areas) visible in semitransparent basal wall by light microscopy. Basal surface with sporadic small, tubular protuberances about 0.07 mm in diameter and up to 0.26 mm long. Boundaries between zooids visible as fine meandering sutures.

Ancestrula and early astogeny not observed.

Remarks. *R. townsendi* resembles *R. curvirostrata* in possessing: 1) a tessellated frontal shield; 2) a primary orifice with a bisinuate proximal margin, median bifurcate lyrula and pair of triangular lateral processes; 3) an asymmetrically set suboral avicularium with a triangular rostrum that partly overhangs the proximal orificial margin; and 4) an ooecium with uniformly scattered pseudopores. At the same time, *R. townsendi* clearly differs from *R. curvirostrata* in that 1) the suboral avicularium is rather short and overhangs the proximal orificial margin in *R. townsendi* but is strongly elongate, extending across and overhanging the entire orifice in *R. curvirostrata*; 2) the marginal areolae are separated by short, sometimes reduced ridges in *R. townsendi*, but by moderately to strongly elongate ridges in *R. curvirostrata*; 3) fully-formed ovicells remain prominent in *R. townsendi*, but ooecia become embedded in the frontal shield of the distal zooid by secondary calcification in *R. curvirostrata*; and 4) all major measurements are generally smaller in *R. townsendi* than in *R. curvirostrata*.

While the holotype specimen (USNM 11032) from the Santa Rosa Island, California, is clearly conspecific with our specimens from the Commander and western Aleutian Islands, the holotype appears to lack oral spines altogether. Furthermore, there appears to be intercolony variation in tessellation, with some specimens (e.g. Fig. 21A, F–H) more coarsely tesselated than others (e.g. Fig. 21D, E).

Ecology. *Rhamphostomella townsendi* is known from depths of 224–977 m on sandy and silty bottoms, encrusting glass sponges and the erect bryozoan *Microporina okadai*.

Distribution. *Rhamphostomella townsendi* is a little-known species originally described from southwest of the Channel Islands, California, USA. It is now also known from two northwestern Pacific localities, including the Pacific slope of Medny Island, Commander Islands, and the Beringian slope of Amchitka Island, Rat Islands, western Aleutian Islands. Thus *R. townsendi* appears to be an Eastern Pacifc boreal, sublittoral to upper bathyal species, extending to the edge of the subtropics.

***Rhamphostomella multirostrata* n. sp.**

(Figs 22, 30I)

Diagnosis. Colony encrusting, multiserial, partly forming small free-growing frills. Zooids large, oblong-hexagonal.

Frontal shield moderately convex, very finely granular. Interareolar ridges reaching avicularian cystid in distal part of zooid. Umbonuloid component extensive. Primary orifice submerged, broadly circular, with very broad median lyrula-like prominence. No condyles. Secondary orifice transversely oval, cormidial; proximolateral curvature incorporating large mucro with two thin-walled symmetrical lateral lappets. 1–2 pairs of long, tubular, basally articulated oral spines around distal curvature of orifice. Suboral aviculiferous mucro very tall, conical to bulbous, finely granular, bearing 3–5 spirally arranged avicularia decreasing in size towards apex. Basalmost main avicularium budding 2–4 smaller avicularia. No adventitious avicularia. Ovicells hyperstomial. Ectooecium smooth, with numerous scattered pseudopores, mostly with no secondary calcification. 4–5 pore chambers in distolateral wall and two multiporous septula in transverse walls. Basal surface of zooids fully calcified, with numerous tubular protuberances.

Material examined. *Holotype*: ZIRAS 1/50545, single large colony detached from sponge, IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 19/15, 13 July 2011, westward from Urup Island, middle Kuril Islands, Sea of Okhotsk, 45°54.2′ N, 149°40.4′ E – 45°54.2′ N, 149°40.0′ E, depth 183–213 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev. *Paratype*: ZIRAS 2/50546, single colony encrusting sponge. IMB Collection, RV *Akademik Oparin*, 41st Expedition, Stn 41/36, 19 July 2011, southeastward from Chiproy Island, middle Kuril Islands, Pacific Ocean, 46°20.5′ N 150°58.0′ E – 46°21.0′ N 150°58.4′ E, depth 438–567 m, Sigsbee trawl, collectors A.P. Tsurpalo and A.V. Chernyshev.

Etymology. This specific name *multirostrata* refers to the multiple avicularian rostra spirally arranged on the aviculiferous suboral mucro.

Type locality. Westward from Urup Island, middle Kuril Islands, Sea of Okhotsk, 45°54.2′ N, 149°40.4′ E – 45°54.2′ N, 149°40.0′ E, depth 183–213 m.

Measurements. ZIRAS 1/50545, Urup Island, Kuril Islands, Sea of Okhotsk (Figs 22A–M, 30I). ZL, 0.93–1.78 (1.22 ± 0.20). ZW, 0.50–0.83 (0.66 ± 0.08). ZD, 0.51–0.74 (n = 2). OrL, 0.21–0.29 (0.24 ± 0.02). OrW, 0.26–0.35 (0.30 ± 0.02). OeL, 0.47–0.73 (0.58 ± 0.06). OeW, 0.37–0.55 (0.47 ± 0.05). Av(s)L, 0.35–0.64 (0.51 ± 0.08). Av(s)2L, 0.21–0.28 (0.24 ± 0.02) (n = 10). Av(s)3L, 0.19–0.25 (0.22 ± 0.02) (n = 10). Av(s)4L, 0.18–0.25 (0.21 ± 0.03) (n = 10). Av(s)5L, 0.14–0.18 (0.16 ± 0.02) (n = 6). Sp(or)L, 0.70–1.05 (0.89 ± 0.15) (n = 4). P(m)N, 18–31 (25). P(oe)N, 42–52 (43) (n = 7).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 22A), forming extensive muff-like encrustations on sponges, attaining 35 × 22 mm in size, partly developing small, free-growing frills, light-brown when dry. Zooids large, oblong-hexagonal to irregularly oval, tapering proximally, arranged in checkered pattern, demarcated by fine sutures between lateral and transverse walls; sutures less visible in older parts of colony (Fig. 22F).

Frontal shield umbonuloid (Fig. 22A, I), thin, flattened in young zooids, moderately convex in older zooids, with very fine surface granulation. Areolae circular to oval, separated by interareolar ridges; ridges elongate and reaching avicularian cystid in distal part of zooid, shorter proximally (Fig. 22A, D). Umbonuloid component extensive, occupying about 70% of length of frontal shield (76% in one measured zooid), with characteristic lineation and accretionary banding (Fig. 22I, J, L). Ring scar discrete (Fig. 22L).

Primary orifice submerged (Fig. 22A, C, J) broadly circular to oval; distal and lateral margins formed by upper part of distal transverse wall, with narrow or distinct shelf distally (Fig. 22A). Distal margin of orifice rounded, proximal margin straight, with low, very broad, median lyrula-like prominence and rounded proximolateral corners. No condyles.

Secondary orifice (Fig. 22B–D) transversely oval, cormidial; distolateral curvature restricted by proximal and lateral vertical walls of daughter and adjacent lateral zooids; proximolateral curvature represented by low peristome incorporating mucro with avicularia medially and forming two symmetrical, thin-walled lappets laterally. One or two pairs of elongate, tubular, basally articulated oral spines around distal curvature of orifice in non-ovicellate zooids (Fig. 22A–D); one pair of spines near proximolateral corners of ooecium in some ovicellate zooids (Fig. 22G–H). Spines long, fragile, easy detached, slightly tilted distally, with strong bases. Situated proximal to orifice, a conical to bulbous, aviculiferous mucro up to 1.34 mm tall; surface finely granular, with 6–9 scattered minute communication pores. Mucro incorporating 3–5 spirally arranged avicularia that decrease in size toward apex; main, most basal avicularium budding 2–4 smaller avicularia.

Cystid of main (basal) avicularium positioned symmetrically relative to proximal margin of zooidal orifice (Fig. 22A), frontal surface (rostral/postmandibular areas) facing distolaterally, crossing zooidal midline; rostrum elongate triangular to elongate oval, pointed, slightly narrowing in middle, with prominent hooked tip, directed distolaterally

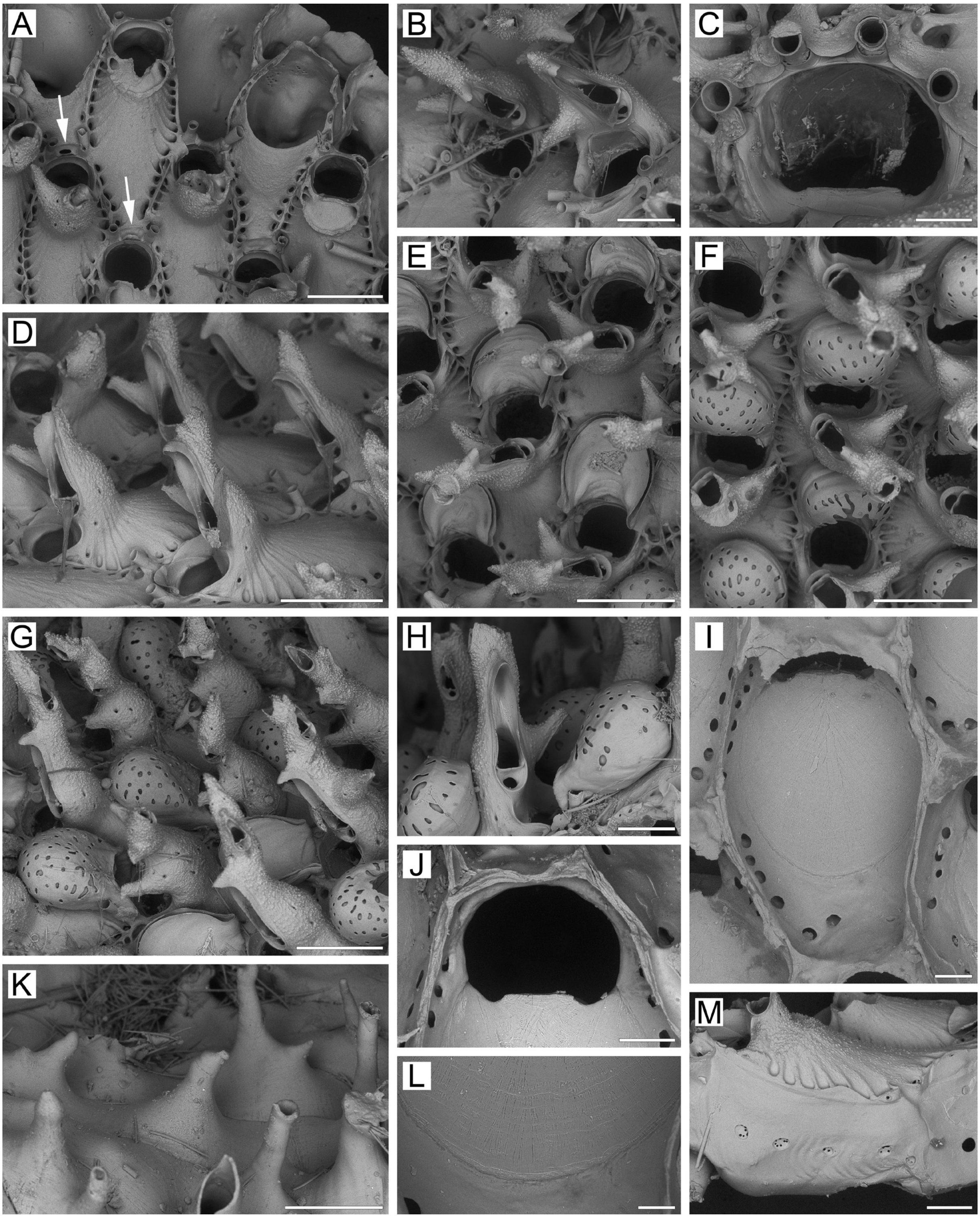

FIGURE 22. *Rhamphostomella multirostrata* **n. sp.** *Holotype*, ZIRAS 1/50545 (Urup Island, Kuril Islands, Sea of Okhotsk). A. Colony margin with developing zooids and main avicularian cystids (arrows, sites of ooecial development). B. Distal view of marginal zooids, showing details of orifice and suboral avicularia. C. Zooidal orifice with broad lyrula and bases of oral spines. D. Oblique view of several zooids, one showing early developmental stage of ooecium. E. Zooids with developing ooecia. F. Frontal view of ovicellate zooids. G. Lateral view of ovicellate zooids. H. Lateral view of distal half of ovicellate zooid. I. Interior of frontal shield, showing lyrula, umbonuloid component and areolae. J. Internal view of primary orifice. K. Basal surface of colony, showing protuberances. L. Interior of frontal shield, showing ring scar and external-wall microstructure of umbonuloid component. M. Lateral view of zooid, showing frontal shield with areolae and interareolar ridges, avicularium and lateral wall with mural pore chambers. Scale bars: A, D–F, G, K, 500 µm; B, H, 250 µm; C, I, J, 100 µm; L, 50 µm; M, 200 µm.

and frontally (Fig. 22B, D, G, H). Palatal foramen triangular, acute or rounded distally, cryptocystal shelf occupying one-third to half of rostrum; opesia oval or ellipsoid, bordered by cryptocyst. Crossbar complete, sometimes with small ligula. Mandible elongate triangular (Fig. 22D). Frontal surface of second suboral avicularium (Fig. 22B, D–H) facing distolaterally, obliquely downwards, rostrum acute, tip sometimes hooked; overall positioned at nearly right angle to rostrum of main avicularium, overhanging zooidal orifice; palatal foramen triangular, restricted distally by cryptocystal shelf; opesia oval or ellipsoidal, bordered by cryptocyst. Crossbar complete. Postmandibular area in main and second suboral avicularia located at more or less similar level relative to zooidal surface. Third and fourth avicularia, when present, almost identical in form and size to one another (Fig. 22G); situated higher, in different positions closer to apex of mucro; frontal surface facing laterally to proximolaterally, occasionally proximally or distolaterally. Rostrum elongate triangular, often with hooked tip, directed frontally or tilted slightly basally. Palatal foramen triangular, restricted distally by cryptocystal shelf; opesia circular, reduced to small, elongate pore, bordered by extensive cryptocyst (Fig. 22G). Crossbar complete, sometimes with small ligula. Fifth avicularium (when present) small, variable in shape (Fig. 22E–G), usually located on side of mucro, with frontal surface facing laterally, elongate triangular rostrum directed frontally; palate triangular. Crossbar complete. Sometimes avicularium located at apex of mucro and facing frontally, with nearly circular to oval rostrum and palate. While most zooids have first to third avicularia, fourth to fifth avicularia frequently absent, particularly in young zooids.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 22F–H); only basal part overgrown by secondary calcification in some instances (Fig. 22F). Ooecium formed by distal autozooid around small, shallow concavity with oval communication pore at bottom, situated in proximalmost part of frontal shield just immediate to distal margin of maternal orifice (Fig. 22A). Ooecium compressed proximally, with straight to slightly concave proximal margin. Ectooecium smooth, with numerous circular, oval to slit-like pseudopores.

Zooids interconnected by 4–5 mural pore chambers (Fig. 22M) in each distolateral wall and two multiporous septula (sometimes with individual pores in between) in basal half of transverse walls (Fig. 22A). In some zooids, transverse walls distally with two recesses separated by medial buttress.

Basal surface of zooids (Figs 22K, 30I) fully calcified, convex, smooth, thin, with numerous tubular protuberances (0.09–0.25 mm in diameter), surface covered with fine, parallel to centripetal lineation. Numerous white spots (presumably less-calcified areas) visible in semitransparent basal wall by light microscopy. Boundaries between zooids recognizable basally by fine sutures.

Ancestrula and early astogeny not observed.

Remarks. The presence of large a suboral mucro bearing 3–5 avicularia distinguishes *R. multirostrata* **n. sp.** from all congeners, making it a unique member of the genus. The suboral aviculiferous mucro and highly pseudoporous ooecium closely resemble similar structures in the lepralioid-shielded genus *Bitectipora* (Gordon 1994). *Bitectipora* species lack a lyrula, having instead a sinusoidal orifice.

Ecology. *Rhamphostomella multirostrata* **n. sp.** was collected from depths of 183–567 m, encrusting glass sponges on gravelly bottoms.

Distribution. Presently known from the Pacific and Sea of Okhotsk coasts of the middle Kuril Islands (Chiproy to Urup), *R. multrostrata* **n. sp.** is a Pacific Asian high-boreal, sublittoral to upper bathyal species.

Rhamphostomella spinigera **Lorenz, 1886**

(Figs 23, 25C, 33E, F)

Cellepora plicata: Smitt 1868a, p. 30, 31 (part), pl. 28, fig. 192.
Rhamphostomella spinigera Lorenz, 1886, p. 12.
Rhamphostomella spinigera: Nordgaard 1906, p. 32, 41, pl. 4, figs 52–55; Osburn 1952, p. 429, pl. 51, fig. 1; Kluge 1962, p. 542, fig. 379; 1975, p. 659, fig. 379; Hayami 1970, p. 332, pl. 36, fig. 11; 1975, p. 89, pl. 17, fig. 2; Gostilovskaya 1978, p. 228, fig. 144.
Rhamphostomella plicata: Waters 1900, p. 92, pl. 11, figs 28, 29; Nordgaard 1905, p. 171, pl. 5, figs 14, 15.

Additional references. *Rhamphostomella spinigera*: Kluge 1906, p. 46; 1907, p. 196; 1908b, p. 553; 1915, p. 386; 1964, p. 190; Osburn 1936, p. 542; 1955, p. 38; Gostilovskaya 1957, p. 455; 1964, p. 219; Hansen 1962, p. 42; Sakagami *et al*. 1980, p. 330; Denisenko 1988, p. 13; 1990, p. 39; 2013, p. 184; Gontar & Denisenko 1989, p. 359; Grischenko 1997, p. 174; 2002, p. 115; 2003b, p. 237; Gontar *et al*. 2001, p. 195; Shunatova & Ostrovsky 2001, p. 118; Kuklinski 2002b, p. 203; Foster 2010, p. 57; Gontar 2010, p. 153.

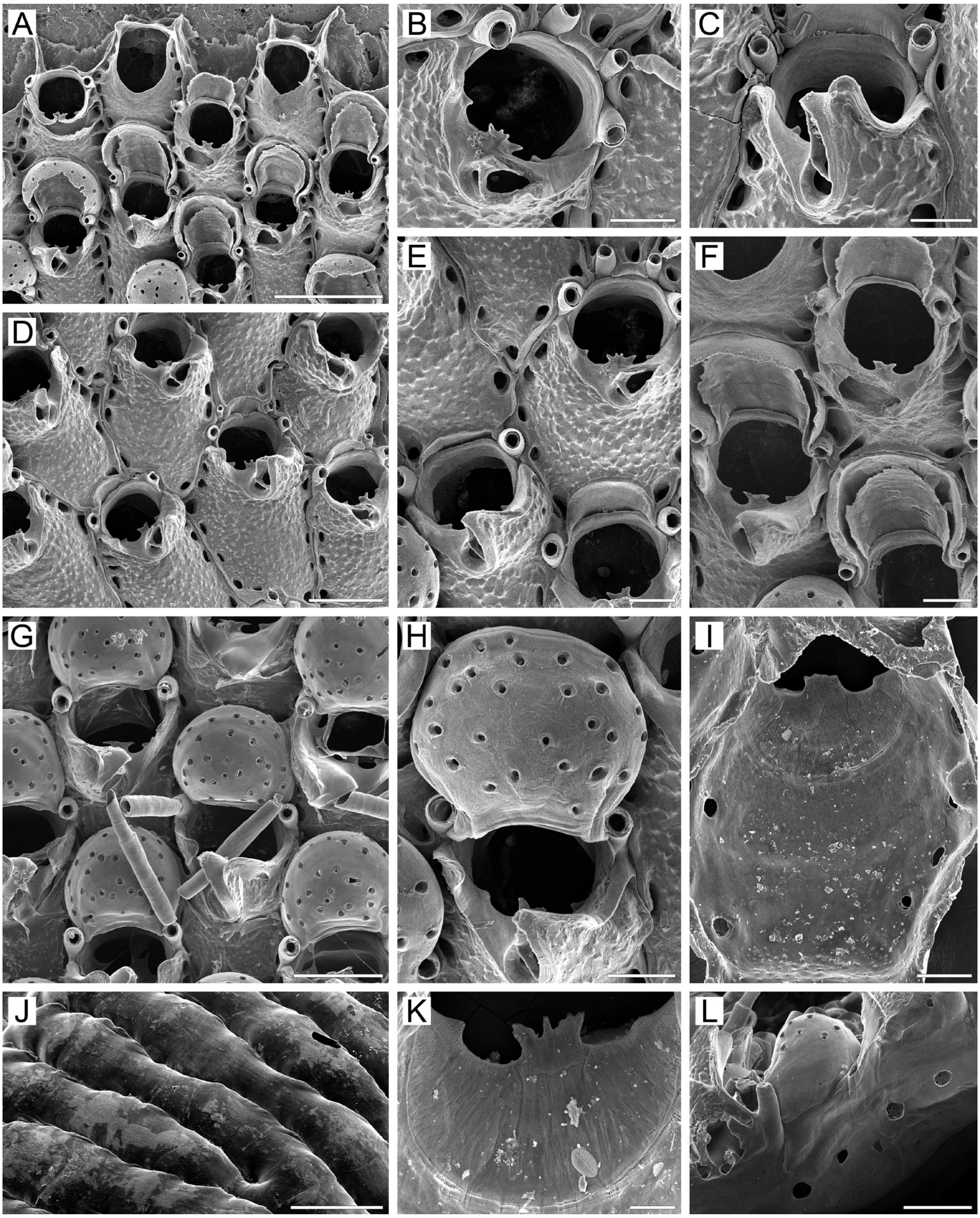

FIGURE 23. *Rhamphostomella spinigera* Lorenz, 1886. A–F, H, I, L. ZIRAS 26/50112 (Medny Island, Commander Islands, Bering Sea). G, J, K. ZIRAS 25/50111 (Bering Island, Commander Islands, Pacific Ocean). A. Colony margin with developing zooids, suboral avicularia and ooecia. B. Orifice with two pairs of oral spines, showing lyrula, lateral denticles and suboral avicularium. C. Zooidal orifice with developing ooecium (partially seen), one pair of oral spines and suboral avicularium. D. Non-ovicellate autozooids (number of oral spines varies from two to four). E. Non-ovicellate zooid (upper right corner) and two zooids with partially developed ooecia, possibly "aborted". F. Zooids with developing ooecia. G. Ovicellate zooids, some with detached articulated oral spines (colony partially cleaned). H. Frontal view of distal part of ovicellate zooid. I. Interior of frontal shield, showing umbo, ring scar and areolae. J. Basal surface of colony. K. Interior of frontal shield, showing ring scar around exterior-wall microstructure of umbonuloid component, and lyrula with lateral denticles. L. Lateral view of zooid, showing ooecium, oral spines, peristomial lappet and lateral wall with mural pore chambers. Scale bars: A, J, 500 µm; B, C, E, F, H, I, 100 µm; D, G, 250 µm; K, 50 µm; L, 200 µm.

Material examined. *Lectotype*: NHMW 92535 (=1884.II.51), single colony encrusting shell of *Chlamys islandica*, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 160–180 m, collector F. Fischer. *Paralectotype*: NHMW 92536 (=1884.II.51), single colony encrusting shell of *Chlamys islandica*, L. Lorenz Collection, II Austro-Hungarian Polar Expedition, 1882–1883, Jan Mayen, depth 160–180 m, collector F. Fischer.

NHMUK (1911.10.1.1585 NHML), two colonies, ex Vienna Museum Natural History Collection, from L. Lorenz, A.M. Norman Collection, Jan Mayen. SMNH-131116, one colony, Swedish Arctic Expedition, 1858, west Spitsbergen, Svalbard and Jan Mayen. ZIRAS 25/50111, one colony, KIENM Collection, Stn 208, 22 July 1991, Podutesnaya Bight, coastal waters of Bering Island, Commander Islands, Pacific Ocean, 55°01.3′ N, 166°06.2′ E, depth 20 m, SCUBA, collector V.V. Oshurkov. ZIRAS 26/50112, one colony encrusting bivalve shell of *Hiatella arctica*, KIENM Collection, Stn 91, 16 July 1992, Korabelnaya Bight, coastal waters of Medny Island, Commander Islands, Bering Sea, 54°41.4′ N, 167°47.2′ E, depth 15 m, SCUBA, collector V.I. Shalukhanov. NHMUK 2013.10.21.7b, one colony encrusting oyster shell, RV *Norseman*, Stn AST–2, 16 July 2011, reef in middle of Boot Bay, coastal waters of Adak Island, Andreanof Islands, Aleutian Islands, Pacific Ocean, 51°44.4′ N, 176°30.3′ W, depth 10–12 m, SCUBA, collector P. Kuklinski.

Additional material. 131 specimens. KIENM Collection (1991) Stns 186, 210, 225; (1992) Stns 4, 5, 37, 38, 39, 54, 58, 64, 88, 89, 90, 91, 97, 98, 99, 126, 127, 135, 136, 137, 142, 143, 145, 147, 150, 151; PIBOC Collection (1991) Stns 17, 20; A.V. Grischenko Collection (1991) Stn 17 (see Appendix 1 for details).

Measurements. ZIRAS 26/50112, Medny Island, Commander Islands, Bering Sea (Fig. 23A–F, H, I, L). ZL, 0.52–0.88 (0.67 ± 0.09). ZW, 0.33–0.48 (0.39 ± 0.04). ZD, 0.34–0.40 (n = 2). OrL, 0.12–0.20 (0.16 ± 0.02). OrW, 0.15–0.21 (0.19 ± 0.02). OeL, 0.20–0.33 (0.27 ± 0.04). OeW, 0.30–0.40 (0.35 ± 0.03). Av(s)L, 0.08–0.25 (0.16 ± 0.04). Sp(or)L, 0.24–0.90 (0.51 ± 0.17) (n = 20). P(m)N, 9–13 (10). P(oe)N, 21–29 (25) (n = 10).

NHMUK 2013.10.21.7b, Adak Island, Aleutian Islands, Pacific Ocean. ZL, 0.37–0.72 (0.52 ± 0.07). ZW, 0.20–0.43 (0.33 ± 0.05). ZD, 0.32–0.38 (n = 2). OrL, 0.14–0.20 (0.16 ± 0.01). OrW, 0.14–0.23 (0.19 ± 0.02). OeL, 0.20–0.48 (0.25 ± 0.05) (n = 23). OeW, 0.22–0.56 (0.30 ± 0.06) (n = 25). Av(s)L, 0.11–0.36 (0.18 ± 0.06). Sp(or)L, 0.05–0.10 (0.08 ± 0.01) (n = 16). P(m)N, 6–15 (10) (n = 15). P(oe)N, 12–27 (24) (n = 12).

NHMW 1884.II.51, Jan Mayen (Fig. 25C). AnL, 0.44 (n = 1). AnW, 0.34 (n = 1). AnOpL, 0.30 (n = 1). AnOpW, 0.24 (n = 1).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 23A), small, more or less circular, attaining 11 mm in maximal dimension, red to bright brown when alive, light brown to pale-yellow when dry. Zooids medium-sized, hexagonal to oval, arranged in quincunx, demarcated by fine sutures between transverse and lateral walls; sutures less visible in older colony parts.

Frontal shield umbonuloid (Fig. 23B, I), thin, moderately convex, covered with small pointed tubercles giving reticulate appearance to zooids. Oval and round areolae along zooidal margins separated by low, short interareolar ridges in distal half of marginal zooids (Fig. 23A); these ridges absent or strongly reduced in older parts of colony (Fig. 23D, E). Interior of frontal shield (Fig. 23I) shows relatively small umbonuloid component, occupying about 30% of length of frontal shield (31% in one measured zooid). Ring scar (Fig. 23K) discrete.

Primary orifice (Fig. 23B, C, E) irregularly quadrangular to transversely oval, with gently straight sides and broadly rounded angles; its distal and lateral margins formed by upper part of distal transverse wall (Fig. 23A, E, F). Distal margin of orifice almost straight or shallow rounded, proximal margin bisinuate, with prominent, median lyrula, normally bifurcate, but sometimes trifid or with four tips. Two triangular acute processes lateral to lyrula. Condyles absent. Four articulated oral spines, medial two of smaller diameter, located around distal curvature of orifice in non-ovicellate zooids (Fig. 23B, E). Normally only two lateral spines found in ovicellate zooids, adjoining proximolateral corners of ooecia (Fig. 23F–H); 3–4 spines can be seen in some zooids with developing ooecia (Fig. 23D). Oral spines usually short in young zooids, and strongly elongated and thicker in older zooids.

Secondary orifice transversely oval, cormidial (Fig. 23B–H); its distolateral curvature slightly above primary orifice, being formed by upper terminal part of distal transverse wall (Fig. 23B); laterally and proximally it is constructed by thin-walled low peristome consisting of two roundly triangular flared lappets, one incorporating cystid of suboral avicularium and forming broad, deep U-shaped, asymmetrically placed pseudosinus in secondary orifice (Fig. 23G); distally, lappets mounted to lateral walls of distolateral zooids, not fused with proximolateral corners of ooecia in ovicellate zooids (Fig. 23B–H).

