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Nudibranch molluscs of Sakhalin Island, Northwestern Pacific: new records and descriptions of two new species

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ABSTRACT. In this paper we investigate a collection of nudibranch molluscs from Sakhalin Is. by means of integrative taxonomy, including morphological analyses, and molecular data from the cytochrome *c* oxidase subunit I, 16S rRNA, Histone H3 and 28S rRNA markers. Material used in this study was collected during two independent research programs: the expedition of the R/V "*Akademic Oparin*" (Russia) to the Sea of Okhotsk, July 2019 at depths of 38–282 m, and the survey of Cape Crillon biodiversity in August 2023, at depths of 0.5–20 m. Our integrative results revealed clear cases of the unknown diversity within some groups of the nudibranch molluscs. Among the dorid nudibranchs, the new species *Adalaria* ***boussoleana*** sp. nov. is described and differs in morphological and molecular characters from other species of the genus. Also, among specimens of the genus *Cadlina* we have detected two genetically distinct groups, one is close to *C. umiushi* and another group likely represents a new species for science. Their morphology is similar to the diagnosis of *C. umiushi* and may represent a case of true cryptic diversity. Among the cladobranch molluscs our results revealed a new species of the genus *Cuthonella* described herein under the name *Cuthonella* ***anastasia*** sp. nov. Four species are recorded for Sakhalin Is. waters for the first time: *Cadlina umiushi, Onchimira cavifera, Eubranchus rupium* and *E. alexeii.* After this paper, the total nudibranch fauna of Sakhalin Is. includes 21 species. Although we have limited numbers of nudibranch species in Sakhalin waters due to low sampling effort, a comparison of the biogeographic affinities of species from different regions is consistent with the presence of a biogeographic boundary between northeastern and southwestern Sakhalin.

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Голожаберные моллюски острова Сахалин, северо-западная часть Тихого океана: новые находки и описание двух новых видов

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РЕЗЮМЕ. В данной работе мы исследуем коллекцию голожаберных моллюсков, собранных в прибрежных водах острова Сахалин, с помощью методов интегративной таксономии, включающие морфологический анализ и молекулярные данные по четырем маркерам: I субъединица цитохром с-оксидазы, 16S рРНК, гистон Н3 и 28S рРНК. Материал, использованный в работе, был собран в ходе двух независимых исследовательских программ: экспедиции НИС «*Академик Опарин*» (Россия) в Охотское море, июль 2019 г. на глубинах 38-282 м, и исследования биоразнообразия мыса Крильон в августе 2023 г., на глубинах 0,5-20 м. Полученные результаты позволили выявить случаи скрытого разнообразия внутри некоторых групп голожаберных моллюсков. Среди голожаберных моллюсков дорид был обнаружен и описан новый для науки вид *Adalaria* **boussoleana** sp. nov., который хорошо отличается от других видов рода по совокупности морфологических и молекулярных данных. Кроме того, среди изученных экземпляров рода *Cadlina* мы обнаружили две генетически различные группы: одна близка к *C. umiushi,* а другая, вероятно, представляет собой новый для науки вид. В то же время морфология обоих видов аналогична диагнозу *C. umiushi*, что, возможно, является примером истинного криптического биоразнообразия. Среди голожаберных моллюсков подотряда Cladobranchia также был обнаружен новый вид рода *Cuthonella,* описанный под названием *Cuthonella* ***anastasia*** sp. nov. Для прибрежных вод острова Сахалин впервые отмечено четыре вида голожаберных моллюсков: *Cadlina umiushi, Onchimira cavifera, Eubranchus rupium* и *E. alexeii*. Всего в фауне Сахалина представлен 21 вид голожаберных моллюсков. Хотя из-за низкой активности сбора проб имеются лишь единичные находки голожаберных моллюсков, сравнение биогеографической принадлежности

видов из разных регионов соответствует наличию биогеографической границы между северо-восточным и юго-западным Сахалином.

Introduction

Studies of the nudibranch fauna of Sakhalin Island (North-West Pacific) are scarce in comparison to adjacent waters of the Sea of Japan and the Sea of Okhotsk. To date, no dedicated studies have been ever published listing the biodiversity of nudibranchs of this area. Several records of nudibranch molluscs from Sakhalin Is. have been reported in the Ph.D. dissertations by N.I. Volodchenko [Volodchenko, 1941a] and A.V. Martynov [Martynov, 1999], for example *Adalaria proxima* (Alder et Hancock, 1854), *Tritonia tetraquetra* (Pallas, 1788), *Dirona pellucida* Volodchenko, 1941, *Coryphella verrucosa* (M. Sars, 1829), *Dendronotus dalli* Bergh, 1879 and some others. Some of papers dealing with the biodiversity of the Sea of Japan or the Sea of Okhotsk nudibranchs also mentioned species collected from Sakhalin coastal waters: *i.e. Trironia tetraquetra* and *Onchidoris muricata* (O. F. Müller, 1776) from Nevelsk [Chichvarkhin, 2016; Chichvarkhin *et al.*, 2018], *Aeolidia papillosa* (Linnaeus, 1761), *Dirona pellucida* from Aniva Bay [Baba, 1935], *Dendronotus patricki* Stout, Wilson et Valdés, 2011 from eastern Sakhalin [Ekimova *et al.*, 2021a], *Coryphella nobilis* Verrill, 1880 from northern Sakhalin [Ekimova *et al.*, 2022a]. Three nudibranch species were described based on material collected from Sakhalin Is. coastal waters: *Colga minichevi* Martynov et Baranets, 2002, *Adalaria ultima* Martynov et Korshunova, 2017, and *Dendronotus pseudodalli* Ekimova *et al.*, 2023 [Martynov, Baranets, 2002; Martynov, Korshunova, 2017; Ekimova *et al.*, 2023a]. In the check-list of free living marine invertebrates of the Far Eastern seas of Russia, twenty two species are mentioned for the southern Kurile Islands and southern Sakhalin [Martynov, 2013], however the exact geographical range of species across this region is not clear. Scarce information on the Sakhalin nudibranch fauna is exceptionally low in comparison to the well-studied and rich biodiversity of the Sea of Japan [Baba, 1960; 1961; Martynov, Roginskaya, 2005; Martynov *et al.*, 2015a, b; Ekimova *et al.*, 2016; 2021b; 2022b; 2023b; Korshunova *et al.*, 2023a], Kurile Islands [Martynov *et al.*, 2015 a,b; Korshunova *et al.*, 2020a,b; 2023b; Korshunova, Martynov, 2022; Martynov, Korshunova, 2020; 2022; Ekimova *et al.*, 2021a; 2023a] and Kamchatka [Martynov *et al.*, 2009; 2015a, b; Korshunova *et al.*, 2016].

