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A new species of the genus *Coryphella* (Gastropoda: Nudibranchia) from the Kuril Islands

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ABSTRACT. A new species of the family Coryphellidae, *Coryphella* ***alexanderi*** sp. nov. is described based on specimens collected in the Kuril Islands, North-West Pacific, from the upper sublittoral to 200 m depth. An integrative analysis was conducted, including a molecular phylogenetic analysis based on four markers (COI, 16S, H3, 28S), an automatic species delimitation method ABGD, and an analysis of the external and internal morphology using light and scanning electron microcopy. The distinctiveness of *Coryphella* ***alexanderi*** sp. nov. is well established both morphologically and genetically, and it differs from externally similar species in radular characters. Phylogenetically *Coryphella* ***alexanderi*** sp. nov. is closely related to *Coryphella trophina,* which occurs sympatrically in the same geographic and bathymetric ranges. *Coryphella* ***alexanderi*** sp. nov. appears to be restricted to the middle and northern Kuril Islands, which is consistent with the high numbers of endemic taxa in this area.

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Новый вид рода *Coryphella* (Gastropoda: Nudibranchia) из прибрежных вод Курильских островов

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РЕЗЮМЕ. Описан новый вид семейства Coryphellidae, *Coryphella* ***alexanderi*** sp. nov., обитающий в северо-западной части Тихого океана, в районе Курильских островов. Данный вид был обнаружен в шельфовых водах в широком диапазоне глубин, от верхней сублиторали до глубины 200 метров. Для его описания был проведен интегративный анализ, включающий молекулярно-филогенетический анализ по четырем маркерам (COI, 16S, H3, 28S), автоматический метод разделения видов ABGD, а также анализ внешней и внутренней морфологии с использованием световой и сканирующей электронной микроскопии. Новый вид *Coryphella* ***alexanderi*** sp. nov. значительно отличается от других видов рода морфологически и генетически. По внешней морфологии он наиболее сходен с северо-тихоокенаским видом *Coryphella sanamyanae,* амфибореальным видом *Coryphella nobilis* и северо-атлантическим видом *Coryphella browni,* однако значительно отличается от них по признакам радулы. Филогенетически данный вид наиболее близок к *Coryphella trophina,* который обитает в том же регионе на сходных глубинах. Находки *C.* ***alexanderi*** sp. nov. ограничены группами северных и средних Курильских островов, что подтверждает предшествующие указания на высокую степень эндемизма фауны морских беспозвоночных данного региона.

Introduction

The Coryphellidae is a monophyletic nudibranch family, with most species described from boreal and polar regions in both hemispheres [Korshunova *et al*., 2017]. This family was recently resurrected following the integrative revision of the highly diverse and polymorphic family Flabellinidae *s.l.* [Korshunova *et al*., 2017]. The study by Korshunova *et al*. [2017] supported the validity of the family Coryphellidae and introduced nine genera for 27 coryphellid species. However, further research indicated that the taxonomical scheme for Flabellinidae *s.l.* proposed by Korshunova *et al*. [2017] might be excessively splitting [Furfaro *et al*., 2021; Ekimova *et al*., in press]. Because of this, Ekimova *et al*. [in press] suggested to unite the entire diversity of the family Coryphellidae within the single genus *Coryphella*. Nevertheless, several new Coryphellidae species were recently described from Norway and the North-West Pacific [Korshunova *et al*., 2017], and it is suspected that diversity of this group might be much higher than previously thought.

In the North-West Pacific only seven Coryphellidae species are currently known: *Coryphella verrucosa* (M. Sars, 1829)*, C. amabilis* (Hirano et

Kuzirian, 1991)*,* *C. nobilis* A. E. Verrill, 1900, *C. sanamyanae* (Korshunova *et al*., 2017)*, C. trophina* (Bergh, 1980)*, C. abei* Baba, 1987, and *C. athadona* Bergh, 1875. All these species are well characterized and have clear distinctive morphological traits [Baba, 1987; Korshunova *et al*., 2017; Ekimova *et al.*, in press]. *Coryphella verrucosa* and *C. nobilis* are amphiboreal species, *C. amabilis* and *C. trophina* display a wide geographic range in the North Pacific, and the other three species are restricted to the Sea of Japan and adjacent areas [Baba, 1987; Roginskaya, 1990; Hirano, Kuzirian, 1991; Jung, Park, 2015; Martynov *et al*., 2016; Korshunova *et al*., 2017; Ekimova *et al.,* in press]. Most species are very abundant in shallow-water hydrozoan communities [Martynov *et al*., 2015; 2016; Chichvarkhin, 2016].

