

A combination of historical collections and newly obtained molecular data contributes to the revision of the genus *Ziminella* (Nudibranchia: Cladobranchia)

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ABSTRACT. The main goal of the present paper is to revise the diversity of the nudibranch genus *Ziminella* and update the geographic ranges of its species, based on historical museum material and newly collected specimens of *Ziminella japonica* (Volodchenko, 1941) from the Sea of Japan. We provide morphological examinations, a molecular phylogenetic analysis based on four markers, and species delimitation analyses of *Ziminella*. Our results indicate that *Z. salmonacea* (Couthouy, 1838) and *Z. circapolaris* Korshunova *et al.*, 2017 represent a single species but display some intraspecific variation in the COI marker (up to 2.54% between individuals). The species delimitation analyses cannot explicitly support the distinct status of *Z. japonica* and *Z. vrijenhoeki* Valdés *et al.*, 2018, but in this case the minimal interspecific *p*-distance in COI comprised 7.95%. Moreover, several differences in the coloration and external morphology are found in specimens from the type localities of these two species. We also show that *Z. japonica* displays high morphological diversity across its putative geographical range. Since this variation could be either intraspecific or interspecific, we suggest that specimens collected outside the type localities and lack molecular data, cannot be precisely identified. The molecular phylogenetic analysis does not support close relationships of the shelf species *Z. japonica* and the abyssal species *Z. abyssa* Korshunova *et al.*, 2017, thus a hypothesis of a shelf origin of the latter species cannot be confirmed by the presented data. Finally, we provide novel evidence on the hidden diversity of flabellinids in the deep-sea waters of the Sea of Japan.

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Сочетание музейных коллекций и новых молекулярных данных способствует ревизии рода голожаберных моллюсков *Ziminella* (Nudibranchia)

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РЕЗЮМЕ. Основная цель настоящей работы – ревизия биологического разнообразия голожаберных моллюсков рода *Ziminella* и уточнение ареалов видов этого рода, с использованием обширного материала из музейных коллекций и недавно собранных образцов *Ziminella japonica* (Volodchenko, 1941) из Японского моря. Мы провели морфологический и молекулярно-филогенетический анализ рода *Ziminella*, основанный на четырех молекулярных маркерах, а также анализ разделения видов. Наши результаты показывают, что *Z. salmonacea* (Couthouy, 1838) и *Z. circapolaris* Korshunova *et al.*, 2017 представляют собой единый вид с высокой внутривидовой изменчивостью в молекулярном маркере COI (до 2.54% между изученными особями). Анализ определения видовых границ не может однозначно подтвердить самостоятельный статус *Z. japonica* и *Z. vrijenhoeki* Valdés *et al.*, 2018, но в данном случае минимальные попарные дистанции

по гену COI составляют 7.95%. Кроме того, были обнаружены некоторые различия в окраске и внешней морфологии между этими видами при анализе образцов из типовых местообитаний. Было также показано, что *Z. japonica* демонстрирует высокое морфологическое разнообразие в пределах предполагаемого географического ареала. Поскольку данная вариативность признаков может быть как внутри- так и межвидовой изменчивостью, мы предполагаем, что особи, собранные за пределами типовых местообитаний и не имеющие молекулярных данных, не могут быть достоверно определены. Молекулярно-филогенетический анализ не подтверждает тесного родства шельфового вида *Z. japonica* и абиссального вида *Z. abyssa* Korshunova *et al.*, 2017, таким образом, гипотеза о шельфовом происхождении последнего вида не может быть подтверждена представленными данными. Наконец, мы приводим новые данные о скрытом разнообразии флабеллинид в глубоководных районах Японского моря.

Introduction

The nudibranch genus *Ziminella* Korshunova *et al.*, 2017 (type species *Eolis salmonacea* Couthouy, 1838) was recently established as a part of the reinstated family Paracoryphellidae [Korshunova *et al.*, 2017]. This genus includes wide-bodied aeolid nudibranchs and encompasses former members of the family Flabellinidae *s.l.* with a well-developed and continuous notal edge, a pleuroproctic anus, a triserial radula with a large central cusp of the rachidian teeth and narrow lateral teeth with minute or reduced denticles on their inner side [Korshunova *et al.*, 2017]. The most peculiar feature that clearly differentiates *Ziminella* from its relatives of the family Paracoryphellidae is absence of any seminal reservoirs in the female part of the hermaphrodite reproductive system [Korshunova *et al.*, 2017]. Currently five species are included in *Ziminella*: *Ziminella salmonacea*, *Ziminella japonica* (Volodchenko, 1941) (originally described as *Coryphella japonica*), *Ziminella abyssa* Korshunova *et al.*, 2017, *Ziminella circapolaris* Korshunova *et al.*, 2017 and *Ziminella vrijenhoeki* Valdés, Lundsten et Wilson, 2018. These species commonly inhabit sandy bottoms with thin silt, or muddy sand from upper subtidal depth to ca. 3500 m depth in the North Atlantic, North Pacific and Arctic waters [Martynov, 2013; Korshunova *et al.*, 2017; Valdés *et al.*, 2018].

Ziminella salmonacea is a common North Atlantic species that was believed to have a wide range in this region as well as adjacent Arctic waters, ranging from the Canadian Arctic Archipelago on the west and to the East Siberian Sea on the east [Kuzirian, 1977; Martynov, 2006]. It was suggested that this species also inhabits the North-West Pacific [Roginskaya, 1978, as *Coryphella stimpsoni* (Verrill,

1879)], however further studies showed that this region is inhabited by other species of the genus [Martynov, 2013]. The identity of *Z. salmonacea* was challenged in the recent revision by Korshunova *et al.* [2017]. They postulated that specimens from the North-West Atlantic coast and Spitzbergen differed from those collected from the Franz Josef Land in a molecular phylogenetic analysis, and also showed different levels of denticulation of the lateral teeth. In Atlantic specimens the lateral teeth can be completely smooth or bear few denticles at the basal part of the teeth, while in specimens from the Franz Josef Land denticles are present on the entire length of the teeth [see Korshunova *et al.*, 2017 for details]. Based on these differences, specimens from the Franz Josef Land were described as a new species *Ziminella circapolaris*. However, no additional revision of the material from the Arctic waters including northeastern parts of the Barents Sea and the Kara Sea was conducted, raising questions on range limits of both *Z. salmonacea s.str.* and *Z. circapolaris*.

Ziminella japonica inhabits deep shallow water to bathyal habitats in the Sea of Japan. It was originally described under the name *Coryphella japonica* based on the material collected from 5 to 42 m depth [Volodchenko, 1941a, b]. The taxonomic status of this species has been questioned in several studies and its synonymy with either *Ziminella salmonacea* (as *Coryphella stimpsoni*, see Roginskaya [1978]) or *Coryphella athadona* Bergh, 1875 [Baba, 1987] was suggested. However, the distinct status of *Z. japonica* was further confirmed by Martynov [1999] (as *Coryphella japonica*) based on the morphological analysis of the type series deposited at the Zoological Institute, Russian Academy of Science (ZIN). Furthermore, a comprehensive morphoanatomical study was published by Martynov [2013] based on the material collected during the deep-sea expeditions of R/V “Vityaz” (1972, 1976) and SoJaBio (2010), including the designation of one of the syntypes examined by Volodchenko as the lectotype for *Z. japonica*. As a result of Martynov [2013] study, the bathymetric range of *Coryphella japonica* was extended to 3620 m [Martynov, 2013]. However, the upper bathymetric limit of *C. japonica* was determined to be either 100 m [Martynov, 2013: table 1], or 120 m [Martynov, 2013: p. 113], since no material corresponding the originally reported depths [Volodchenko, 1941b] was found in the type series [Martynov, 1999]. Martynov [2013] showed a significant morphological variability in radular morphology of studied specimens, including the wide range of denticles shapes on the rachidian teeth [Martynov, 2013: pl. 4, 5], which also corroborated previous observations by Roginskaya [1978]. This variation has been addressed in a subsequent work by Korshunova *et al.* [2017] in which a new species *Ziminella abyssa* Korshunova *et al.*, 2017 was established for specimens from the

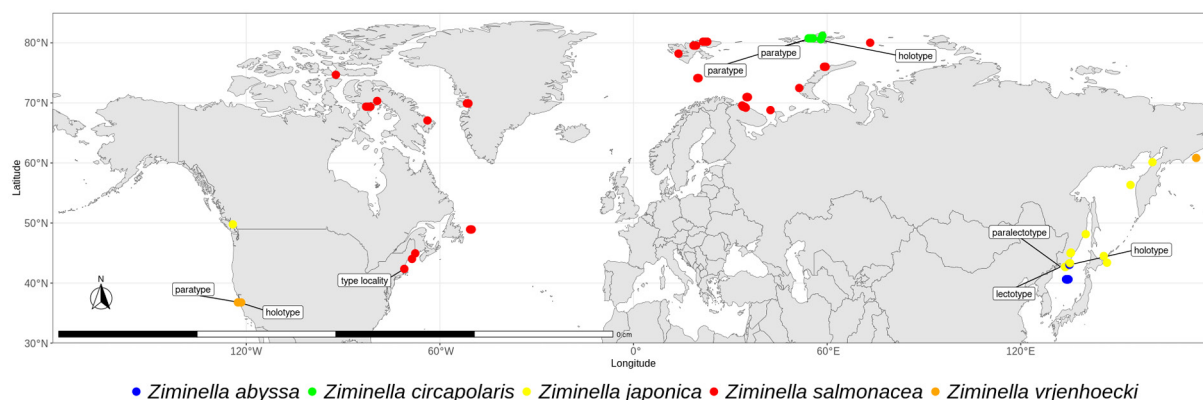


FIG. 1. Map of the Northern Hemisphere (Mercator projection) showing collection sites of *Ziminella* specimens studied herein (including GenBank data) and the type locality of each species.

РИС. 1. Карта Северного полушария (проекция Меркатора) с указанием точек сбора особей рода *Ziminella*, использованных в работе (включая образцы из ГенБанка), а также типового местонахождения каждого вида.

deep-water basin of the Sea of Japan. In fact, the type material of *Ziminella abyssa* in Korshunova *et al.* [2017] almost entirely overlapped with the specimens used in the redescription of *Z. japonica* [Martynov, 2013: p. 112], except the type material of the latter species and several additional specimens collected from 295–994 m depth, but no synonymy was indicated [see Korshunova *et al.*, 2017, p. 20]. Also, neither formal redescription of *Z. japonica s.str.* was provided, nor molecular data, although its external morphology and internal characters (radula, jaws and reproductive system) were illustrated [Korshunova *et al.*, 2017, p. 90]. *Ziminella japonica* was also recorded from the North-East Pacific, specifically from British Columbia from 20 m depth [Behrens, 2004; Calder *et al.*, 2015], where it was found feeding on *Similiclava nivea* Calder *et al.*, 2015.

Finally, the species *Ziminella vrijenhoeki* was the most recently described species of the genus [Valdés *et al.*, 2018] based on deep-sea material from the continental slope off California, with depth ranging from 595 to 1018 m. This species was further reported from 660 m in depth on the Bering Sea slope (the North-West Pacific) [Ekimova *et al.*, 2021a]. It was suggested that *Z. vrijenhoeki* differs from *Z. salmonacea* by having shorter rachidian teeth and larger denticles, and from *Z. japonica* – in coloration. Further phylogenetic research based on three molecular markers [Valdés *et al.*, 2018] showed that *Z. circapolaris* was nested within *Z. salmonacea*, raising doubts on the validity of the former species.

Based on the available information on the genus *Ziminella*, it is clear that several serious gaps exist in our knowledge on the morphological and genetic diversity and distribution of its species. Some phylogenetic analyses do not support the distinct status of *Z. circapolaris* [Valdés *et al.*, 2018] and the

geographical range of this species and the closely related *Z. salmonacea* is not well established. Differences between *Z. vrijenhoeki* and *Z. japonica* are also ambiguous, as the reproductive system was not described in detail for *Z. japonica* and the coloration of this species is not known in its native geographical range, close to the type locality (the Sea of Japan). Also, no molecular data for *Z. japonica* are available to date. The main goal of the present paper is to revise *Ziminella* diversity and update the distribution ranges of its species, based on the historical museum material and newly collected specimens of *Ziminella japonica* from the Sea of Japan.