The application of molecular methods to taxonomic studies has led to the discovery of numerous pseudocryptic taxa within different families of northwestern Pacific nudibranch molluscs [Korshunova *et al.*, 2016; 2020a,b; 2023b; Ekimova *et al.*, 2019; 2021a,b; 2023a, b; Ekimova, 2022 and others]. Considering this, all previous records of nudibranchs from Sakhalin Island needs a modern re-evaluation with the help of DNA barcoding methods.

In this paper we investigate a collection of nudibranch molluscs from Sakhalin Is. collected during two independent surveys covering different regions of Sakhalin Is. coastal waters and depths from 0.1 to 282 m. For each species we provide a morphological diagnosis, new bathymetric and geographic records as well as molecular data. We also summarize all available data on nudibranch biodiversity and distribution in this area.

Material and methods

Material collection

Material used in this study was collected during two independent research programs. 25 nudibranch specimens were sampled near eastern and northeastern shores of Sakhalin Is. during the expedition of R/V "*Akademic Oparin*" (Russia) to the Sea of Okhotsk, July 2019 at depths of 38–282 m. Additionally, 28 specimens were collected from southern Sakhalin in the vicinity of Cape Crillon in August 2023, at depths of 0.5–20 m. Specimens found during the first survey were sampled using an Agassiz Trawl (AGT) and during the second survey specimens were collected by snorkeling and diving. All living specimens were photographed in the lab and preserved in 96% EtOH to prevent DNA degradation. Voucher specimens were deposited in the collections of the National Scientific Center of Marine Biology (MIMB). Detailed sampling localities and voucher numbers for each specimen are given in Table S1.

External morphology and spicular complex

All collected specimens were used for the examination of their external morphology under a stereomicroscope. We also studied the spicular complex of a putative new species of the genus *Adalaria.* In this case, the specimen was studied by means of X-ray microtomography using a SkyScan 1272 microtomograph (Bruker MicroCT, Belgium). The SkyScan 1272 settings were as follows: Al filter radiation, acceleration voltage – 60 kV, current – 166 μA, resolution – 7.4 μm, crystal rotation angle – 0.150 grad., 2 scans in one position, exposure – 2823 msec. For reconstruction of the shadow image array, the NRecon software package (BrukerMicroCT) was used, since it can neutralize the artefacts caused by the instrument and provide a grey scale diapason corresponding to X-ray absorption, and, consequently, to chemical composition of the sample. Microtomographic sections obtained were analyzed using the CTVox software packages. Also, pieces of the mantle

Table 1. Amplification and sequencing primers and PCR conditions.

Табл. 1. Праймеры, использованные для амплификации и секвенирования, и условия ПЦР.

Marker	Primers	PCR conditions	Reference
Cytochrome c oxidase subunit I	**LCO1490** GGT CAA CAA ATC ATA AAG ATA TTG G **HCO2198** TAA ACT TCA GGG TGA CCA AAA AAT CA	5 min - 95°C, 35x[15 s - 95°C, 45 s - 45°C, 1 min - 72°C], 7 min - 72°C	Folmer *et al.* 1994
	jgLCO TNT CNA CNA AYC AYA ARG AYA TTG G **jgHCO** ANA CYT CNG GRT GNC CRA ARA AYC A	5 min - 95°C, 10x[30 s – 95°C, 1 min - 52°C (-0.5°C/cycle), 1 min - 72°C], 30x [30 s – 95°C, 1 min – 48°C, 1 min - 72°C], 7 min - 72°C	Geller *et al.*, 2013
	polyLCO GAY TAT WTT CAA CAA ATC ATA AAG ATA TTG G **polyHCO** TAM ACT TCW GGG TGA CCA AAR AAT CA		Carr *et al.*, 2011
16S rRNA	**16Sar-L** CGC CTG TTT ATC AAA AAC AT **16S R** CCG RTY TGA ACT CAG CTC ACG	5 min - 95°C, 35x[20 s - 95°C, 30 s - 52°C, 45 s - 72°C], 7 min - 72°C	Palumbi *et al.* 1991 Puslednik and Serb 2008
Histone H3	**H3AF** ATG GCT CGT ACC AAG CAG ACV GC **H3AR** ATA TCC TTR GGC ATR ATR GTG AC	5 min - 95°C, 35x[15 s - 94°C, 30 s - 50°C, 45 s - 72°C], 7 min - 72°C	Colgan *et al.*, 1998
Sequencing	**M13F** TGT AAA ACG ACG GCC AGT **M13R** CAG GAA ACA GCT ATG ACT	n/a	n/a