In this paper an additional North-West Pacific species of the genus *Coryphella* is described from the Kuril Islands, North-West Pacific, based on the integrative approach combining morphological and molecular data.

Material and methods

The material examined was collected in two localities: (1) one specimen was collected in the northern Kuril Islands (exact locality and coordinates are not available) during the "Aquatilis Expedition" [Semenov, 2013], and four specimens were collected during the expedition of the R/V "*Akademik Oparin*" (cruise 56, Russia) at one site: Urup Is., 46°17.0 N 150°17.0 E. The holotype and paratypes are deposited in the collections of the National Scientific Center of Marine Biology, MIMB. One paratype is deposited in the collection of Zoological Museum of Lomonosov Moscow State University, White Sea Branch (ZMMU WS).

Molecular methods

Molecular methods included obtaining of the four molecular markers commonly used in Flabellinidae *s.l.* systematics: cytochrome *c* oxidase subunit I, 16S rRNA, histone H3 and 28S rRNA [Korshunova *et al*., 2017; Ekimova *et al*., in press]. DNA extraction, amplification, and sequencing followed methods described in Ekimova *et al*. [2019, 2020]. All newly obtained sequences were submitted to NCBI GenBank (Table S1). Raw reads for each gene were assembled and checked for ambiguities and low-quality data in Geneious R10 (Biomatters, Auckland, New Zealand). Edited sequences were verified for contamination using the BLAST-n algorithm run over the GenBank nr/nt database [Altschul *et al*., 1990]. For phylogenetic reconstruction, dataset obtained in previous comprehensive study on the family Coryphellidae was used for the analysis [Korshunova *et al*., 2017]. Indel-rich regions of the 16S alignment were identified and removed in Gblocks 0.91b [Talavera, Castresana, 2007] with the least stringent settings. Sequences were concatenated by a simple biopython script following Chaban *et al*. [2019]. Phylogenetic reconstruction was conducted for the concatenated multi-gene partitioned datasets. The best-fit nucleotide evolution models were tested in the MEGA7 [Kumar *et al*., 2016] based on the Bayesian Information Criterion (BIC) for each partition. The Bayesian phylogenetic analysis (BI) and estimation of posterior probabilities was 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 10^7 generations. Maximum likelihood phylogeny inference (ML) was performed in the HPC-PTHREADS-AVX option of RaxML HPC-PTHREADS 8.2.12 [Stamatakis, 2014] with 1000 pseudoreplicates under the GTRCAT model of nucleotide evolution. Bootstrap values were placed on the best tree found with SumTrees 3.3.1 from DendroPy Phylogenetic Computing Library 3.12.0 [Sukumaran, Holder, 2010]. Final phylogenetic tree images were rendered in FigTree 1.4.0 and further modified in Adobe illustrator CS 2015. For computational species delimitations methods, the COI alignment was used; in addition, the nuclear H3 alignment was analysed to identify species-specific polymorphisms. To confirm the status of clades recovered in our analysis as distinct species we used the Automatic Barcode Gap Discovery (ABGD) method [Puillandre *et al*., 2012] that detects breaks in the distribution of intra- and interspecific distances referred to as the "barcode gap" without any prior species hypothesis. The ABGD analysis was run on the online version of the program (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) with the following settings: Pmin = 0.001, Pmax = 0.2, Steps = 10; X = 1.0; Nb bins = 20 and three proposed models – Jukes Cantor (JC69), Kimura (K80) and Simple distance. COI sequences were aligned for ABGD analysis with the MUSCLE [Edgar, 2004] algorithm in MEGA7 [Kumar *et al*., 2016]. *P*-distances for COI alignment were calculated in MEGA7 [Kumar *et al*., 2016].