Material and Methods

Material

The material used in this study included both historical collections retrieved from deposited at Zoological Institute RAS (St. Petersburg, Russia: ZIN) and at Museum of A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences (Vladivostok, Russia: MIMB). Additional material on the species *Ziminella japonica* was collected during the 64 cruise of R/V “Akademic Oparin” (Russia) to the Sea of Japan, July–August 2021, at depths of 100–250 m. This material was collected by an Agassiz trawl and then photographed in the lab, fixed in 96% EtOH and stored at -20 °C to prevent DNA degradation. The newly collected specimens were deposited at MIMB. Detailed sampling localities and voucher numbers for each studied specimen (including historical collections) are given in Table S1, their collection sites are shown on the map (Fig. 1), the specimens for which only genetic data from GenBank is available were also included (Table S2).

Morphological studies

The external and internal morphology of 27 specimens was examined, including the digestive and reproductive systems. The buccal mass of each specimen was extracted and soaked in hypochlorite solution to dissolve connective and muscle tissues. Since most of the specimens and their buccal mass were large, this may cause the degradation of radular teeth during long incubation in hypochlorite solution. Therefore, for most radulae the anterior and posterior portions were processed separately. The isolated radula and the jaws were rinsed in distilled water, air-dried, mounted on an aluminium stub, and sputter-coated with gold for visualization under a JEOL JCM7000 (JEOL, Japan) and Quattro (Thermo Scientific, USA) scanning electron microscopes (SEM). To study the reproductive system, specimens were dissected from the dorsal side along the midline and examined under a stereomicroscope. Also, 15 slides of isolated radulae of *Ziminella* spp. from ZIN collection were analysed under the light microscope.

Molecular analysis

Among historical collections no samples were available for the phylogenetic analysis, since most of them were old and initially fixed in formalin. Therefore, for the DNA extraction only fresh specimens of *Z. japonica* collected from the Sea of Japan in 2021 (during the 62 cruise of R/V “*Akademik Oparin*”) were used (3 specimens, see Tables S1, S2). Additionally, for the phylogenetic analysis we used all *Ziminella* specimens available in public databases (GenBank, Biodiversity of Life Database: BOLD) (Table S2). During the preparation of the alignments, it became clear that the histone H3 of *Z. vrijenhoeki* deposited in GenBank (voucher MIMB42255, accession number MZ766234) is a result of contamination with *Carronella pellucida* (Alder et Hancock, 1843) sequence. Therefore, for this voucher we additionally re-sequenced this marker, and also obtained 18S rRNA sequence data (Table S2).

Total genomic DNA was extracted following the invertebrate protocol of the Canadian Centre for DNA Barcoding [Ivanova *et al.*, 2006]. Extracted DNA was used as a template for amplification of partial mitochondrial cytochrome c oxidase subunit I and 16S rRNA, and nuclear histone H3, 28S rRNA and 18S rRNA. Reaction conditions and primers are available in Table S3. Polymerase chain reactions were performed with an “HS Taq” kit (Eurogen Lab, Russia), following the manufacturer’s protocol. For sequencing, 2 μ L of amplicons were purified by EtOH + Ammonium acetate precipitation [Osterburg *et al.*, 1975] and used as a template for the sequencing reactions with a NovaDye Terminator v3.1 sequencing kit by GeneQuest. Sequencing reactions were analyzed using an ABI 3500 Genetic Analyser (Ap-

plied Biosystems) or Locus 1616 Genetic Analyser (Helicon). All novel sequences were submitted to NCBI GenBank (Table S2).

Data processing and phylogenetic analysis

All raw reads for each gene were assembled and checked for ambiguities and low-quality data in Geneious R10 [Kearse *et al.*, 2012]. Edited sequences were verified for contamination using the BLAST-n algorithm run over the GenBank nr/nt database [Altschul *et al.*, 1990]. The genera *Chlamylla* Bergh, 1886, *Paracoryphella* Miller, 1971 and *Polaria* Korshunova *et al.*, 2017 were chosen as close outgroups, and representatives of the family Tritoniidae – as distant outgroups according to Korshunova *et al.* [2017]. Original data and publicly available sequences were aligned with the MUSCLE [Edgar, 2004] algorithm in MEGA 7 [Kumar *et al.*, 2016]. Additionally, all protein-coding sequences were translated into amino acids to verify reading frames and check for stop-codons. Resulting alignments comprised 650 bp for COI, 326 bp for H3, 396 bp for 16S and 315 bp for 28S. Phylogenetic reconstructions were conducted for the concatenated multi-gene partitioned dataset. The best-fit nucleotide evolution model for MrBayes phylogeny reconstruction method were selected in ModelTest-NG v0.1.7 [Darriba *et al.*, 2020]. The Bayesian phylogenetic analyses and estimation of posterior probabilities were performed in MrBayes 3.2 [Ronquist, Huelsenbeck, 2003]. Markov chains were sampled at intervals of 500 generations. The analysis was initiated with a random starting tree and ran for 5×10^6 generations. The analysis was converged and terminated when the standard deviation of split frequencies reached <0.01 . The Maximum likelihood analysis was conducted in raxmlGUI 2.0 [Edler *et al.*, 2021] with automatically estimated pseudo-replicate number defined by the autoMRE algorithm [Pattengale *et al.*, 2010] under the GTRCAT approximation, applied to each partition individually. Final phylogenetic tree images were rendered in FigTree 1.4.0.

To verify the molecular species boundaries, we also performed Assemble Species by Automatic Partitioning analysis (ASAP) [Puillandre *et al.*, 2021]. The COI alignment was used and three available models were tested, the remaining settings were set to default. For species *Ziminella salmonacea* and *Z. circapolaris* the haplotype network based on the COI dataset was constructed using PopART 1.7 (<http://popart.otago.ac.nz>, assessed on 23 January, 2025) with the TCS network algorithm [Clement *et al.*, 2002]. Uncorrected *p*-distances were calculated based on COI alignment in MEGA 7 [Kumar *et al.*, 2016]. In the case of *Z. japonica* and *Z. vrijenhoeki*, a partial 18S rRNA gene (~1200 bp) was also obtained and studied to identify the phylogenetically important substitutions.

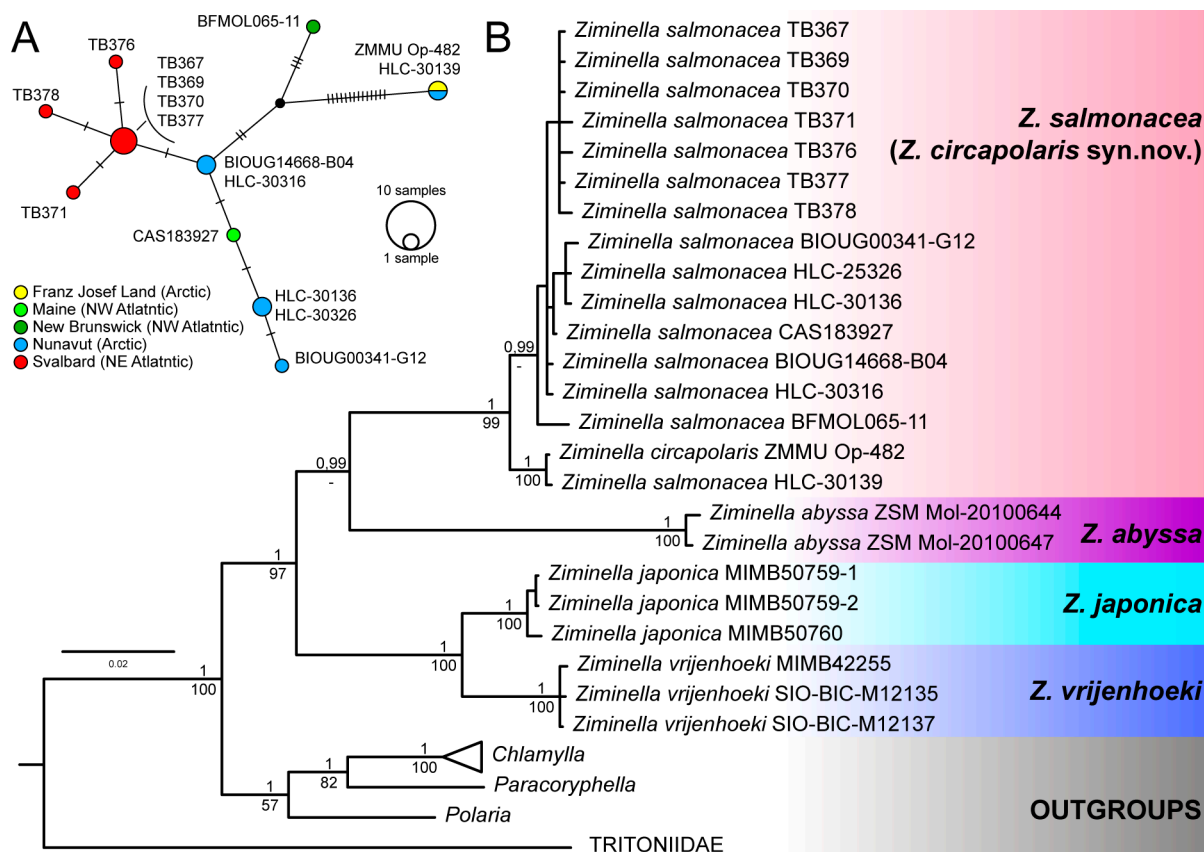


FIG. 2. Results of molecular phylogenetic analysis. **A.** COI haplotype network of *Ziminella salmonacea* and *Ziminella circapolaris* produced with TCS method in PopART. Colors of circles refer to the geographic origin of each haplotype. The relative size of circles is proportional to the number of sequences of that same haplotype. **B.** Molecular phylogenetic hypothesis of the family Paracoryphellidae, Bayesian Inference, concatenated dataset of four markers (COI + 16S + H3 + 28S), genera are collapsed to a single branch, except representatives of *Ziminella*. Numbers above branches indicate posterior probabilities from Bayesian Inference, numbers below branches – bootstrap support from Maximum Likelihood.

РИС. 2. Результаты молекулярно-филогенетического анализа. **A.** Сеть гаплотипов COI *Ziminella salmonacea* и *Ziminella circapolaris*, полученная методом TCS в PopART. Цвета кружков обозначают географическое происхождение каждого гаплотипа. Относительный размер кружков пропорционален количеству последовательностей одного и того же гаплотипа. **B.** Молекулярно-филогенетическое дерево семейства Paracoryphellidae, построенное на основании комбинированного датасета (COI + 16S + H3 + 28S) при помощи байесовского анализа, все клады сколлапсированы, кроме представителей рода *Ziminella*. Значения над ветвями обозначают апостериорные вероятности. Значения под ветвями обозначают поддержки бутстрепа.

Results

Molecular phylogenetic analysis and population genetic structure

The results of the molecular analyses are presented in Fig. 2 and Fig. S1. The Bayesian (BI) and Maximum likelihood (ML) results were generally similar (Fig. 2B, Fig. S1). Both analyses supported the monophyly of the genus *Ziminella* (posterior probabilities from BI (PP) = 1; bootstrap support from ML (BS) = 97). Also, both analyses supported the monophyly of *Ziminella abyssa*, *Z. japonica* and *Z. vrijenhoeki*, as well as sister relationships of the two latter species (PP = 1; BS = 100 in all cases). *Ziminella salmonacea* and *Z. circapolaris* formed a single clade (PP = 1; BS = 97), and the monophyly

of *Z. salmonacea* was compromised in both analyses. First of all, *Z. circapolaris* (the holotype) clustered with *Z. salmonacea* HLC-30139 from Nunavut (PP = 1; BS = 100). In BI analysis this clade was recovered sister to the clade containing the rest *Z. salmonacea* specimens (PP = 0.99). In ML these two species nested within the rest *Z. salmonacea* diversity. Finally, in BI analysis *Z. abyssa* was recovered sister to *Z. salmonacea* and *Z. circapolaris* clade (PP = 0.99), but ML did not resolve its relationships with other *Ziminella* species (BS = 25, see Fig. S1).

The COI-based TCS haplotype network of *Z. salmonacea* and *Z. circapolaris* (Fig. 2A) was well-structured and corroborated the results of the molecular phylogenetic analysis (Fig. 2B). Specimens of *Z. salmonacea* (excluding specimen HLC-30139) were represented by 8 haplotypes with poor

Table 1. Intra- and interspecific uncorrected p-distances (%) based on the COI gene.