were dissected and placed in bleach (10% NaOCl solution) at room temperature for 5–20 minutes. Then, the spicules were washed with distilled water. Spicule preparations were examined with a Leica DM 2500 (Leica, Germany) and a Nikon Eclipse 200 (Nikon, Japan) light microscopes, and scanning electron microscopes (SEM) JEOL JSM 6380LA or JEOL JSM 7000 (JEOL, USA). The spicule measurements were carried out under a light microscope or scanning electron microscope using a scale segment or an electronic ruler. The length of multiaxial spicules was determined by measuring the length of the main (largest) axis. Examinations were performed with the SEMs listed above.

Anatomical studies

In the case of potentially new taxa, the internal morphology was examined for 11 specimens, 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 until connective and muscle tissues were completely dissolved. The radula, the jaws or labial cuticle were then 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). For the study of the reproductive system, specimens were dissected from the dorsal side along the midline and examined under a stereomicroscope.

DNA extraction, amplification, and sequencing

For most specimens we aimed to sequence the barcoding marker COI (partial fragment of *cytochrome c oxidase* subunit I) to confirm the initial identification. In addition, in taxa with expected cryptic biodiversity we also obtained mitochondrial 16S rRNA and nuclear Histone *H3* to reconstruct their phylogenetic relationships. Total genomic DNA was extracted from tissue samples preserved in 96% EtOH (Table S1) following the invertebrate protocol of the Canadian Center for DNA Barcoding [Ivanova *et al.*, 2006]. Polymerase chain reactions were performed with an "HS Taq" kit (Eurogen Lab, Russia), following the manufacturer's protocol. Reaction conditions and primers are available in Table 1.

For sequencing, 1 µL of successful 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 sequencing kit by GeneQuest. Sequencing reactions were analyzed using an ABI 3500 Genetic Analyser (Applied Biosystems). All novel sequences were submitted to NCBI GenBank (Table S1).

Data processing and phylogenetic reconstruction

All raw reads for each gene were assembled and checked for ambiguities and low-quality data in Geneious R10. Edited sequences were verified for contamination using the BLAST-n algorithm run on the GenBank nr/nt database [Altschul *et al.*, 1990]. In the case of the genera *Cadlina, Adalaria, Onchimira*, and *Cuthonella* phylogenetic reconstructions were performed. For this purpose, we incorporated in our analyses molecular datasets obtained in previous studies: *Cadlina* [Korshunova *et al.*, 2020b; Do *et al.* 2020; Ekimova *et al.*, 2021a]; *Adalaria* and *Onchimira* [Hallas *et al.*, 2017]; *Cuthonella* [Korshunova *et al.*, 2020b]. For the rest of the biodiversity only a BLAST-n search was done. 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 acid sequences to verify reading frames and check for stop-codons. Saturation was checked by plotting for all specimens including outgroup the total number of pairwise differences (transitions and transversions) against uncorrected p-distances. Indel-rich regions of the 16S alignment were identified and removed in Gblocks 0.91b [Talavera, Castresana, 2007] with the least stringent settings. Phylogenetic reconstructions were conducted for the concatenated multi-gene partitioned datasets. The best-fit nucleotide evolution model for MrBayes phylogeny and Maximum Likelihood reconstruction methods were selected in MEGA7 [Kumar *et al.*, 2016]. Multi-gene analyses were done by applying evolutionary models separately to partitions representing single markers. The Bayesian phylogenetic analyses and estimation of posterior probabilities were performed in MrBayes 3.2 [Ronquist, Huelsenbeck, 2003]. Analyses were initiated with a random starting tree and ran for 10^7 generations. Maximum likelihood phylogeny inference 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. Final phylogenetic tree images were rendered in FigTree 1.4.0 and further modified in Adobe illustrator CS 2015. Uncorrected *p*-distances were calculated based on COI alignments in MEGA 7 [Kumar *et al.*, 2016].

Results

Our molecular and morphological data revealed 13 nudibranch species belonging to the genera *Cadlina, Adalaria, Onchimira, Dendronotus, Eubranchus, Cuthonella,* and *Aeolidia.* We identified a clear case of cryptic biodiversity within the genera *Cadlina, Adalaria* and *Cuthonella,* for the latter two genera two species are described as new to science herein.

For described species which identity was confirmed by morphological and molecular data, we provide only brief descriptions; the new species are described in full. Molecular and morphological data for four species (*Dendronotus dalli, D. pseudodalli, D. patricki*, *Coryphella nobilis*) have already been published in dedicated taxonomical papers [Ekimova *et al.*, 2022a; 2023a], they are listed here for consistency.