Cystid of suboral avicularium (Fig. 23A, F) small, strongly elevated, with dimpled surface and single communication pore, asymmetrically situated on left or right near orifice margin. Frontal surface (rostral/postmandibular areas) slightly concave (Fig. 23B, C), crossing zooidal midline, facing proximolaterally. Rostrum oblong oval, tapering distally, or triangular, pointed, occasionally hooked terminally, directed ditstolaterally and frontalwards. Palate semielliptical to triangular, with rounded distal end; foramen triangular with acute tip; opesia semicircular. Crossbar complete.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 23F–H, L), ooecium not overgrown by secondary calcification. Ooecium formed by distal autozooid; ooecial fold developing at colony periphery concurrently with formation of frontal shield of distal zooid (Fig. 23A). Ooecium narrowing at proximolateral corners, with straight or weakly concave proximal margin that may have several minor wrinkles. Ectooecium with scattered small circular pseudopores.

Zooids interconnected by two mural pore chambers (Fig. 23L) in each distolateral wall. Communication pores spread through basal part of transverse walls either as horizontal "band" or form two multiporous septula.

Basal surface of zooids (Fig. 23J) fully calcified, smooth, inflated, lacking white spots and protuberances. Boundaries between zooids indicated basally by deep undulating grooves laterally and indistinct sutures transversely.

Ancestrula tatiform (Fig. 25C), longitudinally oval, with fully calcified basal wall. Opesia longitudinally oval, with eight periopesial spines evenly distributed around opesial margin. Ancestrula budding triplet of periancestrular zooids distally and distolaterally (right zooid undeveloped); periancestrular zooids similar to but smaller than subsequent zooids, bearing four hollow articulated oral spines around distal curvature of orifice.

Remarks. In the constant presence of long oral spines *R*. *spinigera* resembles *R*. *echinata* **n. sp.**, but differs in having the frontal shield tuberculate vs tessellated in the latter.

Ecology. *Rhamphostomella spinigera* has been recorded from 7–234 m depth on hard bottoms such as rock faces (including crevices), boulders and blocks, encrusting shells of bivalve molluscs (*Hiatella arctica*, *Monia macrochisma*, etc.), gastropods (*Cryptonatica jantostoma*, and others), barnacles, tubes of serpulid and spirorbid polychaetes, bryozoans (*Myriapora orientalis*, lichenoporid cyclostomes) and calcareous red algae (*Lithothamnion* sp.). It is also known as a component of the cryptic community met in the cavities formed by the crustose coralline red alga *Clathromorphum nereostratum* and has been found on the brown alga *Agarum clathratus*.

Kluge (1962, 1975) noted that colonies of *R*. *spinigera* loosely overgrow the substratum. In contrast, we observed colonies of this species tightly attached to various substrates.

Distribution. This is a high-boreal-Arctic, sublittoral species. Numerous Arctic records were summarized by Kluge (1962, 1975) and Gontar & Denisenko (1989). In the Arctic it has been reported from the Barents Sea (Bidenkap 1900a; Waters 1900; Nordgaard 1905; Kluge 1906, 1962, 1975; Kuznetsov 1941; Denisenko 1988, 1990), White Sea (Kluge 1907; Gostilovskaya 1957, 1978; Shunatova & Ostrovsky 2001), Kara Sea (Nordgaard 1912; Kluge 1962, 1975; Denisenko 2021), Laptev Sea (Gontar & Denisenko 1989), Chukchi Sea (Gontar 2010), Point Barrow, Alaska, Beaufort Sea (Osburn 1952, 1955), Canadian Arctic Archipelago (Nordgaard 1906; Osburn 1932, 1936), Baffin Bay (Hansen 1962), Davis Strait (Kluge 1962, 1975; Hansen 1962), Labrador (Gontar & Denisenko 1989), western Greenland (Henning 1896; Kluge 1908b; Osburn 1936; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1916; Denisenko & Blicher 2021), Greenland Sea (Gontar & Denisenko 1989), Jan Mayen Island (Lorenz 1886), Norwegian Sea (Gontar & Denisenko 1989), Franz Josef Land (Denisenko 1990) and Spitsbergen (Gontar et *al*. 2001; Kuklinski 2002b). In the northwestern Pacific it has been documented in the Bering Sea from the shelf of the Commander Islands (Grischenko 1997, 2002, 2003b; our data). Northeastern Pacific localities include Canoe Bay (Osburn 1952), Cook Inlet (Foster 2010) and Kodiak Island, Gulf of Alaska (our data).

R. *spinigera* has also been reported from Miocene and Neogene deposits in northern Japan (Hayami 1970, 1975).

Rhamphostomella echinata n. sp.

(Fig. 24)

Rhamphostomella sp.: Grischenko 1997, p. 176; 2002, p. 115.

Diagnosis. Colony encrusting, multiserial. Zooids small, hexagonal. Frontal shield moderately convex, uniformly tessellated, with a few marginal areolae. No interareolar ridges. Umbonuloid component small. Suboral mucro absent. Primary orifice irregularly oval to quadrangular; proximal margin bisinuate, with median bifurcated to multiply branched lyrula and small, lateral, triangular processes. Condyles absent. Secondary orifice irregularly oval, cormidial, just slightly above primary orifice. 2–3 pairs of very long tubular, articulated oral spines with massive bases on lateral margins of secondary orifice, conferring spinose appearance to colony. Suboral avicularian cystid very small, with finely dimpled surface. Rostrum short, oval, slightly elevated. Mandible spatulate, with rounded distal end. Crossbar incomplete. No adventitious avicularia. Ovicell hyperstomial. Ectooecium with small scattered pseudopores, no secondary calcification. 2–3 pore chambers in distolateral wall, and 1–2 multiporous septula in transverse walls. Basal surface of zooids fully calcified, with tubular protuberances.

Material examined. *Holotype*: ZIRAS 1/50126, one colony fragment, IMB Collection, Stn 158/393, 18 September 1973, Kitolovnaya Bank, Medny Island, coastal waters of Medny Island, Commander Islands, Bering Sea, 55°02.2′ N, 167°10.9′ E, depth 60 m, rock dredge, collector S.D. Vavilin. *Paratype*: NHMUK 2013.10.21.3, one colony encrusting oyster shell, RV *Norseman*, Stn LT–2, 3 July 2011, Longshot, East of Square Bay, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°26.6′ N, 179°12.2′ E, depth 10 m, SCUBA, collector P. Kuklinski.

NHMUK 2013.10.21.4, one colony, RV *Norseman*, Stn LT–1, 4 July 2011, Longshot, South of Crown Reefer Point, coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands, Bering Sea, 51°27.3′ N, 179°11.4′ E, depth 13 m, SCUBA, collector P. Kuklinski.

Additional material. 14 specimens. IMB Collection (1973) Stns 108/284, 150/385, 151/386, 160/395, 173/408; KIENM Collection (1992) Stns 5, 39, 140 (see Appendix 1 for details).

Etymology. The specific name *echinata* alludes to the spinose appearance of the colony, with numerous oral spines.

Type locality. Kitolovnaya Bank, coastal waters of Medny Island, Commander Islands, Bering Sea, 55°02.2′ N, 167°10.9′ E, depth 60 m.

Measurements. ZIRAS 1/50126, Medny Island, Commander Islands, Bering Sea (Fig. 24A–L). ZL, 0.52–0.78 (0.64 ± 0.06). ZW, 0.32–0.45 (0.39 ± 0.04). ZD, 0.28–0.35 (*n* = 2). OrL, 0.18–0.25 (0.23 ± 0.02). OrW, 0.20–0.25 (0.22 ± 0.02). OeL, 0.27–0.33 (0.30 ± 0.02) (*n* = 20). OeW, 0.27–0.33 (0.31 ± 0.02) (*n* = 20). Av(s)L, 0.06–0.11 (0.08 ± 0.01) (*n* = 20). Sp(or)L, 0.39–1.05 (0.77 ± 0.14). P(m)N, 5–10 (7) (*n* = 12). P(oe)N, 18–22 (20) (*n* = 5).

NHMUK 2013.10.21.3, Amchitka Island, Aleutian Islands, Bering Sea. ZL, 0.49–0.80 (0.61 ± 0.07). ZW, 0.25–0.48 (0.35 ± 0.05). ZD, 0.27–0.32 (*n* = 2). OrL, 0.18–0.27 (0.23 ± 0.02). OrW, 0.18–0.27 (0.22 ± 0.02). OeL, 0.21–0.31 (0.26 ± 0.02). OeW, 0.21–0.35 (0.31 ± 0.03). Av(s)L, 0.05–0.10 (0.08 ± 0.01). Sp(or)L, 0.16–0.69 (0.37 ± 0.11). P(m)N, 3–8 (6) (*n* = 20). P(oe)N, 6–21 (15).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 24A), irregular in form, small, attaining 5 mm in maximal dimension, bright brown when alive, light brown or pink when dry. Zooids small, oval, rectangular or hexagonal, arranged in checkered pattern, demarcated by fine undulating sutures between lateral and transverse walls; sutures recognisable in all parts of colony.

Frontal shield moderately convex in distal half, flattened proximally, uniformly tessellated, with a few circular to oval areolae along zooidal margins. Interareolar ridges absent. Interior of frontal shield (Fig. 24I) with thin discrete ring scar (Fig. 24K). Umbonuloid component small, occupying 15–26% of length of frontal shield.

Primary orifice (Fig. 24A, C, D) irregularly oval to quadrangular with broadly rounded angles; distal and lateral margins formed by upper part of distal transverse wall. Distal wall of orifice shallowly rounded or nearly straight, proximal margin bisinuate, with prominent, median, bifurcate, trifid or multiply branched lyrula and small, lateral, triangular processes, often looking like acute spinules, 1–4 in number on each side (Fig. 24A, B). Condyles absent.

Secondary orifice (Fig. 24D–H) irregularly oval to quadrangular, cormidial; distolateral curvature just slightly above primary orifice, formed by upper terminal part of distal transverse wall (Fig. 24C, D); proximally restricted by asymmetrically placed cystid of suboral avicularium. Usually, two or three pairs of tubular, articulated oral spines along lateral margins of secondary orifice, two (less frequently three) pairs in ovicellate zooids (Fig. 24A–H); spines very long, sometimes exceeding length of zooid, with thick bases, weakly bent (Fig. 24E, F), giving distinctive spinose appearance to colony.

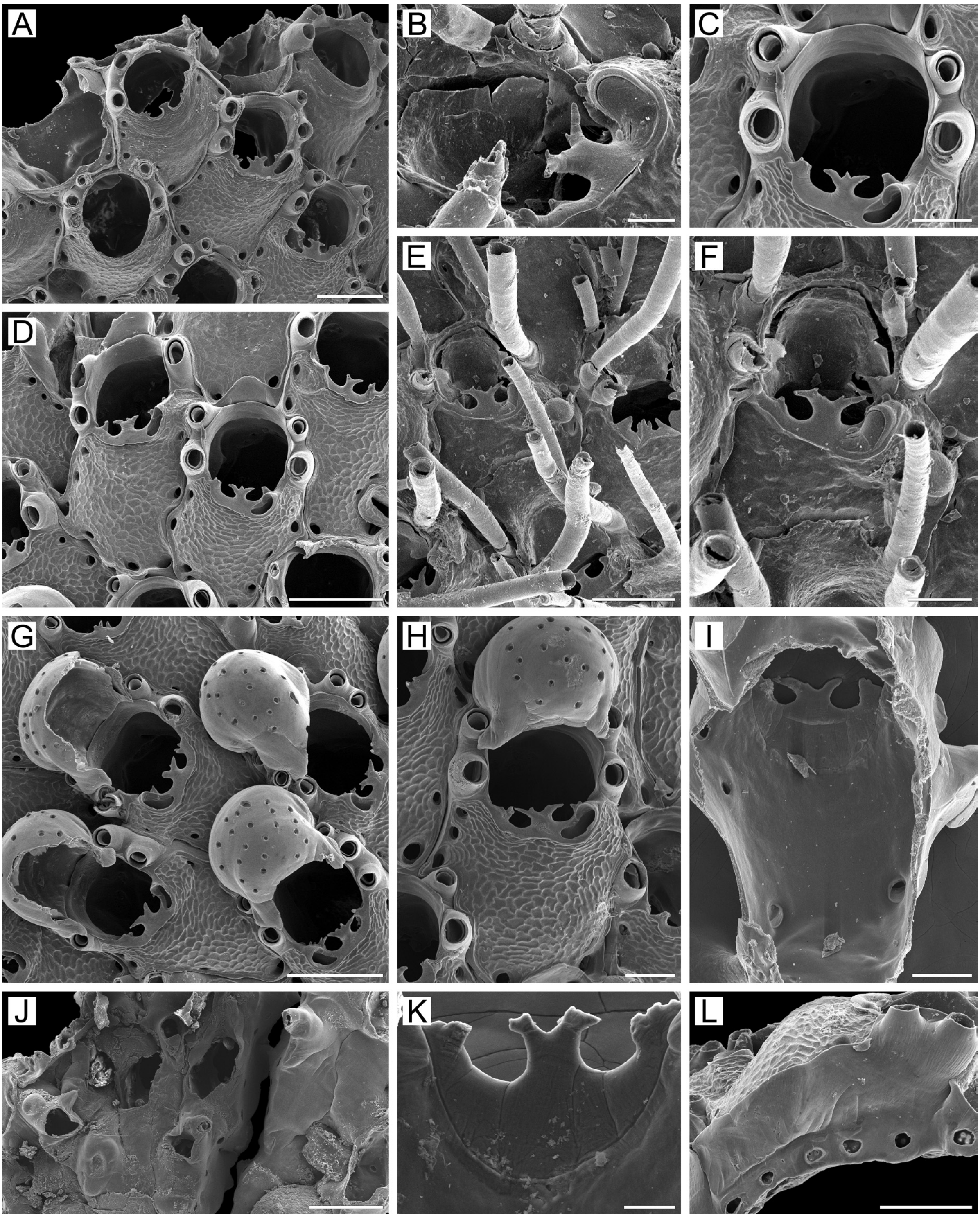

FIGURE 24. *Rhamphostomella echinata* **n. sp.** *Holotype*, ZIRAS 1/50126 (Medny Island, Commander Islands, Bering Sea). A. Colony margin with developing and fully formed young zooids. B. Lateral view of orifice, showing branching lyrula, four spinules, suboral avicularium and bases of oral spines; non-bleached colony. C. Orifice of non-ovicellate zooid showing lyrula, lateral denticles and bases of oral spines. D. Group of non-ovicellate zooids, showing dimpled frontal shields and early stages of ooecial formation. E. Non-ovicellate zooids with long oral spines; unbleached colony. F. Close-up of non-ovicellate zooid, unbleached. G. Group of zooids with broken and completed ooecia. H. Single ovicellate zooid, showing details of orifice, spine bases and ooecium. I. Interior of frontal shield, showing lyrula, lateral denticles, umbo, ring scar and areolae. J. Basal surface of colony, showing protuberances. K. Interior of frontal shield, showing ring scar and umbonuloid component with lyrula and lateral denticles. L. Lateral view of zooid, showing frontal shield, oral spines and lateral wall with mural pore chambers. Scale bars: A, D, E, G, 250 µm; B, K, 50 µm; C, F, H, I, 100 µm; J, 500 µm; L, 200 µm.

Cystid of suboral avicularium (Fig. 24B–D, F–H) very small, flattened, surface finely dimpled, with single minute communication pore situated proximally, on left or right side relative to orifice. Frontal surface (rostral/postmandibular areas) of avicularium curved to one side, out of zooidal midline, facing obliquely proximolaterally. Rostrum short, oval, slightly elevated, directed distolaterally and frontally. Mandible spatulate, with rounded distal end (Fig. 24B, F), palate of similar shape, forming blunt angle with postmandibular area; opesia semioval. Crossbar incomplete, visible as two indictinst denticles.

No adventitious avicularia.

Ovicells hyperstomial (Fig. 24G, H), ooecium not overgrown by secondary calcification. Ooecium formed by distal autozooid, ooecial fold developing at colony periphery, concurrently with frontal shield of distal zooid (Fig. 24D). Ooecium flattened laterally, proximal margin weakly concave with minor wrinkles. Ectooecium with numerous small, circular uniformly scattered pseudopores. Bases of distalmost oral spines appressed to sides of ooecium.

Zooids interconnected by 2–3 mural pore chambers (Fig. 24L) in each distolateral wall and 1–2 multiporous septula (sometimes with individual pores in between) or line of individual pores in basal half of transverse walls.

Basal surface of zooids (Fig. 24J) fully calcified, flattened to moderately convex, with long, tubular protuberances (up to 0.24 mm long, 0.11–0.27 mm in diameter) (Fig. 24J). Boundaries between zooids indicated basally by irregular undulation and sutures.

Ancestrula and early astogeny not observed.

Remarks. *Rhamphostomella echinata* **n. sp.** clearly differs from congeners in the following combination of characters: 1) small zooid size; 2) two or three pairs of very long, basally articulated oral spines, frequently exceeding zooid length and conferring a distinctive spiny appearance to the colony; 3) wide, massive spine bases; 4) a bisinuate proximal orificial margin, with a bifurcate or multi-pronged median process and irregular lateral processes; and 5) a very small, frontally curved suboral avicularium.

Rhamphostomella spinigera has a generally similar proximal margin of the primary orifice and distolateral oral spines with large bases, but in *R. spinigera*, the spines are straight and situated along the distal curvature of the orifice, whereas in *R. echinata* **n. sp.** they are slightly curved, and their bases are arranged laterally along the orifice. Among other differences, the frontal shield is tuberculate in *R. spinigera* but tesselated in *R. echinata* **n. sp.**, and the suboral avicularium differ in morphology between the two species.

Ecology. This species has been collected from from depths of 10–100 m on hard bottoms, including rock, boulders and pebbles. Colonies encrust serpulid tubes, oyster shells, hydroid stolons, articulated red algae, other bryozoans (*Tricellaria beringia* and lichenoporid cyclostomes) and crab carapaces.

Distribution. Based on known records, which include several localities from the shelf zone of the Commander Islands (Grischenko 1997, 2002; and our data) and Beringian coastal waters of Amchitka Island, Rat Islands, and the western Aleutian Islands, *R. echinata* **n. sp.** is a Pacific high-boreal, sublittoral species.

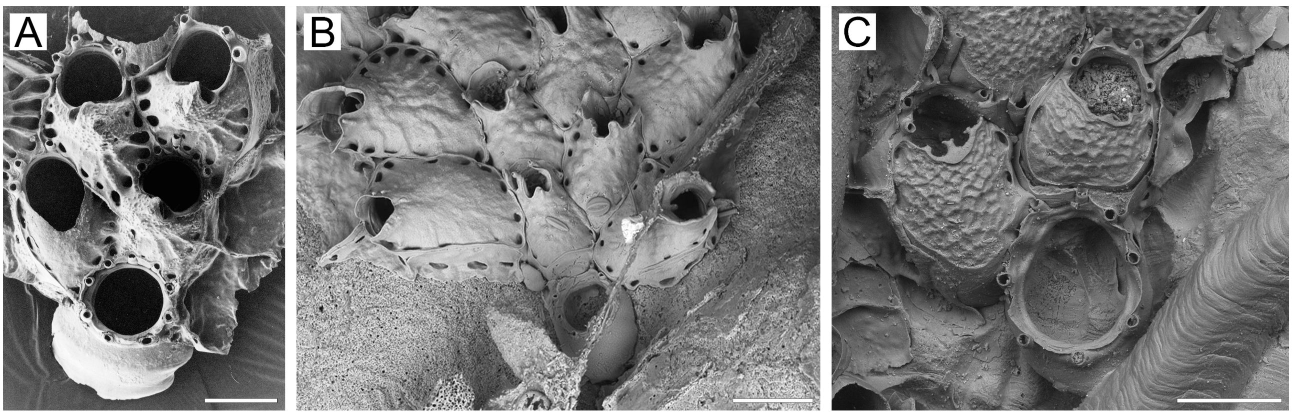

FIGURE 25. Ancestrulae with periancestrular zooids in colonies of three *Rhamphostomella* species. A. *R. scabra*, A.V. Grischenko Collection (western Kamchatka shelf, Sea of Okhotsk). B. *R. sibirica*, P. Kuklinski Collection (Beringian coastal waters of Amchitka Island, Rat Islands, western Aleutian Islands). C. *R. spinigera*, *Paralectotype*, NHMW 92536 (Jan Mayen), initial part of colony. Scale bars: 250 µm.

***Rhamphostomella*? *peristomata* Gontar, 1993**
(Fig. 26)

Rhamphostomella peristomata Gontar, 1993a, p. 12, fig. 5.

Material examined. *Holotype*: ZIRAS 1/44568, colony encrusting shell, 26 August 1969, off Cape Levashov, Paramushir Island, northern Kuril Islands, Pacific Ocean, depth 32 m, SCUBA, collector A.N. Golikov.

Remarks. Gontar (1993a) described *Rhamphostomella peristomata* from Paramushir Island, northern Kuril Islands. She mentioned a finely granulated to "fine-meshed" pattern on the frontal wall; a rounded primary orifice with a medium-sized lyrula on the proximal border; an irregularly oval peristomial secondary orifice; and a small avicularium with rounded mandible "between the primary and secondary orifices close to proximal border of the first one, somewhat to the right or left of the center of this border" (see Gontar 1993a, p. 12, fig. 5). Ovicells were absent in Gontar's specimen.

SEM examination of the holotype colony (Fig. 26) revealed that this specimen has: 1) a non-cormidial secondary orifice in a low tubular peristome formed entirely by elevation of the frontal wall of the maternal zooid and lacking sutures (both external and internal); 2) a well-developed distal zooidal wall, forming the distal part of peristome with the distal orifical margin separated from the distal zooidal margin by a distance of half to one-quarter orifice length, and 3) 2–5 areolae (often small) along the distal margin of the zooid.

This set of characters is atypical for *Rhamphostomella*. No other species in the genus has a subterminal orifice, with areolae extending around the distal zooidal margin. Accordingly, *R. peristomata* is here only tentatively attributed to this genus, pending further data on morphology and genetics.

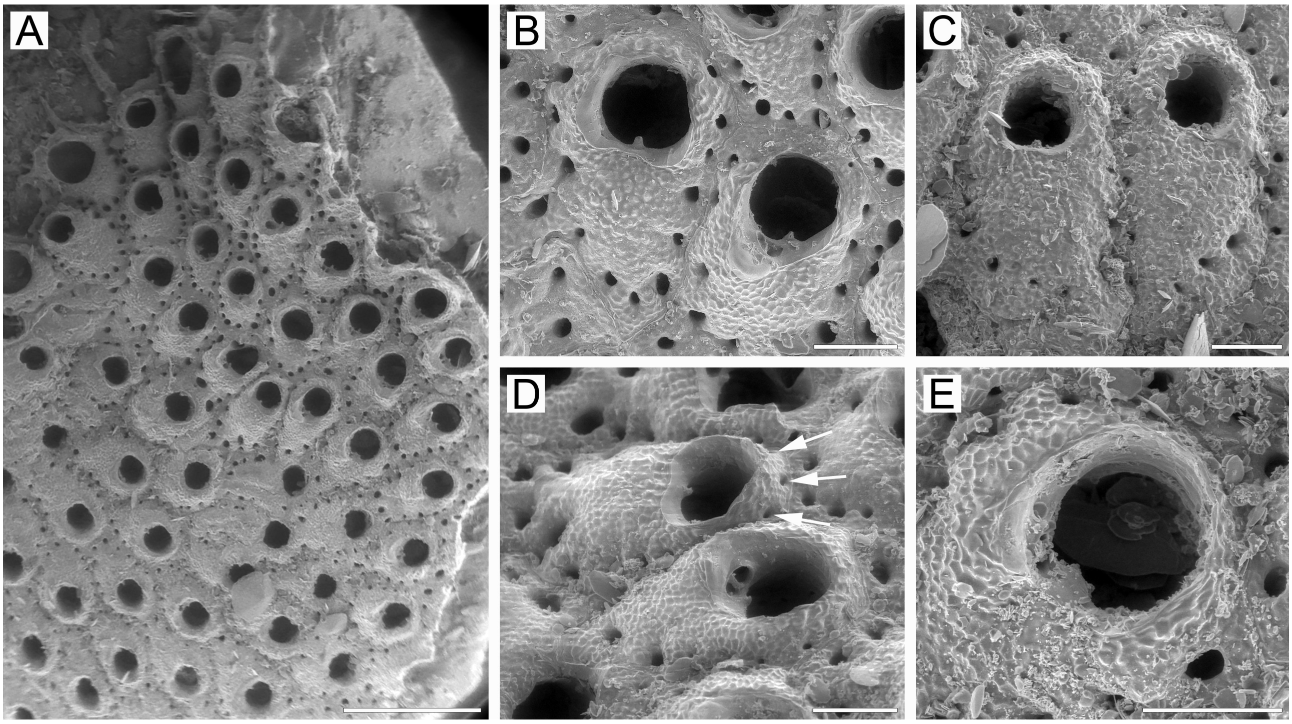

FIGURE 26. *Rhamphostomella*? *peristomata* Gontar, 1993. ZIRAS 1/44568 (Paramushir Island, Kuril Islands, Pacific Ocean). A. General view of part of holotype colony. B, C. Frontal view of two autozooids, showing orifices with median lyrula, and small avicularium on internal proximolateral surface of one peristome. D. Lateral view of two zooids, showing enlarged distal area of frontal wall with series of marginal areolar pores (arrows) and small peristomial avicularium. E. Distal half of autozooid, showing circular secondary orifice and lyrula. Scale bars: A, 1 mm; D–E, 200 µm.

Genus *Mixtoscutella* n. gen.

Type species: *Cellepora ovata* Smitt, 1868, by original designation.

Diagnosis. Colony encrusting, multiserial, unilaminar. Frontal shield mixed, comprising a much-reduced umbonuloid area beneath suboral avicularium, corresponding externally to suboral avicularium, and extensive, uniformly pseudoporous lepralioid area. Primary orifice with or without lyrula, with condyles. Secondary orifice cormidial, with very low peristome. Suboral adventitious avicularium always present. Large adventitious avicularia present in some species. Ovicell hyperstomial, often becoming less prominent due to secondary calcification overgrowing ooecium; with pseudopores. Mural pore chambers and multiporous septula present. Basal wall fully calcified, without protuberances.

Etymology. The name refers to the mixed nature of the frontal shield.

Species included. *Mixtoscutella ovata* (Smitt, 1868a), *M. ussowi* (Kluge, 1908a), *M. cancellata* (Smitt, 1868a), *M. harmsworthi* (Waters, 1900), and *M. androsovae* (Gontar, 1979).

Remarks. Apart from two species examined in detail (*M. ovata* and *M. ussowi*) and transferred from *Rhamphostomella* (Figs 27, 28), we illustrate here three other taxa, including two little-known species (Fig. 29), that display a combination of characters (mixed frontal shield and suboral avicularium) warranting their placement in *Mixtoscutella*.

Mixtoscutella androsovae (Gontar, 1979) [= *Smittina androsovae* Gontar, 1979 (p. 244, fig. 4)] is known only from its type locality at Cape Nerpochka on the Pacific side of Simushir Island, middle Kuril Islands, from 30 m depth (paratype, ZIRAS 2/43716) (Fig. 29A–C).

The high-boreal-Arctic species, *M. harmsworthi* (Waters, 1900) [= *Schizoporella harmsworthi* Waters, 1900 (p. 65, pl. 9, figs 10–12)], widely distributed in Arctic seas (see Kluge 1962 for details) has been detected in Avacha Gulf, eastern Kamchatka (ZIRAS 52/50568, KIENM Collection, RV *Nazarovsk*, Stn 141, 11 May 1988, 53°41.0′ N, 160°04.0′ E, depth 75 m) (Fig. 29D–F).

The rarely reported *M. cancellata* (Smitt, 1868) [=*Escharella porifera* forma *cancellata* Smitt, 1868a (p. 9, 75, pl. 24, figs 40, 41)], originally described from Spitsbergen (see also Nordgaard 1906; Kluge 1962; Kuklinski 2002b), has been documented from Point Barrow, Alaska (Osburn 1953) and the Chukchi Sea (Gontar 2010), and was recently found on the western slope of the Kamchatka Peninsula, Sea of Okhotsk (ZIRAS 1/50572, KIENM Collection, RV *Agat*, Stn 1–K–1, 1 June 2008, 58°00.0′ N, 155°43.0′ E, depth 285 m) (Fig. 29G–I).