Таблица 1. Внутри- и межвидовые нескорректированные попарные дистанции (в %), посчитанные по гену COI.

| Species | 1 | 2 | 3 | 4 | 5 |
|--|--------|--------|--------|--------|-------|
| <i>Z. circapolaris</i> + <i>Z. salmonacea</i> HLC30139 | 0 | | | | |
| <i>Z. salmonacea</i> | 2.54% | 1.35% | | | |
| <i>Z. vrijenhoeki</i> | 16.41% | 15.91% | 0.03% | | |
| <i>Z. japonica</i> | 16.24% | 15.74% | 7.95% | 0.85% | |
| <i>Z. abyssa</i> | 17.60% | 18.10% | 19.12% | 19.97% | 0.06% |

geographic structure, differing in 1–5 substitutions. *Ziminella circapolaris* had the same haplotype as *Z. salmonacea* HLC-30139 from Western Greenland, this haplotype differed from the rest of *Z. salmonacea* diversity by 16 substitutions.

Species delimitation

The results of ASAP analysis based on three different models were similar (Fig. S2). In all cases the lowest ASAP scores (1.5) were received by two different species partitions with four or three candidate species. In the first case, the analysis recovered *Z. salmonacea* + *Z. circapolaris*, *Z. abyssa*, *Z. japonica* and *Z. vrijenhoeki* as distinct. In the second case, *Z. japonica* and *Z. vrijenhoeki* were recovered in a single partition. None of the analysis supported the distinct status of *Z. circapolaris*.

The *p*-distance values of COI marker are shown in Table 1. Overall, with the exception of *Z. circapolaris*, the minimal interspecific distance varied from 7.95% (between *Z. japonica* and *Z. vrijenhoeki*) to 19.95% (between *Z. abyssa* and *Z. japonica*). *Z. circapolaris* was identical to *Z. salmonacea* from Nunavut (HLC-30139), and both specimens demonstrated a *p*-distance of 2.43% to the rest of *Z. salmonacea*. The maximal intraspecific diversity within *Z. salmonacea* (without HLC30139) comprised 1.35%. We also did not identify the phylogenetically important substitutions between *Z. circapolaris* and *Z. salmonacea* in available nuclear markers (H3, 28S), as well as between *Z. vrijenhoeki* and *Z. japonica* (H3, 28S, 18S).

Summarizing the results of the molecular analysis and the morphological data (discussed below in the Systematic part), we can conclude that *Z. salmonacea* and *Z. circapolaris* represent a single species but has intraspecific variation in the COI marker. Also, the ASAP analysis cannot explicitly support the distinct status of *Z. japonica* and *Z. vrijenhoeki* (Fig. S1), but in this case the *p*-distance is much higher than between *Z. salmonacea* and *Z. circapolaris* (Table 1), which allow us to putatively consider these two species as distinct until more data from different localities becomes available (see Remarks section of *Z. japonica*).

Taxonomic descriptions

Order Nudibranchia de Blainville, 1814
Suborder Cladobranchia
Willan & Morton, 1984
Superfamily Fionoidea Gray, 1857
Family Paracoryphellidae Miller, 1971

Genus *Ziminella* Korshunova *et al.*, 2017

Type species. *Eolis salmonacea* Couthouy, 1838, by original designation.

Diagnosis. Body wide; head rounded; notal edge present, well-developed, continuous; rhinophores smooth to rugose; cerata in rows, attached directly to notum, unstalked; anus pleuroproctic on posterior right side of body; oral glands absent; jaws triangular with denticulated masticatory process; triserial radula; rachidian teeth with strong elevated blunt cusp and large denticles on each side; lateral teeth narrow, triangular, with minute denticles on inner edge or denticles absent; seminal receptacles absent; vas deferens long; penial gland absent; unarmed penis.

Species included: *Ziminella abyssa* Korshunova *et al.*, 2017, *Ziminella japonica* (Volodchenko, 1941), *Ziminella salmonacea* (Couthouy, 1838), *Ziminella vrijenhoeki* Valdés *et al.*, 2018.

Ziminella salmonacea (Couthouy, 1838)
(Figs 3 A–C, 4–6)

Eolis salmonacea Couthouy, 1838: 68–69, pl. 1, fig. 2.

Ziminella circapolaris Korshunova *et al.*, 2017: 22–23, fig. 13 – **syn. nov.**

For a full list of synonyms see McDonald [2009].

Type material. For *Z. salmonacea* the type material is not known [Martynov, 2006]. The type material for *Z. circapolaris* **syn. nov.** (Holotype ZMMU Op-598) is hosted at Zoological Museum of Lomonosov Moscow State University.

Material studied. Barents Sea, 70°58'N 37°07'E, 161–170 m depth, coll. Knipowitsch N., 19.07.1899, ZIN24520 (4 spm). Barents Sea, Teriberskaya Guba, 110–146 m depth, coll. Knipowitsch N., 21.07.1894, ZIN24526 (1 spm). Barents Sea, Novaya Zemlya, Gorbovy Isl., 11 m depth, coll. Ushakov P.V., Gorbunov, 04.09.1927, ZIN24527 (2 spm). Barents Sea, 69°34'30.0"N 32°00'31.0"E, 202 m depth, coll. Knipowitsch N., 13.07.1899, ZIN24528 (3 spm). Bar-

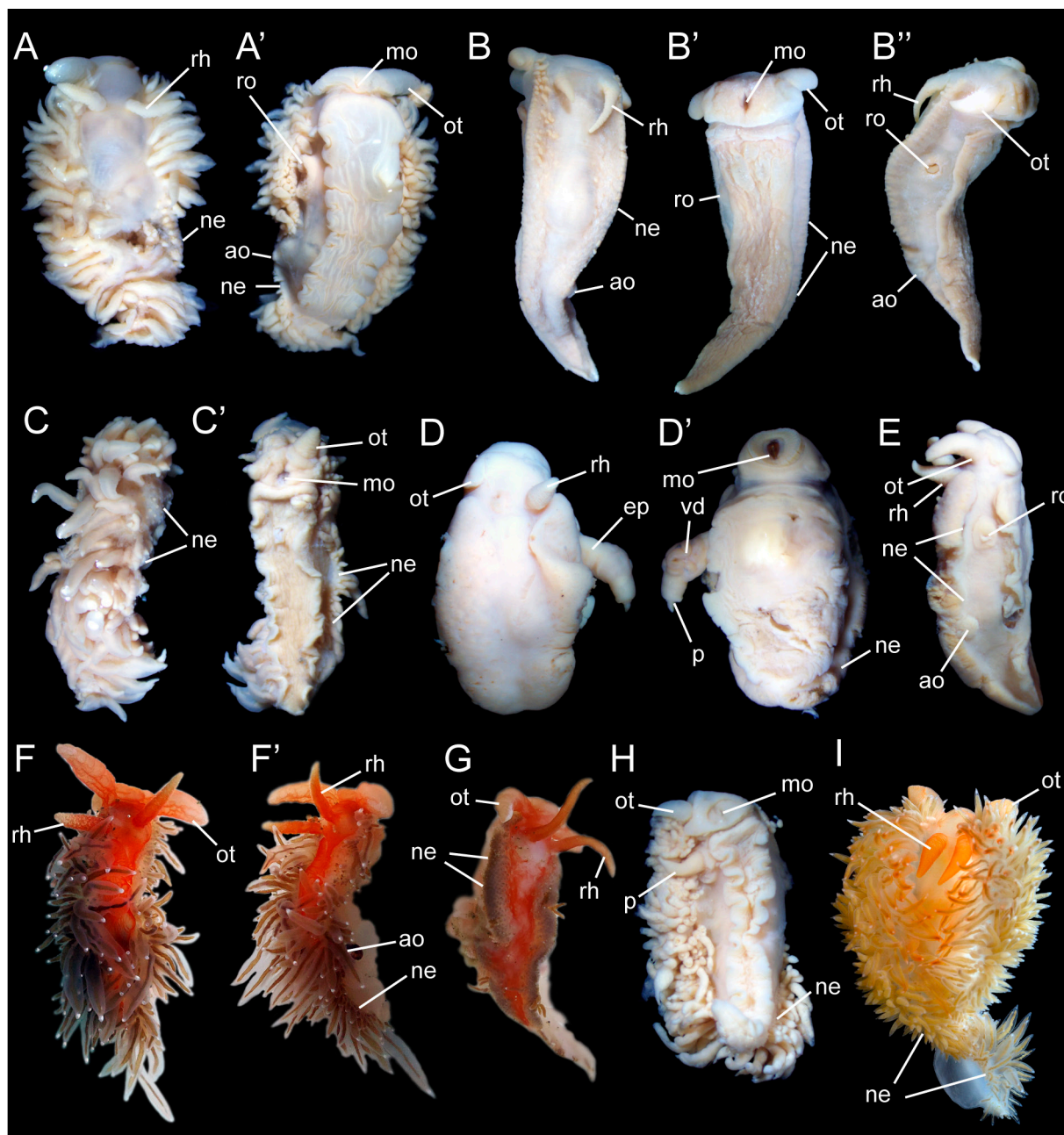


FIG. 3. External morphology of different *Ziminella* species. **A.** *Ziminella salmonacea*, ZIN63740 from (A) dorsal side, (A') ventral side. **B.** *Ziminella salmonacea*, ZIN63739 from (B) dorsal side, (B') ventral side, (B'') lateral side. **C.** *Ziminella salmonacea*, ZIN63746 (*Z. circapolaris* syn. nov.) from (C) dorsal side, (C') ventral side. **D.** *Ziminella abyssa*, ZIN63735-1 from (D) dorsal side and (D') ventral side. **E.** *Ziminella abyssa*, ZIN63735-4 from lateral side. **F.** *Ziminella japonica* MIMB50760 from (F) dorsal side and (F') dorsolateral side. **G.** *Ziminella japonica* MIMB50759-1 from dorsal side. **H.** *Ziminella* sp. from British Columbia, ZIN63760 from ventral side. **I.** *Ziminella vrijenhoeki* MIMB42255 from dorsal side. Abbreviations: ao – anal opening; ep – everted penis; mo – mouth; ne – notal edge; ot – oral tentacles; p – penis; rh – rhinophore; ro – reproductive opening; vd – vas deferens. Photo credits: **A–E, H.** Irina Ekimova; **F–G.** Olga Chichvarkhina; **I.** Anastasia Mayorova.

РИС. 3. Внешняя морфология различных видов рода *Ziminella*. **A.** *Ziminella salmonacea*, ZIN63740 с (A) дорсальной стороны, (A') вентральной стороны. **B.** *Ziminella salmonacea*, ZIN63739 с (B) дорсальной стороны, (B') вентральной стороны, (B'') латеральной стороны. **C.** *Ziminella salmonacea*, ZIN63746 (*Z. circapolaris* syn. nov.) с (C) дорсальной стороны, (C') вентральной стороны. **D.** *Ziminella abyssa*, ZIN63735-1 с (D) дорсальной стороны и (D') вентральной стороны. **E.** *Ziminella abyssa*, ZIN63735-4 с латеральной стороны. **F.** *Ziminella japonica* MIMB50760 с (F) дорсальной стороны и (F') дорсолатеральной стороны. **G.** *Ziminella japonica* MIMB50759-1 с дорсальной стороны. **H.** *Ziminella* sp. из Британской Колумбии, ZIN63760 с вентральной стороны. **I.** *Ziminella vrijenhoeki* MIMB42255 с дорсальной стороны. Обозначения: ao – анальное отверстие; ep – вывернутый penis; mo – рот; ne – край нотума; ot – оральные щупальца; p – penis; rh – ринофор; ro – половое отверстие; vd – семяпровод. Авторство фотографий: **A–E, H.** Ирина Екимова; **F–G.** Ольга Чичвархина; **I.** Анастасия Майорова.

ents Sea, 74°08'N 20°00'E, 155 m depth, coll. Knipowitsch N., 16.04.1900, ZIN24529 (1 spm). Barents Sea, 74°08'N 20°00'E, 155 m depth, coll. Knipowitsch N., 16.04.1900, ZIN24530 (1 spm). Barents Sea, Novaya Zemlya, 72°29'N 51°21'E, 73–74 m depth, coll. Knipowitsch N., 19.07.1901, ZIN24531 (2 spm). Barents Sea, 70°58'N 37°07'E, 161–170 m depth, coll. Knipowitsch N., 19.07.1899, ZIN24532 (1 spm). Barents Sea, Ura Bay, 69°23'00.0"N 32°55'00.0"E, 271 m depth, coll. Knipowitsch N., 26.05.1901, ZIN24533 (1 spm). Kara Sea, 80°1.5'N 73°20'E, 41 m depth, coll. Vagin, 18.08.1934, ZIN24535 (2 spm). Barents Sea, Kola Bay, 220 m depth, coll. Knipowitsch N., 11.06.1898, ZIN24537 (1 spm). Barents Sea, Ura Bay, 235 m depth, coll. Knipowitsch N., 17.06.1902, ZIN24540 (1 spm). Barents Sea, 69°18'14.8"N 33°41'57.4"E, 72 m depth, coll. Knipowitsch N., 28.06.1898, ZIN24545 (1 spm). Franz Josef Land, Heiss Is., 5–7 m in depth, coll. Pushkin, 01.02.1982, ZIN63736 (1 spm). NW Atlantic, off Newfoundland, 48°55.5'N 50°31.4'W, 230–237 m depth, coll. Nesis K.N., 14.07.1959, ZIN63739 (3 spm). Western Greenland, 69°55'1"N 51°16.2"W, 7 m depth, coll. Sirenko B.I., 21.07.1993, ZIN63740 (12 spm). Barents Sea, Novaya Zemlya, Gorbovy Isl., 11 m depth, coll. Ushakov P.V., 04.09.1927, ZIN63741 (3 spm). Franz Josef Land, Apollonov Is., 3–4 m depth, coll. Averintsev, 30.09.1992, ZIN63746 (1 spm).