Taxonomic descriptions

Order Nudibranchia de Blainville, 1814
Suborder Doridina Odhner, 1934
Superfamily Chromodoridoidea Bergh, 1891
Family Cadlinidae Bergh, 1891

Cadlina umiushi Korshunova, Picton, Sanamyan et Martynov, 2015
(Figs 1C–E, H, I, L, M, P; 2A)

Material studied: MIMB48043, 1 specimen, dissected, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05.372'N, 142°13.612'E, 20 m in depth, 20.08.2013, coll. A. Plaksin, A. Semenov. MIMB48042, 1 specimen, dissected, same locality, date and collectors as MIMB48043.

Type locality: Sea of Japan, Peter the Great Bay, Bolshoy Pelis Is., 5–7 m depth.

Diagnosis: Length 13–24 mm (preserved specimens). Notum semitransparent white, rounded anteriorly, posteriorly, covered with numerous yellow rounded spots on dorsal side. Large yellow subepidermal glands on dorsolateral sides of notum. Well-defined yellow line around notal edge. Buccal bulb with labial cuticle, formed by bifid to trifid or rarely unicuspidal rodlets. Radular formula: 73 × 21–27.1.21–27. Rachidian tooth trapezoid, elongate, slightly narrowed apically, with 5–7 denticles, sometimes with bifurcations, inner denticles larger than outer denticles. Lateral teeth hook-shaped with up to 12 denticles. Reproductive system triaulic (Fig. 2A). Ampulla massive, convoluted, muscular. Penis armed with small, densely arranged hamate spines. Vas deferens long and winding, with long expanded prostatic part, narrowing near penis. Receptaculum seminis small, oval; bursa copulatrix large, rounded, muscular.

Molecular data: A BLAST-n search of COI sequence resulted 99.53% identical to 2 sequences of *Cadlina umiushi* (type specimens, MN224067 and MN224068) thus confirming the species identity of our samples.

Distribution: This species was originally described from the Sea of Japan, Peter the Great Bay and adjacent areas, *e.g.* Spokoinaya Bay, Rudnaya