Morphological studies

All collected specimens were used for the examination of their external morphology under a stereomicroscope. The internal morphology of three specimens was also examined, including the digestive and reproductive systems. The buccal mass of each specimen was extracted and soaked in proteinase K solution for 2 hours at 60 ºC to dissolve connective and muscular tissues. The 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 JSM 6380 scanning electron microscope (SEM). Features of

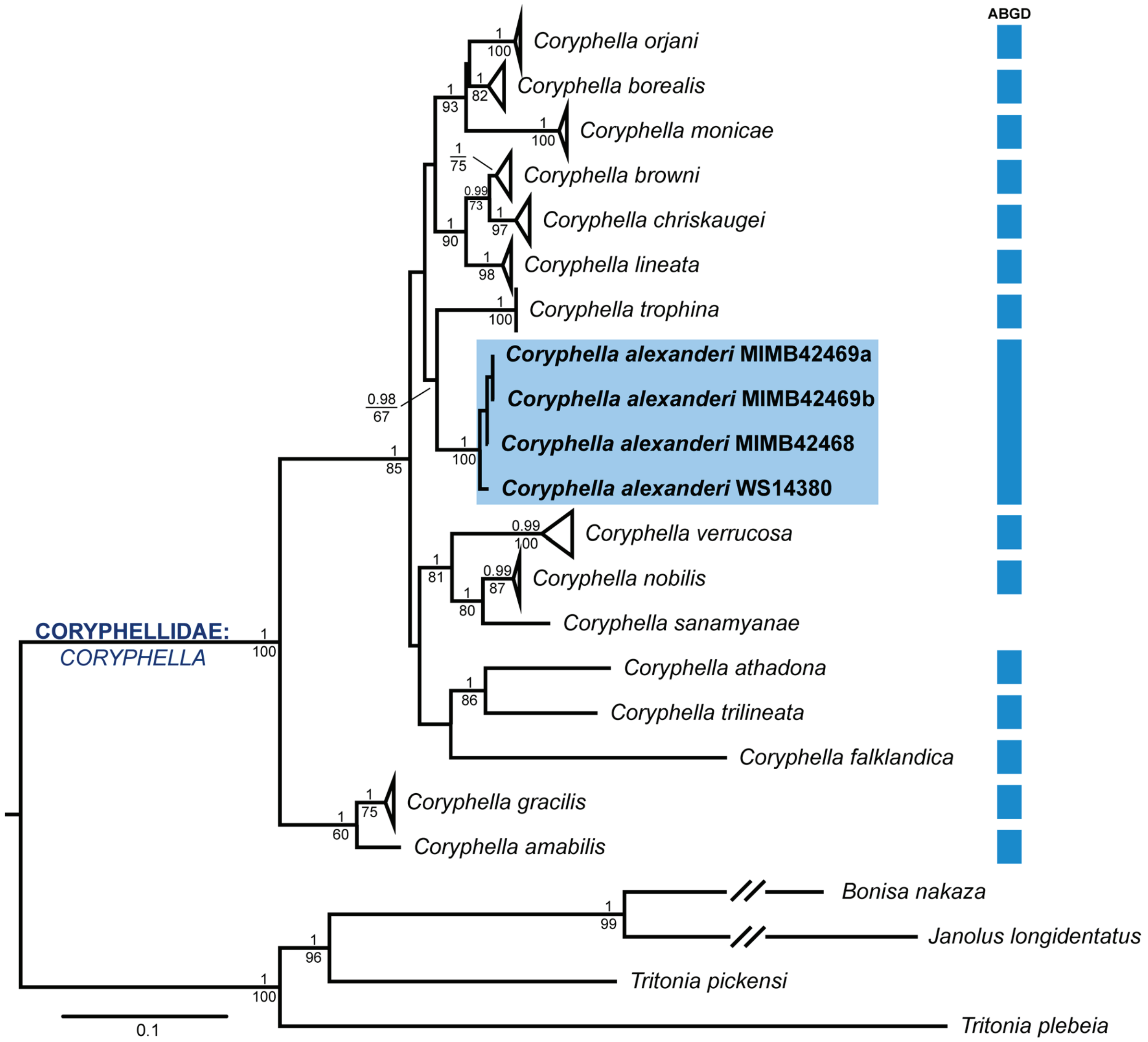

FIG. 1. Maximum likelihood phylogenetic tree of the genus *Coryphella* based on the concatenated dataset COI+16S+H3+28S. Numbers above branches indicate the posterior probabilities from Bayesian Inference (for PP > 0.95), numbers below branches – bootstrap values from Maximum likelihood (for BS > 60%). Blocks on the right indicate ABGD species delimitation results based on COI dataset. For *Coryphella sanamyanae* the ABGD analysis was not conducted since this species lacks COI data.