Type locality. Charles River, Massachusetts, USA.

Description. *External morphology* (based on studied specimens): Body length up to 40 mm. Body wide. Foot wide, anterior corners short, rounded. Notal edge well-developed, continuous, forming short elevation above lateral body sides. Oral tentacles elongated, conical. Rhinophores smooth to rugose, longer and thinner than oral tentacles. Cerata in distinct rows, attached directly to well-defined notal edge. Cerata fusiform to cylindrical, lateral cerata much smaller than dorsal. Digestive gland diverticula filling more than half of ceratal volume. Anal opening on right side below notal edge, at beginning of posterior half of body. Reproductive opening on right side, on anterior part of body, surrounded by slightly folded region.

Coloration [after Kuzirian, 1977; 1979; Roginskaya, 1987]: Background body color milky-white. Oral tentacles and rhinophores beige to light orange with distal white stripe. Cerata orange-tan to deep red-brown, distal tip with white ring.

Internal morphology (based on studied specimens): Jaws oval-triangular with well-developed masticatory border bearing several rows of low blunt denticles or elevations. Radular formula: 19–32 × 1.1.1. Rachidian teeth massive, triangular. Central cusp strong, conical and elongated, non-compressed by adjacent denticles. From 4 to 11 small sharp and slightly curved denticles on each side of cusp, commonly from 6 to 9, denticles of about same size. Lateral teeth narrow, slightly curved blades with variable denticulation. From 0 to 29 denticles on inner side, locating at base, on first half or on entire length of tooth. Reproductive system diaulic. Ampulla long,

narrow and convoluted. Vas deferens extremely long with slightly expanded prostatic part. Penis conical to slightly folded. Seminal receptacle absent.

Distribution. This species possesses a wide geographic and bathymetric distribution in the North Atlantic and adjacent Arctic waters. Based on Kuzirian [1979], Roginskaya [1987], Korshunova *et al.* [2017], and the material from BOLD and ZIN collections, the known range of *Z. salmonacea* includes Massachusetts, Maine, Bay of Fundy, New Brunswick, Newfoundland, Western Greenland, waters off Canadian Arctic Archipelago, Iceland, Northern Norway, Svalbard, Franz Josef Land and the Barents, the White and the Kara seas, on depths from 3 to 271 m.

Remarks. Our morphological and molecular data suggest that *Z. salmonacea* and *Z. circapolaris* should be considered a single species. *Ziminella circapolaris* was described based on specimens from the Franz Josef Land, as it “forms a separate sister clade to *Z. salmonacea*” [Korshunova *et al.*, 2017: 22]. According to Korshunova *et al.* [2017] these two species differ in the denticulation of the lateral teeth, as in *Z. circapolaris* the “denticulation runs up to very end of the lateral teeth, and the teeth are always denticulated”, while in *Z. salmonacea* the denticles are restricted to the first half of the laterals [Korshunova *et al.*, 2017: 23]. Finally, it was noted that the separate status of *Z. circapolaris* is “concordant with a considerable level of endemism of the nudibranch fauna of Franz Josef Land” [Korshunova *et al.*, 2017: 23]. Our data suggests that none of above-mentioned arguments could be used to delineate these species. First of all, the specimen from BOLD database (HLC-30139) collected from the Canadian Arctic, has the same haplotype as *Z. circapolaris* (Fig. 2A), rejecting the idea of endemic status for the latter. Although *Z. salmonacea* and *Z. circapolaris* (with an inclusion of HLC-30139) formed two distinct clades on the BI tree, the ML analysis did not separate them (Fig. 2B, Fig. S1). The validity of *Ziminella circapolaris* was not supported by the species delimitation analysis (even if we consider HLC-30139 represents the same species), and this species also does not show any difference from *Z. salmonacea* in sequenced nuclear markers (H3). Finally, we have studied a large collection of *Z. salmonacea* deposited in ZIN, including the slides with isolated radulae (Tables S1, S4). Accordingly, the lateral teeth denticulation varies greatly in specimens collected across distant localities, in a single locality (including Franz Josef Land) or even at the same site (Fig. 4, 5). In fact, several specimens from Franz Josef Land possess weakly denticulated (Table S4, Figs 5 B, C) or even almost smooth (Table S4, Figs 5 D, G, H) lateral teeth. At the same time, dense denticulation was observed in a specimen from Severnaya Zemlya Is. (Table S4, Figs 5 J–L). Specimens from the North-

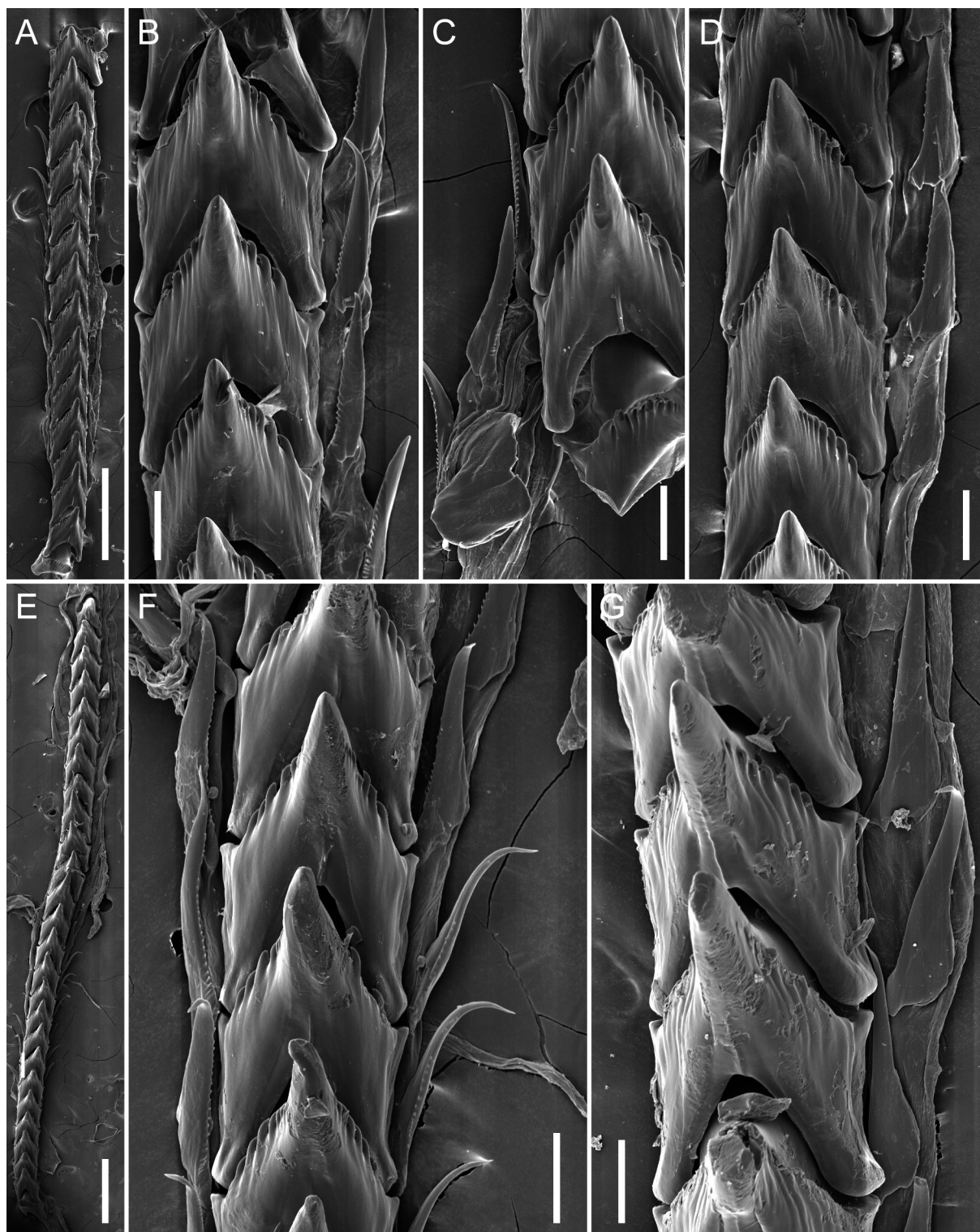


FIG 4. Radular morphology of *Ziminella salmonacea* from northwestern Atlantic. **A.** ZIN63740, specimen 22 mm in length (preserved), posterior radular portion. **B, C.** Same specimen, rachidian and lateral teeth. **D.** ZIN63740, specimen 21 mm in length (preserved), rachidian and lateral teeth. **E.** ZIN63739, specimen 10 mm in length (preserved), radula. **F.** Same specimen, rachidian and lateral teeth. **G.** ZIN63739, specimen 23 mm in length (preserved), rachidian and lateral teeth. Scale bars: A, E = 500 μ m; B–D, F, G = 100 μ m.

FIG 4. Морфология радулы *Ziminella salmonacea* из северо-западной Атлантики. **A.** ZIN63740, особь 22 мм длиной (фикс.), задняя часть радулы. **B, C.** Та же особь, центральные и латеральные зубы. **D.** ZIN63740, особь 21 мм длиной (фикс.), центральный и латеральные зубы. **E.** ZIN63739, особь 10 мм длиной (фикс.), радула. **F.** Та же особь, центральные и латеральные зубы. **G.** ZIN63739, особь 23 мм длиной (фикс.), центральные и латеральные зубы. Масштабные линейки: A, E = 500 μ m; B–D, F, G = 100 μ m.