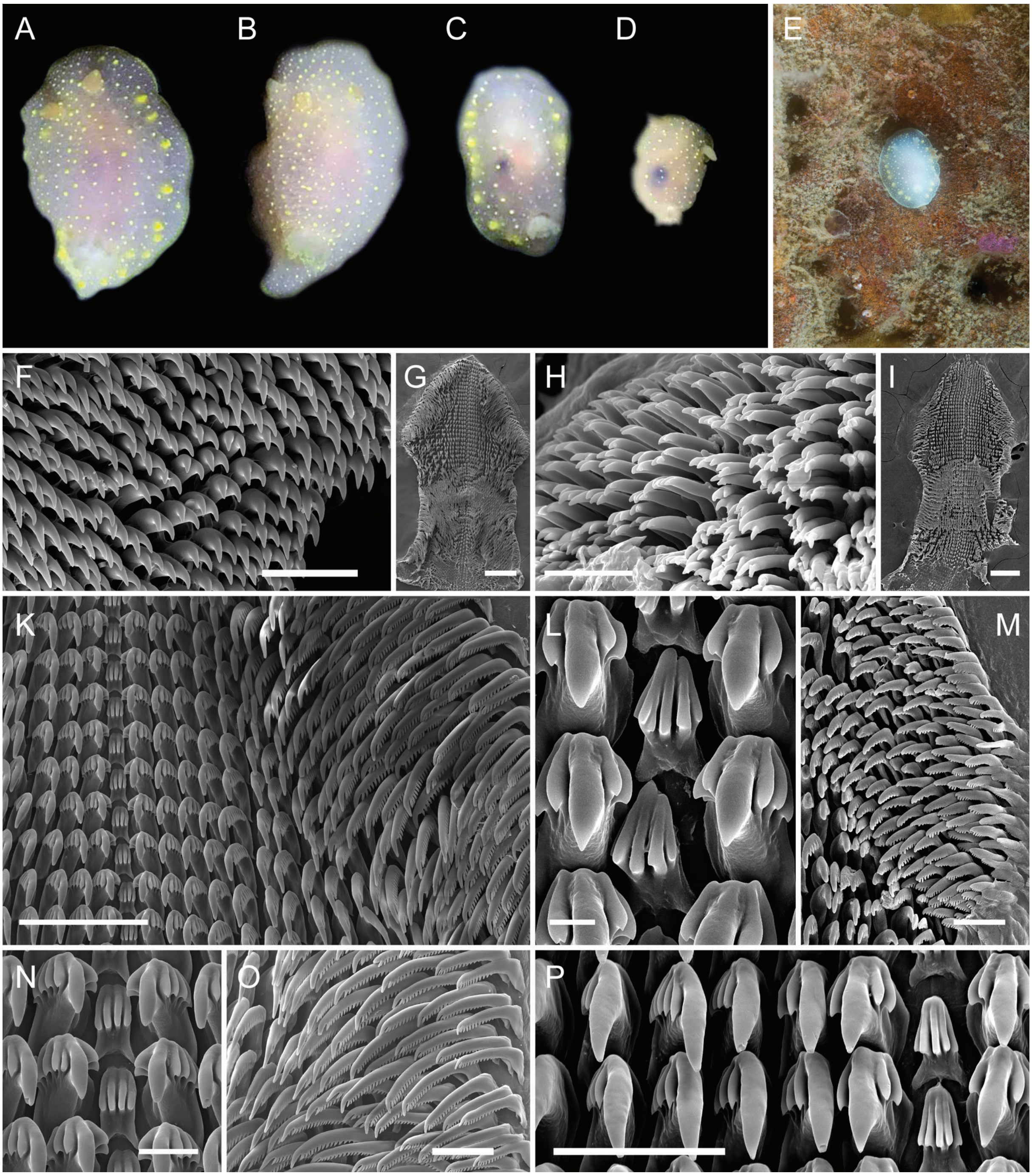

FIG. 1. External and internal morphology of *Cadlina* spp. from Aniva Bay. **A.** *Cadlina* sp. MIMB48044. **B.** *Cadlina* sp., MIMB48045. **C.** *Cadlina umiushi,* MIMB48042. **D.** *Cadlina umiushi,* MIMB48043. **E.** *Cadlina umiushi,* MIMB48042, in natural environment. **F.** *Cadlina* sp., MIMB48045, labial cuticle rodlets. **G.** *Cadlina* sp., MIMB48045, radula. **H.** *Cadlina umiushi*, MIMB48043, labial cuticle rodlets. **I.** *Cadlina umiushi,* MIMB48043, radula. **K, N, O.** *Cadlina* sp., MIMB48045, anterior radular portion, details of teeth morphology. **L, M, P.** *Cadlina umiushi,* MIMB48043, anterior radular portion, details of teeth morphology. Scale bars: F, H, N = 20 µm; G, I = 250 µm; K = 100 µm; L = 10 µm; M, O, P = 50 µm. Photo credits: **A – D.** Anton Plaksin; **E.** Alexander Semenov.

РИС. 1. Внешняя и внутренняя морфология *Cadlina* spp. из залива Анива. **A.** *Cadlina* sp. MIMB48044. **B.** *Cadlina* sp., MIMB48045. **C.** *Cadlina umiushi,* MIMB48042. **D.** *Cadlina umiushi,* MIMB48043. **E.** *Cadlina umiushi,* MIMB48042 в естественной среде. **F.** *Cadlina* sp., MIMB48045, родлеты лабиальной кутикулы. **G.** *Cadlina* sp., MIMB48045, радула. **H.** *Cadlina umiushi*, MIMB48043, родлеты лабиальной кутикулы. **I.** *Cadlina umiushi,* MIMB48043, радула. **K, N, O.** *Cadlina* sp., MIMB48045, передняя часть радулы, детали морфологии зубов. **L, M, P.** *Cadlina umiushi,* MIMB48043, передняя часть радулы, детали морфологии зубов. Масштабные линейки: F, H, N = 20 µm; G, I = 250 µm; K = 100 µm; L = 10 µm; M, O, P = 50 µm. Авторство фотографий: **A – D.** Антон Плаксин; **E.** Александр Семенов.