РИС. 1. Молекулярно-филогенетическое дерево для рода *Coryphella,* построенное на основании комбинированного выравнивания (COI+16S+H3+28S) методом максимального правдоподобия. Значения над ветвями обозначают апостериорные вероятности (> 0.95). Значения под ветвями обозначают поддержки бутстрепа (> 60%). Голубые блоки справа обозначают результат делимитационного ABGD теста. Для *Coryphella sanamyanae* результаты ABGD теста отсутствуют, поскольку последовательности COI этого вида недоступны в открытых базах данных.

the jaws were examined by optical stereomicroscopy and SEM. For study of the reproductive system specimens were dissected from the dorsum along the midline and examined under a stereomicroscope.

Results

Phylogenetic analysis

The concatenated analysis of four markers (COI+16S+H3+28S) revealed well-resolved and highly supported trees at the species level using both BI and ML (Fig. 1). The topology of BI and ML tree was similar, except for the deeper relationships and the position of *Coryphella falklandica* Eliot, 1907. The new species represented a highly supported clade [PP (posterior probability from BI) = 1; BS (bootstrap support from ML) = 100], which was recovered as sister to *Coryphella trophina* with moderate support (PP = 0.98; BS = 67). This clade was sister to a monophyletic group representing by the North-East Atlantic species: *Coryphella lineata* (Lovén, 1846), *C. chriskaugei* (Korshunova *et al*., 2017)*, C. browni* Picton, 1980*, C. monicae* (Korshunova *et al*., 2017)*, C. borealis* Odhner, 1922*, C. orjani* (Korshunova *et al*., 2017), but these relationships were not supported.

Species delimitation

The ABGD analysis supported the initial species hypothesis with 15 species-level groups in the initial partition (Fig. 1), supporting the identity of all monophyletic species clades except *C. sanamyanae,* for which no COI data was available. All studied specimens from the Kuril Islands appeared in a single group. The lowest *p*-distance in COI marker (Table 1) was found between the new species and *Coryphella lineata* (6.74%). Maximum intraspecific distance within the new species was 2.07%. Analysis of the H3 dataset showed a high genetic divergence of the new species from other *Coryphella* species, with a minimum divergence of 3 substitutions between the new species and *Coryphella orjani.*

Table 1. Minimum interspecific uncorrected p-distances (%) based on the COI gene between *Coryphella* ***alexanderi*** sp. nov. and other *Coryphella* species.

Табл. 1. Минимальные межвидовые нескорректированные *p*-дистанции по гену COI между *Coryphella* ***alexanderi*** sp. nov. и другими видами рода *Coryphella.*

Species	p-distance value
Coryphella amabilis	12.61
Coryphella athadona	12.09
Coryphella borealis	7.94
Coryphella browni	7.77
Coryphella chriskaugei	9.15
Coryphella gracilis	12.44
Coryphella falklandica	16.75
Coryphella lineata	6.74
Coryphella monicae	10.71
Coryphella nobilis	10.36
Coryphella orjani	9.50
Coryphella sanamyanae	n/a
Coryphella trilineata	12.95
Coryphella trophina	9.33
Coryphella verrucosa	11.92

Taxonomic description

Order Nudibranchia de Blainville, 1814
Suborder Cladobranchia William & Morton, 1984
Superfamily Fionoidea J. E. Gray, 1857
Family Coryphellidae Bergh, 1889
Genus *Coryphella* J. E. Gray, 1850

Coryphella ***alexanderi*** sp. nov.
(Figs 2–4)

ZooBank registration: urn:lsid:zoobank.org:act:E49D9E1E-78F7-44EE-AB89-11D75A1B955F

Type material. Holotype MIMB42468, partly dissected, radula and jaws mounted on SEM stub. Paratypes: MIMB42469, three specimens, two dissected, same locality and collector as holotype. ZMMU WS14380, one specimen, dissected, northern Kuril Is., coordinates not available, 10-20 m depth, 04.08.2016, coll. Alexander Semenov.

Type locality. Sea of Okhotsk, Urup Is., 46°17.0’N, 150°17.0’E, 148–198 m depth, 05.07.2019, coll. Anastassya Maiorova.