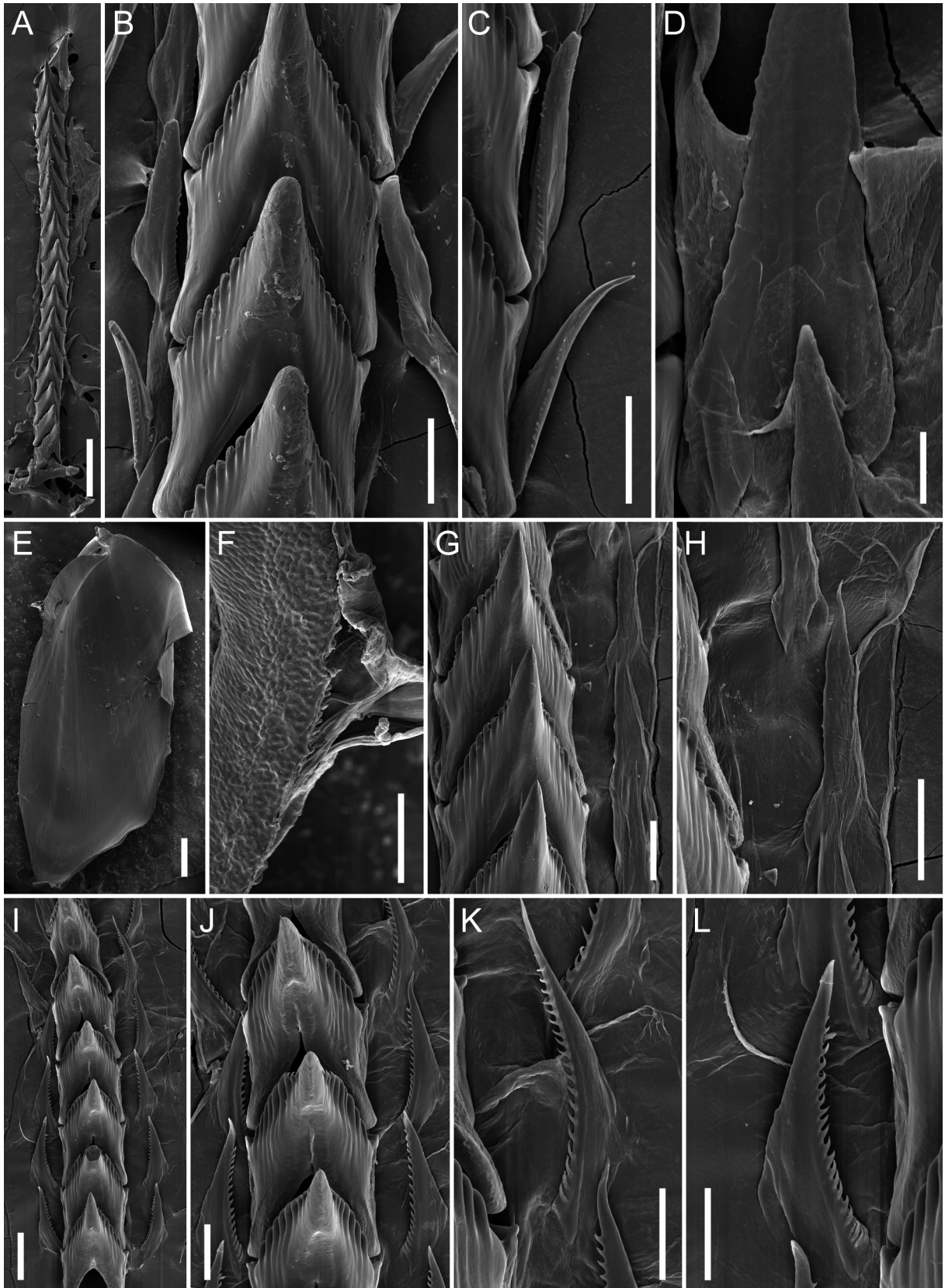


FIG. 5. Radular and jaw morphology of *Ziminella salmonacea* from Franz Josef Land (= *Z. circapolaris* syn. nov.) and Novaya Zemlya Is. A–F. ZIN63746, specimen 20 mm in length (preserved). G, H. ZIN63736, specimen 12 mm in length (preserved). I–L. ZIN63741, specimen 19 mm in length (preserved). A. Posterior radular portion. B. Rachidian and lateral teeth. C. Lateral teeth with well-defined denticles. D. Lateral tooth lacking developed denticles. E. Right jaw plate. F. Denticulation of masticatory border. G. Rachidian and lateral teeth. H. Lateral tooth. I. Posterior radular portion. J. Rachidian and lateral teeth. K, L. Lateral teeth. Scale bars: A, E = 500 μ m; B, C, F–I = 100 μ m; D = 30 μ m; J–L = 50 μ m.

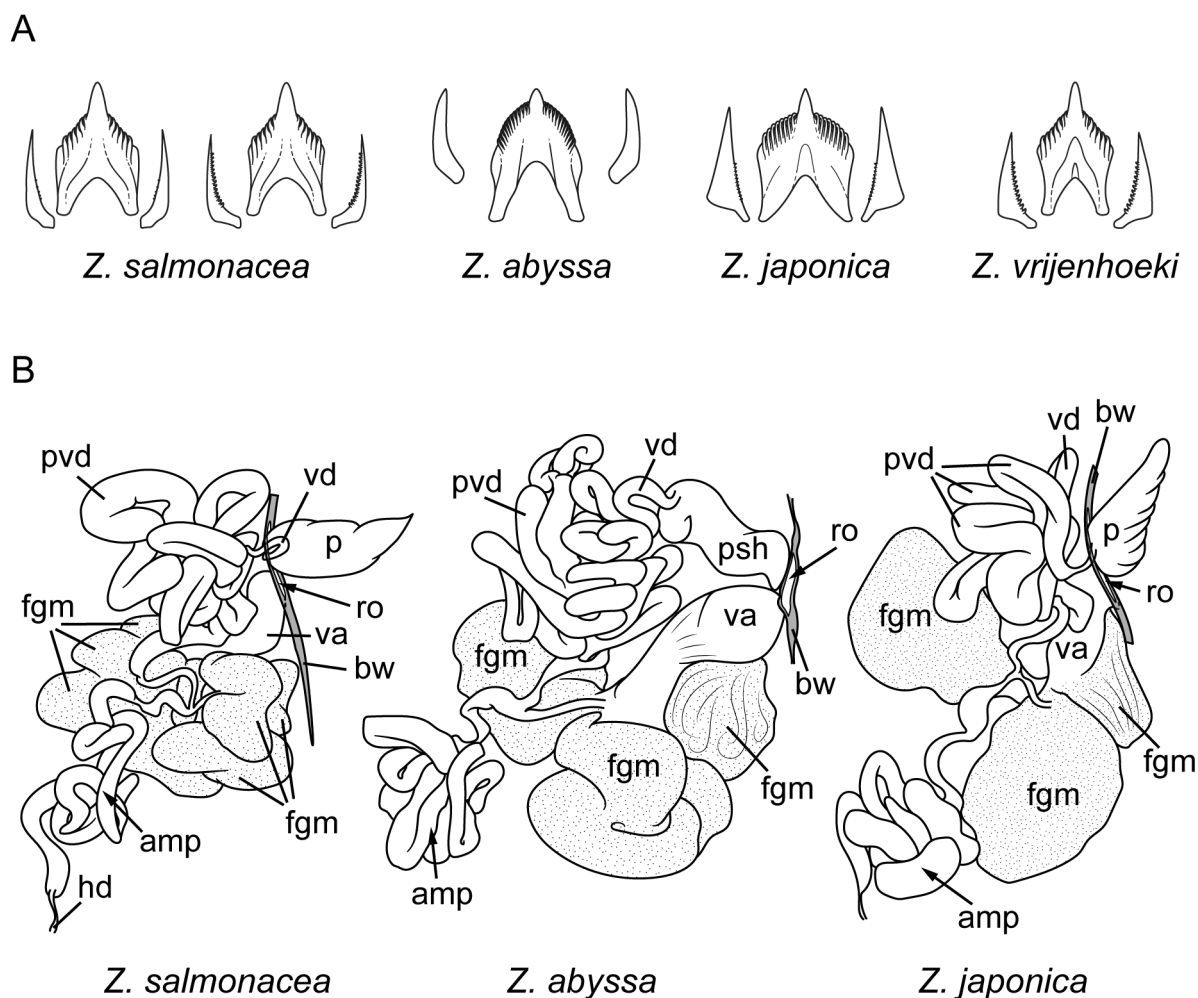


FIG. 6. Schematic overviews of radulae and reproductive system of studied *Ziminella* species. **A.** Radulae. **B.** Reproductive system. Abbreviations: amp – ampulla; bw – body wall; fgm – female gland mass; hd – hermaphrodite duct; p – penis; psh – penial sheath; pvd – prostatic vas deferens; ro – reproductive opening; va – vagina; vd – vas deferens.

РИС. 6. Схемы строения радулы и половой системы у изученных видов *Ziminella*. **A.** Радулы. **B.** Половая система. Обозначения: amp – ампулла; bw – стенка тела; fgm – комплекс женских желез; hd – гермафродитный проток; p – пенис; psh – сумка пениса; pvd – простатическая часть семяпровода; ro – половое отверстие; va – вагина; vd – семяпровод.

West Atlantic and western Arctic sectors also showed variability in denticulation (Fig. 4, Table S4) and the same has already been reported for the specimens of *Z. salmonacea* collected close to the type locality [Morse, 1971]. Moreover, in the SEM image of *Z. salmonacea* radula provided by Korshunova *et al.* [2017], the denticulation reaches the top of the lateral teeth [Korshunova *et al.*, 2017: fig. 15G]. Thus, we consider this variability to be intraspecific rather than interspecific. It was previously suggested that this variation could be ontogenetic, as Morse [1971] indicated that lateral teeth commonly have fewer

denticles on the anterior part of the radular ribbon. In our material, this tendency is not traceable overall (Table S4), although in some radulae the anterior radular portion may possess denser denticulation of the lateral teeth.

Ziminella salmonacea shows minor but consistent morphological differences with other species of the genus. From *Z. abyssa* it differs by consistently fewer number of denticles on the rachidian teeth (from 10 to 19 in *Z. abyssa*), also in the latter species the lateral teeth never have well-developed denticles (Fig. 7). In *Ziminella japonica* and *Z. vrijenhoeki* the lateral

РИС. 5 (предыдущая страница). Морфология радулы и челюстей *Ziminella salmonacea* с Земли Франца-Иосифа (= *Z. circumpolaris* syn. nov.) и Новой Земли. **A–F.** ZIN63746, особь 20 мм длиной (фикс.) **G, H.** ZIN63736, особь 12 мм длиной. **I–L.** ZIN63741, особь 19 мм длиной. **A.** Задняя часть радулы. **B.** Центральные и латеральные зубы. **C.** Латеральные зубы с хорошо выраженными зубчиками. **D.** Латеральные зубы без выраженных зубчиков. **E.** Правая челюстная пластинка. **F.** Зазубренность жевательного отростка. **G.** Центральные и латеральные зубы. **H.** Латеральный зуб. **I.** Задняя часть радулы. **J.** Центральные и латеральные зубы. **K, L.** Латеральные зубы. Масштабные линейки: **A, E** = 500 μ m; **B, C, F–I** = 100 μ m; **D** = 30 μ m; **J–L** = 50 μ m.

teeth have much wider base, with denticulation always occurring in the first half of its internal edge (Fig. 9) [Valdés *et al.*, 2018]. Also, *Z. japonica* has different coloration with distinct orange to reddish dorsal surface and rhinophores (Figs 3F, G).

Ziminella abyssa Korshunova *et al.*, 2017
(Figs 3 D, E, 6, 7)

Ziminella abyssa Korshunova *et al.*, 2017: 20, 21, fig. 12.

Coryphella stimpsoni – Roginskaya, 1978: 169–177, fig. 1, 2, *partim* (not of Verrill, 1879).

Coryphella japonica – Martynov, 2013: 112–114 (*partim*), pl. 1.1–10, pl. 4, pl. 6.1–4, pl. 7.1–3 (not of Volodchenko, 1941).

Type material. Holotype ZSM Mol-20100647 deposited at Bavarian State Collection of Zoology, Munich. 153 paratypes (ZMMU Op-248–Op-250, Op-252, Op-253, Op-255–Op-259, Op-264) deposited at Zoological Museum of Lomonosov Moscow State University.

Material studied. Sea of Japan, R/V “*Vityaz*”, st. 6658, 40°37'8"N 134°07'0"E, 3580 m depth, 16.06.1972, ZIN63735 (6 spm). All specimens were dissected.

Type locality. Sea of Japan, 43°01'42.9"N 135°04'32.7"E, 2676 m depth.

Description. *External morphology* (based on studied specimens): Body length up to 25 mm. Body wide. Foot wide, anterior corners short, rounded. Notal edge well-developed, continuous, forming short elevation above lateral body sides. Oral tentacles elongated, conical. Rhinophores slightly rugose, same length as oral tentacles, thinner than oral tentacles. Cerata in distinct rows, attached directly to well-defined notal edge. Anal opening on right side below notal edge, at beginning of posterior half of body. Reproductive opening on right side, on anterior part of body.

Coloration [after Korshunova *et al.*, 2017]: Background body color translucent milky-white. Rhinophores light orange at base and pale on rest of length. Cerata dark violet.