Mixtoscutella ovata **(Smitt, 1868)**

(Figs 27, 33G)

Cellepora ovata Smitt, 1868a, p. 31, pl. 28, fig. 197.
Cellepora ovata: Smitt 1868b, p. 485; Hincks 1877, p. 105, pl. 11, fig. 5.
Rhamphostomella ovata: Nordgaard 1906, p. 32, 41, pl. 4, fig. 56; Kluge 1962, p. 540, fig. 377; 1975, p. 657, fig. 377; Osburn 1912a, p. 245, pl. 26, fig. 63; 1933, p. 54, pl. 11, figs 5, 6; 1952, p. 432, pl. 50; Androsova 1958, p. 170, fig. 101; Gostilovskaya 1978, p. 227, fig. 143; Winston & Hayward 2012, p. 121, fig. 77; Grischenko 2013, p. 177, figs. 1q–r.
Discopora ovata: Nordgaard 1918, p. 78.

Additional references. *Rhamphostomella ovata*: Kluge 1908a, p. 533; 1928, p. 257; 1929, p. 22; 1961, p. 141; Osburn 1936, p. 542; 1955, p. 38; Gostilovskaya 1957, p. 455; 1968, p. 70; Hansen 1962, p. 40; Powell & Crowell 1967, p. 343; Powell 1968a, p. 2312; 1968b, p. 257; Gontar 1980, p. 18; 1990, p. 132; 1993b, p. 202; 1994a, p. 145; 2010, p. 153; Denisenko 1988, p. 13; 1990, p. 39; 2008, p. 187; 2011, p. 14; 2013, p. 184; Gontar & Denisenko 1989, p. 354; Grishankov 1995, p. 48; Kubanin 1997, p. 123; Gontar *et al*. 2001, p. 195; Shunatova & Ostrovsky 2001, p. 115, 118; Shunatova & Nielsen 2002, p. 263, fig. 1b; Grischenko 2002, p. 115; Kuklinski 2002b, p. 203; 2009, p. 228; Denisenko & Kuklinski 2008, p. 48; Ostrovsky 2009, p. 175, fig. 78a; 2013, p. 8, figs 1.11c, 2.41a; Denisenko *et al*. 2016, p. 366.

Material examined. *Lectotype*: SMNH-Type-9303, six fragments from one colony, Swedish Arctic Expedition, July 1861, Red Bay, west Spitsbergen, Svalbard and Jan Mayen, depth 64 m, mud. *Paralectotype*: SMHM-Type-9305, small colony growing on eroded fragment of another cheilostome, Swedish Arctic Expedition, September 1861, Advent Bay, Isfjord, west Spitsbergen, Svalbard and Jan Mayen, depth 35 m, mud with stones.

NHMUK 1911.10.1.1581A, one colony, ex Swedish Museum Natural History, from F.A. Smitt Collection, Spitsbergen. NHMW 44378, one colony fragment, Kola Haven, collector H. Kluge [before 1907]. ZIRAS 36/50120, three colony fragments detached from broken shells of the bivalve mollusc *Chlamys* sp., MFRT *Rodino*, 12 September 1992, about 32 km from Cape Hayryuzova, western Kamchatka shelf, Sea of Okhotsk, 57°36.2′ N, 156°09.0′ E, depth 78–81 m, crab trap, collector A.V. Grischenko. P. Kuklinski Collection, two colony fragments, Russian-

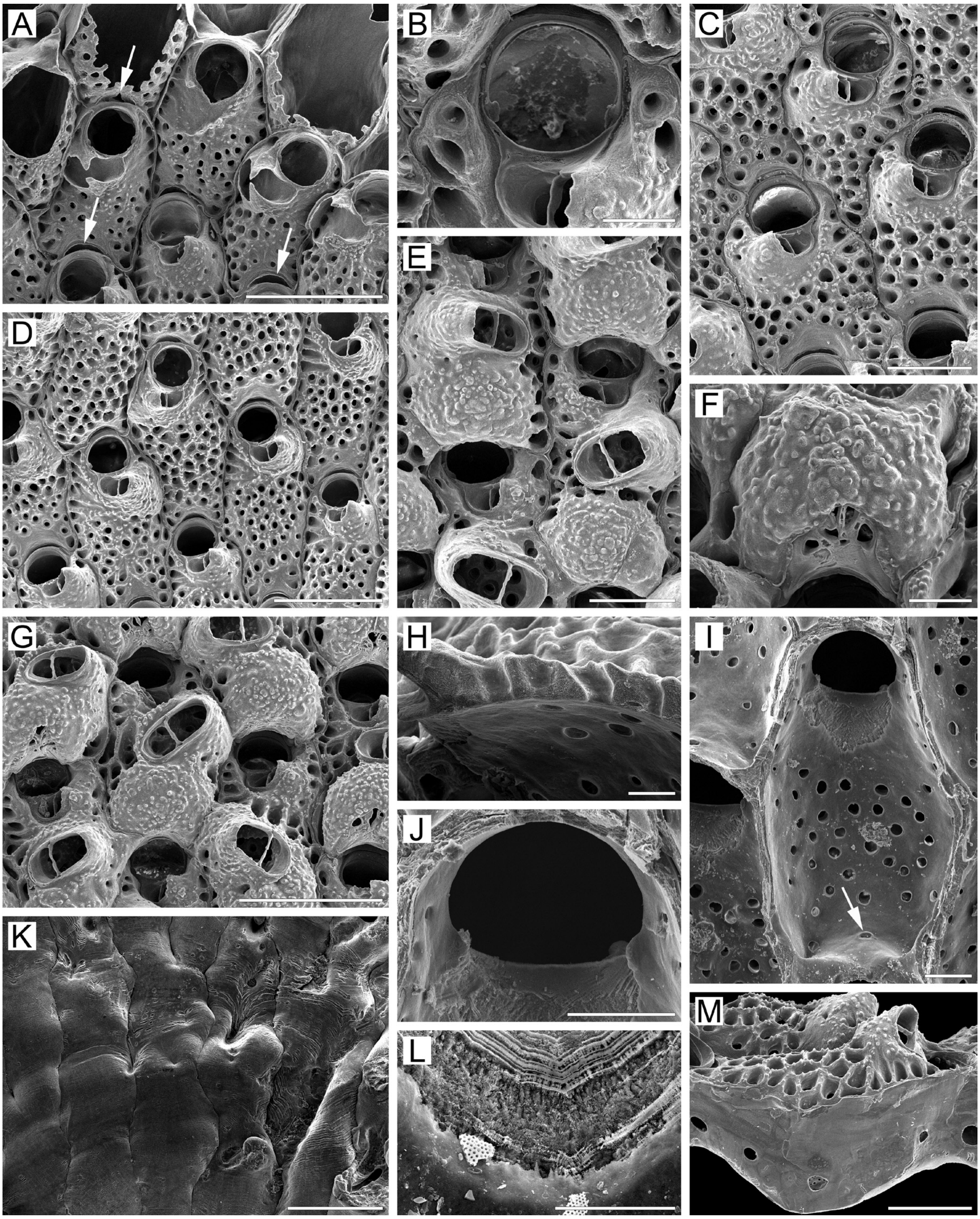

FIGURE 27. *Mixtoscutella ovata* (Smitt, 1868). ZIRAS 36/50120 (western Kamchatka, Sea of Okhotsk). A. Colony margin with young and developing zooids (arrows, sites of ooecial development). B. Zooidal orifice, showing condyles, and suboral avicularium. C, D. Non-ovicellate zooids in young part of colony. E. Ovicellate zooids in older part of colony, showing ovicells, and suboral and adventitious avicularia. F. Ooecium covered by secondary calcification, except in proximal triangular area with pseudopores. G. Area of colony with ovicellate zooids and adventitious avicularia. H. Longitudinal section through frontal shield, showing interior of umbonulomorph suboral area and adjacent pseudoporous lepralioid shield. I. Interior of frontal shield with umbonuloid component, ring scar, areolae (smaller lateral openings in upper part of zooid), pseudopores and ooecial pore (arrow). J. Internal view of primary orifice with condyles. K. Basal surface of colony. L. Interior of frontal shield, showing blurred ring scar and exterior wall microstructure of umbonuloid component. M. Lateral view of zooid, showing frontal shield, suboral avicularium and lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, F, I, J, 100 µm; C, E, 250 µm; H, L, 50 µm; M, 200 µm.

German Expedition Transdrift 1, RV *Ivan Kireev*, Stn 48, 18 August 1993, Laptev Sea, 74°30.0′ N, 137°05.0′ E, depth 22 m, rock dredge, collectors M.K. Schmid and D. Piepenburg.

Measurements. ZIRAS 36/50120, western Kamchatka, Sea of Okhotsk (Fig. 27A–M). ZL, 0.51–0.77 (0.63 ± 0.08). ZW, 0.32–0.53 (0.41 ± 0.05). ZD, 0.39–0.68 (*n* = 2). OrL, 0.12–0.16 (0.14 ± 0.01). OrW, 0.15–0.20 (0.18 ± 0.02). OeL, 0.20–0.27 (0.23 ± 0.02). OeW, 0.28–0.38 (0.35 ± 0.03). Av(s)L, 0.12–0.17 (0.14 ± 0.01). Av(ad)L, 0.17–0.32 (0.23 ± 0.04). P(f)N, 29–40 (36) (*n* = 10). P(oe)N, 2–7 (4) (*n* = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 27A), more or less circular or irregular in form, up to 22 mm in maximal dimension, yellow to pink-yellowish when alive, light brown to light yellow when dry. Zooids of medium size, oblong-hexagonal, oval to pyriform or rectangular, arranged in checkered pattern, demarcated by fine undulating sutures between lateral and transverse walls; sutures barely discernible in older parts of colony.

Frontal shield (Fig. 27A, C, D) moderately convex, finely granulated, combining both umbonuloid and lepralioid portions. Marginal areolae lateral to orifice separated by short interareolar ridges, indicating umbonuloid area; rest of shield uniformly pseudoporous, with pits of various sizes and shapes (from circular and drop-like to oval and irregular), corresponding to lepralioid part. Pseudopores becoming more sunken and frontal shield coarsely reticulate with age, with 2–3 pseudopores sometimes lying in single depression (Fig. 27G). Interior of frontal shield (Fig. 27I) showing mixed nature. Ring scar irregular (Fig. 27I, L), forming boundary between umbonuloid exterior-wall and extra-umbonuloid interior-wall microstructure. Umbonuloid component small, occupying about 20% of length of frontal shield (22% in one measured zooid).

Primary orifice (Fig. 27A, B, J) broadly circular to transversely oval; distal and lateral margins formed by upper terminal part of distal transverse wall, incidentally with narrow rim and forming small, blunt condyles at proximolateral corners. Proximal margin shallow to moderately concave (Fig. 27B, J), without lyrula. No oral spines.

Secondary orifice (Fig. 27B) round to asymmetrically oval, cormidial; distolateral curvature formed by low, vertical thickening of proximal wall of daughter zooid and, occasionally, by lateral walls of adjacent distolateral zooids; proximally restricted by cystid of suboral avicularium on one side and very low thickening of frontal shield on opposite side, together forming inconspicuous peristome.

Cystid of suboral avicularium (Fig. 27A–E) relatively small, broad, elevated, with coarsely granular surface and 1–4 minute communication pores, situated on left or right relative to orifice. Frontal surface (rostral/postmandibular areas) of avicularium slightly curved, concave, crossing zooidal midline, facing obliquely laterally. Rostrum (Fig. 27B–D) elevated, short, lingulate, with weakly denticulate margin, directed laterally and frontally. Palatal foramen conforming to shape of rostrum, no cryptocystal shelf; opesia semioval. Crossbar complete.

Large adventitious avicularia developing in older areas of colony, occupying central to proximal part of frontal shield, frequently extending to marginal area of adjoining lateral zooid. Avicularian cystid broad, with coarsely granular surface (Fig. 27E, G) and 2–5 minute communication pores. Frontal surface of avicularium facing obliquely distolaterally to proximolaterally, and frontally. Rostrum elevated, elongate oval to lingulate; palatal foramen conforming to shape of rostrum; opesia semioval. Crossbar complete.

Ovicells hyperstomial at all stages, cleithral (Fig. 27E–G). Ooecium formed by distal autozooid around shallow crescentic concavity with communication pore at bottom, situated in proximalmost part of frontal shield adjacent to distal margin of maternal primary orifice (Fig. 27A, C, D); pore leads to communication canal connecting ooecial and visceral coeloms, opening on inner side of frontal shield as oval communication pore near transverse wall (Fig. 27I). Ooecium hemispherical, with weakly concave proximal margin and round to slit-like pseudopores, some occluded by secondary calcification, sometimes visible in limited subtriangular area of proximal surface of ectooecium (Fig. 27F). Ectooecium initially smooth, rapidly overgrown by secondary calcification proceeding from frontal shields of daughter and adjacent zooids, frontal surface becoming granulated (except proximally), with 1–2 divergent sutures dividing calcification contributed by different surrounding zooids (Fig. 27F).

Zooids interconnected by two mural pore chambers in each distolateral wall (Fig. 27M). Communication pores form horizontal "band" or two multiporous septula in basal half of transverse walls.

Basal surface of zooids (Fig. 27K) fully calcified, moderately convex, smooth or with coarse transverse lineation, lacking evident protuberances. Boundaries between zooids recognizable by fine, sinuous incisions.

Ancestrula and early astogeny not observed.

Remarks. Winston & Hayward (2012) mentioned neither condyles nor large adventitious avicularia in describing this species from the northwestern Atlantic. In contrast to our material, their colonies were loosely attached to substrata. Additionally, ooecia were almost free of secondary calcification, and the medial convex area had only a single pseudopore near the proximal margin, whereas ooecia in our specimens were heavily calcified, with several pseudopores of various sizes and shapes.

Ecology. *Mixtoscutella ovata* was recorded at depths of 3.5–582 m, mainly on mixed bottoms including silt, gravel and shells. Colonies encrusted brown and red algae, hydroid stolons, other cheilostome bryozoans (*Stomachetosella* sp.), mollusc shells, brachiopods and hydrocorals.

Distribution. This is a boreal-Arctic, circumpolar, sublittoral to upper bathyal species. Numerous Arctic records include the Barents Sea (Smitt 1868a; Kluge 1915, 1929, 1962, 1975; Denisenko 1988, 1990), White Sea (Gostilovskaya 1957, 1978; Grishankov 1995; Shunatova & Ostrovsky 2001; Shunatova & Nielsen 2002; Ostrovsky 2009, 2013), Kara Sea (Nordgaard 1912; Kluge 1929, 1962, 1975; Denisenko 2021), Laptev Sea (Kluge 1929, 1962, 1975; Gontar 1990), East Siberian Sea (Kluge 1929, 1962, 1975; Gontar 1994a; Denisenko 2011), Chukchi Sea (Kluge 1929, 1962, 1975; Denisenko 2008; Denisenko & Kuklinski 2008; Gontar 2010), Point Barrow, Beaufort Sea, Alaska (Osburn 1952, 1955), Canadian Arctic Archipelago (Nordgaard 1906; Osburn 1932, 1936), Baffin Bay (Hansen 1962), Davis Strait (Kluge 1962, 1975; Hansen 1962), Hudson Bay (Gontar & Denisenko 1989), Labrador (Hincks 1877; Gontar & Denisenko 1989), western Greenland (Smitt 1868b; Kluge 1908b; Levinsen 1914; Osburn 1919; Denisenko & Blicher 2021), eastern Greenland (Levinsen 1916; Denisenko & Blicher 2021) [Smitt (1868b) just mentioned Greenland], Franz Josef Land (Denisenko 1990), Iceland (Hincks 1877); Spitsbergen (Smitt 1868b, Gontar *et al*. 2001; Kuklinski 2002b, 2009) and northern Norway (Nordgaard 1918). In the northwestern Atlantic it is recorded along the eastern coast of North America from the Gulf of St Lawrence (Whiteaves 1901; Gontar & Denisenko 1989), Gulf of Maine, Woods Hole and Cape Cod (Osburn 1912a, 1933; Powell 1968b; Winston & Hayward 2012). The only locality known from the northeastern Atlantic is the Faroe Islands (Denisenko *et al*. 2016). In the northwestern Pacific it has been reported from Anadyrskiy Gulf in the Bering Sea (Kluge 1961; Grischenko 2002) and from the waters along the eastern coast of the Kamchatka Peninsula including Kamchatskiy Gulf, Kronotsky Gulf (Kubanin 1997; Grischenko 2002), Avacha Gulf (Kluge 1961; Kubanin 1997; Grischenko 2002), Sea of Okhotsk in the waters along the southeast coast of Sakhalin Island (Kluge *et al*. 1959; Kluge 1961), Shantar Archipelago (Kluge 1961), western Kamchatka shelf (our data) and the Kuril Islands including Iturup, Zelenyy, Shikotan and South Kuril Strait (Kluge *et al*. 1959; Kluge 1961; Gontar 1980, 1993b), Sea of Japan, in the waters of the southwestern coast of Sakhalin Island (Androsova 1958; Kluge 1961) and continental slope of the northern part of the Sea of Japan (Grischenko 2013). Northeastern Pacific records include Olga Bay and Leonard Harbor, Gulf of Alaska, and Punuk Island in the northeastern Bering Sea (Osburn 1952).

Mixtoscutella ussowi (Kluge, 1908)

(Figs 28, 33H)

Schizoporella ussowi Kluge, 1908a, p. 527, figs 2a–c.
Hippodiplosia ussowi: Kluge 1953, p. 175; 1961, p. 135; 1962, p. 501, fig. 348; 1975, p. 609, fig. 348; Androsova 1958, p. 139, fig. 62; Kluge *et al*. 1959, p. 212.
Hippodiplosia smitti: Osburn 1933, p. 330, pl. 9, fig. 6.
Hippoporina ussowi: Gontar & Denisenko 1989, p. 358; Denisenko 1990, p. 37; 2013, p. 184; Grischenko 1997, p. 189; Shunatova & Ostrovsky 2001, p. 115.
Rhamphostomella ussowi: Winston & Hayward 2012, p. 124, fig. 80.

Material examined. *Lectotype*: ZIRAS 4/2331, single colony fragment, Stn 8, 27 June 1876, estuary of Mezen River, White Sea, dredge, collector K.S. Merezhkovsky.

ZIRAS 13/13526, colony fragment, summer 1897, Zajatskie Islands of the Solovetskiy Archipelago, Onego Bay, White Sea, dredge, collector G.A. Kluge. ZIRAS 14/50567, colony fragment, KIENM Collection, RV *Nazarovsk*, Stn 394, 18 September 1988, Korfa Gulf, eastern Kamchatka Peninsula, Bering Sea, 60°07.0′ N, 165°57.0′ E, depth 48 m, rock dredge, collector A.V. Rzhavsky.

Additional material. Seven specimens. IMB Collection, Commander Intertidal Expedition (1972) Stn 194/2; KIENM Collection (1992) Stns 54, 88 (see Appendix 1 for details).

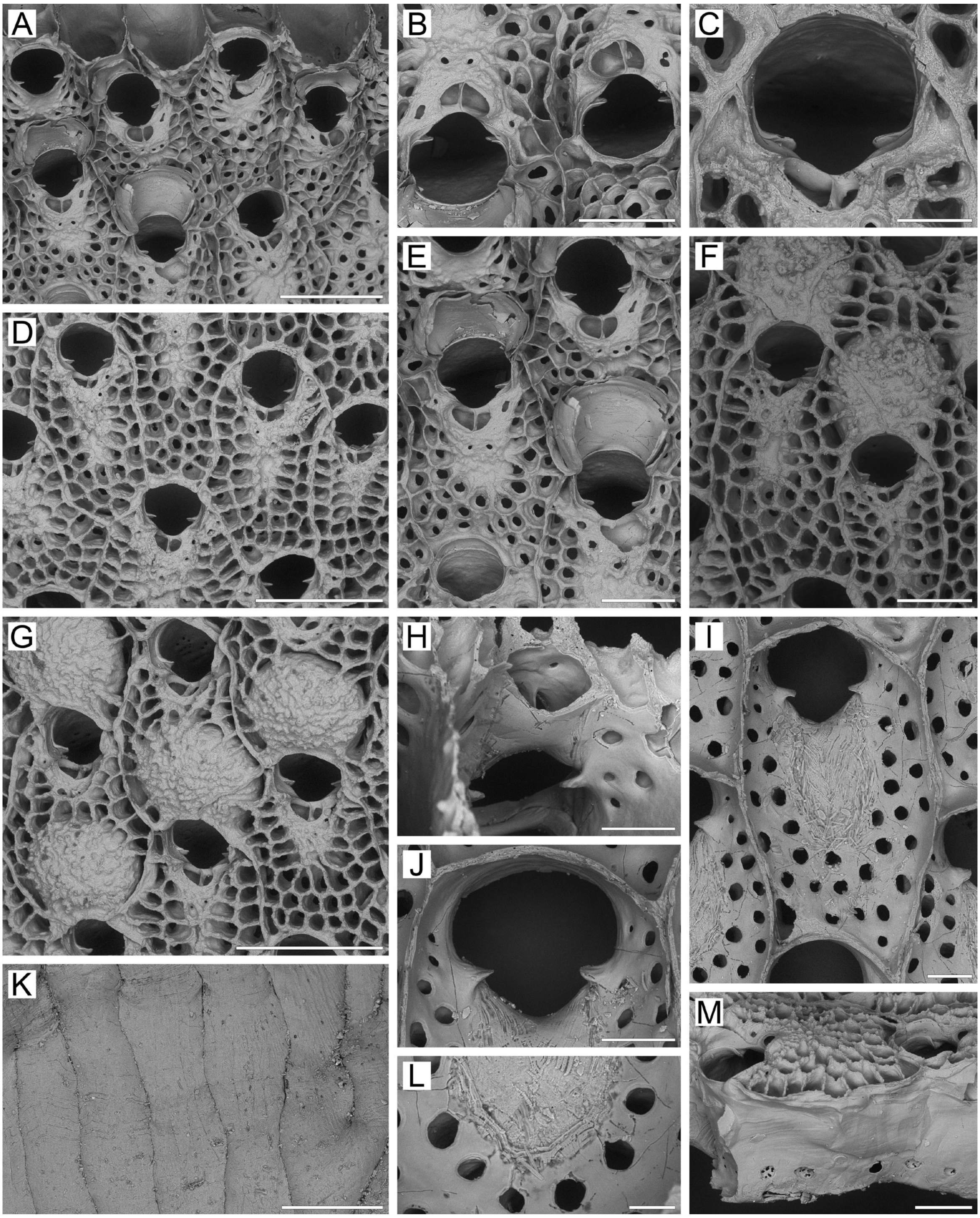

FIGURE 28. *Mixtoscutella ussowi* (Kluge, 1908). ZIRAS 14/50567 (Korfa Gulf, eastern Kamchatka, Bering Sea). A. Colony margin with developing zooids and ooecia. B. Distal view of two zooids, showing details of orifice and suboral avicularia. C. Orifice of non-ovicellate zooid, showing condyles and suboral avicularium. D. Group of non-ovicellate zooids. E. Zooids with developing ovicells close to colony periphery. F, G. Ovicellate zooids in older part of colony, showing ovicells with ooecia covered by secondary calcification and sutures between secondary calcification arising from distal and distolateral zooids. H. Transverse section through frontal shield, showing interior of proximal margin of orifice, umbonulomorph suboral area with adjacent pseudoporous shield, and cavity of suboral avicularian chamber. I. Interior of frontal shield, showing primary orifice with condyles and elongate suboral umbonuloid component surrounded by pseudoporous lepralioid shield. J. Internal view of primary orifice. K. Basal surface of colony. L. Interior of frontal shield, showing blurred ring scar and umbonuloid component surrounded by pseudoporous lepralioid area. M. Lateral view of zooid, showing frontal shield and lateral wall with mural pore chambers. Scale bars: A, D, G, K, 500 µm; B, E, F, 250 µm; C, H–J, 100 µm; L, 50 µm; M, 200 µm.

Measurements. ZIRAS 14/50567, Korfa Gulf, eastern Kamchatka, Bering Sea (Fig. 28A–M). ZL, 0.67–1.13 (0.91 ± 0.11). ZW, 0.37–0.70 (0.54 ± 0.07). ZD, 0.60–0.78 (n = 2). OrL, 0.20–0.25 (0.23 ± 0.01). OrW, 0.21–0.25 (0.23 ± 0.01). OeL, 0.35–0.43 (0.39 ± 0.02) (n = 15). OeW, 0.36–0.44 (0.39 ± 0.02) (n = 15). Av(s)L, 0.09–0.14 (0.11 ± 0.01). P(f)N, 32–49 (42) (n = 10).

Description. Colonies encrusting, multiserial, unilaminar (Fig. 28A), roughly circular, up to 11 × 8 mm in maximal dimension, bright-yellow to beige when alive, light yellow when dry. Zooids of medium size, oblong-hexagonal, oval to irregularly polygonal, arranged in quincunx, delineated by undulating fused lateral walls.

Frontal shield mixed, comprising umbonuloid and lepralioid components (Fig. 28A, D, F), flattened to moderately convex and coarsely granular medially. Proximal to orifice is narrow imperforate area, extending along zooidal midline and corresponding to umbonuloid part of shield. Extensive peripheral area, corresponding to lepralioid part of shield, bearing numerous pseudopores lying in large, deep, polygonal (square, trapezoid, rectangular) infundibular depressions. With age, frontal shield appearing increasingly reticulate (Fig. 28F, G). Interior of frontal shield (Fig. 28I) showing mixed structure. Ring scar indistinct (Fig. 28L), forming irregular boundary between umbonuloid exterior wall and extra-umbonuloid interior wall microstructure. Narrow umbonuloid component occupying more than 50% length of frontal shield (55% in one measured zooid), corresponding to external imperforate area. Adjacent pseudoporous area surrounding imperforate region (Fig. 28I, J, L), corresponding to lepralioid part of shield. One or two small areolae (connecting hypostegal and visceral coelomic cavities) visible lateral to primary orifice (Fig. 28B, C), as smallest pores in shield interior (Fig. 28I, J).

Primary orifice (Fig. 28A, B, C, J) roughly circular to pyriform; distal and lateral margins formed by upper terminal part of distal transverse wall. Condyles usually narrow triangular, with acute or rounded tips. Distal margin of orifice rounded, proximal margin with deep, wide U-shaped sinus. No oral spines or lyrula.

Secondary orifice (Fig. 28D, E, G) rounded to transversely oval, generally repeating form of primary orifice, cormidial; restricted distally by vertical thickening of proximal wall of daughter zooid and, occasionally, by adjacent zooids (Fig. 28C–E); proximal curvature formed by distal side of avicularian cystid connecting to weakly elevated, very small lateral lappets from frontal shield; in ovicellate zooids, these low lappets connecting with proximolateral corners of ooecium (Fig. 28E, F, G).

Cystid of suboral avicularium small, only slightly broadened and elevated (Fig. 28A–G), situated medially proximal to orifice, surface finely to coarsely granular, with 3–4 minute communication pores. Avicularian frontal surface (rostral/postmandibular areas) angular, crossing zooidal midline, facing obliquely distally. Rostrum low (Fig. 28B, C), short, oval, transversely oriented, directed distolaterally to laterally, forming blunt angle with postmandibular area. Palate short, lingulate, foramen repeating shape of palate; opesia semicircular. Crossbar complete.

Ovicells initially hyperstomial, becoming subimmersed and even appearing endozooidal (Fig. 28E–G) as consequence of overgrowth by secondary calcification from frontal shields of daughter and adjacent zooids; surface coarsely granular, with 1–2 divergent sutures subdividing secondary calcification from contiguous zooids (Fig. 28F–G). Ooecium formed by distal autozooid, ooecial fold developing at colony margin concurrently with formation of frontal shield of distal zooid (Fig. 28A). Fully completed ooecia with concave proximal margin; pseudopores not seen.

Zooids interconnected by 1–2 mural pore chambers in each distolateral wall (Fig. 28M). Communication pores forming two multiporous septula or spread randomly in basal half of transverse walls.

Basal surface of zooids (Fig. 28K) fully calcified, flattened, textured with coarse, parallel or irregular lineation, without protuberances. Boundaries between zooids recognizable by fine incisions.

Ancestrula and early astogeny not observed.

Remarks. In his original description, Kluge (1908a) assigned this species to *Schizoporella*. It was subsequently placed in *Hippodiplosia* (Osburn 1933; Kluge 1953, 1962, 1975) or *Hippoporina* (Denisenko 1990, 2013; Grischenko 1997). Winston & Hayward (2012) tentatively assigned it to *Rhamphostomella*, pointing out that it is strikingly similar to *M. ovata* and does not belong in either of the superfamilies Smittinoidea or Schizoporelloidea, in which species formerly assigned to *Hippodiplosia* are now classified, warranting a deeper investigation of its morphology.

Winston & Hayward (2012) considered the single series of large marginal pores to be areolae. However, the underside of the frontal shield shows 1–2 areolae laterally to the zooidal orifice in the vicinity of the umbonuloid part of the shield. Although the marginal pseudopores have an areolar position, we doubt that they are similar in function (long suspected in lepralioid pseudoporous shields, in which it is assumed that there is an organic continuity between the hypostegal and visceral coeloms). Winston & Hayward (2012, p. 124) also wrote that the ooecia have "imperforate calcification", but presented no evidence of this. All ooecia were covered by secondary calcification in our material, so the presence or absence of ooecial pseudopores remains unresolved.