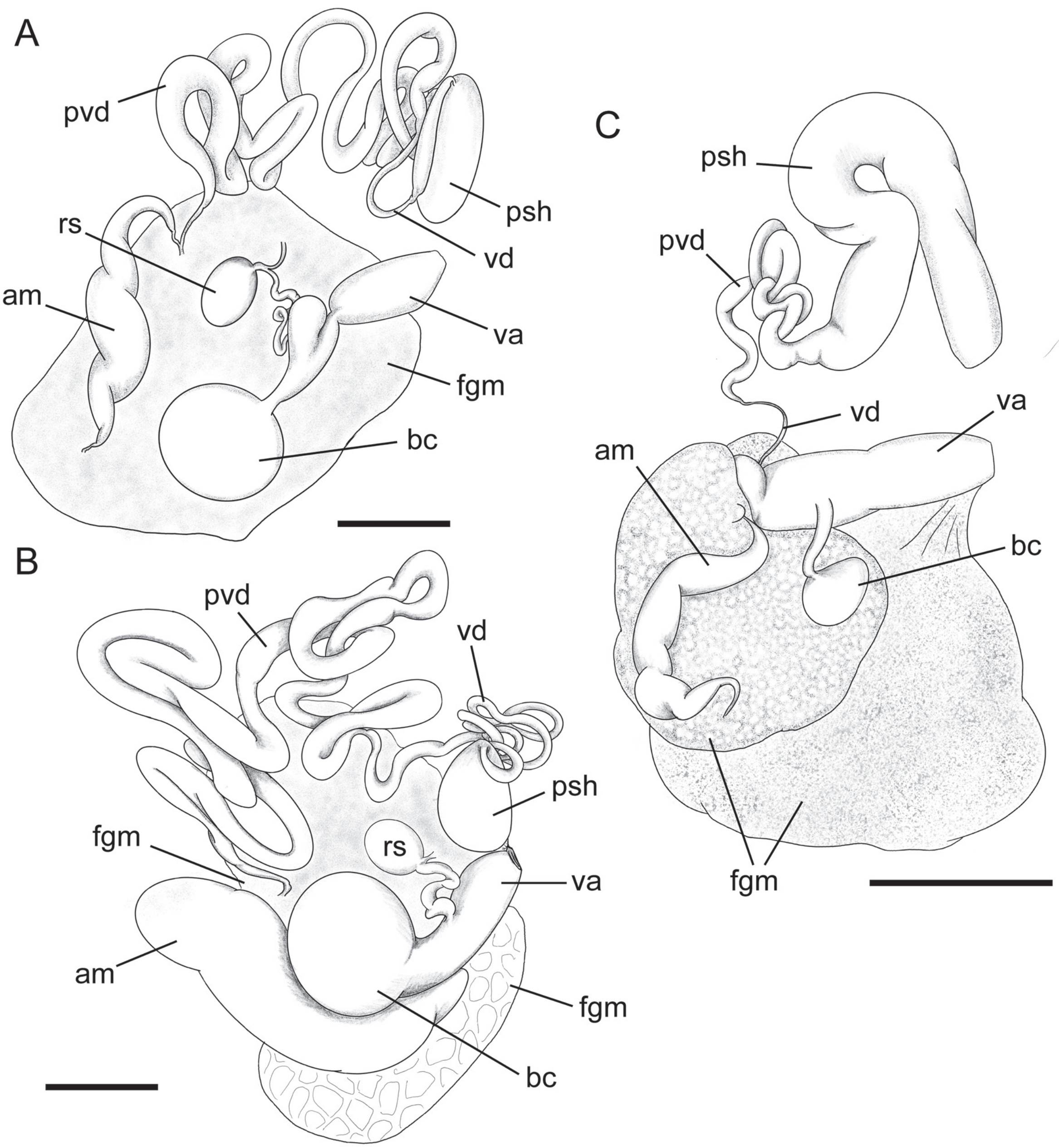

FIG. 2. Reproductive system morphology of *Cadlina* spp. from Aniva Bay and *Adalaria* ***boussoleana*** sp. nov. from the Sea of Okhotsk. **A.** *Cadlina umiushi,* MIMB48042. **B.** *Cadlina* sp., MIMB48045. **C.** *Adalaria* ***boussoleana*** sp. nov. MIMB48047. Abbreviations: am = ampulla; bc = bursa copulatrix; fgm = female gland mass; p = penis; pr = prostate; psh = penial sheath; pvd = prostatic vas deferens; rs = receptaculum seminis; va = vagina; vd = vas deferens. Scale bars: A, B = 1 mm; C = 5 mm.

РИС. 2. Половая система *Cadlina* spp. из залива Анива и *Adalaria* ***boussoleana*** sp. nov. из Охотского моря. **A.** *Cadlina umiushi,* MIMB48042. **B.** *Cadlina* sp., MIMB48045. **C.** *Adalaria* ***boussoleana*** sp. nov. MIMB48047. Сокращения: am = ампулла; bc = копулятивная сумка; fgm = комплекс женских желез; p = пенис; pr = простата; psh = сумка пениса; pvd – простатическая часть семяпровода, rs – семяприемник; va – вагина; vd – семяпровод. Масштабные линейки: A, B = 1 мм; C = 5 мм.

Bay [Martynov *et al.*, 2015a,b; Korshunova *et al.*, 2020a; Chichvarkhin, 2016]. It was discovered further south, in the Sea of Japan waters of South Korea [Do *et al.*, 2020]. Our results extend the geographical range of this species to southern parts of the Sea of Okhotsk (Aniva Bay).

Remarks: Specimens from Aniva Bay show slight morphological differences from the type specimens of *C. umiushi*: the latter have mostly bifid and rarely trifid rodlets of the labial cuticle, and their rachidian teeth are trapezoid, bearing 5–6 denticles almost equal in size or slightly larger [Korshunova *et al.*, 2020a]. In specimens from Aniva Bay the rodlets are commonly bifid and trifid, with rare unicuspid elements (Fig. 1H), the rachidian tooth is elongated trapezoid, commonly with 5–6 large denticles among which central denticles are the largest.