Internal morphology (based on studied specimens): Jaws massive, oval-triangular with well-developed masticatory border bearing several rows of low blunt denticles or elevations. Radular formula:

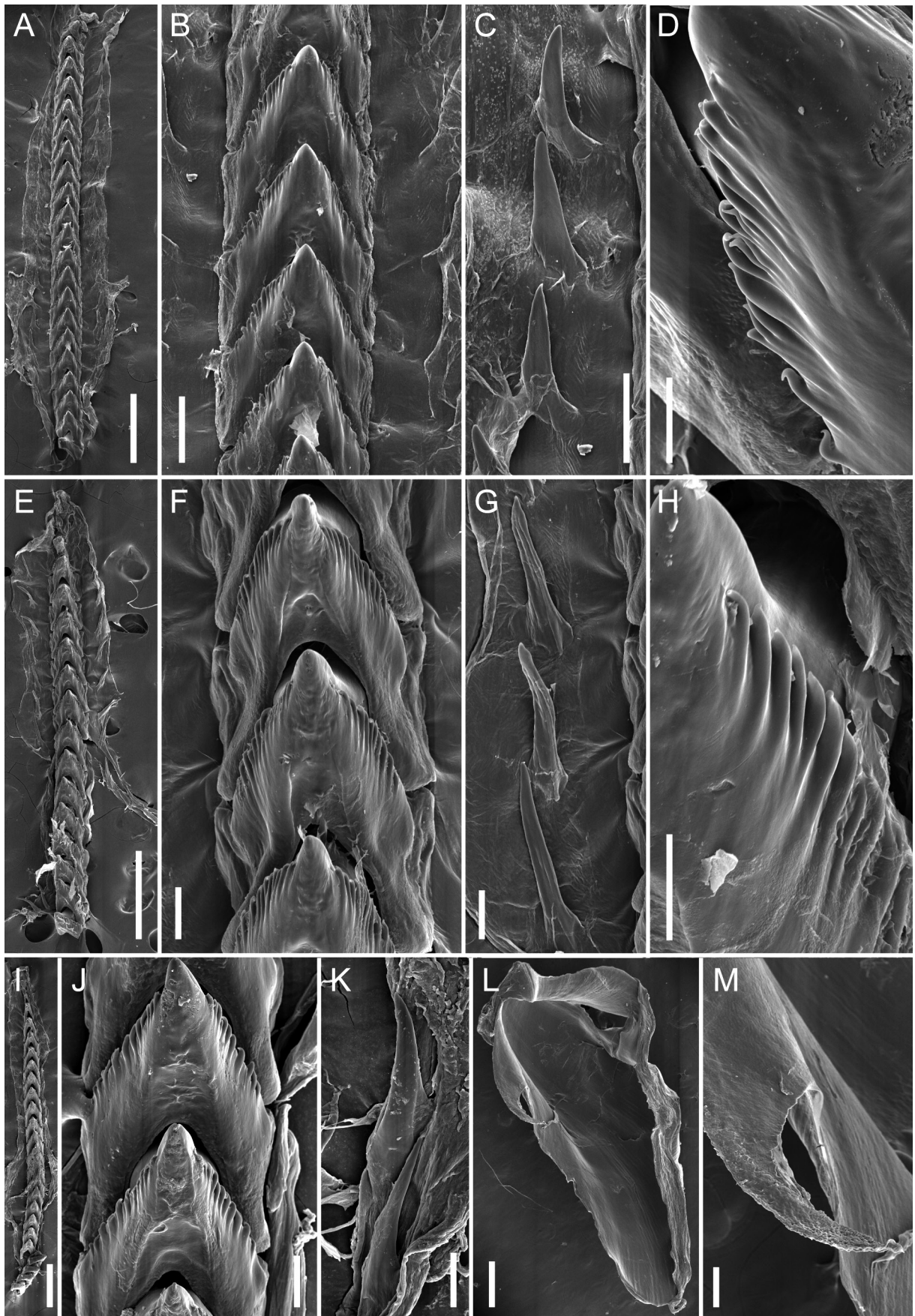
22–31 × 1.1.1. Rachidian teeth large, triangular. Central cusp conical, wide and rather short, non-compressed by adjacent denticles. From 10 to 19 small slightly curved denticles on each side of cusp, sometimes bifurcated, commonly different in size. Lateral teeth narrow, slightly curved triangle blades, no denticulation traceable. Reproductive system diaulic. Ampulla long, narrow and convoluted. Vas deferens extremely long with slightly expanded prostatic part. Penis slightly folded, elongated when everted. Seminal receptacle absent.

Distribution. Currently this species is known only from the Sea of Japan [Roginskaya, 1978; Martynov, 2013; Korshunova *et al.*, 2017; this study], however further studies and sampling in adjacent regions are needed.

Remarks. This species was described based on historical collections (sampling by the R/V “*Vityaz*” in 1972–1976) and materials from the SoJaBio expedition in 2010 [Korshunova *et al.*, 2017]. The historical samples have been studied initially by Roginskaya [1978] and Martynov [2013], and were identified as either *Coryphella stimpsoni* or *Coryphella japonica* respectively. Furthermore, the collection of material suitable for the molecular studies allowed researchers to reconsider the deep-sea material of *Z. japonica* as a distinct species *Z. abyssa* [Korshunova *et al.*, 2017], although sequences of true *Z. japonica* were not available for comparison. Our results support the distinct status of *Z. abyssa* from *Z. japonica* (Fig. 2B), however our investigation of the radular morphology showed several differences with the original description of *Z. abyssa* (Fig. 7). Roginskaya [1978], Martynov [2013], and Korshunova *et al.* [2017] have reported on the irregular denticulation or even smooth rachidian teeth. Roginskaya [1978] suggested that the high variability in denticulation of lateral and rachidian teeth was a result of radular wearing. Martynov [2013] identified asymmetrically effaced rachidian teeth and also suggested this was a result of feeding on burrowing sea anemones of the family Edwardsiidae. Korshunova *et al.* [2017] considered the irregular denticulation of the rachidian teeth to be a specific trait differentiating *Z. abyssa* from the remaining species of the genus. According

FIG. 7 (following page). Radular and jaw morphology of *Ziminella abyssa* ZIN63735. **A.** Specimen 18 mm in length, posterior radular portion. **B.** Same specimen, rachidian teeth. **C.** Same specimen, lateral teeth. **D.** Same specimen, rachidian tooth denticulation. **E.** Specimen 16 mm in length, posterior radular portion. **F.** Same specimen, rachidian teeth. **G.** Same specimen, lateral teeth. **H.** Same specimen, rachidian tooth denticulation. **I.** Specimen 20 mm in length, radula. **J.** Same specimen, rachidian teeth. **K.** Same specimen, lateral teeth. **L.** Specimen 18 mm in length, right jaw plate. **M.** Same specimen, masticatory border denticulation. Scale bars: A, E, I, L = 500 µm; B, C, M = 100 µm; D, H = 30 µm; F, G, J, K = 50 µm.

РИС. 7. Морфология радулы и челюстей *Ziminella abyssa* ZIN63735. **A.** Особь 18 мм в длину (фикс.), задняя часть радулы. **B.** Та же особь, центральные зубы. **C.** Та же особь, латеральные зубы. **D.** Та же особь, зазубренность центрального зуба. **E.** Особь 16 мм в длину (фикс.), задняя часть радулы. **F.** Та же особь, центральные зубы. **G.** Та же особь, латеральные зубы. **H.** Та же особь, зазубренность центрального зуба. **I.** Особь 20 мм в длину (фикс.), радула. **J.** Та же особь, центральные зубы. **K.** Та же особь, латеральные зубы. **L.** Особь 18 мм в длину, правая челюстная пластинка. **M.** Та же особь, зазубренность жевательного отростка. Масштабные линейки: А, Е, I, L = 500 µm; В, С, М = 100 µm; D, H = 30 µm; F, G, J, K = 50 µm.



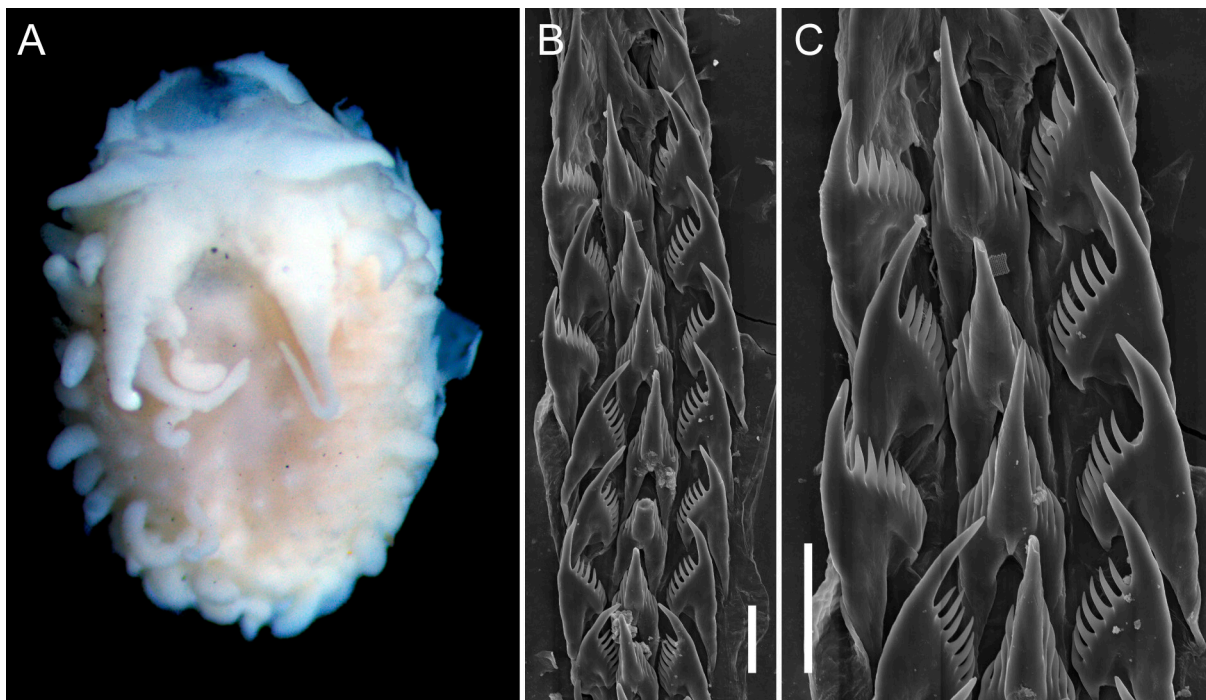


FIG. 8. External and internal morphology of *Polaria polaris* (MIMB49484) from the Sea of Japan. **A.** Fixed specimen (4 mm in length) from dorsal side, buccal mass removed. **B, C.** Rachidian and lateral teeth. Scale bars: 50 μ m.

РИС. 8. Внешняя и внутренняя морфология *Polaria polaris* (MIMB49484) из Японского моря. **A.** Фиксированный экземпляр (4 мм длиной) с дорсальной стороны, буккальная масса отпрепарирована. **B, C.** Центральные и латеральные зубы радулы. Масштабные линейки: 50 μ m.

to the latter authors, denticles of the rachidian teeth are commonly “fold-like or fork-like”, sometimes greatly irregular, and the larger denticles are typically intermingled with the smaller ones, which is an obvious trait of studied juvenile specimen [Korshunova *et al.* 2017: 20, fig. 12I]. In our material the denticles on the rachidian teeth were not highly irregular (Figs 7 F, H, J), but in several specimens their size was different and some of denticles were branched (Fig. 7D). We did not detect any specific pattern of denticulation, like regular intermingling of larger denticles with smaller ones. Also, the anterior teeth rows had the same denticulation as the posterior teeth, with no sign of teeth wearing. Moreover, Korshunova *et al.* [2017] described small denticles on internal edge of the lateral teeth, however the referred figures display either only rachidian teeth [Korshunova *et al.*, 2017: 20, figs 12 F–H] or smooth lateral teeth [Korshunova *et al.*, 2017: fig. 12E]. In our material the lateral teeth were smooth with no evidence for any denticulation (Figs 7 C, G, K).