Ecology. *Mixtoscutella ussowi* has been recorded from depths of 1–100 m on seafloors of rock, shell and silt. Colonies encrust pebbles, mollusc shells, barnacles, other bryozoans and brown and red algae.

Distribution. This is a boreal-Arctic, circumpolar, sublittoral species. Arctic records include White Sea (Kluge 1908; Gostilovskaya 1957; Gontar & Denisenko 1989; Shunatova & Ostrovsky 2001), Barents Sea (Kluge 1962, 1975; Gontar & Denisenko 1989; Denisenko 1990), Kara Sea (Kluge 1962, 1975; Gontar & Denisenko 1989; Denisenko 2021), western Greenland (Osburn 1933; Gontar & Denisenko 1989; Denisenko & Blicher 2021) and eastern Greenland (Denisenko & Blicher 2021). There are North Atlantic records from Mount Desert Island, Cape Ann, and Isles of Shoals, Massachusetts, northeastern North America (Osburn 1933; Winston & Hayward 2012). In the northern Pacific *M. ussowi* has been reported from the Bering Sea (Kluge 1962, 1975), including the Commander Islands (Grischenko 1997, 2002), and it was recently found in Korfa Gulf, eastern Kamchatka (our data). In the Sea of Okhotsk, it has been reported from shallow waters along the southeast coast of Sakhalin Island, in Sakhalin Gulf, and near the Shantar Archipelago (Kluge 1961, 1962, 1975). In the Sea of Japan, it has been reported from northern Primorye (Androsova 1958; Kluge 1961) and along the southwestern coast of Sakhalin Island (Kluge *et al*. 1959).

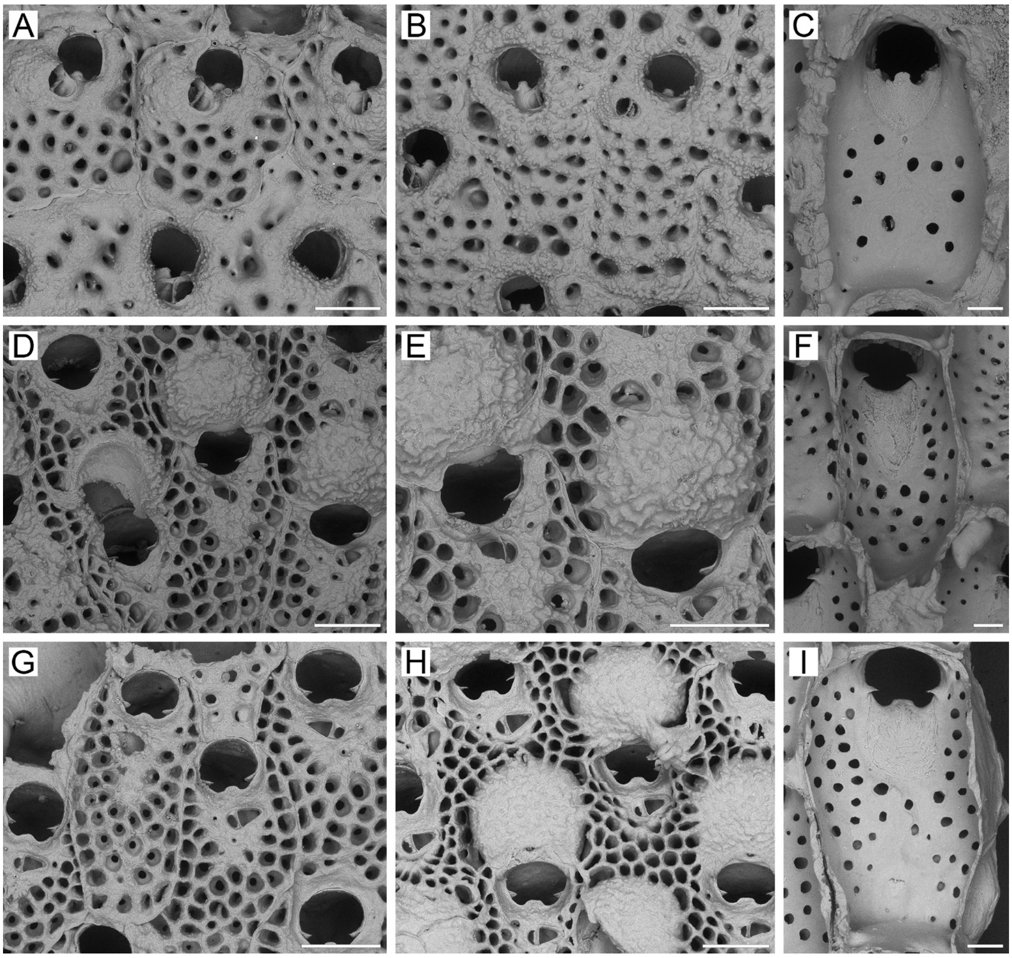

FIGURE 29. Known species of *Mixtoscutella* from the northern Pacific. A–C. *M. androsovae* (Gontar, 1979). *Paratype*, ZIRAS 2/43716 (Cape Nerpochka, off Pacific side of Simushir Island, middle Kuril Islands). D–F. *M. harmsworthi* (Waters, 1900). ZIRAS 52/50568, KIENM Collection (Avacha Gulf, eastern Kamchatka, Pacific Ocean). G–I. *M. cancellata* (Smitt, 1868). ZIRAS 1/50572, KIENM Collection (western Kamchatka, Sea of Okhotsk). A. Colony margin. B. Group of non-ovicellate zooids. C. Interior of frontal shield, showing small umbonuloid component and lepraliomorph area. D. Zooids with ovicells (one ooecium broken). E. Ovicellate zooids, showing details of orifice and suboral avicularium. F. Interior of frontal shield, showing umbonuloid component and lepraliomorph area. G. Colony margin. H. Ovicellate zooids, showing details of orifice and suboral avicularium. I. Interior of frontal shield, showing umbonuloid component and lepraliomorph area. Scale bars: A, B, D, E, G, H, 250 μm; C, F, I, 100 μm.

Discussion

Morphology

Frontal shield. Our study has revealed that both *Rhamphostomella* and *Rhamphostomella*-like species have a frontal shield comprising a suboral umbonuloid area, typically capped frontally by an avicularian cystid, and a post-umbonuloid, non-pseudoporous or pseudoporous lepralioid area. For the species with a pseudoporous lepralioid area, we have introduced the genus *Mixtoscutella.* This genus adds to the growing list of genera, both fossil and Recent, that have a combined umbonuloid-lepralioid frontal shield morphology, with the umbonuloid component varying in size relative to the lepralioid component, which may be non-pseudoporous or pseudoporous. Families including such genera are Lepraliellidae, Siphonicytaridae, Phidoloporidae, Umbonulidae, Adeonidae, Inversiulidae, Smittinidae, Bitectiporidae, Petraliidae and Stomachetosellidae (Gordon & Voigt 1996; Gordon 2000), with additional ascophoran families anticipated to contain genera with mixed shields.

Rhamphostomella itself shows wide variation in the size of the umbonuloid component among species. In our material, the umbonuloid component was smallest in *R. echinata* (15–25% of frontal shield length) and *R. bilaminata* (about 35%), and largest in *R. aspera* and *R. tatarica* (about 80% and 90%, respectively). The other species we examined showed intermediate ranges from about 40% (*R. plicata*, *R. cellata*) to 45% (*R. hincksi*), 50% (*R. scabra*, *R. morozovi*), 60% (*R. costata*, *R. cristata*, *R. alutacea*, *R. radiatula*, *R. sibirica*, and *R. townsendi*), 65% (*R. gigantea*), 70% (*R. commandorica*, *R. pacifica*, *R. curvirostrata*, and *R. obliqua*) and 75% (*R. microavicularia*, *R. aleutica*, and *R. multirostrata*), with 60% most frequent. In comparison, in two species of *Mixtoscutella*, the umbonuloid component comprised about 20% (*M. ovata*) and 50% (*M. ussowi*). *Rhamphostomella* thus shows a clear trend towards reduction of the umbonuloid component, and more than half of all the species we studied have in fact a mixed/transitional frontal shield with a prominent non-pseudoporous lepralioid component.

A pseudoporous frontal shield is more derived than an umbonuloid frontal shield (Gordon 2000); hence, *Mixtoscutella* is more derived (evolved later) than *Rhamphostomella*. The earliest-known strictly umbonuloid-shielded cheilostome is the Santonian (Late Cretaceous) genus *Staurosteginopora* (Arachnopusiidae) (Voigt 1991); the earliest evidence of reduction in size of the umbonuloid area, with an inferred post-umbonuloid ascus extension, is the Danian (early Paleocene) genus *Schizemiellopsis* (?Lepraliellidae) (Voigt 1987; Gordon & Voigt 1996). Given that fully pseudoporous lepralioid frontal shields are not known until the Paleocene (Brezina *et al*. 2021), it is inferred that a mixed frontal shield having a pseudoporous component probably originated in the Late Cretaceous, but as Gordon & Taylor (2015) pointed out, lepralioid ascophorans are rare in the Paleocene globally, so the time of their origination remains a mystery.

Gordon (2000) noted the implications of the presence of both a ring scar and pseudopores in the same frontal shield. The ring scar indicates the place of attachment of the margin of the membranous frontal wall, which functions as an ascus or compensation sac. However, the area occupied by the ascus in this instance is presumably too small for the hydrostatic mechanism to function effectively, and a post-umbonuloid extension to the ascus is inferred. Theoretically, this could be achieved in two ways. Either the edge of the compensation sac peels back from the ring scar after initial ontogeny of the autozooid, or the sac remains attached to the ring scar and a balloon-like extension differentiates proximally from it. Careful study of zooidal ontogeny is needed to determine if either or both of these developmental scenarios are true.

Another implication concerns the origin of pseudopores. Gordon (2000) suggested that they evolved from marginal areolae, which communicate laterally with the visceral coelom. Inasmuch as areolae are known to "branch" in young (as in *Rhamphostomella scabra*) or old (*R. aspera*) zooids during development of the frontal calcification, more than one opening can be seen in the frontal surface of a shield, but these converge to a single canal beneath. In mixed shields, pseudopores occur outside the perimeter of the ring scar, and it is conceivable that they originated by multiplication of areolae. Alternatively (or additionally), pseudopores may simply be loci where, for energetic or other functional reasons, calcification does not occur (Gordon 2000).

Inasmuch as it is clear that pseudoporous frontal shields have originated from umbonuloid ancestors many times in evolution, the possibility exists that this has also happened in the species here included in *Mixtoscutella* and that the genus may not be monophyletic. This can be determined by using molecular sequence data.

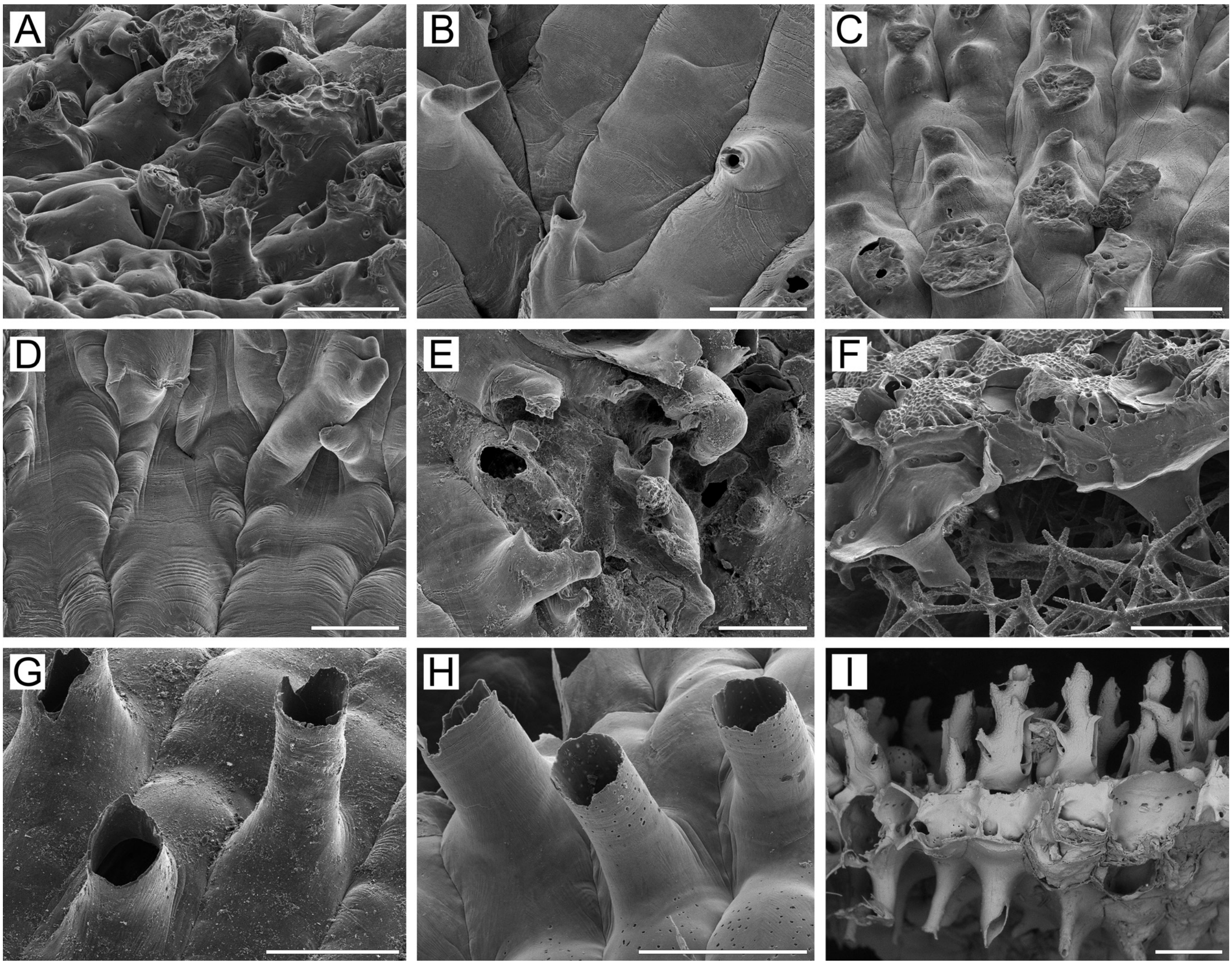

FIGURE 30. Basal colony surface in some *Rhamphostomella* species. A. *R. scabra*, ZIRAS 93/50106 (Bering Island, Commander Islands, Pacific Ocean), colony fragment developed above irregular substrate, showing broken protuberances and pits formed above sponge spicules. B. *R. commandorica*, ZIRAS 1/50125 (Medny Island, Commander Islands, Pacific Ocean), colony fragment, showing smooth surface with rare thin protuberances. C. *R. cristata*, ZIRAS 2/50110 (Medny Island, Commander Islands, Pacific Ocean), colony area growing above crustose coralline algae *Lithothamnion* sp., showing regular series of columnar protuberances with broad bases. D. *R. gigantea*, ZIRAS 3/50129 (western Kamchatka shelf, Sea of Okhotsk), colony detached from internal side of broken shell of bivalve mollusc *Chlamys* sp. E. *R. pacifica*, ZIRAS 1/50124 (Kronotsky Gulf, eastern Kamchatka, Pacific Ocean), colony developed above irregular substratum. F. *R. curvirostrata*, NHMUK 1964.1.2.7 (Pacific coast of North America), colony margin with developing zooids, supported by long tubular processes. G. *R. hincksi*, USNM 11130 (Point Barrow, Alaska, Beaufort Sea), basal surface with long tubular protuberances. H. *R. sibirica*, ZIRAS 34/50113 (Medny Island, Commander Islands, Bering Sea), basal surface with long tubular protuberances. I. *R. multirostrata*, ZIRAS 1/50545 (Urup Island, Kuril Islands, Sea of Okhotsk), colony detached from a sponge, showing marginal zooids with regular series of tubular protuberances. Scale bars: 500 µm.

Ovicells. Ovicells in *Rhamphostomella* have ooecia of the so-called “lepralielliform type” that is widespread among both umbonuloid and lepralioid cheilostomes (Ostrovsky 2009, 2013). Early stages of calcification of the ooecial fold (consisting of the rudimentary ecto- and endooecium) have the shape of a “double-disc” (Figs 7E, 12A, E, 16E, 18A, B, 19A, E, 20B, E, 21A, 22E, 23A), further growth of which results in the formation of a “spherical” ooecium of two calcified walls (apart from pseudopores in the ectooecium) with a slit-like coelom in between. The ooecial coelom is connected with the visceral coelom of the distal autozooid via a short canal that opens on both sides as two central communication pores, one (upper) near and distal to the primary orifice of the maternal zooid and another (lower) on the underside of the frontal shield of the distal zooid. The shape, size and position of the lower pore are subject to considerable variation.

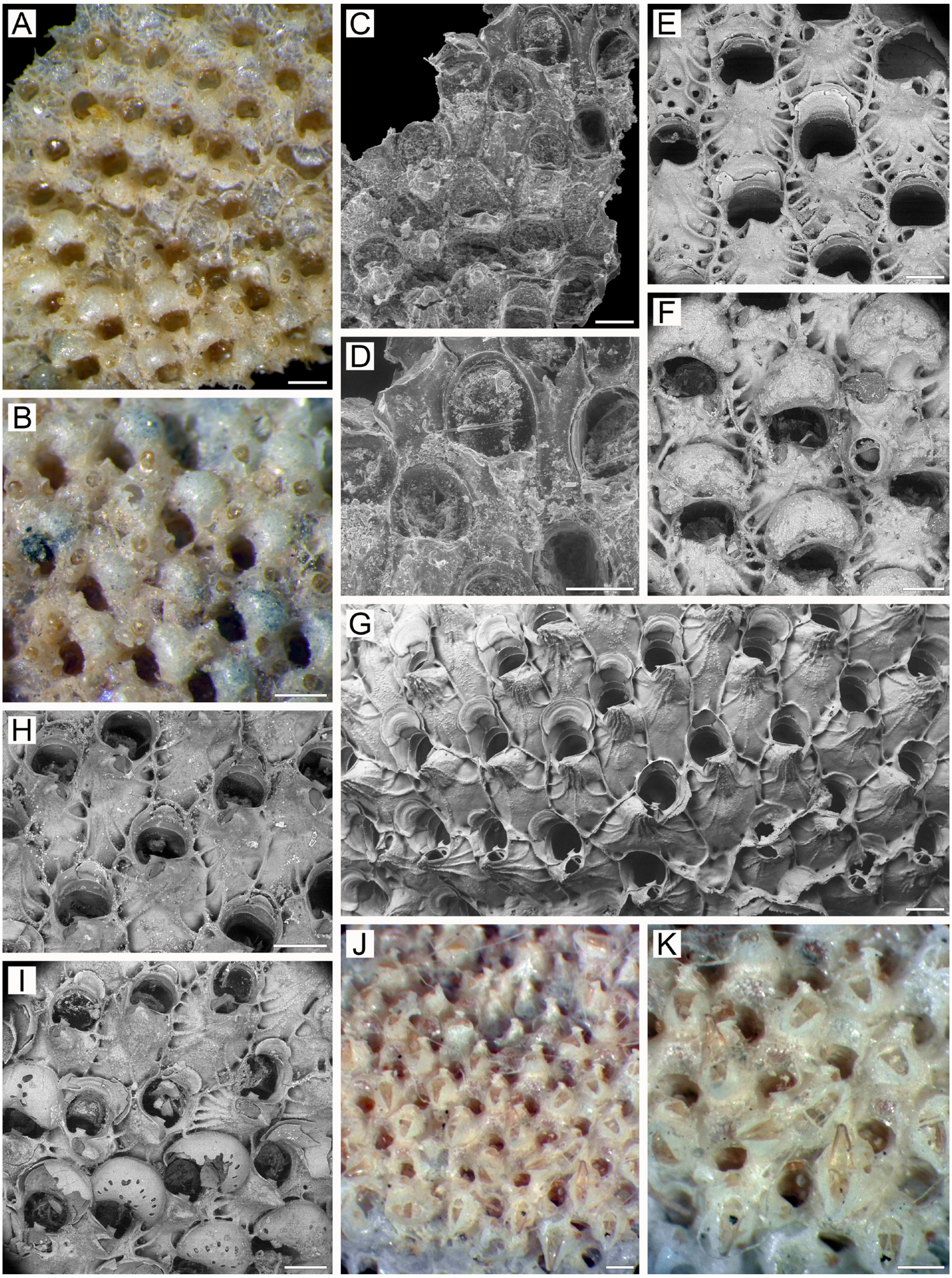

FIGURE 31. Type specimens of *Rhamphostomella* species. A, B. *Rhamphostomella scabra* (Fabricius, 1824). *Neotype*, SMNH-Type-9304 (Hammerfest, Norway, North Atlantic Ocean). C, D. *Desmacystis sandalia* (Robertson, 1900) (junior synonym of *Rhamphostomella scabra orientalis* Kluge, 1961). *Holotype*, ZIRAS 1/8801 (Cape Vkhodnoy Reef, Bering Island, Pacific Ocean). E, F. *Rhamphostomella sollers* (Canu & Bassler, 1929) (junior synonym of *Rhamphostomella scabra*). *Syntype*, USNM 8136 (Cape Tsiuka, Sangar Strait, Sea of Japan). G. *Rhamphostomella costata* Lorenz, 1886. *Lectotype*, NHMW 92531 (Jan Mayen). H, I. *Rhamphostomella magnirostris* (Canu & Bassler, 1928) (junior synonym of *Rhamphostomella costata*). *Syntype*, USNM 7579 (Cedar Keys, western Florida, Gulf of Mexico). J, K. *Rhamphostomella cristata* (Hincks, 1889). *Neotype*, NHMUK 1911.10.1.1576A (Gulf of St Lawrence, Atlantic Ocean). Scale bars: A, B, J, K, 500 µm; C–I, 250 µm.

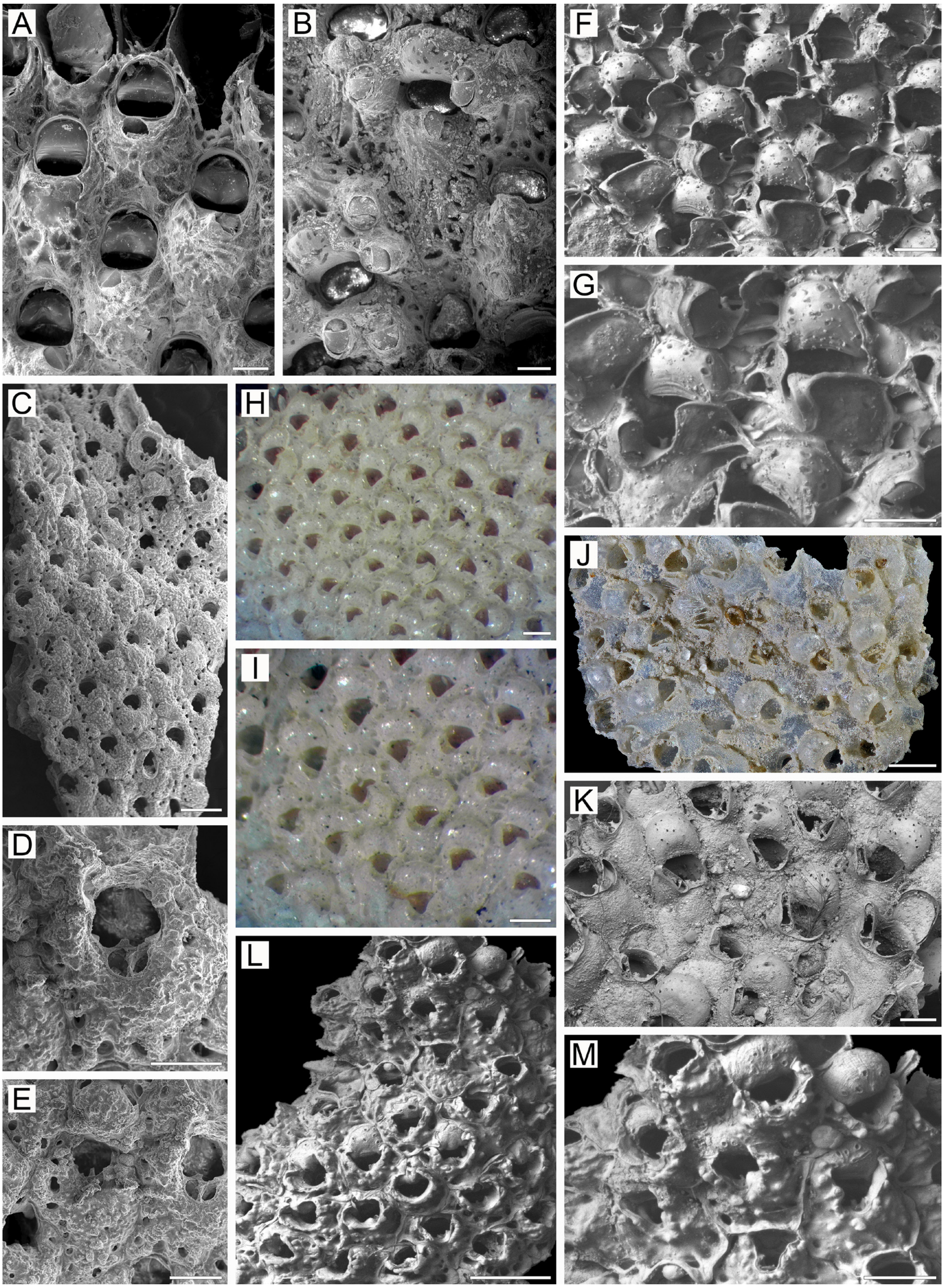

FIGURE 32. Type specimens of *Rhamphostomella* species. A, B. *Rhamphostomella gigantea* Osburn, 1952. *Holotype*, USNM 11033 (Point Barrow, Alaska, Beaufort Sea). C–E. *Rhamphostomella alutacea* Gontar, 1993. *Holotype*, ZIRAS 1/44569 (Krabovaya Bight, Shikotan Island, Lesser Kuril Ridge, Pacific Ocean). F, G. *Rhamphostomella bilaminata* (Hincks, 1877). *Neotype*, NHMUK 1911.10.1.1580A (Gaspe, Gulf of St Lawrence, Atlantic Ocean). H, I. *Rhamphostomella hincksi* Nordgaard, 1906. *Neotype*, NHMUK 1976.8.6.39pt (about 22 km westwards from Medvezhii Island, western Barents Sea). J, K. *Rhamphostomella plicata* (Smitt, 1868). *Lectotype*, SMNH-Type-1696 (Waygat Islands, Hinlopen Strait, Svalbard and Jan Mayen). L, M. *Rhamphostomella radiatula* (Hincks, 1877). *Neotype*, NHMUK 1911.10.1.1592 (Iceland). Scale bars: A, B, D–G, K, M, 250 µm; C, H, I, J, L, 500 µm.