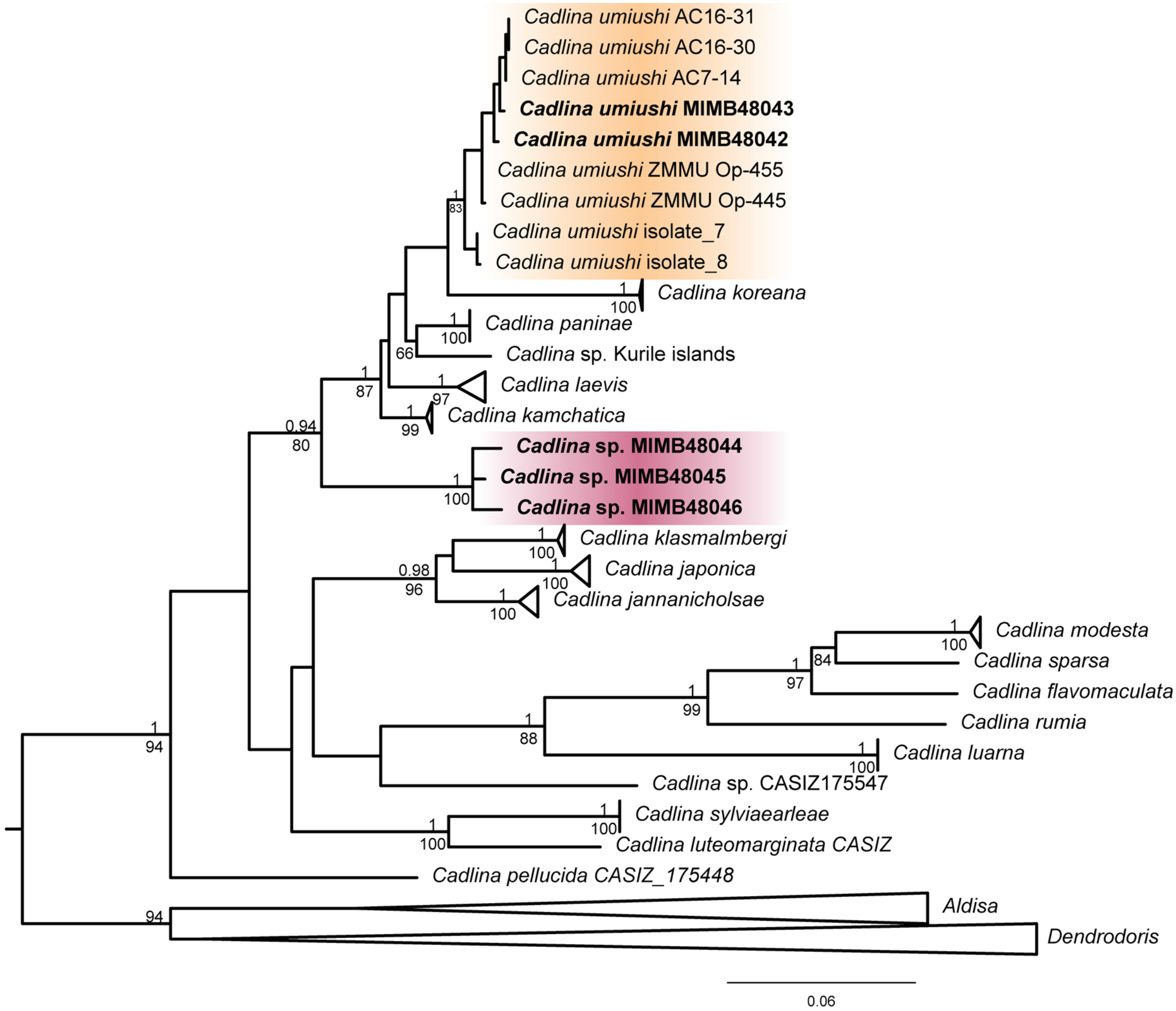

FIG. 3. Molecular phylogenetic hypothesis of genus *Cadlina*, Maximum Likelihood, concatenated dataset of three markers (COI + 16S + H3), species-level clades and outgroups are collapsed to a single branch, except target species from Sakhalin Is. Numbers above branches indicate posterior probabilities from Bayesian Inference (values higher than 0.9 are shown), numbers below branches – bootstrap support from Maximum Likelihood (in %, values higher than 60% are shown).

РИС. 3. Молекулярно-филогенетическое дерево для рода *Cadlina*, построенное на основании комбинированного датасета при помощи метода максимального правдоподобия (COI + 16S + H3), клады видового уровня сколлапсированы, кроме клад изучаемых видов с о. Сахалин. Значения над ветвями обозначают апостериорные вероятности (показаны значения более 0.9). Значения под ветвями обозначают поддержки бутстрепа (в %, показаны значения более 70%).

Cadlina sp.
(Figs 1A, B, F, G, K, N, O; 2B)

Material studied: MIMB48044, 1 specimen, the Sea of Okhotsk, Aniva Bay, Anastasia Cape, 46°00.727'N, 142°10.671'E, 5–15 m in depth, 22.08.2023, coll. A. Plaksin, A. Semenov. MIMB48045, MIMB48046, 2 specimens, dissected, collection locality, date and collectors are same as MIMB48044.

Diagnosis: Length 20–26 mm (preserved specimens). Notum semitransparent white, rounded in front and posteriorly, covered with numerous yellow rounded spots on dorsal side. Large yellow subepidermal glands on dorsolateral sides of notum. Well-defined yellow line around notal edge. Buccal bulb with labial cuticle, formed by bifid rodlets. Radular formula: 67 × 17–24.1.17–24. Rachidian tooth trapezoid, with 4–5 denticles, almost equal in size. Lateral teeth hook-shaped with up to 18 denticles. Reproductive system triaulic (Fig. 2B). Ampulla large, slightly convoluted. Penis armed with small, densely arranged hamate spines. Prostatic part of vas deferens long and winding, non-prostatic portion of vas deferens formed several dense loops near penial sheath. Receptaculum seminis small, oval; bursa copulatrix large, rounded, muscular, connecting to vagina by wide duct.

Molecular data: On both Bayesian (BI) and Maximum likelihood (ML) phylogenetic trees (Fig. 3) *Cadlina* sp. from Aniva Bay was recovered as a derived monophyletic group (posterior probability from BI, PP = 1; bootstrap support from ML, BS = 100). This clade is sister to monophyletic group, uniting Atlantic species of the *Cadlina laevis* (Linnaeus, 1767) species complex (PP = 0.94; BS = 80). The *C. laevis* species complex includes *C. kamchatica* Korshunova *et al.*, 2015 from Kamchatka, *C. laevis s.str.* from NE Atlantic and Arctic, *Cadlina* sp. and *C. paninae* Korshunova *et al.*, 2020 from the Kurile Islands, *Cadlina koreana* Do *et al.*, 2020 from the Sea of Japan and *Cadlina umiushi* from the Sea of Japan and Aniva Bay (PP = 1; BS = 87).

Distribution: This species is found only in the Sea of Okhotsk, Aniva Bay.