Description. *External morphology* (Fig. 2). Body length up to 22 mm. Body narrow, tapering to tail. Rhinophores about two times longer than oral tentacles. Rhinophores smooth with thin wrinkles. Anterior foot corners present. Notal edge reduced, discontinuous. Cerata in continuous rows, not united in separated groups. Anus pleuroproctic. Reproductive opening on right side under anterior ceratal rows.

Coloration (Fig. 2). Background color of body translucent milky-white. Dorsal side of oral tentacles with opaque white pigment dots. Opaque white line on back side of rhinophores, becoming pigment white band on rhinophoral tip. Tail with white line. Digestive gland diverticula inside cerata from orange to pale brown. Cnidosac area white, with thin, white pigmen band.

Internal morphology (Figs 3, 4). Jaw triangle plate with strong masticatory process (Fig. 3A). It bears at least 9 rows of small denticles (Fig. 3B). Outer denticles simply serrated, especially on masticatory edge (Fig. 3C). Radular formula: 15–17 x 1.1.1 (Fig. 3D, H). Rachidian tooth triangular, with long sharp cusp, and 5–9 large sharp denticles on each side. Cusp usually longer than denticles. Lateral teeth widened, triangular, with attenuated outer basal processes and up to 14 denticles on inner side. Reproductive system diaulic (Fig. 4). Ampulla large, folded. Vas deferens of moderate length, widened in proximal prostatic part. Distinct distal and proximal receptaculum seminis, both small muscular sacs. Penis broad, conical.

Distribution. This species is only known from the middle and northern Kuril Islands.

Ecology. This species has a wide bathymetric range, being found in both upper (10–20 m in depth) and deep (down to 200 m in depth) shallow waters, and it is very likely it inhabits intermediate depths as well. In upper shallow-water it was found on *Rhizorhagium roseum* M. Sars, 1874 and *Eudendrium* sp. (Fig. 2A).

Remarks. Both morphological and molecular analyses support the distinctiveness of *Coryphella* ***alexanderi*** sp. nov. from other species in the genus. The external morphological characters of this new species shows the most resemblance to the North-West Pacific species *Coryphella sanamyanae,* the amphiboreal species *C. nobilis* A. E. Verrill, 1880, and the North-East Atlantic species *C. browni,* as it