Ziminella abyssa is clearly different from other described species considered distinct herein. The main differences are observed in radular characters, as this species has the highest number of denticles on the rachidian teeth among *Ziminella*, and these denticles commonly have different sizes. Also, in our material smooth lateral teeth were detected, which could be another distinctive feature of this species.

It is possible that the coloration or some external features could be also different from those in other *Ziminella* species, but we do not have newly collected material to confirm this.

It is important to notice that both Martynov [2013] and Korshunova *et al.* [2017] identified a 2 mm specimen (ZMMU Op-264) to be a member of *Ziminella abyssa*. This specimen has very distinct rachidian teeth with narrow and long central cusps, highly protruding from the tooth surface [Korshunova *et al.*, 2017: fig. 12I]. This morphology is not typical for *Ziminella*, but is found in other Paracoryphellidae, such as *Chlamylla intermedia* (Bergh, 1899), *Paracoryphella parva* (Hadfield, 1963), *Polaria polaris* (Volodchenko, 1946), see for example Korshunova *et al.* [2017], although no records of these species are known for the deep-sea waters of the Sea of Japan. We have studied a ‘juvenile’ specimen from the Sea of Japan collected from 3427–3431 m in depth (MIMB49484). The external appearance of this specimen (Fig. 8A) is very similar to that of the ‘juvenile’ ZMMU Op-264 [Martynov, 2013: pl. 2.9], in particular they have similar body width and arrangement of oral tentacles and rhinophores; the bases of the rhinophores are closely together (Fig. 8A), which is not typical for *Ziminella* (Fig. 3). The study of the radula of MIMB49484 shows that it has similar morphology to that of *Polaria polaris*: the rachidian teeth are triangular and bear

long central cusps, and the lateral teeth are wide with large sharp denticles on the inner edge and long cusp (Figs 8 B, C). *Polaria polaris* has a wide distribution in the Arctic waters [Martynov, 2006 as *Coryphella polaris*], and was also recorded from the Sea of Okhotsk and the southern Kuril Islands with a bathymetric limit of 325 m depth [Martynov *et al.*, 2015]. Our discovery extends its geographical range to the Sea of Japan, and its bathymetric range to 3431 m depth. Taking into account the external similarity between MIMB49484 and ZMMU Op-264, and also the different radular morphology of the latter from typical *Ziminella*, we consider ZMMU Op-264 does not belong to *Ziminella abyssa*. Nevertheless, we cannot precisely identify the species of ZMMU Op-264 as its rachidian teeth morphology does not fit the diagnosis of any described paracoryphellid species. This fact, along with the discovery of *P. polaris* in the abyssal depths of the Sea of Japan, suggests the species diversity of this area is much higher than previously thought and further dedicated studies with comprehensive sampling for molecular analysis are needed.

Ziminella japonica (Volodchenko, 1941)
(Figs 3 F, G, 6, 9 A–I, L, M)

Coryphella japonica Volodchenko, 1941b: 57, pl. 3.3, pl. 4.1; Martynov, 1998: 207; Martynov, 2006: 284–285, pl. 13: 6 A, B; Martynov, 2013: 112–114 (*partim*), pl. 1.11, 1.12, pl. 2.1–2.8, pl. 5.1–8.

Coryphella stimpsoni – Roginskaya, 1878: 169–177, *partim* (not of Verrill, 1879).

Type material. Lectotype (dissected): ZIN24615, Sea of Japan, off Askold Is., 120 m depth, coll. Derzhavin, 25.06.1928 (designated by Martynov [2013]). Paralectotype ZIN63758, dissected, same locality, depth and collector as in lectotype.

Additional material studied: Sea of Japan, R/V “*Akademich Oparin*”, st. 80, 43°18.7′N 135°10.0′E, 219 m depth, coll. O.V. Chichvarikhina, 09.07.2021, MIMB50759 (2 spm). Sea of Japan, R/V “*Akademich Oparin*”, st. 56, 44°58.3′N 136°53.1′E, 120 m depth, coll. O.V. Chichvarikhina, 04.07.2021, MIMB50760 (1 spm). Sea of Japan, R/V “*Krasny Yakut*”, st. 119/4, 45°05.3′N 136°56′E, 115 m depth, coll. P.V. Ushakov, 10.07.1930, ZIN63756 (1 spm). Sea of Japan, R/V “*Leitenant Dydymov*”, st. 431, 48°08′30.0″N 140°08′30.0″E, 122 m depth, coll. Soldatov, 15.09.1913, ZIN63759 (1 spm).

Type locality. Sea of Japan, off Askold Is., 120 m depth.

Description (based on studied specimens). *External morphology:* Body length up to 14 mm (preserved). Body wide. Foot wide, anterior corners short, rounded. Notal edge well-developed, continuous, elevations not extended above lateral body sides. Oral tentacles short, wide, conical. Rhinophores rugose, same size as oral tentacles, thinner than oral tentacles. Cerata in distinct rows, attached directly to well-defined notal edge. Cerata fusiform to cy-

lindrical, lateral cerata much smaller than dorsal. Digestive gland diverticula filling from 1/3 to 3/4 of ceratal volume. Anal opening on right side right below notal edge, at beginning of posterior half of body. Reproductive opening on right side on anterior part of body.

Coloration: Background body color pinkish-white. Dorsal side of body lacking cerata, oral tentacles and rhinophores covered with extensive orange to reddish pigment, which becoming paler to peachy on tips of cerata and oral tentacles. Cerata orange-tan to deep red-brown, distal tip with white ring.

Internal morphology (based on studied specimens): Jaws massive, oval-triangular with well-developed masticatory border bearing several rows of low blunt denticles or elevations. Radular formula: 17–28 × 1.1.1. Rachidian teeth massive, triangular. Central cusp strong, conical, elongated, non-compressed by adjacent denticles. From 6 to 11 small sharp and slightly curved denticles on each side of cusp, commonly from 7 to 9, denticles of about same size. Denticles may be ramified to 2–4 smaller denticles. Lateral teeth triangular plates, denticulation always present on first half. From 7 to 19 denticles on inner side. Reproductive system diaulic. Ampulla long, narrow and convoluted. Vas deferens extremely long with slightly expanded prostatic part. Penis conical or slightly folded. Seminal receptacle absent.

Distribution. The Sea of Japan from 115 to 528 m in depth [Martynov, 2013; Korshunova *et al.*, 2017; present study]. Specimens with similar morphology are also known from the Sea of Okhotsk, the Southern Kuril Islands and from the British Columbia from depth of 20 m to 560 m (this study), but molecular data are needed for confirmation of their species identity (see below).

Remarks. The type material (lectotype ZIN24615) of *Z. japonica* was dissected and no slides of the radula and jaws of these specimens was available for study. At the same time, the original description provides the illustrations of the radular morphology [Volodchenko, 1941b: pl. 4-1], which corroborates well with our morphological investigations. The external morphology of specimens collected from adjacent areas to the type locality and at the same depths (minimum distance ~250 km) corroborates with the initial description and the external morphology of the type material (see Volodchenko [1941b]: pl. 3.3, and Martynov *et al.* [2013]: pl. 1.11, 1.12). *Ziminella japonica* shows several consistent differences with *Z. abyssa* and *Z. salmonacea*. Accordingly, *Z. abyssa* has more denticles on the rachidian teeth and shorter central cusps, and its lateral teeth are smooth and narrow (Fig. 7), while in *Z. japonica* laterals are triangular and bear small sharp denticles at first half of teeth (Fig. 9 D, G–I). *Ziminella japonica* differs from the Arctic-Atlantic species *Z. salmonacea* by the shape of the rachidian

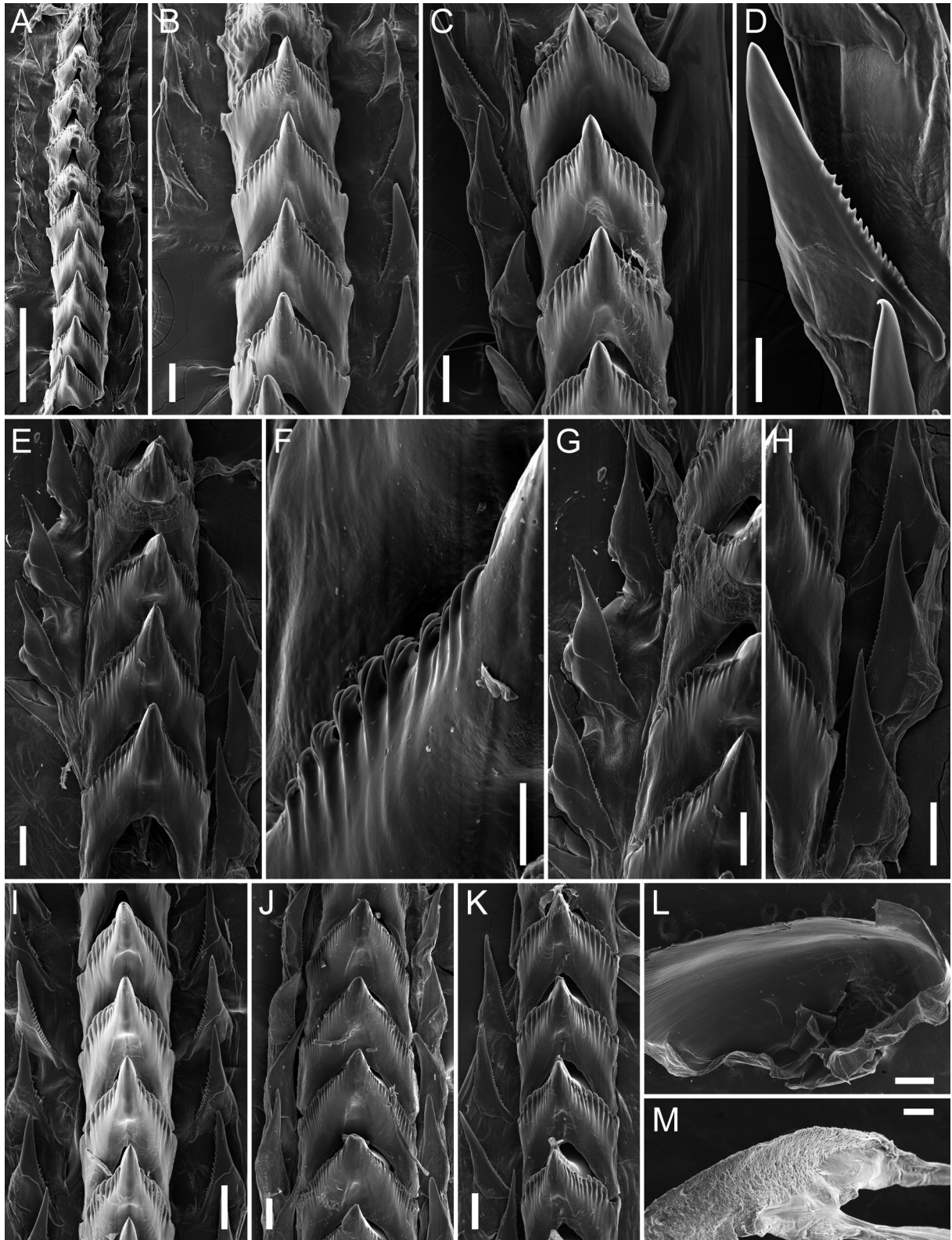


FIG. 9. Radular and jaw morphology of *Ziminella japonica* and *Ziminella* sp. **A–D, L, M.** *Ziminella japonica*, MIMB50759-1, specimen 13 mm in length (preserved). **E–H.** *Ziminella japonica*, ZIN63759, specimen 14 mm in length (preserved). **I.** *Ziminella japonica*, MIMB50760, specimen 14 mm in length (preserved). **J.** *Ziminella* sp., ZIN63764, specimen 38 mm in length (preserved). **K.** *Ziminella* sp., ZIN63757, specimen 23 mm in length (preserved). **A.** Posterior radular portion. **B, C.** Rachidian and lateral teeth. **D.** Lateral tooth. **E.** Rachidian and lateral teeth. **F.** Rachidian tooth with highly ramified denticles. **G, H.** Lateral teeth and denticulation of rachidian teeth. **I–K.** Rachidian and lateral teeth. **L.** Right jaw plate. **M.** Denticulation of masticatory border. Scale bars: A, L = 500 μ m; B, C, E, G–K, M = 100 μ m; D, F = 50 μ m.

teeth (elongate-triangular in *Z. salmonacea*, while in *Z. japonica* they are clearly wider). Also, they show differences in the shape of lateral teeth (with narrow bases in *Z. salmonacea*, wide base in *Z. japonica*; in the former species lateral teeth are also slightly curved). The molecular analyses showed that *Z. japonica* from the Sea of Japan forms a separate clade, which is distinct from all other species of the genus (Fig. 2B). Minimal interspecific differences were identified between *Z. japonica* and the North-Pacific bathyal species *Z. vrijenhoeki* (Table 1). Both these species are very similar morphologically. It was suggested that they differ in coloration [Valdés *et al.*, 2018]. Although Valdés *et al.* [2018] compared *Z. vrijenhoeki* with specimens from British Columbia, which possess cream to pinkish coloration with white or beige cerata [Behrens, Hermosillo, 2005; Calder *et al.*, 2015], true *Ziminella japonica* from the Sea of Japan has orange to reddish dorsum and dark rhinophores and cerata (Fig. 3 F, G). This coloration is different from both *Z. vrijenhoeki* and specimens of “*Z. japonica*” from British Columbia [Calder *et al.*, 2015; Valdés *et al.*, 2018]. There were also reports on different penial morphology of these species, as *Z. vrijenhoeki* has a folded penis, while it is conical in *Z. japonica* [Valdés *et al.*, 2018]. Our results do not confirm this, since specimens from British Columbia have a folded penis (Fig. 3H), and in the North-West Pacific *Z. japonica* the penis may have a different shape, and we suggest this is likely a result of tissue contraction during fixation. Although slight differences may be identified between radulae of these species, *Z. japonica* shows considerable variation in radular characters across the putative geographic range (Fig. 9). For instance, we have found a specimen (ZIN63759, the Sea of Japan) in which denticles on the rachidian teeth were highly branched, making the denticles to be brush-like (Figs 9 E–H).