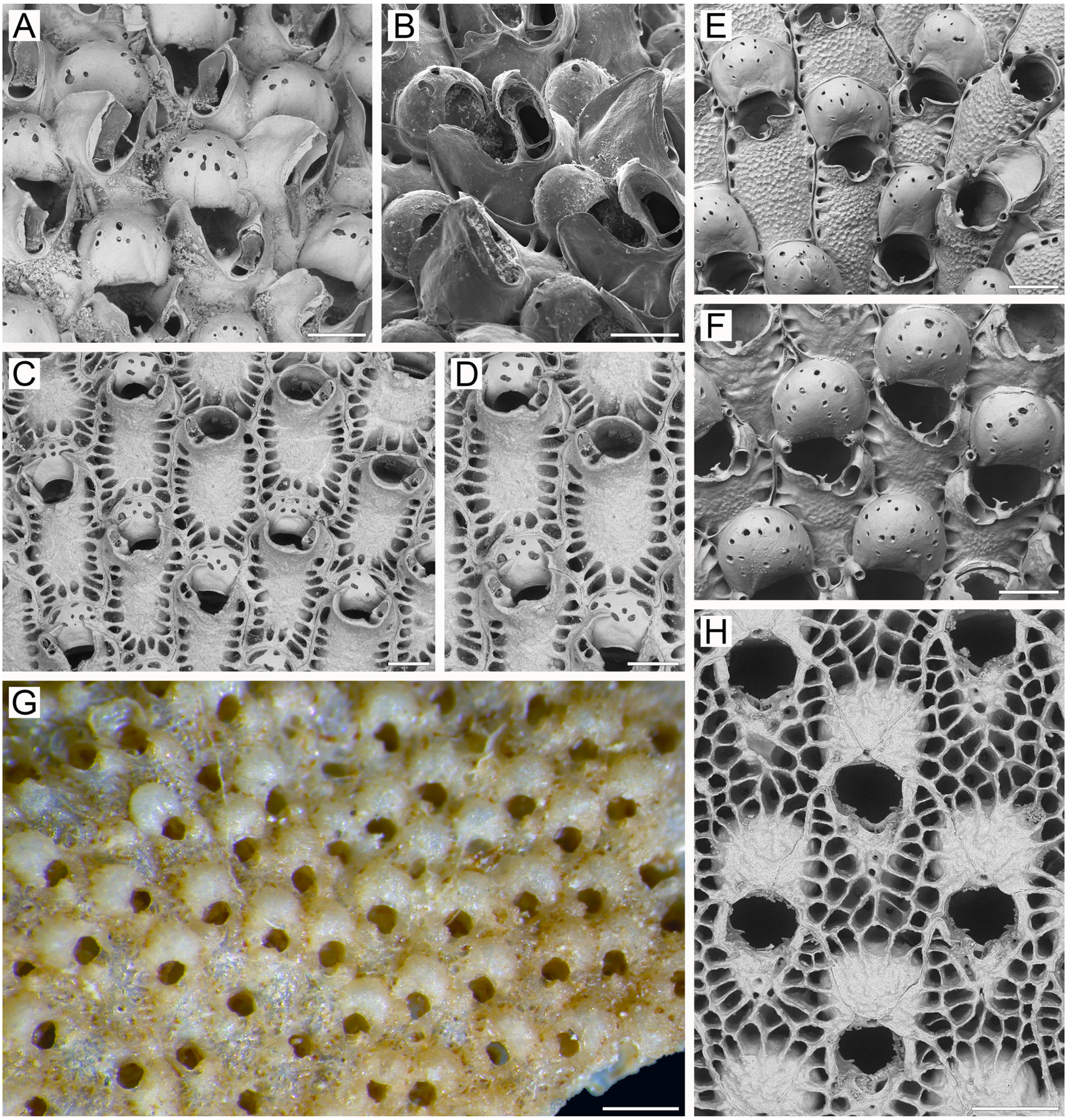

FIGURE 33. Type specimens of *Rhamphostomella* and *Mixtoscutella* species. A, B. *Rhamphostomella sibirica* (Kluge, 1929). *Lectotype*, ZIRAS 1/50730 (Laptev Sea). C, D. *Rhamphostomella tatarica* (Androsova, 1958). Paratype, ZIRAS 2/3852 (Tatar Strait, Sea of Japan). E, F. *Rhamphostomella spinigera* Lorenz, 1886. *Lectotype*, NHMW 92535 (Jan Mayen). G. *Mixtoscutella ovata* (Smitt, 1868). *Lectotype*, SMNH-Type-9303 (Red Bay, west Spitsbergen, Svalbard and Jan Mayen). H. *Mixtoscutella ussowi* (Kluge, 1908). *Lectotype*, ZIRAS 4/2331 (estuary of Mezen River, White Sea). Scale bars: A–F, H, 250 µm; G, 500 µm.

The ooecium is formed by the distal autozooid, but the timing of its formation is different in different species. In 11 of the species studied (*R. aleutica*, *R. bilaminata*, *R. curvirostrata*, *R. plicata*, *R. radiatula*, *R. hincksi*, *R. sibirica*, *R. tatarica*, *R. townsendi*, *R. spinigera*, and *R. echinata*), the ooecial fold grows at the colony periphery during formation of the distal zooid, and particularly, its frontal shield. This pattern is most widespread among cheilostomes, both anascans and ascophorans (reviewed in Ostrovsky 1998, 2009, 2013; for anascans, see e.g.

Ostrovsky & Schäfer 2003; Ostrovsky *et al*. 2003, 2009a; Moosbrugger *et al*. 2012) and is clearly an ancestral character, one that is encountered in Cretaceous calloporids (Ostrovsky & Taylor 2005a).

A more advanced pattern is known only in ascophorans (Ostrovsky 2009, 2013). In this instance, formation of the ooecium is postponed, and the double-disc stage grows proximal to the colony periphery (sometimes considerably so). Ooecium-producing zooids have a fully formed frontal shield, and the ooecial fold is formed around the shallow oval or crescentic concavity situated in the proximalmost part of the frontal shield, just immediate to the distal margin of the maternal primary orifice. This concavity has its own membranous cover, with the coelom underneath isolated from the surrounding hypostegal coelom of the distal zooid. The concavity also has a communication pore at the bottom that leads to the communication canal connecting the ooecial and visceral coeloms. Another 11 of the species we studied showed this pattern (*R*. *scabra*, *R*. *commandorica*, *R*. *costata*, *R*. *cristata*, *R*. *gigantea*, *R*. *microavicularia*, *R*. *morozovi*, *R*. *pacifica*, *R*. *aspera*, *R*. *obliqua*, and *R*. *multirostrata*). We have no data on early ovicellogenesis in *R*. *alutacea*, and *R*. *cellata*.

Initially, ovicells in all the species we studied are hyperstomial (=prominent), in which half or more of the brood cavity is above the colony surface. In many species, the ooecium remains clear of secondary calcification (*R*. *aleutica*, *R*. *aspera*, *R*. *cellata*, *R*. *obliqua*, *R*. *plicata*, *R*. *townsendi*, *R*. *spinigera*, and *R*. *echinata*), or only its basal part is overgrown (*R*. *cristata*, *R*. *bilaminata*, and *R*. *multirostrata*). In contrast, in some other species, ovicells eventually become subimmersed (*R*. *scabra*, *R*. *microavicularia*, *R*. *morozovi*, *R*. *pacifica*, *R*. *curvirostrata*, *R*. *hincksi*, and *R*. *sibirica*) or even have the appearance of endozooidal ovicells (*R*. *commandorica*, *R*. *costata*, *R*. *gigantea*, *R*. *alutacea*, *R*. *radiatula*, and *R*. *tatarica*), with the ooecium being embedded (e.g. strongly or sometimes almost completely overgrown) in secondary calcification. This, however, has nothing to do with true endozooidal ovicells in which the brood cavity occupies the proximal part of the distal zooid and is not situated above it (Ostrovsky 2008, 2009, 2013; Ostrovsky *et al.* 2009b).

The number, size, pattern of distribution and shape of ectooecial pseudopores vary widely. Among others, *R*. *gigantea* has elongate pseudopores giving a costate appearance to the ooecia. The perforations seen in bleached specimens are actually covered by cuticle and are of course not open in life. This similarity is obviously only superficial and not related to the "costate" origin of the ooecia in the "neocheilostomes" (Ostrovsky 1998, 2002; Ostrovsky & Taylor 2004, 2005b). The very thinly calcified endooecium appears damaged in most ovicells in our material.

Ostrovsky's (2009, 2013) study using histological sections showed that the opening of the ovicell is plugged by the ooecial vesicle and sealed by the zooidal operculum in *R*. *costata*, *R*. *bilaminata*, and *R*. *radiatula*. The ovicells in these species are thus cleithral, although we defer extrapolating this variable character to all species in this genus. SEM study showed that the relative position of the ovicell opening and zooidal orifice may differ greatly, and histological sections or direct observations of live colonies are required to demonstrate the actual type of ovicell closure among species.

In *Mixtoscutella*, ovicell structure and development correspond to that in *Rhamphostomella*. Interestingly, ooecia are formed by distal autozooids at the colony periphery in *M*. *ussowi*, whereas they form in more central areas of the colony in *M*. *ovata*. Secondary calcification may cover the entire ooecium in *M*. *ussowi*. We found no ovicells with fully-formed ectooecium not covered by secondary calcification among colonies of this species, and are not aware if there are pseudopores at any stage of development; Kluge (1962, 1975), however, noticed a central ooecial [pseudo]pore. It also should be noted that ovicells are cleithral in *M*. *ovata* (Ostrovsky 2009, 2013).

Multiporous septula. Each zooid buds 1–3 daughter zooids distally and distolaterally. The morphology of the transverse wall and associated communication organs varies. The transverse wall can be uniformly flat or slightly arched distally (Figs 1A, 5A). In many instances, however, it is flat or weakly arched only in the upper half, thus becoming "bi-sided", i.e. with two opposite "slopes" or "swollen chambers" joined distally under the sharp angle in the lower/basal half of the wall (Figs 3A, 4A). In the latter case, the lower part of the transverse wall forms two recesses that frontally look like two opposite porous "slopes" (when flat) or "chambers" (when swollen) expanding to the cavity of the maternal zooid. Both variants can occur in the same colony (e.g. in *R*. *commandorica*).

Simple (flat or concave) transverse walls either have a wide, horizontal porous area/"band" (thus, each is a common multiporous septulum) sometimes added to by random individual pores and/or small groups above the "band", or bear 1–4 separate pore plates (again, multiporous septula) of various shapes and sizes that sometimes overlap. In transverse walls with recesses, the opposite lateral "slopes"/"chambers" are each provided with a multiporous septulum (Fig. 3A), sometimes consisting of two or three small pore-plates. In some instances, these two septula are "interconnected" by individual pores situated in between. In *R. commandorica*, *R. cristata* and some other species, the recesses of the transverse wall are separated by prominent buttresses, conferring the appearance of basal pore chambers (Figs 2A, 4A). Transverse walls may bear on their distal side two short triangular shelves above each multiporous septulum. These parts of the transverse wall are situated below the frontal shield and continue along the lateral zooidal wall as a narrow flange (*R. costata*, *R. gigantea*, and *R. bilaminata*; see e.g. Fig. 3A).

Ecology

Bathymetry. Bathymetrically, *Rhamphostomella* is unequally represented by two groups. One includes nine (37%) sublittoral to upper-bathyal species (*R. scabra*, *R. costata*, *R. microavicularia*, *R. pacifica*, *R. bilaminata*, *R. curvirostrata*, *R. obliqua*, *R. townsendi*, and *R. multirostrata*) occurring at shelf and upper slope depths (0–950 m); the other includes fifteen (63%) sublittoral species (*R. commandorica*, *R. cristata*, *R. gigantea*, *R. morozovi*, *R. aleutica*, *R. alutacea*, *R. aspera*, *R. cellata*, *R. hincksi*, *R. plicata*, *R. radiatula*, *R. sibirica*, *R. tatarica*, *R. spinigera*, and *R. echinata*) restricted to the shelf zone (0–300 m). Twenty-one species (88%) are relatively eurybathic, inhabiting broad depth ranges (Table 1). Three (12%) species (*R. morozovi*, *R. alutacea*, and *R. cellata*) are presumably relatively stenobathic, inhabiting narrower depth ranges (116–146, 55–81 and 1.8–9.1 m respectively) in the middle and upper sublittoral (although small number of records allows only preliminary statement). Some populations of *R. scabra*, *R. costata*, and *R. sibirica* occur in the middle to low horizons of the intertidal zone (Dick & Ross 1988; Barnes & Dick 2000; Kubanin 1997; Grischenko 2004).

Three of the five presently known species of *Mixtoscutella* (*M. ussowi*, *M. androsovae*, and *M. cancellata*) have been recorded from sublittoral depths. The other two, *M. ovata* and *M. harmsworthi*, have a wider range, including the sublittoral and upper bathyal zones (Kluge 1962, 1975; Grischenko 2013; our data).

Substrata. Although all of the species examined were collected from hard, soft and mixed areas of seafloor, they seem to be better represented in benthic assemblages on hard bottoms. Colonies can attach to a variety of substrata (Table 1), having the capacity to rise up over irregularities in a fair proportion of *Rhamphostomella* species. Usually, colonies encrust hard substrata such as pebbles, gravel and shells (especially bivalves), barnacles and calcareous polychaete tubes, but they are also found on various algae, hydroids, hydrocorals, sponges, bryozoans, ascidians, crustacean carapaces and sea urchin tests.

The basal walls of zooids in at least fifteen (63%) species produce elongate tubular or columnar protuberances (Fig. 30), with the longest detected in *R. hincksi* (0.47 mm), *R. plicata* (0.60 mm) and *R. curvirostrata* (0.67 mm), and with maximal diameter in *R. microavicularia* and *R. pacifica* (0.39 mm), *R. gigantea* (0.42 mm) and *R. cristata* (0.59 mm). In *R. curvirostrata*, these protuberances occasionally reach 1.55 mm in length (Fig. 30F) and possess terminal rootlets. Many *Rhamphostomella* colonies with basal protuberances were partially to entirely elevated over the substratum, with strongly reduced attachment by zooidal basal walls. Some such colonies were noted to colonize a range of allelopathically active substrata, such as sponges and crustose red algae; at least nine (37%) species (Table 1) were recorded on the surface of sponges (Figs 9A, 11A, 21A, J, 22K, 30F, I), including three species (*R. aleutica*, *R. aspera*, and *R. multirostrata*) currently known particularly to be sponge epibionts. Some colonies of *R. cristata* (Figs 4K, 30C) also encrusted surfaces of the crustose coralline red alga *Lithothamnion* sp.

Basal protuberances have been described in some other living and fossil cheilostome taxa—for instance, in *Robertsonidra* (see Robertson 1908; Tilbrook 2006) and *Bertorsonidra* (Rosso *et al*. 2010) and *Chaperiopsis* (Gordon 1992), due to convergent evolution.

The comparatively large size of both zooids (with mean length equal to or exceeding 1 mm in fourteen species) and colonies (usually exceeding 20 mm, sometimes reaching 50 mm across), frequently elevated above the substratum by basal protuberances, presumably confers an advantage to many *Rhamphostomella* species in boundary interactions with other encrusting bryozoans. The elevation of growing margins by means of protuberances could be a method to prevent or to slow overgrowth by neighbouring spatial competitors. Also, long oral spines tilted forward appear to represent an additional mode of protection for marginal zooids in *R. multirostrata*, *R. spinigera*, and *R. echinata*.

Habitat-generating species. Some *Rhamphostomella* species can provide a habitat for other benthic invertebrates. Their colonies contribute to the substrate complexity, thus greatly affecting the biodiversity (discussed in Sokolover *et al*. 2018). For instance, colonies of *R. sibirica* frequently form complex multilayered aggregations, with free slit-like spaces in between adjoining colony layers (see also the Remarks section for this species). These spaces provide a niche for spirorbid polychaetes and juvenile crustaceans (Kubanin 1976). We observed that species with

TABLE 1. Ecological data for *Rhamphostomella* and *Mixtoscutella* species.

Taxa	Depth (m)	Bottom type	Substrata	Temp. (°C)	Salinity (‰)
R. scabra	0–460	Rock, boulders, blocks, gravel, sand, silt	Shells, sponges, ascidians, polychaete tubes, shingles	-1.9–4.3	34.40–34.96
R. commandorica	10–250	Boulders, pebbles, silt	–	–	–
R. costata	0–308	Rock, boulders, blocks	Shells, algae, hydroids, polychaete tubes, bryozoans, shingles	-1.9–3.2	23.80–34.96
R. cristata	10–197	Rock, boulders, blocks, gravel, silt	Shells, shingles, polychaete tubes, hydroids, bryozoans	-1.7	–
R. gigantea	33.5–176	Rock, gravel, sand, silt	Shells, pebbles, polychaete tubes	–	–
R. microavicularia	264–480	–	Barnacles, sponges	–	–
R. morozovi	116–146	Pebbles, gravel, sand, silt	–	–	–
R. pacifica	97–490	Pebbles, silted sand	Shells, pebbles	–	–
R. aleutica	224–235	–	Sponges	4.3	–
R. alutacea	55–81	Shells, gravel, sand, silt	Shells, sea urchin tests	–	–
R. aspera	264–274	–	Sponges	–	–
R. bilaminata	4–435	Silt, sand, shells	Shells, hydroids, ascidians, bryozoans, crustaceans	-1.9–9.6	27.09–29.39
R. cellata	1.8–9.1	–	Shells	–	–
R. curvirostrata	10–566	Rock	Shells, polychaete tubes, sponges, shingles	–	–
R. hincksi	10–270	Gravel, shells, sand, silt	Shells, bryozoans	-1.6–1.5	32.18–34.83
R. obliqua	10–435	Pebbles, shells	Shells	–	–
R. plicata	12–146	Sand, shells, gravel	Shells, bryozoans, ascidians	-1.6–1.8	33.77–34.27
R. radiatula	2–280	Rock, boulders, blocks, gravel, sand, silt, shells	Shells, algae, ascidians, bryozoans, polychaete tubes, sponges, barnacles	-1.6–9.6	26.53–34.27
R. sibirica	0–170	Rock, boulders, shingles, gravel, sand, silt	Shells, algae, sponges, hydroids, ascidians, bryozoans, gravel	-1.6–13.5	29.96–34.83
R. tatarica	30–117	Sand, silt	Shells, gravel	–	–
R. townsendi	224–977	Pebbles, silt	Sponges, bryozoans	4.3	–
R. multirostrata	183–567	Gravel, pebbles	Sponges	–	–
R. spinigera	7–234	Rock, boulders, blocks	Shells, algae, polychaete tubes, bryozoans, barnacles	-1.9–6.1	27.09–34.54
R. echinata	10–100	Rock, shingles, boulders	Algae, polychaete tubes, hydroids, bryozoans, crustaceans	–	–
M. ovata	3.5–582	Gravel, shells, silt	Shells, algae, hydroids, bryozoans, brachiopods, hydrocorals	-1.7–13.5	26.91–34.83
M. ussowi	1–100	Rock, shells, silt	Shells, shingles, barnacles, bryozoans, algae	6.5–10.7	26.90–27.38
M. androsovae	15–30	Rock	Rock	–	–
M. harmsworthi	30–365	Rock, shells, silt	Shells, rock	-1.9–10.4	26.90–34.96
M. cancellata	133–285	–	Barnacles, bryozoans	–	–

TABLE 2. Geographical distributions of species of *Rhamphostomella* and *Mixtoscutella*.

Taxa	Localities																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
R. scabra	+	+		+	+	+	+		+	+	+					+	+	+	+	+	+	+	+	+
R. costata	+	+		+	+	+	+	+	+	+	+				+	+	+	+	+	+	+	+	+	+
R. bilaminata	+	+		+	+	+	+	+	+	+	+	+			+	+		+	+	+	+	+	+	+
R. hincksi		+		+	+	+	+	+		+	+		+		+	+	+		+		+	+		+
R. plicata	+	+			+	+	+			+	+		+	+		+	+	+	+	+	+	+		+
R. radiatula		+			+	+	+		+	+	+		+		+	+	+	+	+	+	+			
R. sibirica	+	+								+	+					+	+		+	+	+	+	+	+
R. cristata		+	+	+	+			+	+		+	+				+	+	+	+		+		+	+
R. spinigera				+	+	+	+		+	+	+	+			+	+	+	+	+	+	+	+		+
R. curvirostrata																								
R. gigantea				+																				+
R. commandorica																								
R. aleutica																								
R. obliqua																								
R. echinata																								
R. alutacea																								
R. pacifica																								
R. microavicularia																								
R. morozovi																								
R. aspera																								
R. multirostrata																								
R. tatarica																								
R. cellata																								
R. townsendi																								
M. ovata	+	+		+	+	+	+	+	+	+	+		+	+		+	+	+	+	+	+	+	+	+
M. ussowi	+									+									+	+	+			
M. harmsworthi		+								+	+				+				+	+	+	+	+	+
M. cancellata																+			+					+
M. androsovae																								

......*continued on the next page*

TABLE 2. (Continued)

Taxa	Localities																				Category
	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
R. scabra		+	+	+		+		+	+	+	+	+									BAC
R. costata		+	+	+		+		+	+	+	+	+				+	+	+	+		BAC
R. bilaminata	+		+			+	+	+				+				+	+	+	+		BAC
R. hincksi						+		+		+							+				BAC
R. plicata		+								+											BAC
R. radiatula			+	+				+			+	+				+		+			BAC
R. sibirica		+	+	+	+		+	+	+	+	+										BAC
R. cristata				+		+					+				+		+	+			HBA
R. spinigera				+											+	+	+	+			HBA
R. curvirostrata				+				+			+		+		+	+		+	+	?	PB
R. gigantea			+			+		+			+			+							PB
R. commandorica				+											+						PHB
R. aleutica					+																PHB
R. obliqua								+							+						PHB
R. echinata				+	+																PHB
R. alutacea						+		+													PAB
R. pacifica			+					+					+								PAB
R. microavicularia								+													PAHB
R. morozovi						+															PAHB
R. aspera								+													PAHB
R. multirostrata								+													PAHB
R. tatarica						+					+										PAHB
R. cellata																			+		EPB
R. townsendi				+	+															+	EPB
M. ovata		+	+			+		+	+	+	+			+				+			BAC
M. ussowi			+	+					+	+	+										BAC
M. harmsworthi			+																		HBA
M. cancellata						+															HBA
M. androsovae								+													PAHB

TABLE 2. Note. Localities: 1. Gulf of Maine; 2. St Lawrence Gulf; 3. Newfoundland; 4. Beaufort Sea; 5. Canadian Arctic Archipelago; 6. Baffin Bay; 7. Davis Strait; 8. Hudson Bay; 9. Labrador; 10. Western Greenland; 11. Eastern Greenland; 12. Greenland Sea; 13. Iceland; 14. Faroe Islands; 15. Jan Mayen; 16. Spitsbergen; 17. Franz-Josef Land; 18. Northern Norway; 19. Barents Sea; 20. White Sea; 21. Kara Sea; 22. Laptev Sea; 23. East-Siberian Sea; 24. Chukchi Sea; 25. Bering Strait; 26. Northwestern part of the Bering Sea (Chaplin Cape, Chukotskiy Cape, Provideniya Bay, Anadyrskiy Gulf, Navarin Cape); 27. Eastern Kamchatka Peninsula; 28. Commander Islands; 29. Amchitka Island, Rat Islands, western Aleutian Islands; 30. Western Kamchatka Peninsula; 31. Northwestern coastal waters of the Sea of Okhotsk (Zavjalov Island, Penzhinskaya, Gizhiginskaya, Yamskaya, and Tauyskaya Inlets, Okhotsk, Ayan); 32. Kuril Islands; 33. Shantar Archipelago; 34. Southeastern Sakhalin Island; 35. Northern part of the Sea of Japan (Tatar Strait, southwestern Sakhalin Island, Primorye, Monneron Island); 36. Pacific coastal waters of Hokkaido Island (Sangar Strait, Akkeshi Bay); 37. Pacific coastal waters of Honshu Island down to Sagami Bay; 38. Northeastern part of the Bering Sea (shelf of Alaska, St Lawrence and Punuk Islands); 39. Adak Island, Andreanof Islands, the Aleutian Islands; 40. Kodiak Island; 41. Cook Inlet; 42. Gulf of Alaska; 43. British Columbia; 44. Lower California (southwest off Channel Islands). Abbreviations: BAC: boreal-Arctic circumpolar; HBA: high-boreal-Arctic; PB: Pacific boreal; PHB: Pacific high-boreal; PAB: Pacific Asian boreal; PAHB: Pacific Asian high-boreal; EPB: Eastern Pacific boreal.

massive, erect foliaceous colonies (*R*. *costata*, *R*. *gigantea*, and *R*. *pacifica*) harbour diverse epibenthic communities, including primarily juvenile barnacles, serpulid and spirorbid worms, ascidians, amphipod and isopod crustaceans, molluscs, ophiuroids, holothurians, hydrozoans and some other erect and encrusting bryozoan species.

Accommodation to benthic communities. In certain types of Arctic and North Pacific benthic assemblages, several *Rhamphostomella* species are highly frequent and abundant. Lukin (1979) reported *R*. *curvirostrata* and *R*. *sibirica* to be common in communities of kelp and the crustose red alga *Clathromorphum loculosum* in the upper sublittoral of Simushir Island, middle Kuril Islands. Similarly, such species as *R*. *cristata*, *R*. *radiatula*, *R*. *sibirica*, and *R*. *spinigera* are typical members of the cryptic community, inhabiting internal cavities formed by the crustose red alga *Clathromorphum nereostratum* in the upper shelf zone (15–40 m depth) of the Commander Islands (Grischenko 1997, 2003b; our data). According to Grishankov (1995), *R*. *bilaminata* and *R*. *radiatula* are highly abundant and form a seafloor biotope in the shallow benthic assemblages of Solovetsky Bay, Onezhsky Gulf, in the White Sea.

Zoogeography

Zoogeographical composition. Rhamphostomella is zoogeographically complex (Table 2). Based on the formal categorization of Golikov (1982), it comprises nine boreal-Arctic species (*R*. *scabra* to *R*. *spinigera*) and fifteen Pacific species (*R*. *curvirostrata* to *R*. *townsendi*) indicating strong predominance of the latter (37.5 to 62.5%).

Boreal-Arctic species include: 1) boreal-Arctic circumpolar species (*R*. *scabra*, *R*. *costata*, *R*. *bilaminata*, *R*. *hincksi*, *R*. *plicata*, *R*. *radiatula*, and *R*. *sibirica*), distributed in Arctic seas around the pole and in boreal zones of the Pacific and Atlantic oceans; and 2) high-boreal-Arctic species (*R*. *cristata* and *R*. *spinigera*), occurring from the Arctic southwards to high-boreal subzones of the Atlantic and Pacific.

Pacific species include: 1) Pacific boreal species (*R*. *curvirostrata* and *R*. *gigantea*), widely distributed in the boreal zone of the Pacific Ocean; 2) Pacific high-boreal species (*R*. *commandorica*, *R*. *aleutica*, *R*. *obliqua*, and *R*. *echinata*), limited in distribution by the high-boreal subzone of the Pacific; 3) Pacific Asian boreal species (*R*. *pacifica* and *R*. *alutacea*), known from the western Kamchatka, Kuril Islands to the Pacific side of Honshu, Japan; 4) Pacific Asian high-boreal species (*R*. *microavicularia*, *R*. *morozovi*, *R*. *aspera*, *R*. *multirostrata*, and *R*. *tatarica*), recorded mostly along western Kamchatka south to the middle Kuril Islands and the northern part of the Sea of Japan; 5) Eastern Pacific boreal species (*R*. *cellata* and *R*. *townsendi*), recorded from Lower California and Vancouver Island, British Columbia westwards to the Commander Islands via the Aleutian Ridge, corresponding to the Oregonian and Aleutian provinces of the Oregonian and Beringian subregions of the boreal Pacific (Golikov *et al*. 1990).

Regional diversity. The diversity of *Rhamphostomella* species (Table 2) varies among regions. Eight species occur in the North Atlantic, ten in the Arctic, and twenty-four in the North Pacific. The pattern of diversity is heterogeneous within the North Pacific Region, with 12 species reported from the northeastern Pacific and 23 of 24 currently known species reported from the northwestern Pacific. Hence, the bulk of diversity is located along the shelf and continental slope of the northwestern Pacific and includes the areas with the highest species richness: western Kamchatka (9 species), Commander Islands (10), and Kuril Islands (14), respectively corresponding to the

Okhotsk or Lamutian, Kurilian and Aleutian provinces of the Beringian subregion of the boreal Pacific (Kussakin 1990). This high diversity is largely the consequence of taxa endemic to the region, as six of the eight newly described species come from various localities in the northwestern Pacific, i.e. the western Kamchatka shelf of the Sea of Okhotsk (*R. morozovi*), middle to southern Kuril Islands (*R. aspera*, *R. microavicularia*, and *R. multirostrata*), and Commander Islands and Amchitka Island of the western stretch of the Commander–Aleutian Ridge (*R. aleutica* and *R. echinata*).

Considering the low diversity and absence of endemic *Rhamphostomella* species in both the North Atlantic and Arctic, the peak of diversity detected in the northwestern Pacific, and the high proportion of regional endemics in the northwestern Pacific, this latter region appears to be the center of origination and speciation for *Rhamphostomella*. The subsequent extension of species into the Arctic and North Atlantic apparently took place via the Bering Strait and then along the shelves of Eurasia and the Canadian Arctic Archipelago.