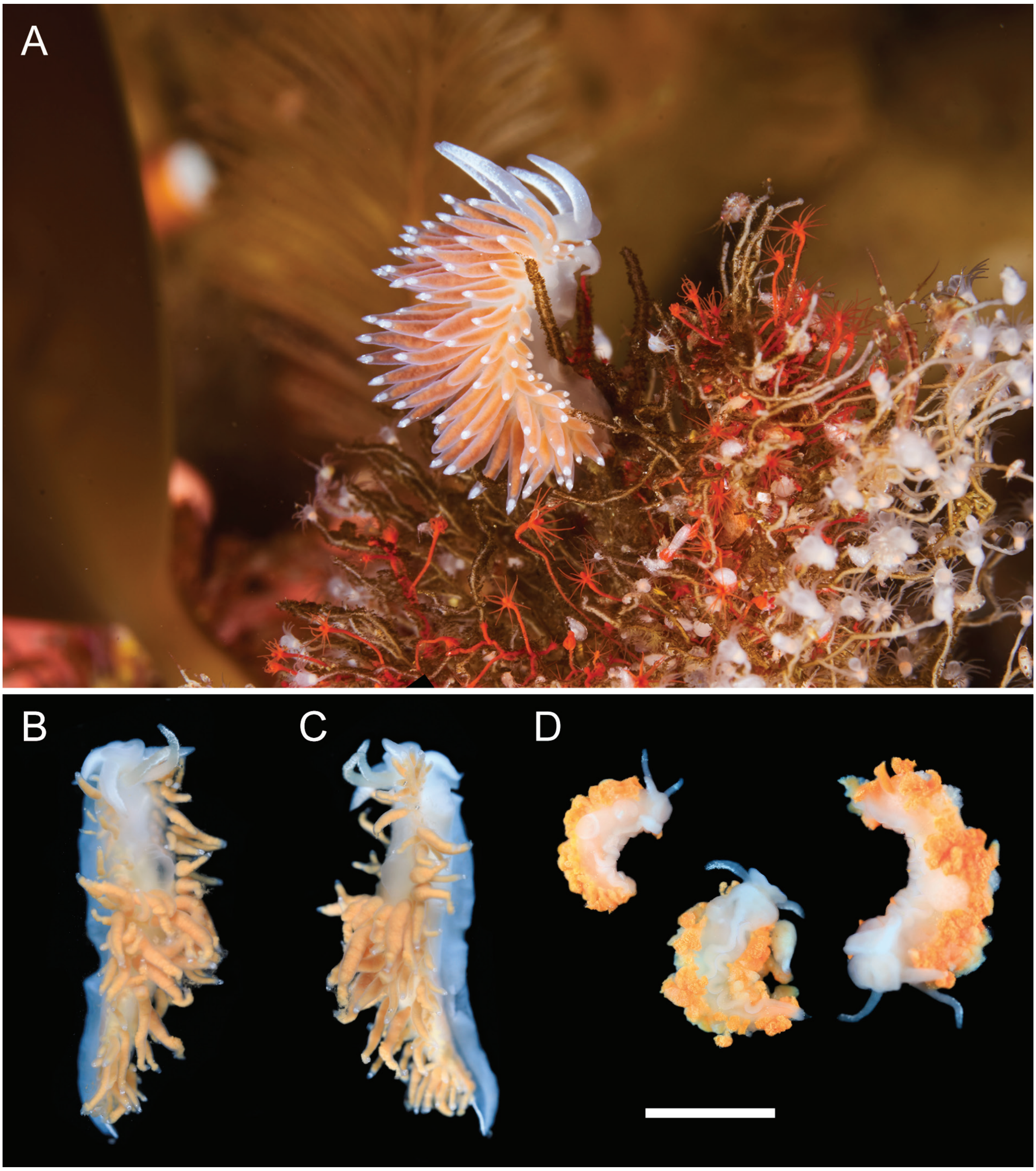

FIG. 2. Living specimens of *Coryphella* ***alexanderi*** sp. nov. **A.** Paratype ZMMU WS14380 in natural environment. **B.** Holotype MIMB42268, dorsal view, specimens was damaged during collection. **C.** Holotype MIMB42268, dorsolateral view. **D.** Paratypes MIMB42269, specimens were damaged during collection. Scale bar: 5 mm. Photo credits: A – Alexander Semenov. B-D – Anastassya Maiorova.

РИС. 2. Прижизненные фотографии *Coryphella* ***alexanderi*** sp. nov. **A.** Паратип ZMMU WS14380 в естественной среде. **B.** Голотип MIMB42268, вид с дорсальной стороны, особь была незначительно повреждена при сборе. **C.** Голотип MIMB42268, вид с дорсолатеральной стороны. **D.** Паратипы MIMB42269, особи были повреждены при сборе. Масштабная линейка: 5 мм. Авторство фотографий: A – Александр Семенов. B–D – Анастасия Майорова.

possesses continuous rows of cerata, reddish color of the digestive gland diverticula, and white rhinophores. However, *Coryphella* ***alexanderi*** sp. nov. differs from all these species by internal anatomical features. First of all, it differs in radular characters, since in *C. nobilis* and *C. sanamyanae* the rachidian tooth possesses a very small central cusp that is usually compressed. *Coryphella browni* has narrower lateral teeth with small cusps and tiny denticles; this species also possesses a single row of denticles on the masticatory edge of the jaws, while in *C.* ***alexanderi*** sp. nov. there are at least 10 rows of serrated den-