We have also studied several specimens from the Sea of Okhotsk and the Kuril Islands (ZIN63757, ZIN63763, ZIN63764, MIMB15111, see Table S1), which we initially identified as *Z. japonica*. Although most of them fit the diagnostic features of *Z. japonica*, a slight variation may be observed in external morphology (body length and shape, the extension of the notal edge). Also, some of these specimens show differences in radular morphology from true *Z. japonica*. For example, in specimen ZIN63764 the rachidian teeth closely resembles those of *Z. abyssa*

(more than 15 denticles and short cusp), but the lateral teeth were similar to those of *Z. salmonacea* (Fig. 9J). Externally, the specimen ZIN63764 has short extensions of notal edge, typical of *Z. japonica*.

To sum up, although minor differences were found between *Z. japonica* and *Z. vrijenhoeki* based on the material from the type locality, the species status of *Z. vrijenhoeki* needs additional verification. We also cannot precisely identify several specimens collected outside the type localities, i.e. specimens from the Sea of Okhotsk, the Kuril Islands, and British Columbia, because no molecular data are available and the morphology and coloration of the living animals is unknown in most cases. Considering the slight variation of radular characters and coloration (e.g., creamy white specimens from British Columbia), we suggest *Z. japonica* could be either a species complex, or there is a single species with considerable intraspecific morphological and genetic variability as a result of wide geographical and bathymetrical distribution.

Ziminella vrijenhoeki Valdés *et al.*, 2018
(Figs 3I, 6)

Ziminella vrijenhoeki Valdés *et al.*, 2018: 415, figs 2D–E, 11–13.

Type material. Holotype SIO-BIC M12137, California, Monterey Bay, 36°46'19.2"N 122°04'58.8"W, 1018 m depth, 13.01.2007. Paratype SIO-BIC M12135, California, Monterey Bay, 36°46'19.6"N 122°04'59.2"W, 595 m depth, 16.11.2009.

Type locality. California, Monterey Bay, 36°46'19.2"N 122°04'58.8"W, 1018 m depth

Detailed descriptions are provided by Valdés *et al.* [2018] and Ekimova *et al.* [2021a]. No additional material was available for study.

Distribution. This species is known from the type locality [Valdés *et al.*, 2018] and was further reported from the Bering Sea, at a depth of 660 m [Ekimova *et al.*, 2021a].

Remarks. Ekimova *et al.* [2021a] have mistakenly reported on the presence of seminal receptacle, which is absent in all *Ziminella*. For now, the range limits of this species cannot be precisely determined as it shares several morphological similarities with *Z. japonica* and no additional material was available for morphological and molecular analysis. Further studies are needed to confirm the species validity

РИС. 9 (на предыдущей странице). Морфология радулы и челюстей *Ziminella japonica*. А–D, L, M. *Ziminella japonica*, MIMB50759-1, особь 13 мм длиной (фикс.). Е–Н. *Ziminella japonica*, ZIN63759, особь 14 мм длиной (фикс.). I. *Ziminella japonica*, MIMB50760, особь 14 мм длиной (фикс.). J. *Ziminella* sp., ZIN63764, особь 32 мм длиной (фикс.). K. *Ziminella* sp., ZIN63757, особь 23 мм длиной (фикс.). А. Задняя часть радулы. В, С. Центральные и латеральные зубы. D. Латеральные зубы. Е. Центральные и латеральные зубы. F. Зазубренность центрального зуба с сильно расщепленными зубчиками. G, H. Латеральные зубы и зазубренность центрального зуба. I–K. Центральные и латеральные зубы. L. Правая челюстная пластинка. M. Зазубренность жевательной поверхности. Масштабные линейки: A, L = 500 μm; B, C, E, G–K, M = 100 μm; D, F = 50 μm.

of *Z. vrijenhoeki* and verify its geographical and bathymetric distribution (see Discussion).

Discussion

Our results allowed to revise the species status and distributional range of *Ziminella* species. We show that *Ziminella salmonacea* represents a widely distributed Arctic-Atlantic species. This is a single species found in the North Atlantic and Arctic waters along with other three Pacific species of *Ziminella* (Fig. 1). This diversity pattern corresponds to the general phylogeographic pattern of trans-Arctic nudibranch molluscs [Ekimova *et al.*, 2023; 2024], where species currently distributed in the Atlantic, have a secondary Atlantic origin, i.e., represent descendants of the Pacific fauna invading the Atlantic Ocean during climatic optima in the Pliocene and Pleistocene [Ekimova *et al.*, 2024]. The range of *Z. salmonacea* is considerable and encompasses a range of environmental conditions, from boreal (in Maine, Massachusetts) to high Arctic latitudes (Greenland, Novaya Zemlya Is., the Kara Sea) (Fig. 1). The genetic diversity is correspondingly high, but genetic population structure does not corroborate the geographic patterns (collection locations of studied specimens) (Fig. 2A). Indeed, our results show that closely related *Z. circapolaris* from the Franz Josef Land cannot be considered a distinct species, or even a subspecies of *Ziminella salmonacea*, as its populations are not separated genetically (Fig. 2) or differ morphologically (Figs 3–5). In the latter case, we have demonstrated that supposed diagnostic features (the denticulation of the lateral teeth) are flexible and vary greatly among specimens from the same locality (including presumable ranges of both *Z. salmonacea* and *Z. circapolaris*), from distant localities, and even within a single specimen (Figs 4, 5). This considerable variation of the radular teeth morphology is characteristic of the trans-Arctic flabellinids (*sensu lato*). For example, the atypically smooth lateral teeth of radula were detected within the White Sea populations of *Coryphella verrucosa* [Ekimova *et al.*, 2022], and it was suggested that underestimation of intraspecific morphological diversity could lead to an overestimation of species diversity [Ekimova *et al.*, 2023].

In the present paper we publish the first molecular phylogeny for the North-West Pacific species *Ziminella japonica* and provide its modern redescription. According to our integrative data, this species is very close to the North-East Pacific species *Z. vrijenhoeki* both morphologically (including high similarities in the morphology of radula, jaws and the reproductive system) and genetically. In the latter case, both species are sister in all phylogenetic trees (Figs 2B, S1), and the species delimitation analysis does not provide a unequivocal result on their species status (Fig. S2).

Although the *p*-distances in COI between *Z. japonica* and *Z. vrijenhoeki* are quite high (up to 8%), we did not detect any differences in studied nuclear markers, including 18S rRNA. The latter was suggested to be a useful independent marker for verification of species distinctness [Ekimova *et al.* 2021b, 2022], therefore the lack of divergence may indicate either an ongoing gene exchange between different distant haplogroups of a single species, or be a result of incomplete lineage sorting [Chaban *et al.*, 2023]. From a morphological point of view, we have identified several differences in the external morphology of these two species (considering only the material with genetically confirmed species affiliation): the coloration and the notal edge extension (see Remarks section of *Z. japonica*). States of these putative diagnostic characters cannot be identified for most specimens in our material, as the coloration is not preserved in fixative and soft tissues may be contracted at different level. As a consequence, precise identification is difficult for most material collected far from the type locality (e.g., the Sea of Okhotsk, including Kurile Islands, British Columbia, and other regions). There are also several pieces of evidence supporting the existence of cryptic diversity, as “*Z. japonica*” from British Columbia possesses a different coloration and wider notal edge [Behrens, Hermosillo, 2004; Cadler *et al.*, 2015] than specimens of *Z. japonica* collected close to the type locality (Figs 3 F, G, H). Also, a specimen from the Kuril Islands (ZIN63764) has a slightly different radular morphology (Fig. 9J) from the true *Z. japonica* collected near the type locality. We suggest identifying all records lacking the genetic data as *Ziminella* sp. until molecular analysis of these specimens is conducted. So far, the confirmed distribution of *Z. japonica* includes only the deep shelf regions of the Sea of Japan, and the range of *Z. vrijenhoeki* encompasses bathyal depths off California and the Bering Sea.

The deep waters of the Sea of Japan have been the subject of considerable attention by marine biologists as it is considered a ‘pseudoabyssal’ area [Ushakov, 1957; Andriashev, 1979; Mironov *et al.*, 2019]. The maximum depth of Sea of Japan is about 3800 m, and its abyssal plane is isolated from the Pacific abyssal area as the four straits of the Sea of Japan are shallow-water and their depth does not exceed 140 m. The abyssal plain of the Sea of Japan has high levels of endemism, and previous studies suggested a closer phylogenetic relationships of its biota with shelf organisms from the Sea of Japan, rather than with the true abyssal Pacific fauna [Mironov *et al.*, 2019]. One of the examples was the recently described *Z. abyssa* [Korshunova *et al.*, 2017], which was for a long time confused with the deep shallow-water species *Z. japonica* [Roginskaya, 1978; Martynov, 2013]. Our novel molecular data for *Z. japonica* confirm the separate species status of *Z.*

abyssa from *Z. japonica*. However both phylogenetic analyses (Figs 2B, S1) show that these two species are not closely related, as *Z. japonica* is sister to the North-East Pacific bathyal species *Z. vrijenhoeki* (Fig. 2B). The position of *Z. abyssa* can be considered unresolved, as it either forms a polytomy with other species (ML analysis, see Fig. S1), or is sister to shelf Arctic-Atlantic species *Z. salmonacea* (BI analysis, Fig. 2B). Therefore, our data cannot univocally identify the centre of *Ziminella* speciation in the North Pacific and a putative shelf origin of *Z. abyssa* remains unverified. It should also be noted that the diversity of the deep waters of the Sea of Japan may be even higher than currently known, as we identified at least two additional paracoryphellid species inhabiting bathyal or abyssal depth (see Remarks section of *Z. abyssa*). All this indicates that the biodiversity of this region could be still largely underestimated and the biogeographic connectivity of its fauna with adjacent regions remain unexplored. Thus, further integrative study of the molluscan fauna from the abyssal plain of the Sea of Japan is a very promising research focus in terms of phylo- and biogeography of the North Pacific.

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Supplementary Material

Table S1. List of specimens used in this study. Voucher numbers, collection locality and collectors are given.

Table S2. List of specimens used for molecular analysis. Voucher numbers, collection locality and GenBank accession numbers are given.

Table S3. Amplification and sequencing primers and PCR conditions.

Table S4. Measurements and radular morphology of *Z. salmonacea* and *Z. circopolaris* based on ZIN collection.

Fig. S1. Maximum likelihood phylogenetic tree based on the concatenated dataset of four markers (COI + 16S + H3 + 28S).

Fig. S2. ASAP results for COI alignment.