Identification keys

1. Frontal shield with marginal pores only; frontal pores absent or very few pores occasionally present in most proximal region of shield. 2
- Frontal shield uniformly porous except in suboral region 25
2. Permanent, basally articulated, tubular oral spines present (Figs 22–24) 3
- Oral spines absent or, if present, only ephemeral, mostly on marginal zooids or/and autozooids from zone of astogenetic change (Figs 3A, 11A, C, E, 21B, D) 5
3. Oral spines (2–3 pairs) arranged along lateral margins of secondary orifice; suboral mucro absent (Fig. 24A–H) . . *R. echinata*
- Oral spines arranged along distolateral curvature of secondary orifice (Figs 22C, 23B); suboral mucro present. 4
4. Suboral mucro very tall, incorporating 3–5 spirally arranged avicularia (Fig. 22D–G) . . . . *R. multirostrata*
- Suboral mucro small, elevated, incorporating cystid of asymmetrically placed suboral avicularium (Fig. 23C) . . *R. spinigera*
5. Both suboral and adventitious frontal avicularia present in fully formed colonies (Figs 1–8); adventitious frontal avicularia can be lacking in young colonies, and within zone of astogenetic change and in zooids close to colony margin in mature colonies 6
- Only suboral avicularia present (Figs 9–21) 13
6. Multiple adventitious frontal avicularia, 2–5 per zooid, situated along lateral margins (Fig. 6A–H) . . . . . . *R. microavicularia*
- Frontal avicularium single per zooid 7
7. Suboral avicularium roughly circular to broadly oval in outline, touching proximal margin of orifice (Figs 2A–G, 8A–H) . . 8
- Suboral avicularium elongate-oval to elongate-triangular in outline. 9
8. Proximal margin of primary orifice with low and wide median prominence (Fig. 2J); frontal surface of suboral avicularium crossing zooidal midline, tilted forwards at about 60–90°, facing distolaterally and slightly overhanging proximal margin of primary orifice (Fig. 2B–D); colony encrusting. . . . . *R. commandorica*
- Proximal margin of primary orifice straight or with very weak median convexity (Fig. 8C, J); frontal surface of suboral avicularium overlapping or, more often, not crossing zooidal midline, facing obliquely upwards (Fig. 8C–E); colony initially encrusting, rapidly forming erect bilamellar expansions . . . . *R. pacifica*
9. Proximal margin of primary orifice with anvil-shaped or trapezoidal median lyrula (Fig. 3B, J) . . . . *R. costata*
- Proximal margin of primary orifice lacking lyrula 10
10. Rostrum of suboral and adventitious avicularia with short terminal hook. 11
- Rostrum of suboral and adventitious avicularia lacking terminal hook. 12
11. Rostrum and palate of suboral and adventitious avicularia broadly triangular to semielliptical, with a blunt tip (Fig. 7B–G); colonies initially encrusting, unilaminar, later rising into bilamellar, fan-like expansions . . . .*R. morozovi*
- Rostrum and palate of suboral and adventitious avicularia elongate-triangular, with acute tip (Fig. 4B–H); colony encrusting . . . . *R. cristata*
12. Orifice bell-shaped, with straight proximal margin (Fig. 5J); condyles well developed; suboral avicularian cystid relatively low, inflated; fully formed ooecia overhanging less than half of primary orifice length; colonies initially encrusting but rapidly forming extensive erect, bilamellar, fan-like expansions; autozooid mean length 1.18–1.45 mm . . . .*R. gigantea*
- Orifice irregularly oval, with weak proximal median prominence (Fig. 1J); condyles absent; suboral avicularian cystid cone-shaped and protruding; fully formed ooecia overhanging half to two-thirds of primary orifice length; colonies nearly always encrusting, only occasionally forming small erect bilamellar frills; autozooid mean length 0.82–1.15 mm . . . . *R. scabra*
13. Suboral avicularium situated on midline, rostrum strictly transversely oriented. 14
- Suboral avicularium situated eccentrically on left- or right-side proximal to orifice 15
14. Secondary orifice with broad pseudosinus; frontal surface of avicularium facing obliquely frontally and easily visible in frontal view (Fig. 10A–H) . . . . *R. alutacea*
- Secondary orifice with narrow U-shaped pseudosinus; frontal surface of avicularium facing obliquely distally, hidden, and barely visible frontally (Fig. 18A–H) . . . . *R. radiatula*
15. Primary orifice lacking lyrula or central process 16
- Primary orifice with lyrula or central process 18

16. Proximal margin of primary and secondary orifices with median U-shaped sinus (Fig. 20B, C, J); suboral avicularium with lingulate rostrum, directed distolaterally outwards, extending over surface of neighboring zooid (Fig. 20D–H) . . . .*R. tatarica*
- Proximal margin of primary orifice straight; cystid of suboral avicularium bulbous or conical, strongly elevated, tilted distally and overhanging the orifice; frontal surface of suboral avicularium elongate-oval in outline; ovicell hyperstomial, with ooecium free of secondary calcification 17
17. Proximal margin of primary orifice with broad, low median prominence (Fig. 11C, I, J); suboral avicularian cystid with acute conical apex (Fig. 11D–G); rostrum of suboral avicularium facing laterally to proximolaterally (Fig. 11B, D–H); interareolar ridges long, prominent, solid, continuing to apex of avicularian cystid (Fig. 11D, E); frontal surface evenly coarse, giving a shaggy appearance . . . . *R. aspera*
- Proximal margin of primary orifice straight (Fig. 16C, I, J); suboral avicularian cystid with blunt apex (Fig. 16H); rostrum of suboral avicularium facing distolaterally to laterally (Fig. 16C, D, F, H); interareolar ridges short and low, reaching only the sides of the avicularian cystid in the distal half of zooid (Fig. 16A, E–G); frontal surface smooth to finely granular, except for the coarsely granulated surface of the avicularian cystid . . . .*R. obliqua*
18. Suboral avicularium with long, curved (Fig. 14A, D–F) or, less frequently, straight rostrum (Fig. 14C, G), crossing the orifice obliquely and reaching/fusing with peristomial lappet on opposite side of peristome (Fig. 14E, H) . . . . *R. curvirostrata*
- Suboral avicularian rostrum shorter and not crossing the orifice obliquely 19
19. Peristomial lappets with marginal, spine-like tubular projections, 2–4 on each side (Fig. 9A, B, D–H) . . . . *R. aleutica*
- Peristomial lappets with smooth edges. 20
20. Frontal shield conspicuously dimpled/tessellated, giving a reticulate appearance 21
- Frontal shield smooth to very finely dimpled. 22
21. Rostrum of suboral avicularium lodged within rim of peristome, slightly curving inwardly to conform to it; rostrum of avicularium to one side of zooidal midline, facing obliquely frontally (Fig. 13C, E, H); mandible semi-oval in non-ovicellate zooids (Fig. 13C, E), roundly triangular in ovicellate zooids (Fig. 13H). . . . . *R. cellata*
- Rostrum of suboral avicularium slightly extending across and overhanging proximal margin of orifice, gently curved, directed obliquely medially to laterally and upwards (Fig. 21B–H); frontal surface of avicularium crossing zooidal midline, facing obliquely proximally to proximolaterally (Fig. 21D, H); mandible elongate-triangular, with rounded or pointed tip (Fig. 21C, E, H) . . . .*R. townsendi*
22. Interareolar ridges short, weakly to moderately developed 23
- Interareolar ridges well-developed, giving strongly costate appearance to frontal shield 24
23. Interareolar ridges lacking or developed only in distal half of autozooid (Fig. 17D–G); zooidal vertical walls moderately raised; frontal surface of suboral avicularium straight, mandible elongate-triangular (Fig. 17C) . . . . *R. plicata*
- Interareolar ridges short, radially arranged (Fig. 12E–H); zooidal vertical walls strongly raised; frontal surface of suboral avicularium slightly curved, mandible elongate-oval (Fig. 12C) . . . . *R. bilaminata*
24. Proximal margin of primary orifice sinuate or occasionally bisinuate, in latter case with small, pointed process (Fig. 15B, I); process occasionally lacking . . . . *R. hincksi*
- Proximal margin of primary orifice concave (Fig. 19B, I), with a median bifid lyrula (Fig. 19C) . . . . *R. sibirica*
25. Both suboral and adventitious frontal avicularia present in fully formed colonies 26
- Only suboral avicularium present in fully developed colonies 27
26. Primary orifice with central tooth (Fig. 29A–C); adventitious frontal and suboral avicularia small, nearly identical in size and form; frontal avicularia located mostly in distal half of zooid . . . . *M. androsovae*
- Primary orifice with shallow concave margin, lacking lyrula (Fig. 27B, J); adventitious frontal avicularia 1.4–1.9 times larger than suboral avicularia, located in central to proximal part of frontal shield (Fig. 27E, G) . . . . *M. ovata*
27. Primary orifice with central denticle (Fig. 29G–I). . . . . *M. cancellata*
- Primary orifice lacking denticle, with U-shaped sinus and sharp, downcurved condyles 28
28. Suboral avicularium adjoining proximal margin of orifice (Fig. 28C); frontal surface of avicularium angular, crossing zooidal midline, tilted ahead, facing obliquely distally (Fig. 28B, D, G) . . . . *M. ussowi*
- Suboral avicularium separated from proximal margin of orifice by distance about equivalent to avicularium width and located slightly laterally from zooidal midline; frontal surface of avicularium straight, facing obliquely upwards (Fig. 29D, E) . . . . *M. harmsworthi*

Acknowledgements

We are grateful to Dr Valentina I. Gontar (Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia), Professor Dr Matthew H. Dick (Hokkaido University, Sapporo, Japan), Ms Nora R. Foster (Museum of the North, University of Alaska, Fairbanks, USA), Dr Alan Cheetham (United States National Museum, Washington DC, USA), Dr Joann Sanner (Smithsonian Institution, Washington DC, USA), Dr Sabine Stöhr (Swedish Museum of Natural History, Stockholm, Sweden), Ms Anita Eschner (Natural History Museum, Vienna, Austria), Dr Emanuela Di Martino and Ms Ann-Helén Rønning (Natural History Museum, University of Oslo), Mr Taras B. Morozov (Kamchatka Research Institute of Fisheries and Oceanography, Petropavlovsk-Kamchatsky, Russia) and Dr Natalya V. Kameneva, Dr Alexei V. Chernyshev, and Dr Alexandra P. Tsurpalo (A.V. Zhirmunsky National Scientific Center of Marine Biology, Vladivostok, Russia) for specimen loans, SEM and optical photos;

Mr Yoshinobu Nodasaka (Hokkaido University, Sapporo, Japan) for assistance in scanning electron microscopy; Professor Shunsuke F. Mawatari (Hokkaido University, Sapporo, Japan) for discussion; Professor Dr Matthew H. Dick (Hokkaido University, Sapporo, Japan) and Professor Dr Antonietta Rosso (University of Catania, Catania, Italy) for thorough peer review. Dr Matthias Obst (Department of Marine Sciences, University of Gothenburg, Sweden), helped with translation of old literature. Professor Dr Claus Nielsen (Natural History Museum of Denmark, University of Copenhagen, Denmark) and Dr Phil Bock (Museum Victoria, Melbourne, Australia) kindly helped with old literature. The present study was partly conducted within a framework of the project "Biodiversity of the World Ocean: taxonomy, bar-coding, phylogenetics, reproductive and evolutionary biology, biogeography" (State Registration No 121082600036-9) (Andrei Grischenko as a participant). Piotr Kuklinski thanks National Science Centre, Poland (grant 2016/23/B/ST10/01936), and Andrew Ostrovsky thanks the Russian Foundation for Basic Research (grant 13-04-00758-a) (research on skeletal morphology) and the Russian Science Foundation (grant 18-14-00086) (research on brooding structures), for financial support. Nina Denisenko work was supported by budget funding of the Russian Academy of Sciences under grant No 1021051402797-9.

References

Abildgaard, P.C. (1806) Descripsit et tabulas. *In*: Müller, O.F. (Ed.), *Zoologica Danica, seu Animalium Daniae et Norvegiae Rariorum ac Minus Notorum Descriptiones et Historia*. Volume 4. Havniae, Copenhagen, pp. 1–46. https://doi.org/10.5962/bhl.title.63796

Andersson, K.A. (1902) Bryozoen, während der schwedischen Expeditionen 1898 und 1899 unter Leitung von Professor A.G. Nathorst und 1900 unter Leitung von Conservator G. Kolthoff gesammelt. *Zoologischer Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 15, 537–560.

Androsova, E.I. (1958) Bryozoa of the order Cheilostomata of the northern part of the Sea of Japan. *Explorations of the Far Eastern Seas of the USSR*, 5, 90–204. [in Russian]

Androsova, E.I. (1977) Bryozoa in the biocenoses of the Arctic Ocean (Franz Josef Land). *Explorations of the Fauna of the Seas*, 14, 194–204. [in Russian with English summary]

Barnes, D.K.A. & Dick, M.H. (2000) Overgrowth competition in encrusting bryozoan assemblages of the intertidal and infralittoral zones of Alaska. *Marine Biology*, 136, 813–822. https://doi.org/10.1007/s002270000253

Bassler, R.S. (1953) Bryozoa. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology*. Geological Society of America & University of Kansas, Lawrence, Kansas, pp. 1–253.

Bennike, O., Hansen, K.B., Knudsen, K.L., Penney, D.N. & Rasmussen, K.L. (1994) Quaternary marine stratigraphy and geochronology in central West Greenland. *Boreas*, 23, 194–215. https://doi.org/10.1111/j.1502-3885.1994.tb00599.x

Bidenkap, O. (1900a) Die Bryozoen. I Teil: Die Bryozoen von Spitzbergen und Konig-Karls-Land. *Fauna Arctica*, 1, 503–540.

Bidenkap, O. (1900b) Zoologische Ergebnisse einer Untersuchungsfahrt des Deutschen Seefischerei-Vereins nach der Bäreninsel und Westspitzbergen, ausgefurt im Sommer 1898 auf S.M.S 'Olga'. III. Die Bryozoen. *Wissenschaftliche Meeresuntersuchungen*, Neue Folge, 4, 249–263.

Bock, P.E. & Gordon, D.P. (2013) Phylum Bryozoa Ehrenberg, 1831. *In*: Zhang, Z.-Q. (Ed.), *Animal Biodiversity*: *An Outline of High-level Classification and Survey of Taxonomic Richness* (Addenda 2013). *Zootaxa*, 3703 (1), 67–74. https://doi.org/10.11646/zootaxa.3703.1.14

Brezina, S., Taylor, P.D., Romero, M.V., Palópolo, E.E. & Casadio, S. (2021) Late Maastrichtian and Danian bryozoans from Northern Patagonia, Argentina. *Cretaceous Research*, 125, 104845. https://doi.org/10.1016/j.cretres.2021.104845

Busk, G. (1852) An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago. *In*: MacGillivray, J. (Ed.), *Narrative of the Voyage of H.M.S. 'Rattlesnake', Commanded by the Late Captain Owen Stanley During the Years 1846–1850; Including Discoveries and Surveys in New Guinea, the Louisiade Archipelago, Etc., to Which is Added the Account of Mr E.B. Kennedy's Expedition for the Exploration of the Cape York Peninsula [Including Mr Carron's Narrative]*. T.W. Boone, London, pp. 343–402.

Cáceres-Chamizo, J.P., Sanner, J., Tilbrook, K.J. & Ostrovsky, A.N. (2017) Revision of the Recent species of *Exechonella* Canu and Bassler in Duvergier, 1924 and *Actisecos* Canu & Bassler, 1927 (Bryozoa, Cheilostomata): Systematics, biogeography and evolutionary trends in skeletal morphology. *Zootaxa*, 4305 (1), 1–79. https://doi.org/10.11646/zootaxa.4305.1.1

Canu, F. (1904) Les bryozoaires du Patagonien. Échelle des bryozoaires pour les terrains Tertiares. *Mémoires de la Société Géologique de France. Paléontologie*, 12, 1–30.

Canu, F. (1908) Iconographie des bryozoaires fossiles de l'Argentine, pt 1. *Anales del Museo Nacional de Buenos Aires*, 10, 245–341.

Canu, F. (1916) Les bryozoaires fossiles des terrains du Sud-Ouest de la France. *Bulletin de la Société Géologique de France*, Série 4, 15, 320–334.
Canu, F. (1919) Les bryozoaires fossiles des terrains du Sud-Ouest de la France. *Bulletin de la Société Géologique de France*, Série 4, 17, 350–361.
Canu, F. & Bassler, R.S. (1917) A synopsis of American early Tertiary cheilostome Bryozoa. *Bulletin of the United States National Museum*, 96, 5–87.
https://doi.org/10.5479/si.03629236.96.1
Canu, F. & Bassler, R.S. (1919) Fossil Bryozoa from the West Indies. *Publications of the Carnegie Institution*, 291, 75–102.
Canu, F. & Bassler, R.S. (1920) North American early Tertiary Bryozoa. *Bulletin of the United States National Museum*, 106, 1–879.
https://doi.org/10.5479/si.03629236.106.i
Canu, F. & Bassler, R.S. (1923) North American later Tertiary and Quaternary Bryozoa. *Bulletin of the United States National Museum*, 125, 1–302.
https://doi.org/10.5479/si.03629236.125.i
Canu, F. & Bassler, R.S. (1929) Bryozoa of the Philippine Region. *Bulletin of the United States National Museum*, 100, 1–685.
Denisenko, N.V. (1984) Species composition and distribution of the Bryozoa in the intertidal of some inlets of the Eastern Murman. *In*: Semyonov, V.N. (Ed.), *Benthos of the Barentz Sea*. Kolsky Division of the Academy of Sciences of the USSR, Appatity, USSR, pp. 71–79. [in Russian]
Denisenko, N.V. (1988) *Distribution and Ecology of Bryozoa of the Barents Sea and Adjacent Areas of the Arctic Ocean*. Unpublished PhD Thesis, Zoological Institute, Leningrad, USSR, 207 pp. [in Russian]
Denisenko, N.V. (1990) Distribution and ecology of Bryozoa of the Barents Sea. Kolsky Scientific Center of the Academy of Sciences of the USSR, Appatity, USSR, 156 pp. [in Russian]
Denisenko, N.V. (2008) Bryozoans of the Chukchi Sea and the Bering Strait. *Explorations of the Fauna of the Seas*, 61, 163–198. [in Russian with English summary]
Denisenko, N.V. (2011) Bryozoans of the East Siberian Sea: History of research and current knowledge of diversity. *In*: Wyse Jackson, P.N. & Spencer Jones, M.E. (Eds.), *Annals of Bryozoology 3: Aspects of the History of Research on Bryozoans*. International Bryozoology Association, Dublin, pp. 1–15.
Denisenko, N.V. (2013) Phylum Bryozoa. Check-list of species of free-living invertebrates of the Russian Far Eastern Seas. *Explorations of the Fauna of the Seas*, 75, 178–188.
Denisenko, N.V. (2021) Bryozoans of the Kara Sea: Estimation of species diversity and patterns of biogeographic composition. *Proceedings of Zoological Institute RAS*, 325 (2), 217–234. [in Russian with English summary]
https://doi.org/10.31610/trudyzin/2021.325.2.217
Denisenko, N.V. & Blicher, M.E. (2021) Bryozoan diversity, biogeographic patterns and distribution in Greenland waters. *Marine Biodiversity*, 51, 73. https://doi.org/10.1007/s12526-021-01213-9
Denisenko, N.V. & Kuklinski, P. (2008) Historical development of research and current state of bryozoan diversity in the Chukchi Sea. *In*: Wyse Jackson, P.N. & Spencer Jones, M.E. (Eds.), *Annals of Bryozoology 2: Aspects of the History of Research on Bryozoans*. International Bryozoology Association, Dublin, pp. 35–50.
Denisenko, N.V., Hayward, P.J., Tendal, O.S. & Sørensen, J. (2016) Diversity and biogeographic patterns of the bryozoan fauna of the Faroe Islands. *Marine Biology Research*, 12 (4), 360–378.
https://doi.org/10.1080/17451000.2016.1148817
Dick, M.H. & Ross, J.R.P. (1986) Intertidal cheilostome bryozoans in rock-pile habitat at Narrow Strait, Kodiak, Alaska. *In*: Nielsen, C. & Larwood, G.P. (Eds.), *Bryozoa: Ordovician to Recent*. Olsen & Olsen, Fredensborg, pp. 87–93.
Dick, M.H. & Ross, J.R.P. (1988) Intertidal Bryozoa (Cheilostomata) of the Kodiak Vicinity, Alaska. *Occasional Paper: Center for Pacific Northwest Studies*. *Western Washington University*, 23, 1–133.
Ehrenberg, C.G. (1831) *Symbolae Physicae. Animalia Evertebrata Exclusis Insectis*. Berolini ex Officina Academica, Berlin, 135 pp.
Fabricius, O. (1780) *Fauna Groenlandica: Systematice Sistens Animalia Groenlandiae Occidentalis Hactenus Indagata, quod Nomen Specificium*. Hafniae & Lipsiae, Copenhagen, 452 pp.
https://doi.org/10.5962/bhl.title.13489
Fabricius, O. (1824) Nye zoologiske bidrag. *Kongelige Danske Videnskabernes Selskab*, 1, 25–80.
Foster, N.R. (2010) *Evaluating a Potential Relict Arctic Invertebrate and Algal Community on the West Side of Cook Inlet*. University of Alaska, Fairbanks, 75 pp.
Ghiurca, V. & Mongereau, N. (1981) La faune de Bryozoaires eocènes d'Europe orientale. *In*: Larwood, G.P. & Nielsen, C. (Eds.), *Recent and Fossil Bryozoa*. Olsen & Olsen, Fredensborg, pp. 93–100.
Golikov, A.N. (1982) On the principles of regionalization and unification of terminology in marine biogeography. *In*: Kusakin, O.G. (Ed.), *Marine Biogeography, Its Subject, Methods, and Principles of Regionalization*. Nauka, Moscow, pp. 94–99. [in Russian]
Golikov, A.N., Dolgolenko, M.A., Maximovich, N.V. & Scarlato, O.A. (1990) Theoretical approaches to marine biogeography. *Marine Ecology Progress Series*, 63, 289–301.
https://doi.org/10.3354/MEPS063289
Gontar, V.I. (1979) Bryozoa of the order Cheilostomata in shallow water off Simushir Island. *In*: Kussakin, O.G. (Ed.), *Biology*

of the Shelf of the Kuril Islands. Nauka, Moscow, USSR, pp. 234–248 [in Russian]
Gontar, V.I. (1980) *Bryozoan Fauna of the Order Cheilostomata of the Kuril Islands Coastal Waters*. Unpublished PhD Thesis, Zoological Institute, Leningrad, USSR, 226 pp. [in Russian]
Gontar, V.I. (1989) Phylum Bryozoa. The list of macrophytes and invertebrates of the macrobenthos of the Avacha Inlet. *In*: Kussakin, O.G. (Ed.), *Hydrobiological Explorations in the Avacha Inlet*. Far East Division of the Academy of Sciences of USSR, Vladivostok, USSR, pp. 113. [in Russian]
Gontar, V.I. (1990) Bryozoa of the Laptev Sea and New Siberian shoals. *Explorations of the Fauna of the Seas*, 37, 130–138. [in Russian with English summary]
Gontar, V.I. (1992) Bryozoan fauna of the order Cheilostomida of the coastal waters of the Kuril Islands. Deposited manuscript in the Department of Scientific Publications of the Scientific-Industrial Ecological Center 'Veras-Eko' and the Zoological Institute of Belarus, Minsk, Belarus. [in Russian]
Gontar, V.I. (1993a) New species of Cheilostomida from the Kuril Islands (Bryozoa). *Zoosystematica Rossica*, 1, 9–12.
Gontar, V.I. (1993b) Phylum Bryozoa. List of invertebrate species of the continental slope of the Kuril Islands. *Exploration of the Fauna of the Seas*, 46, 200–203. [in Russian]
Gontar, V.I. (1994a) Distribution and ecology of Bryozoa in the coastal waters of the Chuan Bay of the East Siberian Sea. *Explorations of the Fauna of the Seas*, 47, 144–147. [in Russian with English summary]
Gontar, V.I. (1994b) Phylum Tentaculata, class Bryozoa. Systematical composition of macrobenthos of the ecosystems of the Chuan Bay of the East-Siberian Sea. *Explorations of the Fauna of the Seas*, 47, 104–106. [in Russian]
Gontar, V.I. (1996) Bryozoa collected by the 'Polarstern' expedition in 1991 and 1993. *Zoosystematica Rossica*, 4, 45–47.
Gontar, V.I. (2010) Benthic fauna of the Bryozoa in Chukchi Sea. *Vestnik Ecologii*, *Lesovedeniya i Landschaftovedeniya*, 10, 139–155. [in Russian with English summary]
Gontar, V.I. (2013) Bryozoa of the Providence Bay of the Bering Sea. *GISAP: Biology, Veterinary Medicine and Agricultural Science*, 2, 30–33. [in Russian]
Gontar, V.I. & Denisenko, N.V. (1989) Arctic Ocean Bryozoa. *In*: Herman, Y. (Ed.), *The Arctic Seas. Climatology, Oceanography, Geology, and Biology*. Van Nostrand Reinhold Company, New York, USA, pp. 341–371. https://doi.org/10.1007/978-1-4613-0677-1_14
Gontar, V.I., Hop, H. & Voronkov, A. Yu. (2001) Diversity and distribution of Bryozoa in Kongsfjorden, Svalbard. *Polish Polar Research*, 22, 187–204.
Gordon, D.P. (1984) The marine fauna of New Zealand: Gymnolaemata from the Kermadec Ridge. *New Zealand Oceanographic Institute Memoir*, 91, 1–198.
Gordon, D.P. (1992) A new species of Chaperiidae (Bryozoa, Gymnolaemata) from New Zealand, with excessive spination. *Abhandlungen der naturwissenschaftlichen Vereins Hamburg*, Neue Folge, 33, 115−120.
Gordon, D.P. (1994) Tertiary bryozoan genera in the present-day Australasian fauna—implications for classification and biogeography. *Invertebrate Taxonomy*, 8, 283−298. https://doi.org/10.1071/IT9940283
Gordon, D.P. (2000) Towards a phylogeny of cheilostomes—morphological models of frontal wall/shield evolution. *In*: Herrera Cubilla, A. & Jackson, J.B.C. (Eds.), *Proceedings of the 11th International Bryozoology Association Conference*. Smithsonian Tropical Research Institute, Balboa, pp. 17–37.
Gordon, D.P. & Grischenko, A.V. (1994) Bryozoan frontal shields: the type species of *Desmacystis*, *Rhamphostomella*, *Rhamphosmittina*, *Rhamphostomellina*, and new genus *Arctonula*. *Zoologica Scripta*, 23, 61–72. https://doi.org/10.1111/j.1463-6409.1994.tb00374.x
Gordon, D.P. & Taylor, P.D. (2015) Bryozoa of the early Eocene Tumaio Limestone, Chatham Island, New Zealand. *Systematic Palaeontology*, 13, 983–1070. https://doi.org/10.1080/14772019.2014.991905
Gordon, D.P. & Voigt, E. (1996) The kenozooidal origin of the ascophorine hypostegal coelom and associated frontal shield. *In*: Gordon, D.P., Smith, A.M. & Grant-Mackie, J.A. (Eds.), *Bryozoans in Space and Time*. National Institute of Water and Atmospheric Research, Wellington, pp. 89–107.
Gostilovskaya, M.G. (1957) Bryozoa of the White Sea. *Materials of Complex Investigations of the White Sea*, 1, 434–471. [in Russian]
Gostilovskaya, M.G. (1964) Bryozoa collected by the expedition in the ice-breaker 'F. Litke' to the north of Franz Josef Land and Spitzbergen. *Transactions of the Institute of Arctic and Antarctic*, 259, 191–228. [in Russian]
Gostilovskaya, M.G. (1968) Bryozoa of the Cheschskaya Inlet of the Barents Sea. *Transactions of the Murmansk Marine Biological Institute of the Academy of Sciences of the USSR*, 17, 58–74. [in Russian]
Gostilovskaya, M.G. (1978) *Bryozoa of the White Sea*. Nauka, Leningrad, USSR, 248 pp. [in Russian]
Gray, J.E. (1848) *List of the specimens of British animals in the collections of the British Museum*. *Part 1*. *Centrionae or radiated animals*. Trustees of the British Museum, London, pp. 91–151.
Grischankov, A.V. (1995) *Fauna and Some Peculiarities of the Benthic Communities Structure of Solovetsky Bay* (*Onezhsky Gulf of the White Sea*). Unpublished PhD Thesis, Saint Petersburg State University, Saint Petersburg, 145 pp. [in Russian]
Grischenko, A.V. (1997) Bryozoans (Ctenostomida, Cheilostomida) of the shelf zone of the Commander Islands. *In*: Rzhavsky, A.V. (Ed.), *Benthic Flora and Fauna of the Shelf Zone of the Commander Islands*. Dalnauka, Vladivostok, pp. 153–192. [in Russian with English summary]

Grischenko, A.V. (2001) Red king crab as the mobile substrate for Bryozoa in the western Kamchatka shelf. *In*: Tokranov, A.M. (Ed.), *Conservation of Biodiversity of Kamchatka and Coastal Waters*: *Materials of the 2nd International Scientific Conference*. KamchatNIRO, Petropavlovsk-Kamchatsky, pp. 46–47. [in Russian]

Grischenko, A.V. (2002) History of investigations and current state of knowledge of bryozoan species diversity in the Bering Sea. *In*: Wyse Jackson, P.N. & Spencer Jones, M.E. (Eds.), *Annals of Bryozoology 2: Aspects of the History of Research on Bryozoans*. International Bryozoology Association, Dublin, pp. 97–116.

Grischenko, A.V. (2003a) *Taxonomy of the Cheilostome Bryozoan Rhamphostomella*. Unpublished MSc Thesis, Hokkaido University, Sapporo, 132 pp.