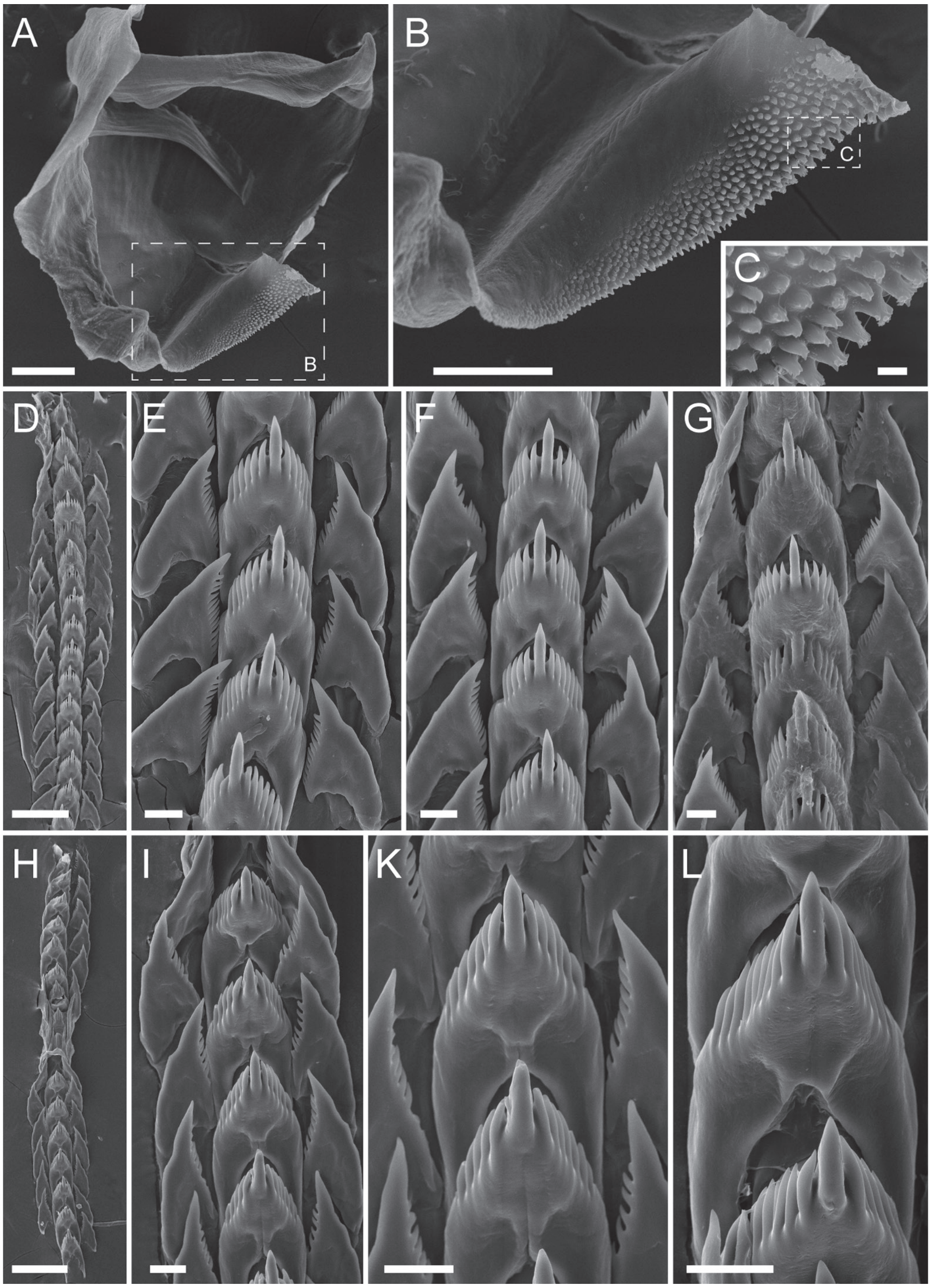

FIG. 3. Buccal armature in *Coryphella* ***alexanderi*** sp. nov. **A.** Holotype MIMB42268, right jaw plate. **B.** Holotype MIMB42268, masticatory border of jaw plate. **C.** Holotype MIMB42268, details of denticulation on masticatory border. **D.** Holotype MIMB42268, radula. **E.** Holotype MIMB42268, anterior radular potion. **F.** Holotype MIMB42268, middle radular potion. **G.** Holotype MIMB42268, posterior radular potion. **H.** Paratype ZMMU WS14380, radula. **I.** Paratype ZMMU WS14380, anterior radular portion. **K.** Paratype ZMMU WS14380, rachidian and lateral teeth. **L.** Paratype ZMMU WS14380, denticulation of rachidian teeth. Scale bars: A, B, H – 150 µm. B – 100 µm. C – 10 µm. E–G, I–K – 30 µm.

FIG. 3. Глоточное вооружение *Coryphella* ***alexanderi*** sp. nov. **A.** Голотип MIMB42268, правая челюстная пластинка. **B.** Голотип MIMB42268, жевательная поверхность челюсти. **C.** Голотип MIMB42268, детали зубчиков жевательной поверхности. **D.** Голотип MIMB42268, радула. **E.** Голотип MIMB42268, передняя часть радулы. **F.** Голотип MIMB42268, средняя часть радулы. **G.** Голотип MIMB42268, задняя часть радулы. **H.** Паратип ZMMU WS14380, радула. **I.** Паратип ZMMU WS14380, передняя часть радулы. **K.** Паратип ZMMU WS14380, центральный и латеральные зубы. **L.** Паратип ZMMU WS14380, особенности зазубренности центрального зуба. Масштабные линейки: A, B, H – 150 µм. B – 100 µм. C – 10 µм. E–G, I–K – 30 µм.

ticles. From other species of the genus *Coryphella* inhabiting the North-West Pacific, *C.* ***alexanderi*** sp. nov. differs by its external morphology. From *C. verrucosa* and *C. amabilis* it differs by having the cerata arranged in continuous rows (in groups in *C. verrucosa* and *C. amabilis*), from *C. trophina* by having almost smooth rhinophores (perfoliated in *C. trophina*); *Coryphella athadona* and *C. abei* possess a Y-marking on head, that is absent in *C.* ***alexanderi***.

Etymology. This species is named after my beloved farther Alexander V. Ekimov, who passed away during the preparation of this manuscript. Alexander V. Ekimov was a researcher in the field of high energy physics, his passion for his work inspired me to become a scientist and his support always encouraged me to be fully dedicated to my research. He will be greatly missed.

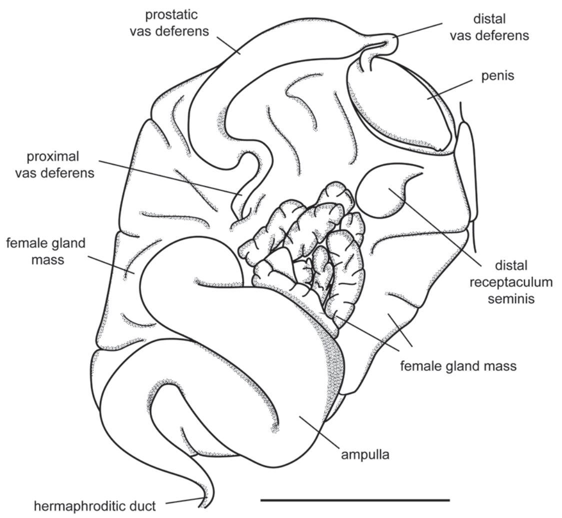

FIG. 4. The reproductive system of *Coryphella* ***alexanderi*** sp. nov. (paratype ZMMU WS14380). Scale bar: 1 mm.

РИС. 4. Половая система *Coryphella* ***alexanderi*** sp. nov. (паратип ZMMU WS14380). Масштабная линейка: 1 mm.

Discussion

The new species *Coryphella* ***alexanderi*** sp. nov. is well characterized both morphologically and genetically (Figs 1–3). Phylogenetically, *C. alexanderi* sp. nov. is close to another North-West Pacific species, *Coryphella trophina* (Fig. 1). But these species have extremely different external and internal morphology [Ekimova *et al*., in press] and have different ecological traits. While *Coryphella* ***alexanderi*** sp. nov. is supposed to be an exclusively cnidarian feeder, being found on *Rhizorhagium roseum* and *Eudendrium* sp. (Fig. 2A), *C. trophina* has a unique diet, which includes either various hydrozoans, or smaller nudibranch species inhabiting same cnidarian colonies [Roginskaya, 1990].

The discovery of *Coryphella* ***alexanderi*** sp. nov. indicates that the knowledge on nudibranch biodiversity in the North-West Pacific in general and in the Kuril Islands in particular, is far from being completely understood. Recently, several new species were described from this area, including representatives of the nudibranch genera *Akiodoris* Bergh, 1879 [Martynov, Korshunova, 2020], *Cadlina* Bergh, 1879 [Korshunova *et al*, 2020a], *Onchidoris* Blainville, 1816 [Martynov, Korshunova, 2017], *Cuthonella* Bergh, 1884 [Korshunova *et al*., 2020b], and *Dendronotus* Alder et Hancock, 1845 [Ekimova *et al.*, 2015; Martynov *et al*., 2020]. Distributional ranges of most of these new taxa are restricted to the Kuril Islands waters, thus possibly indicating high degree of endemism in the area.

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SUPPLEMENTARY MATERIAL

Table S1. List of specimens used in this study. Voucher numbers, collection locality and GenBank accession numbers are given. Sequences obtained for this study are highlighted in bold.

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