Grischenko, A.V. (2003b) Bryozoa as a component of endolithofauna of crustose coralline algae of the shelf zone of the Commander Islands. *In*: Tokranov, A.M. (Ed.), *Conservation of Biodiversity of Kamchatka and Coastal Waters*: *Materials of the 4th International Scientific Conference*. KamchatNIRO, Petropavlovsk-Kamchatsky, pp. 235–238. [in Russian]

Grischenko, A.V. (2004) Intertidal Bryozoa of the Commander Islands. *In*: Tokranov, A.M. (Ed.), *Conservation of Biodiversity of Kamchatka and Coastal Waters*: *Materials of the 5th Scientific Conference*. KamchatNIRO, Petropavlovsk-Kamchatsky, pp. 38–43. [in Russian]

Grischenko, A.V. (2013) First record of a bathyal bryozoan fauna from the Sea of Japan. *Deep-Sea Research II*, 86–87, 172–180.
https://doi.org/10.1016/j.dsr2.2012.08.003

Grischenko, A.V. (2014) First data on intertidal Bryozoa of the Koni Peninsula, Sea of Okhotsk. *Bulletin of Perm University*, Zoology, 4, 16–23. [in Russian with English summary]

Grischenko, A.V. (2015) To the cheilostome bryozoan fauna from the continental slope of western Kamchatka. *In*: Tokranov, A.M. (Ed.), *Conservation of Biodiversity of Kamchatka and Coastal Waters*: *Materials of 16th International Scientific Conference*. Kamchatpress, Petropavlovsk-Kamchatsky, pp. 37–42. [in Russian]

Grischenko, A.V., Gordon, D.P. & Taylor, P.D. (1999) A unique new genus of cheilostomate bryozoan with reversed-polarity zooidal budding. *Asian Marine Biology*, 15, 105–117.

Grischenko, A.V. & Mawatari, S.F. (2002) *Kubaninella*: a new genus of Adeonidae (Bryozoa: Cheilostomata) from the western Kamchatka shelf of the Sea of Okhotsk. *In*: Wyse Jackson, P.N., Buttler, C.J. & Spencer Jones, M.E. (Eds.), *Bryozoan Studies 2001*: *Proceedings of the 12th International Bryozoology Association Conference*. Balkema, Lisse, pp. 125–130.

Grischenko, A.V. & Ivanyushina, E.A. (2002) Hermatypic Bryozoa of the shelf zone of the Commander Islands. *In*: Tokranov, A.M. (Ed.), *Conservation of Biodiversity of Kamchatka and Coastal Waters*: *Materials of the 3rd Scientific Conference*. KamchatNIRO, Petropavlovsk-Kamchatsky, pp. 32–35. [in Russian]

Guha, A.K. & Gopikrishna, K. (2007) Some fossil ascophoran bryozoan taxa from Tertiary sequences of western Kachchh, Gujarat. *Journal of the Palaeontological Society of India*, 52, 195–222.

Hansen, B.K. (1962) Bryozoa. The Gotthaab Expedition 1928. *Meddelelser om Grønland*, 81, 3–74.

Harmer, S.F. (1957) The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora. II. *Siboga Expedition*, 28d, 641–1147.

Hayami, T. (1970) Miocene Bryozoa from southwest Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, 79, 316–336.

Hayami, T. (1973) The recent Cheilostomata (Bryozoa) from Kyuroku-Scima, Northern Honshu, Japan. *Saito Ho-on Kai Museum Research Bulletin*, 42, 47–56.

Hayami, T. (1975) Neogene Bryozoa from northern Japan. *Science Reports of the Tohuku University, Sendai*, Series 2, Geology, 45, 83–126.

Hayward, P.J. (1975) A new species of epiphytic bryozoan from the Aegean Sea. *Cahiers de Biologie Marine*, 16, 207–212.

Hayward, P.J. & Ryland, J.S. (1979) British Ascophoran Bryozoans. Key and notes for the identification of the species. *In*: Kermack, D.M. & Barnes, R.S.K. (Eds.), *Linnean Society synopses of the British Fauna. New Series. Vol. 14*. Academic Press, London, pp. 1–312.

Hayward, P.J. & Thorpe, J.P. (1988) New genera of Antarctic cheilostome Bryozoa. *Cahiers de Biologie Marine*, 29, 277–296.

Hennig, A.H. (1896) Bryozoer från Westgrönland, samlade af Dr Ohlin under 'the Peary auxiliary expedition' ar 1894. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 53, 351–365.

Hincks, T. (1877) On Polyzoa from Iceland and Labrador. *Annals and Magazine of Natural History*, Series 4, 19, 97–112.
https://doi.org/10.1080/00222937708682099

Hincks, T. (1889) The Polyzoa of the St. Lawrence, a study of arctic forms. *Annals and Magazine of Natural History*, Series 6, 3, 424–433.
https://doi.org/10.1080/00222938909460362

Hirose, M. (2010) *Cheilostomatous Bryozoa (Gymnolaemata) from Sagami Bay, with Note on Bryozoan Diversity and Faunal Changes over the Past 130 years*. Unpublished PhD Thesis, Hokkaido University, Sapporo, 180 pp.

d'Hondt, J.-L. (1985) Contribution à la systématique des Bryozoaires Eurystomes. Apports récents et nouvelles propositions. *Annales des Sciences Naturelles*, *Zoologie et Biologie Animale*, 7, 1–12.

Kataoka, J. (1957) Bryozoa from the Daishaka Formation (Pliocene) Minami-Tsugaru-gun, Aomori Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan*, New Series, 28, 143–153.

Kessler, D.W. (1985) Alaska's Saltwater Fishes and Other Sea Life: A Field Guide. Alaska Northwest Publications, Anchorage, Alaska, 358 pp.

Kluge, G.A. (1906) Zoologische Ergebnisse einer Untersuchungsfahrt des Deutschen Seefischerei-Vereins nach der Bäreninsel und Westspitzbergen, ausgefurt im Sommer 1898 auf S.M.S. 'Olga'. VIII. Ergänzungsbericht über die von der 'Olga'–Expedition gesammelten Bryozoen. *Wissenschaftliche Meeresuntersuchungen*, Neue Folge, 8, 31–55.
Kluge, G.A. (1907) Kritische Erörterungen zu den Bryozoologischen Arbeiten von K. Chworostansky. *Archiv für Naturgeschichte*, 1, 181–204.
Kluge, G.A. (1908a) Beiträge zur Kenntnis der Bryozoen des Weissen Meeres. *Annual Reports of the Zoological Museum of the Imperial Academy of Sciences*, *Saint Petersburg*, 12, 515–540.
Kluge, G.A. (1908b) Zur Kenntnis der Bryozoen von West-Grönland. *Annual Reports of the Zoological Museum of the Imperial Academy of Sciences, Saint Petersburg*, 12, 546–554.
Kluge, G.A. (1915) Bryozoa. *In*: Derjugin, K. (Ed.), *Fauna of the Kolsky Gulf and Conditions of its Existence*. *Zapiski Academii Nauk*, Series 8, 34, 376–393. [in Russian]
Kluge, G.A. (1928) Bryozoa. *In*: Derjugin, K. (Ed.), *Fauna of the White Sea and Conditions of its Existence. Issledovanija Morey USSR*, 7–8, 253–258. [in Russian]
Kluge, G.A. (1929) Die Bryozoen des sibirischen Eismeers. *Raboty Murmanskoy Biologicheskoy Stantsii*, 3, 1–33.
Kluge, G.A. (1952) Bryozoa of the Chukchi Sea and the Bering Strait. *In*: Ushakov, P.V. (Ed.), *Far North-East of the USSR. Vol. 2. Fauna and Flora of the Chukchi Sea*. Academy of Sciences of the USSR, Moscow, Leningrad, USSR, pp. 138–168. [in Russian]
Kluge, G.A. (1953) Class Bryozoa. *In*: Ushakov, P.V. (Ed.), *Fauna of the Sea of Okhotsk and Conditions of its Existence*. Academy of Sciences of the USSR, Leningrad, USSR, pp. 169–179. [in Russian]
Kluge, G.A. (1955) Bryozoa. *In*: Ushakov, P.V. (Ed.), *Atlas of Invertebrates of the Far Eastern Seas of the USSR*. Academy of Sciences of the USSR, Moscow, Leningrad, USSR, pp. 99–109. [in Russian]
Kluge, G.A. (1961) Species list of Bryozoa of the Far Eastern Seas of the USSR. *Explorations of the Far Eastern Seas of the USSR*, 7, 118–143. [in Russian]
Kluge, G.A. (1962) Bryozoa of the northern Seas of the USSR. *Identification Keys on the Fauna of the USSR*, 76, 1–584. [in Russian]
Kluge, G.A. (1964) Bryozoa from the region of Franz-Josef Land. *Transactions of the Institute of Arctic and Antarctic*, 259, 181–190. [in Russian]
Kluge, G.A. (1975) *Bryozoa of the Northern Seas of the USSR*. Amerind Publishing, New Delhi, 711 pp.
Kluge, G.A., Androsova, E.I. & Gostilovskaya, M.G. (1959) Class Bryozoa. The list of marine fauna of the southern Sakhalin and southern Kuril Islands. *Explorations of the Far Eastern Seas of the USSR*, 6, 173–256. [in Russian]
Kubanin, A.A. (1975) Bryozoa of the order Cheilostomata of the Peter the Great Gulf of the Sea of Japan. *In*: Zevina, G.B. (Ed.), *Fouling in the Japan and Okhotsk Seas*. Far Eastern Branch of the Academy of Sciences of the USSR, Vladivostok, USSR, pp. 108–136. [in Russian with English summary]
Kubanin, A.A. (1976) Intertidal Bryozoa of Zavyalov Island (Sea of Okhotsk). *Biologiya Morya*, 1, 30–35. [in Russian with English summary]
Kubanin, A.A. (1997) Phylum Tentaculata, subphylum Bryozoa. *In*: Kussakin, O.G., Ivanova, M.B. & Tsurpalo, A.P. (Eds.), *A check-list of Animals, Plants and Fungi from the Intertidal Zone of Far Eastern Seas of Russia*. Dalnauka, Vladivostok, pp. 119–125. [in Russian]
Kuklinski, P. (2002a) Bryozoa of the high Arctic fjord—a preliminary study. *In*: Wyse Jackson, P.N., Buttler, C.J. & Spencer Jones, M.E. (Eds.), *Bryozoan Studies 2001: Proceedings of the 12th International Bryozoology Association Conference*. Balkema, Lisse, pp. 175–182.
Kuklinski, P. (2002b) Fauna of Bryozoa from Kongsfjorden, West Spitsbergen. *Polish Polar Research*, 23, 193–206.
Kuklinski, P. (2009) Ecology of stone-encrusting organisms in the Greenland Sea – a review. *Polar Research*, 28, 222–237. https://doi.org/10.1111/j.1751-8369.2009.00105.x
Kuklinski, P. & Bader, B. (2007a) Diversity, structure and interactions of encrusting lithophyllic macrofaunal assemblages from Belgica Bank, East Greenland. *Polar Biology*, 30, 709–717. https://doi.org/10.1007/s00300-006-0228-0
Kuklinski, P. & Bader, B. (2007b) Comparison of bryozoan assemblages from two contrasting Arctic shelf regions. *Estuarine, Coastal and Shelf Science*, 73, 835–843. https://doi.org/10.1016/j.ecss.2007.03.024
Kuklinski, P. & Taylor, P.D. (2009) Mineralogy of Arctic bryozoan skeletons in a global context. *Facies*, 55, 489–500. https://doi.org/10.1007/s10347-009-0179-3
Kussakin, O.G. (1990) Biogeography of isopod crustaceans in the Boreal Pacific. *Bulletin of Marine Science*, 46, 620–639.
Kuznetsov, V.V. (1941) The dynamic of the biocenoses *Microporella ciliata* in the Barents Sea. *Transactions of the Zoological Institute of the Academy of Science of the USSR*, 7, 114–139. [in Russian]
Labracherie, M. & Sigal, J. (1976) Les Bryozoaires cheilostomes des formation Éocène inférieur du Site 246 (crosiere 25, Deep Sea Drilling Project). *In*: Pouyet, S. (Ed.), *Bryozoa 1974*. Université Claude Bernard, Lyon, pp. 449–466.
Lagaaij, R. (1952) The Pliocene Bryozoa of the Low Countries and their bearing on the marine stratigraphy of the North Sea region. *Mededelingen van de Geologische Stichting*, 5, 6–233.
Levinsen, G.M.R. (1887) Bryozoer fra Kara-Havet. *Dijmphna Togtets Zoologisk Botanisk Udbytte, Kjøbenhavn*, 1887, 305–328.

Levinsen, G.M.R. (1909) *Morphological and Systematic Studies on the Cheilostomatous Bryozoa*. Nationale Forfatteres Forlag, Copenhagen, 431 pp.
https://doi.org/10.5962/bhl.title.5690

Levinsen, G.M.R. (1914) Conspectus Faunae Groenlandicae. Bryozoa, Endoprocta, Pterobranchia og Enteropneusta. *Meddelelser om Grønland*, 23, 545–634.

Levinsen, G.M.R. (1916) Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906–1908. Bryozoa. *Meddelelser om Grønland*, 43, 432–472.

Li, Z.P. (1990) Bryozoaires de Montbrison-Fontbonau (Drôme) et comparison avec les autres faunes Miocènes du Bassin Rhôdanien méridional. *Nouvelles Archives du Museum d'Histoire Naturelle Lyon*, 27, 1–126.
https://doi.org/10.3406/mhnly.1990.1098

Lorenz, L. von (1886) Bryozoën von Jan Mayen. *Die Internationale Polarforschung 1882–1883. Die Österreichische Polarstation von Jan Mayen*, 3, 83–100.

Lukin, V.I. (1979) Macrobenthic communities of the upper subtidal zone off Simushir Island. *In*: Kussakin, O.G. (Ed.), *Biology of the Shelf of the Kuril Islands*. Nauka, Moscow, USSR, pp. 11–60. [in Russian]

Lütken, C.F. (1877) Bryozoa. *In*: Rink, J.H. (Ed.), *Danish Greenland: Its People and its Products*. H.S. King, London, pp. 443–444.

Martha, S.O., Vieira, L.M., Souto-Derungs, J., Grischenko, A.V., Gordon, D.P. & Ostrovsky, A.N. (2021) Gymnolaemata, Cheilostomata. *In*: Schwata, T. (Ed.), *Phylum Bryozoa*. De Gruyter, Berlin, pp. 317–424.
https://doi.org/10.1515/9783110586312-011

Mawatari, S. (1956) Cheilostomatous Bryozoa from the Kuril Islands and neighbouring district. *Pacific Science*, 10, 113–135.

Mawatari S. (1963) Bryozoa of the eastern shore of Noto Peninsula. *Annual Report of the Noto Marine Laboratory of the Faculty of Science, University of Kanazawa*, 3, 5–10.

Mawatari, S. (1965) Phylum Tentaculata. *In*: Okada, Y., Uchida, S. & Uchida, T. (Eds.), *New Illustrated Encyclopedia of the Fauna of Japan*. Hokuryu-Kan, Tokyo, pp. 582–633. [in Japanese]

Mawatari, S.F. & Mawatari, S. (1981) A preliminary list of cheilostomatous bryozoans collected along the coast of Hokkaido. *Proceedings of the Japanese Society of Systematic Zoology*, 21, 41–58.

MacGinitie, G.E. (1955) Distribution and ecology of the marine invertebrates of Point Barrow, Alaska. *Smithsonian Miscellaneous Collections*, 128, 1–201.

Moosbrugger, M., Schwaha, T., Walzl, M.G., Obst, M. & Ostrovsky, A.N. (2012) The placental analogue and the pattern of sexual reproduction in the cheilostome bryozoan *Bicellariella ciliata* (Gymnolaemata). *Frontiers in Zoology*, 9, 29.
https://doi.org/10.1186/1742-9994-9-29

Nordgaard, O. (1896) Systematisk Fortegnelse over de i Norge hidtil observerede arter af marine Polyzoa. I. Cheilostomata. *Bergens Museums Aarborg 1894–1895*, 2, 1–34.

Nordgaard, O. (1900) Polyzoa. *The Norwegian North-Atlantic Expedition, 1876–1878*, Zoology, 27, 1–30.
https://doi.org/10.5962/bhl.title.58194

Nordgaard, O. (1905) Bryozoa or Polyzoa. Hydrographical and Biological Investigations in Norwegian Fiords. *Bergens Museums Meereskrifter*, 2, 164–174.

Nordgaard, O. (1906) Bryozoa from the second 'Fram' Expedition 1898–1902. Reports of the second Norwegian Arctic Expedition of the 'Fram' 1898–1902. *Videnskabs Selskabet i Kristiania*, 8, 1–44.

Nordgaard, O. (1907a) Bryozoaires. *In*: Grieg, M.G. (Ed.), *Mémoire de Invertebres du Fond. Duc d'Orléan, Croisière Océanographique Accomplie à Bord de la Belgica dans la Mer du Grönland 1905*. s.n., Bruxelles, pp. 503–567.

Nordgaard, O. (1907b) Bryozoen von dem norvegischen Fischereidampfer 'Michael Sars' in den Jahren 1900–1904 gesammelt. *Bergens Museums Aarborg 1907*, 2, 3–20.

Nordgaard, O. (1912) Bryozoaires. Duc d'Orleans Campagne Arctiques de 1907. Charles Bulens, Bruxelles, 43 pp.

Nordgaard, O. (1918) Bryozoa from the Arctic regions. *Tromsø Museums Aarshefter*, 40, 1–99.

Nordgaard, O. (1923) Bryozoa. *Report of the scientific results of the Norwegian expedition to Novaya Zemlya 1921*, 17, 1–19.

Nordgaard, O. (1924) Bryozoa from Iceland. *Det Kongelige Norske Videnskabers Selskabs Skrifter*, 2, 1–16.

Nordgaard, O. (1929) Bryozoa. *The Norwegian Northern Polar Expedition with the "Maud" 1918–1925. Scientific Results*, 5, 1–10.

Norman, A.M. (1876) Preliminary report of the biological results of a cruise in HMS 'Valorous' to Davis Strait in 1875. *Proceedings of the Royal Society of London*, 25, 202–215.

Norman, A.M. (1903) Notes on the natural history of East Finnmark. Polyzoa. *Annals and Magazine of Natural History*, Series 7, 11, 567–598.
https://doi.org/10.1080/00222930308678717

Norman, A.M. (1906) Greenlandic Polyzoa. *Annals and Magazine of Natural History*, Series 7, 17, 90–93.
https://doi.org/10.1080/00222930608562494

O'Donoghue, C.H. (1925) Notes on certain Bryozoa in the collection of the University of Washington. *Publication of Puget Sound Biological Station*, 5, 15–23.

O'Donoghue, C.H. & O'Donoghue, E. (1923) A preliminary list of the Bryozoa (Polyzoa) from the Vancouver Island Region. *Contributions to Canadian Biology and Fisheries,* New Series, 1, 143–201.
https://doi.org/10.1139/f22-010

O'Donoghue, C.H. & O'Donoghue, E. (1925) List of Bryozoa from the vicinity of Puget Sound. *Publications of Puget Sound Biological Station*, 5, 75–108.

O'Donoghue, C.H. & O'Donoghue, E. (1926) A second list of Bryozoa (Polyzoa) from the Vancouver Island Region. *Contributions to Canadian Biology and Fisheries*, New Series, 3, 47–131. https://doi.org/10.1139/f26-003

Osburn, R.C. (1912a) The Bryozoa of the Woods Hole region. *Bulletin of the United States Bureau of Fisheries*, 30, 205–265. https://doi.org/10.5962/bhl.title.1325

Osburn, R.C. (1912b) Bryozoa from Labrador, Newfoundland, and Nova Scotia, collected by Dr. Owen Bryant. *Proceedings of the United States National Museum*, 43, 275–289. https://doi.org/10.5479/si.00963801.43-1933.275

Osburn, R.C. (1919) Bryozoa of the Crocker Land Expedition. *Bulletin of the American Museum of Natural History*, 41, 603–624.

Osburn, R.C. (1923) Bryozoa. *Report of the Canadian Arctic Expedition, 1913–1918*, 8, 1–13.

Osburn, R.C. (1932) Biological and oceanographic conditions in Hudson Bay, 6. Bryozoa of Hudson Bay and Strait. *Contributions to Canadian Biology and Fisheries*, 7, 363–376. https://doi.org/10.1139/f32-029

Osburn, R.C. (1933) Bryozoa of the Mount Desert Region. *In*: Procter, W. (Ed.), *Biological Survey of the Mount Desert Region*. Wistar Institute of Anatomy and Biology, Philadelphia, Pennsylvania, pp. 291–385.

Osburn, R.C. (1936) Bryozoa collected in the American Arctic by Captain R.A. Bartlet. *Journal of the Washington Academy of Science*, 26, 538–543.

Osburn, R.C. (1952) Bryozoa of the Pacific Coast of America. Part 2, Cheilostomata–Ascophora. *Allan Hancock Pacific Expedition*, 14, 271–611.

Osburn, R.C. (1953) Bryozoa of the Pacific Coast of America. Part 3, Cyclostomata, Ctenostomata, Entoprocta and addenda. *Allan Hancock Pacific Expedition*, 14, 613–841.

Osburn, R.C. (1955) The circumpolar distribution of Arctic-Alaskan Bryozoa. *In*: *Essays in the Natural Sciences in Honor of Captain Allan Hancock*. Allan Hancock Foundation, University of Southern California, Los Angeles, California, pp. 29–38.

Ostrovsky, A.N. (1998) Comparative studies of ovicell anatomy and reproductive patterns in *Cribrilina annulata* and *Celleporella hyalina* (Bryozoa: Cheilostomatida). *Acta Zoologica*, 79, 287–318. https://doi.org/10.1111/j.1463-6395.1998.tb01280.x

Ostrovsky, A.N. (2002) Brood chambers in cribrimorphs evolved by fusion of costae: Further arguments. *In*: Wyse Jackson, P.N., Buttler, C.J. & Spencer Jones, M.E. (Eds.), *Bryozoan Studies 2001*. A.A. Balkema Publishers, Lisse, pp. 247–255.

Ostrovsky, A.N. (2008) Brood chambers in cheilostome Bryozoa: Diversity and revised terminology. *In*: Hageman, S.J., Key, M.M. & Winston, J.E. (Eds.), *Bryozoan Studies 2007: Proceedings of the 14th International Bryozoology Association Conference*. *Virginia Museum of Natural History Special Publication*, 15, 195–204.

Ostrovsky, A.N. (2009) *Evolution of Sexual Reproduction in the Bryozoan Order Cheilostomata* (*Gymnolaemata*). Saint Petersburg State University, Saint Petersburg, 402 pp. [in Russian with English Summary]

Ostrovsky, A.N. (2013) *Evolution of Sexual Reproduction in Marine Invertebrates*: *Example of Gymnolaemate Bryozoa*. Springer Verlag, Dordrecht, 356 pp. https://doi.org/10.1007/978-94-007-7146-8

Ostrovsky, A.N., Nielsen, C., Vávra, N. & Yagunova, E.B. (2009a) Diversity of the brooding structures in calloporid bryozoans (Gymnolaemata: Cheilostomata): Comparative anatomy and evolutionary trends. *Zoomorphology*, 128, 13–35. https://doi.org/10.1007/s00435-008-0070-8

Ostrovsky, A.N., O'Dea, A. & Rodrígues F. (2009b) Comparative anatomy of internal incubational sacs in cupuladriid bryozoans and the evolution of brooding in free-living cheilostomes. *Journal of Morphology*, 270, 1413–1430. https://doi.org/10.1002/jmor.10767

Ostrovsky, A.N. & Schäfer, P. (2003) Ovicell structure in *Callopora dumerilii* and *C. lineata* (Bryozoa, Cheilostomatida). *Acta Zoologica*, 84, 15–24. https://doi.org/10.1046/j.1463-6395.2003.00121.x

Ostrovsky, A.N., Schäfer, P. & Gordon, D.P. (2003) Ultrastructure and development of the ooecial walls in some calloporid bryozoans. *Zoologischer Anzeiger*, 242, 223–240. https://doi.org/10.1078/0044-5231-00100

Ostrovsky, A.N. & Taylor, P.D. (2004) Systematics of Upper Cretaceous calloporid bryozoans with primitive spinose ovicells. *Palaeontology*, 47, 775–793. https://doi.org/10.1111/j.0031-0239.2004.00379.x

Ostrovsky, A.N. & Taylor, P.D. (2005a) Early stages of the ovicell development in the calloporid *Wilbertopora* (Bryozoa: Cheilostomata) from the Upper Cretaceous of the USA. *In*: Moyano, G.I.G., Cancino, J.M. & Wyse Jackson, P.N. (Eds.), *Bryozoan Studies 2004*: *Proceedings of the 13th International Bryozoology Association Conference*. A.A. Balkema Publishers, Lisse, pp. 223–230.

Ostrovsky, A.N. & Taylor, P.D. (2005b) Brood chambers constructed from spines in fossil and Recent cheilostome bryozoans. *Zoological Journal of the Linnaean Society*, 144, 317–361.

https://doi.org/10.1111/j.1096-3642.2005.00179.x
Pouyet, S. (1997) Les Bryozoaires du Badenien (Miocène Moyen) d'Olimpow Pologne. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, 145, 1–124.
Powell, N.A. (1967) Polyzoa (Bryozoa) – Ascophora from north New Zealand. *Discovery Reports*, 34, 199–393.
Powell, N.A. (1968a) Bryozoa (Polyzoa) of Arctic Canada. *Journal Fishery Research Board Canada*, 25, 2269–2320. https://doi.org/10.1139/f68-202
Powell, N.A. (1968b) Studies on Bryozoa (Polyzoa) of the Bay of Fundy Region. 2. Bryozoa from fifty fathoms, Bay of Fundy. *Cahiers de Biologie Marine*, 9, 247–259.
Powell, N.A. & Crowell, G.D. (1967) Studies on Bryozoa (Polyzoa) of the Bay of Fundy Region. 1. Bryozoa from the intertidal zone of Minas Basin and Bay of Fundy. *Cahiers de Biologie Marine*, 8, 331–347.
Robertson, A. (1900) Papers from the Harriman Alaska Expedition. 6. The Bryozoa. *Proceedings of the Washington Academy of Sciences*, 2, 315–340.
Robertson, A. (1908) The encrusting chilostomatous Bryozoa of the west coast of North America. *University of California Publications of Zoology*, 4, 253–344.
Rogick, M.D. (1956) Bryozoa of the United States Navy's 1947–1948 Antarctic Expedition, I–IV. *Proceedings of the U.S. National Museum*, 105, 221–317.
https://doi.org/10.5479/si.00963801.105-3358.221
Rosso, A., Sciuto, F. & Sinagra, A. (2010) *Bertorsonidra* n. gen. (Bryozoa, Cheilostomata) for *Tremopora prenanti* Gautier, 1955, a rare species from the Mediterranean. *Zoosystema*, 32, 457–467.
https://doi.org/10.5252/z2010n3a7
Römer, F. (1863) Beschreibung der Norddeutschen tertiären Polyparien. *Palaeontographica. Abteilung A, Palaeozoologie-Stratigraphie*, 9, 199–246.
Ryland, J.S. (1969) A nomenclatural index to 'A History of the British Marine Polyzoa' by T. Hincks (1880). *Bulletin of the British Museum of Natural History, Zoology*, 17, 207–260.
https://doi.org/10.5962/bhl.part.10340
Ryland, J.S. & Hayward, P.J. (1991) Erect Bryozoa. Marine flora and fauna of the northeastern United States. *NOAA Technical Report NMFS*, 99, 1–47.
Sakagami, S., Arakawa, S. & Hayami, T. (1980) Checklist and bibliography of Japanese Cenozoic fossil Ectoprocta (Bryozoa), 1935–1978. *In*: Igo, H. & Noda, H. (Eds.), *Professor Saburo Kanno Memorial Volume*. University of Tsukuba, Ibaraki, pp. 317–338.
Shunatova, N.N. & Ostrovsky, A.N. (2001) Individual autozooidal behaviour and feeding in marine bryozoans. *Sarsia*, 86, 113–142.
https://doi.org/10.1080/00364827.2001.10420468
Shunatova, N.N. & Nielsen, C. (2002) Putative sensory structures in marine bryozoans. *Invertebrate Biology*, 121, 262–270. https://doi.org/10.1111/j.1744-7410.2002.tb00066.x
Smitt, F.A. (1868a) Kritisk forteckning ofver Skandinaviens Hafs-Bryozoer. Part 4. *Öfversigt af Kongliga Vetenskaps-Academiens Förhandlingar*, 25, 3–320.
Smitt, F.A. (1868b) Bryozoa marina in regionibus arcticis et borealibus viventia recensuit. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlinger*, 24, 443–487.
Smitt, F.A. (1878a) Recensio animalium Bryozoarum e mari arctico, quae ad paeninsulam Kola, in itinere anno 1877. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlinger*, 35, 19–32.
Smitt, F.A. (1878b) Recensio systematica animalium Bryozoorum, quae in itineribus, annis 1875 et 1876 ad insulas Novaja Semlja. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlinger*, 35, 11–26.
Sokolover N., Ostrovsky A.N. & Ilan, M. (2018) *Schizoporella errata* (Bryozoa, Cheilostomata) in the Mediterranean Sea: Abundance, growth rate, and reproductive strategy. *Marine Biology Research*, 14, 868–882.
https://doi.org/10.1080/17451000.2018.1526385
Soule, J.D., Soule, D.F. & Chaney, H.W. (1995) The Bryozoa. *In*: Blake, J.A., Chaney, H.W., Scott, P.H. & Lissner, A.L. (Eds.), *Taxonomic Atlas of the Santa Maria Basin and Western Santa Barbara Channel*. Santa Barbara Museum of Natural History, Santa Barbara, California, pp. 1–344.
Tarasova, N.A. (1983) *Fauna of bryozoans of the northeastern Sea of Japan*. Unpublished Diploma Thesis, Far East State University, Vladivostok, USSR, 48 pp. [In Russian]
Taylor, P.D. (2021) Pleistocene bryozoans from the Clyde Clay Formation of Scotland, and the Holocene retreat of cold-water species. *Taxonomy*, 1, 69–82.
https://doi.org/10.3390/taxonomy1020008
Tilbrook, K.J. (2006) Cheilostomatous Bryozoa from the Solomon Islands. *In*: Chaney, H.W. (Ed.), *Studies in Biodiversity. Vol. 3*. Santa Barbara Museum of Natural History, California, Santa Barbara, pp. 1–385.
Verrill, A.E. (1879) Bryozoa. *In*: *Preliminary check-list of the Marine Invertebrate of the Atlantic Coast from the Cape Cod to Gulf of St Lawrence*. Private Publication, New Haven, Connecticut, pp. 28–31.
Verrill, A.E. & Smitt, F. (1873) Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Report of the US Commissioner of Fish and Fisheries*, 1, 295–778.
https://doi.org/10.5962/bhl.title.11688

Vigneaux, M. (1949) Révision des Bryozoaires néogènes du Bassin d'Aquitaine et essai de classification. *Mémoires de la Société Géologique de France,* New Series, 28, 1–153.
Voigt, E. (1987) Die Bryozoen des Klassischen Dano Montiens von Mons (Belgien). *Mémoires Pour Servir à l'Explication des Cartes Géologiques et Minières de la Belgique*, 17, 1–161.
Voigt, E. (1991) Mono- or polyphyletic evolution of cheilostomatous bryozoan divisions? *In*: Bigey, F.P. (Ed.), *Bryozoaires Actuels et Fossiles*: *Bryozoa Living and Fossil*. *Bulletin de la Société des Sciences Naturelles de 'Ouest de la France*, Mémoire H.S., 1, 505–522.
Waeschenbach, A., Taylor, P.D. & Littlewood, D.T.J. (2012) A molecular phylogeny of bryozoans. *Molecular Phylogenetics and Evolution*, 62, 718–735.
https://doi.org/10.1016/j.ympev.2011.11.011
Waters, A.W. (1891) North-Italian Bryozoa. *Quarterly Journal of the Geological Society, London*, 47, 1–34.
https://doi.org/10.1144/GSL.JGS.1891.047.01-04.03
Waters, A.W. (1900) Bryozoa from Franz Josef Land, collected by the Jackson-Harmsworth Expedition, 1896–1897. *Journal of the Linnean Society of London*, Zoology Series, 28, 43–105.
https://doi.org/10.1111/j.1096-3642.1900.tb01745.x
Watling, L., Guinotte, J., Clark, M.R. & Smith, C.R. (2013) Proposed biogeography of the deep ocean floor. *Progress in Oceanography*, 111, 91–112.
https://doi.org/10.1016/j.pocean.2012.11.003
Whiteaves, J. (1874) On recent deep-sea dredging operations in the Gulf of St Lawrence. *American Journal of Science and Arts*, Series 2, 7, 1–9.
https://doi.org/10.2475/ajs.s3-7.39.210
Whiteaves, J. (1901) *Catalogue of the Marine Invertebrates of Eastern Canada*. Geological Survey of Canada, Ottawa, 271 pp.
https://doi.org/10.4095/216086
Winston, J.E. & Hayward, P.J. (2012) The marine bryozoans of the northeast coast of the United States: Maine to Virginia. *Virginia Museum of Natural History Memoir*, 11, 1–180.
https://doi.org/10.5962/bhl.title.11688

APPENDIX 1. Station data for additional material (see "Material examined" sections).

E.F. Guryanova Collection (1931). Bering Island, Commander Islands.
223 (26 March 1931) Cape Severniy, 55°22.2′ N, 65°57.5′ E, lower intertidal horizon, small boulders.

Institute of Marine Biology (IMB) Collection (1972). "Commander Intertidal Expedition". Shoreline of Medny Island, Commander Islands. Collector M.B. Ivanova.
194/2 (3 July 1972) Port Preobrazhenskoye, Beringian coast of Medny Island, 54°47.6′ N, 167°34.5′ E, shoreline drift of broken shells of bivalve mollusc *Monia macrochisma*.

Institute of Marine Biology (IMB) Collection (1972). "First Commander Expedition", RV *Krylatka*. Coastal waters of Medny Island, Commander Islands. SCUBA. Collector V.I. Lukin.
5/12 (10 July 1972) Cape Peschany, 54°49.6′ N, 167°33.7′ E, depth 5 m, rocky plateau.
6/16 (10 July 1972) Cape Peschany, 54°49.7′ N, 167°33.9′ E, depth 10 m, blocks.
31/93 (16 July 1972) Cape Palata, 54°33.7′ N, 167°55.2′ E, depth 20 m, rocky plateau.
32/99 (17 July 1972) Bight Poludennaya, 54°45.3′ N, 167°32.0′ E, depth 20 m, rocky plateau.
34/104 (17 July 1972) Cape Peschany, 54°49.7′ N, 167°34.0′ E, depth 15 m, rocky plateau.
59/167 (24 July 1972) Cape Sivuchy, 54°50.3′ N, 167°26.1′ E, depth 15 m, vertical rocky face.

Institute of Marine Biology (IMB) Collection (1973). "Second Commander Expedition", RV *Rakitnoye*. Coastal waters of Commander Islands. BI, Bering Island. MI, Medny Island. SCUBA (depth 5–20 m), rock dredge (depth 40–250 m). Collectors G.T. Belokonev, V.I. Lukin, B.I. Sirenko and S.D. Vavilin.
108/284 (10 September 1973) MI, on the beam of Cape Yugo-Vostochny, 54°27.3′ N, 168°09.5′ E, depth 80 m, rock.
110/290 (11 September 1973) MI, Cape Vodopadskiy, 54°38.5′ N, 167°45.7′ E, depth 20 m, rock face.
110/292 (11 September 1973) MI, Cape Vodopadskiy, 54°38.5′ N, 167°45.7′ E, depth 20 m, rock face.
113/302 (11 September 1973) MI, Cape Vodopadskiy, 54°38.7′ N, 167°45.8′ E, depth 5 m, blocks.
113/305 (11 September 1973) MI, Cape Vodopadskiy, 54°38.7′ N, 167°45.8′ E, depth 5 m, blocks.
113/306 (11 September 1973) MI, Cape Vodopadskiy, 54°38.7′ N, 167°45.8′ E, depth 5 m, blocks.
149/384 (17 September 1973) MI, on the beam of Cape Yugo-Vostochny, 54°23.3′ N, 168°10.3′ E, depth 110–150 m, rock, pebbles.
150/385 (18 September 1973) MI, Kitolovnaya Bank, 54°54.3′ N, 167°20.0′ E, depth 40 m, rock.
151/386 (18 September 1973) MI, profile: Medny Island – Kitolovnaya Bank, 54°56.0′ N, 167°19.0′ E, depth 60 m, pebbles,

sand.

158/393 (18 September 1973) MI, Kitolovnaya Bank, 55°02.2′ N, 167°10.9′ E, depth 60 m, rock, broken shells.

160/395 (18 September 1973) MI, Kitolovnaya Bank, 55°02.5′ N, 167°12.7′ E, depth 100 m, pebbles.

173/408 (19 September 1973) MI, on the beam of Rock Sivuchy, 54°49.0′ N, 167°26.0′ E, depth 40 m, rock.

215/536 (25 September 1973) BI, on the beam of Cape Ostrovnoy, 54°49.0′ N, 166°22.3′ E, depth 20 m, rock face.

217/558 (27 September 1973) BI, Cape Polovinny, 54°59.2′ N, 166°27.1′ E, depth 10 m, rock face with cracks and ledges.

224/582 (2 October 1973) MI, Bight Poludennaya, 54°36.8′ N, 167°21.5′ E, depth 130–250 m, silt, pebbles.

229/587 (3 October 1973) MI, on the beam of Cape Vodopadskiy, 54°29.3′ N, 167°34.1′ E, depth 150–200 m, sand, pebbles.

233/591 (3 October 1973) MI, on the beam of Cape Vodopadskiy, 54°38.6′ N, 167°43.5′ E, depth 40 m, rock face.

Institute of Marine Biology (IMB) Collection (2011). RV *Akademik Oparin*, 41st Expedition. Sea of Okhotsk and Pacific Ocean along southern to middle Kuril Islands shelf and slope. Sigsbee trawl. Collectors A.P. Tsurpalo and A.V. Chernyshev.

3/1 (7 July 2011) northeastward from Kunashir Island, Sea of Okhotsk, 44°36.6′ N, 146°26.4′ E – 44°36.6′ N, 146°25.9′ E, depth 180–200 m, sand, gravel.

11/7 (10 July 2011) westward from Iturup Island, Sea of Okhotsk, 45°14.6′ N, 147°24.7′ E – 45°15.0′ N, 147°25.0′ E, depth 242–490 m.

16/12 (13 July 2011) westward from Urup Island, Sea of Okhotsk, 46°02.5′ N, 149°55.7′ E – 46°02.1′ N, 149°55.3′ E, depth 121–130 m, sand.

18/14 (13 July 2011) westward from Urup Island, Sea of Okhotsk, 45°53.6′ N, 149°43.5′ E – 45°53.6′ N, 149°43.1′ E, depth 97–108 m.

19/15 (13 July 2011) westward from Urup Island, Sea of Okhotsk, 45°54.2′ N, 149°40.4′ E – 45°54.2′ N, 149°40.0′ E, depth 183–213 m, gravel, pebbles.

20/16 (13 July 2011) Urup Strait, northeastward from Urup Island, Sea of Okhotsk, 46°15.9′ N, 150°26.5′ E – 46°15.9′ N, 150°26.6′ E, depth 120–125 m.

22/17 (16 July 2011) eastward from Simushir Island, Pacific Ocean, 46°57.9′ N, 152°17.3′ E – 46°57.2′ N, 152°17.2′ E, depth 450 m, gravel.

24/19 (16 July 2011) eastward from Simushir Island, Pacific Ocean, 46°54.3′ N, 152°07.4′ E – 46°55.1′ N, 152°06.8′ E, depth 113–134 m, gravel, sand.

27/22 (17 July 2011) eastward from Simushir Island, Pacific Ocean, 47°04.3′ N, 152°14.5′ E – 47°04.1′ N, 152°15.2′ E, depth 80–110 m, gravel, sand.

29/24 (17 July 2011) eastward from Simushir Island, Pacific Ocean, 46°57.8′ N, 152°17.3′ E – 46°57.8′ N, 152°14.5′ E, depth 350–440 m, sand with broken shells.

31/26 (17 July 2011) eastward from Simushir Island, Pacific Ocean, 47°02.9′ N, 152°13.6′ E – 47°03.4′ N, 152°14.7′ E, depth 82–115 m, shells, pebbles.

37/32 (19 July 2011) southeastward from Chiproy Island, Pacific Ocean, 46°20.4′ N, 150°58.2′ E – 46°20.8′ N, 150°58.3′ E, depth 440–566 m.

39/34 (19 July 2011) southeastward from Chiproy Island, Pacific Ocean, 46°20.7′ N, 150°58.7′ E – 46°21.3′ N, 150°58.8′ E, depth 436–480 m, broken barnacles.

41/36 (19 July 2011) southeastward from Chiproy Island, Pacific Ocean, 46°20.5′ N, 150°58.0′ E – 46°21.0′ N, 150°58.4′ E, depth 438–567 m.

42/37 (20 July 2011) Urup Strait, southward from Chiproy Island, Pacific Ocean, 46°22.7′ N, 150°51.2′ E – 46°22.8′ N, 150°51.7′ E, depth 135–140 m.

43/38 (20 July 2011) Urup Strait, southward from Chiproy Island, Pacific Ocean, 46°23.9′ N, 150°46.3′ E – 46°23.8′ N, 150°46.6′ E, depth 142–150 m.

48/42 (21 July 2011) westward from Urup Island, Sea of Okhotsk, 45°56.1′ N, 149°42.4′ E – 45°56.1′ N, 149°43.3′ E, depth 462–490 m.

55/47 (26 July 2011) westward from Iturup Island, Sea of Okhotsk, 45°01.2′ N, 147°00.9′ E – 45°01.5′ N, 147°01.3′ E, depth 150–350 m.

56/48 (26 July 2011) westward from Iturup Island, Sea of Okhotsk, 45°16.0′ N, 147°23.2′ E – 45°16.7′ N, 147°23.5′ E, depth 425–460 m.

60/50 (28 July 2011) eastward from Iturup Island, Pacific Ocean, 45°16.7′ N, 148°46.3′ E – 45°16.5′ N, 148°46.2′ E, depth 140 m.

63/53 (29 July 2011) northward from Iturup Island, Sea of Okhotsk, 45°45.1′ N, 148°33.2′ E – 45°44.5′ N, 148°33.5′ E, depth 264–274 m.

64/54 (29 July 2011) northward from Iturup Island, Sea of Okhotsk, 45°43.6′ N, 148°14.0′ E – 45°44.1′ N, 148°14.2′ E, depth 350–435 m.

Kamchatka Institute of Ecology and Nature Management (KIENM) Collection (1988). RV *Nazarovsk*. Coastal waters of eastern Kamchatka Peninsula. Rock dredge. Collector A.V. Rzhavsky.

86 (16 May 1988) Avacha Gulf, 53°03.0′ N, 160°05.0′ E, depth 118 m.

114 (24 May 1988) Avacha Gulf, 52°54.0′ N, 160°03.0′ E, depth 142 m.

118 (28 May 1988) Avacha Gulf, 52°53.0′ N, 160°08.0′ E, depth 176 m, stones.
119 (24 May 1988) Avacha Gulf, 52°54.0′ N, 160°01.0′ E, depth 141 m, gravel.
141 (11 May 1988) Avacha Gulf, 53°41.0′ N, 160°04.0′ E, depth 75 m, sand.
148 (11 May 1988) Avacha Gulf, 53°39.0′ N, 160°06.0′ E, depth unknown, sand with gravel.
170 (9 May 1988) Avacha Gulf, 53°22.0′ N, 160°07.0′ E, depth 136 m, silty sand.
182 (11 May 1988) Avacha Gulf, 53°36.0′ N, 160°07.0′ E, depth 100 m, sand with gravel and broken shells.
238 (11 June 1988) Kronotsky Gulf, 54°53.0′ N, 162°15.0′ E, depth 122 m.
326 (23 September 1988) Litke Strait, 58°50.0′ N, 163°21.0′ E, depth 48 m, silty sand with gravel.
348 (23 September 1988) Litke Strait, 58°51.0′ N, 163°23.0′ E, depth 49 m, silt with gravel and broken shells.
380 (24 September 1988) Litke Strait, 59°26.0′ N, 163°35.0′ E, depth 29 m, stones.
394 (18 September 1988) Korfa Gulf, 60°07.0′ N, 165°57.0′ E, depth 48 m, silt with gravel and broken shells.
406 (20 September 1988) Korfa Gulf, 60°09.0′ N, 165°43.0′ E, depth 33 m, gravel.

Kamchatka Institute of Ecology and Nature Management (KIENM) Collection (1991). Coastal waters of Bering Island, Commander Islands. SCUBA. Collecting frame 0.25 m^2. Collectors D.D. Danilin, V.V. Oshurkov and V.I. Shalukhanov.
186 (17 July 1991) Bight Poludennaya, 54°58.5′ N, 166°09.6′ E, depth 20 m, rock face, pebbles.
196–197 (18 July 1991) Cape Monati, 54°40.1′ N, 166°40.0′ E, depth 14–15 m, top of the block, broken shells.
198–199 (18 July 1991) Cape Monati, 54°40.2′ N, 166°40.0′ E, depth 8–9 m, blocks.
203 (20 July 1991) Cape Ostrovnoy, 54°49.2′ N, 166°22.2′ E, depth 5–7 m, rock face.
208, 210 (22 July 1991) Bight Podutesnaya, 55°01.3′ N, 166°06.2′ E, depth 20 m, rocky plateau.
215 (30 July 1991) profile: Cape Vkhodnoy Reef – Toporkov Island, 55°11.9′ N, 165°56.9′ E, depth 15 m, boulders, pebbles, broken shells.
217 (30 July 1991) profile: Cape Vkhodnoy Reef – Toporkov Island, 55°12.0′ N, 165°56.7′ E, depth 25 m, rocky plateau with silty stones and pebbles.
219 (31 July 1991) profile: Cape Vkhodnoy Reef – Toporkov Island, 55°12.0′ N, 165°56.7′ E, depth 25 m, silty rocky plateau with boulders and accumulations of broken shells.
220–221 (31 July 1991) profile: Cape Vkhodnoy Reef – Toporkov Island, 55°11.9′ N, 165°57.1′ E, depth 10 m, blocks.
225–226 (2 August 1991) Rock Ariy Kamen, 55°12.8′ N, 165°46.9′ E, depth 25 m, rock face.
227–228 (2 August 1991) Rock Ariy Kamen, 55°12.7′ N, 165°47.1′ E, depth 10 m, rock face.
229–230 (2 August 1991) Rock Ariy Kamen, 55°12.7′ N, 165°47.1′ E, depth 4–5 m, vertical rock face covered by bryozoan *Myriapora orientalis*.
236 (2 August 1991) Toporkov Island, 55°12.4′ N, 165°55.4′ E, depth 11 m, vertical rock face covered by bryozoan *Phidolopora elongata.*

Kamchatka Institute of Ecology and Nature Management (KIENM) Collection (1992). Coastal waters of Medny Island, Commander Islands. SCUBA. Collecting frame 0.25 m^2. Collectors V.V. Oshurkov, A.V. Rzhavsky, K.E. Sanamyan and V.I. Shalukhanov.
3 (17 June 1992) Cape Gladkiy, 54°44.5′ N, 167°45.1′ E, depth 15 m, rock face.
4–5 (17 June 1992) Cape Gladkiy, 54°44.5′ N, 167°45.3′ E, depth 20 m, pebbles, boulders.
7 (21 June 1992) Cape Gladkiy, 54°44.5′ N, 167°45.1′ E, depth 10 m, rock face, boulders.
19 (23 June 1992) Cape Popovskiy, 54°42.7′ N, 167°45.1′ E, depth 5 m, steep rocky slope with shelves.
20 (25 June 1992) Cape Popovskiy, 54°42.8′ N, 167°45.4′ E, depth 15 m, rock face.
25, 27 (2 July 1992) Bight Gladkovskaya, 54°44.1′ N, 167°44.0′ E, depth 2 m, rock face with sparse boulders.
28–30 (3 July 1992) Cape Glupyshynye Stolby, 54°38.0′ N, 167°56.4′ E, depth 14 m, blocks.
32 (3 July 1992) Cape Glupyshynye Stolby, 54°38.1′ N, 167°56.2′ E, depth 4–5 m, blocks.
34 (3 July 1992) Cape Glupyshynye Stolby, 54°38.1′ N, 167°56.2′ E, depth 10–12 m, blocks.
37–39 (4 July 1992) Rocks Bobroviye Kamni, 54°52.9′ N, 167°26.6′ E, depth 21–25 m, rocky plateau.
43–44 (4 July 1992) Rocks Bobroviye Kamni, 54°52.8′ N, 167°26.2′ E, depth 9–11 m, blocks.
46 (4 July 1992) Rocks Bobroviye Kamni, 54°52.7′ N, 167°26.2′ E, depth 5 m, rock face.
53–54 (5 July 1992) Cape Matveya, 54°51.1′ N, 167°31.4′ E, depth 20 m, blocks.
55–57 (5 July 1992) Cape Matveya, 54°51.0′ N, 167°31.3′ E, depth 10 m, steep rocky slope with shelves.
58 (5 July 1992) Cape Matveya, 54°51.0′ N, 167°31.3′ E, depth 15 m, rock face with crevices and boulders.
61, 63 (8 July 1992) Cape Matveya, 54°51.0′ N, 167°31.3′ E, depth 5–7 m, blocks.
64–66 (9 July 1992) Bight Gavrilovskaya, 54°47.6′ N, 167°28.7′ E, depth 20 m, vertical rocky face.
67–68 (9 July 1992) Bight Gavrilovskaya, 54°47.7′ N, 167°29.2′ E, depth 10 m, blocks with sand lenses.
69 (9 July 1992) Bight Gavrilovskaya, 54°47.7′ N, 167°29.2′ E, depth 10 m, vertical rock face.
70–72 (9 July 1992) Bight Gavrilovskaya, 54°47.7′ N, 167°28.9′ E, depth 15 m, blocks.
75 (9 July 1992) Bight Gavrilovskaya, 54°47.7′ N, 167°29.2′ E, depth 5 m, blocks.
76–77 (11 July 1992) Rock Korabelny Stolb, 54°39.3′ N, 167°44.0′ E, depth 15 m, blocks with sand lenses.
79, 81 (11 July 1992) Rock Korabelny Stolb, 54°39.3′ N, 167°44.0′ E, depth 5–6 m, rock face.
87 (11 July 1992) Rock Korabelny Stolb, 54°39.1′ N, 167°44.0′ E, depth 18–19 m, rock face with drifts of sand.

88–90 (16 July 1992) Bight Korabelnaya, 54°41.6′ N, 167°47.5′ E, depth 20 m, top of the block.
91 (16 July 1992) Bight Korabelnaya, 54°41.4′ N, 167°47.2′ E, depth 15 m, rock face.
94, 96 (17 July 1992) Cape Drovyanye Stolby, 54°31.2′ N, 168°05.5′ E, depth 15 m, rocky face.
97–99 (17 July 1992) Cape Drovyanye Stolby, 54°31.4′ N, 168°05.8′ E, depth 22–23 m, rock face with cracks.
100 (17 July 1992) Cape Drovyanye Stolby, 54°31.1′ N, 168°05.3′ E, depth 9–12 m, rock face.
105 (17 July 1992) Cape Drovyanye Stolby, 54°31.1′ N, 168°05.2′ E, depth 5 m, blocks.
110–111 (18 July 1992) Bight Korabelnaya, 54°41.3′ N, 167°47.0′ E, depth 10 m, blocks.
113 (20 July 1992) Rock Sivuchy, 54°50.3′ N, 167°26.1′ E, depth 15 m, boulders with sand lenses.
116–118 (20 July 1992) Rock Sivuchy, 54°50.2′ N, 167°25.8′ E, depth 25 m, silty rocky plateau with sand lenses.
119–121 (20 July 1992) Rock Sivuchy, 54°50.3′ N, 167°26.1′ E, depth 10 m, rock face with cracks.
124 (23 July 1992) Rock Sivuchy Kamen, 54°47.4′ N, 167°39.3′ E, depth 20 m, rock face.
125–127 (23 July 1992) Rock Sivuchy Kamen, 54°47.4′ N, 167°39.3′ E, depth 30 m, rock face.
128–130 (23 July 1992) Rock Sivuchy Kamen, 54°47.4′ N, 167°39.3′ E, depth 15 m, rocky plateau with crevices.
132–133 (23 July 1992) Rock Sivuchy Kamen, 54°47.4′ N, 167°39.3′ E, depth 10 m, rocky plateau with crevices.
135–137 (24 July 1992) Cape Gladkiy, 54°44.7′ N, 167°45.2′ E, depth 32 m, rock face.
140 (24 July 1992) Cape Zhirovoy, 54°46.0′ N, 167°43.5′ E, depth 31 m, rock face.
142–143 (28 July 1992) Cape Lebyazhy, 54°35.9′ N, 167°52.1′ E, depth 30 m, rock face.
144–146 (28 July 1992) Cape Lebyazhy, 54°36.0′ N, 167°52.3′ E, depth 20 m, rock face.
147–148 (28 July 1992) Cape Zhirovoy, 54°45.9′ N, 167°43.5′ E, depth 16 m, rock face.
150–152 (10 August 1992) Cape Gladkiy, 54°44.8′ N, 167°45.3′ E, depth 46 m, rock face.

Kamchatka Institute of Ecology and Nature Management (KIENM) Collection (2008). RV *Agat*. Slope of western Kamchatka Peninsula, Sea of Okhotsk. Bottom-grab "Ocean–50", collector S.G. Korostylyov.
1–K–1 (1 June 2008) 58°00.0′ N, 155°43.0′ E, depth 285 m, pebbles.

A.V. Grischenko Collection (1990). Intertidal zone of Bering Island, Commander Islands.
5 (28 July 1990) Cape Vkhodnoy Reef, 55°11.5′ N, 165°58.6′ E, shoreline drift of *Laminaria dentigera*, on rhizoids.
15 (28 July 1990) Cape Vkhodnoy Reef, 55°11.5′ N, 165°58.6′ E, shoreline drift of *Alaria fistulosa*, on rhizoids.

A.V. Grischenko Collection (1991). Intertidal zone of Bering Island, Commander Islands.
10 (22 July 1991) Cape Vkhodnoy Reef, 55°11.5′ N, 165°58.6′ E, middle intertidal horizon, rocky pool, lower face of boulders.
17 (8 August 1991) Cape Vkhodnoy Reef, 55°11.5′ N, 165°58.6′ E, shoreline drift, on gastropod shell *Cryptonatica jantostoma*.

A.V. Grischenko Collection (1992). Intertidal zone of Medny Island, Commander Islands.
1 (30 June 1992) Bight Gladkovskaya, 54°44.3′ N, 167°43.9′ E, rocky reef with boulders and crevices, middle intertidal horizon, lower face of boulders.
7–8 (28 July 1992) Bight Gladkovskaya, 54°44.3′ N, 167°43.9′ E, shoreline drift of crustose coralline algae fragment *Clathromorphum nereostratum*.

Pacific Institute of Bioorganic Chemistry (PIBOC) Collection (1991). RV *Akademik Oparin*, 14th Expedition. Northern Pacific. Sigsbee trawl. Collector A.V. Smirnov.
5 (2 August 1991) South-East off Medny Island, 54°12.0′ N, 168°37.3′ E, depth 569 m, silt.
14 (12 August 1991) near Kodiak Island, Gulf of Alaska, 58°23.9′ N, 150°55.8′ W, depth 64 m, sand.
15 (12 August 1991) near Kodiak Island, Gulf of Alaska, 58°22.4′ N, 150°56.8′ W, depth 61 m, sand.
16 (12 August 1991) near Kodiak Island, Gulf of Alaska, 58°21.0′ N, 150°59.6′ W, depth 57 m, broken shells.
17 (12 August 1991) near Kodiak Island, Gulf of Alaska, 57°58.2′ N, 151°07.5′ W, depth 83 m, sand with broken shells.
18 (12 August 1991) near Kodiak Island, Gulf of Alaska, 57°44.4′ N, 151°05.5′ W, depth 68 m, sand with broken shells.
19 (12 August 1991) near Kodiak Island, Gulf of Alaska, 57°43.4′ N, 151°04.0′ W, depth 69 m, sand with broken shells.
20 (12 August 1991) near Kodiak Island, Gulf of Alaska, 57°42.8′ N, 151°00.9′ W, depth 70 m, sand with broken shells.
41 (24 August 1991) North-West off Bering Island, 55°36.3′ N, 164°51.9′ E, depth 158 m.
44 (24 August 1991) North-West off Bering Island, 55°35.4′ N, 165°00.4′ E, depth 205 m.
58 (3 September 1991) coastal waters off Schumschu Island, Kuril Islands, 50°39.5′ N, 156°43.0′ E, depth 66 m, sand.
89 (10 September 1991) coastal waters of Lesser Kuril Ridge, 43°40.5′ N, 146°45.2′ E, depth 102 m.
91 (10 September 1991) coastal waters of Lesser Kuril Ridge, 43°25.3′ N, 146°25.4′ E, depth 103 m.

Kamchatka Research Institute of Fisheries and Oceanography (KamchatNIRO) Collection (2013). RV *Professor Probatov*. Coastal waters of western Kamchatka Peninsula, Sea of Okhotsk. Bottom-grab "Ocean–50" (Stns 62–82), Sigsbee trawl (Stn 189). Collector T.B. Morozov.
62 (16 August 2013) 57°14.9′ N, 155°37.7′ E, depth 116 m, pebbles, gravel.

63 (15 August 2013) 57°39.4′ N, 155°57.1′ E, depth 100 m, pebbles, with broken shells admixture.
69 (8 August 2013) 57°00.0′ N, 155°00.0′ E, depth 132 m, gravel, sand, silt.
82 (11 August 2013) 58°09.0′ N, 156°03.0′ E, depth 146 m, pebbles, silty sand.
189 (6 August 2013) 56°23.3′ N, 154°17.5′ E, depth 197 m, sand with pebbles admixture.