Remarks: This species shows similarities in external features with the sympatric species *Cadlina umiushi* (Fig. 1): it has a semitrasparent notum, with yellow spots on the dorsal sides, well-defined subepidermal glands on the notal edges and a yellow line around the notal edge. Internally its radular morphology matches the description of *Cadlina* sp. from the Kuril Islands and the type specimens of *Cadlina umiushi*: [see Korshunova *et al.*, 2020a for details]. At the same time, COI-based genetic data shows high divergence from all species comprising the *C. laevis* species complex [*C. laevis, C. kamchatica, C. paninae, C. umiushi, Cadlina* sp. *sensu* Ekimova *et al.*, 2021a] and thus, most likely the species from Aniva Bay represents a new species for science. The complicated taxonomy of the *Cadlina laevis* species group has been already highlighted in the previous studies [Korshunova *et al.*, 2020a; Ekimova *et al.*, 2021a]. Here we follow the suggestion by Ekimova *et al.* [2021a] that further studies of NW Pacific specimens are needed to confirm the species status of putative *Cadlina* new taxa due to the high level of variation in external and internal characters and the limited available material for study.

Superfamily Onchidoridoidea Gray, 1827
Family Onchidorididae Gray, 1827

Adalaria ***boussoleana*** sp. nov.
(Figs 2C, 4, 5)

Zoobank registration: urn:lsid:zoobank.org:act:B1249966-6553-466D-A81E-715C146F0F79

Type material: Holotype MIMB48047, dissected, the Sea of Okhotsk, Bay of Patience, 47°42.5’N, 144°30.3’E, 209–240 m in depth, 28.07.2019, coll. A. Mayorova.

Type locality: Sea of Okhotsk, Bay of Patience, 47°42.5’N, 144°30.3’E, 209–240 m in depth.

External morphology (Fig. 4A, B)*:* Body length 24 mm. Max width 10 mm. Body rounded anteriorly and gradually narrowing posteriorly. Rhinophores conical and massive, with 14 lamellae, retractable, rhinophoral sheaths bear 7 spiculate elongated tubercles on their edges. Notum densely covered by long and narrow tubercles bearing long spicules. On dorsal side smaller tubercles also common. 13 multipinnate branchial leaves forming horseshow ring around anal opening, gill cavity absent. Reproductive opening on right anterior side, atrium forming spiral fold. Large oral veil with distinct lateral processes on both sides.

Coloration (Fig. 4A, B): Notum uniform milky-white. Foot and head same color as notum. Rhinophores yellowish.

Internal morphology (Fig. 4C–I)*:* Spicule complex performed by mono-, di-, and multiaxons. Multiaxons most abundant. Several spicules, especially mono- and diactines may bear minute spines on surface, irregularly placed. Tubercles formed by vertical tracts continuing by stellular tract in upper notal parts, spicule types mixed. Notal edge formed by triactines, which densely packed and oriented by different angles to each other, concatenated by their central short rays.

Buccal pump large, prominent, rounded, with narrow short stalk. Peripheral muscle narrow, covering up to third part of pump width. Radular formula: 32 × 5–6.1.5–6 (Fig. 5). Rachidian tooth rectangular, with vertical folds. Lateral teeth massive, beak-shaped with wide base, its cusp edge bearing 0–7 reduced minute denticles. Marginal teeth triangular, lacking distinct denticles, slightly folded, inner marginal teeth larger than outer.

Reproductive system triaulic (Fig. 2C). Ampulla narrow, with two distinct folds. Penial sheath massive, large, convoluted. Vas deferens moderate in length, highly convoluted, prostatic part indistinct. Vagina massive, slightly narrowing to seminal receptacle region. Bursa copulatrix rounded, distinct, connecting to middle vagina part by short duct.

Molecular data: This species forms a derived singleton on the Onchidorididae phylogenetic trees (Fig. 6) with a highly supported (PP = 1; BS = 85) sister relationship with *Adalaria slavi* Martynov, Korshunova, Sanamyan et Sanamyan, 2009. Although most onchidoridid genera were recovered as monophyletic (*i.e. Onchidoris, Atalodoris, Idaliadoris, Acanthodoris, Onchimira*), the genus *Adalaria* was polyphyletic in both ML and BI analyses. It is arranged into two clades and two singletons with unresolved basal relationships between them and

РИС. 4 (на след. стр.). Внешняя морфология и спикульный комплекс *Adalaria* ***boussoleana*** sp. nov, голотип MIMB48047. **A.** Прижизненная фотография, вид с дорсальной стороны. **B.** Прижизненная фотография, вид с латеральной стороны, справа. **C, D, E.** Спикульный комплекс: (**C**) вид с дорсальной стороны, (**D**) с вентральной стороны, (**E**) с латеральной стороны. **F.** Спикулы жаберного аппарата. **G.** Спикулы ринофоров с боковой стороны. **H.** Спикулы звездчатого тракта в основании туберклов, передняя часть тела. **I.** Моноаксоны. **J.** Диаксоны. **K.** Мультиаксоны. Обозначения: sc = спикулы жаберного аппарата; sf = спикулы ноги; sne = спикулы края нотума; srh = спикулы ринофора; srht = спикулы туберклов по краю кармана ринофора; sst = спикулы звездчатого тракта. Авторство фотографий: **A, B.** Анастасия Майорова.

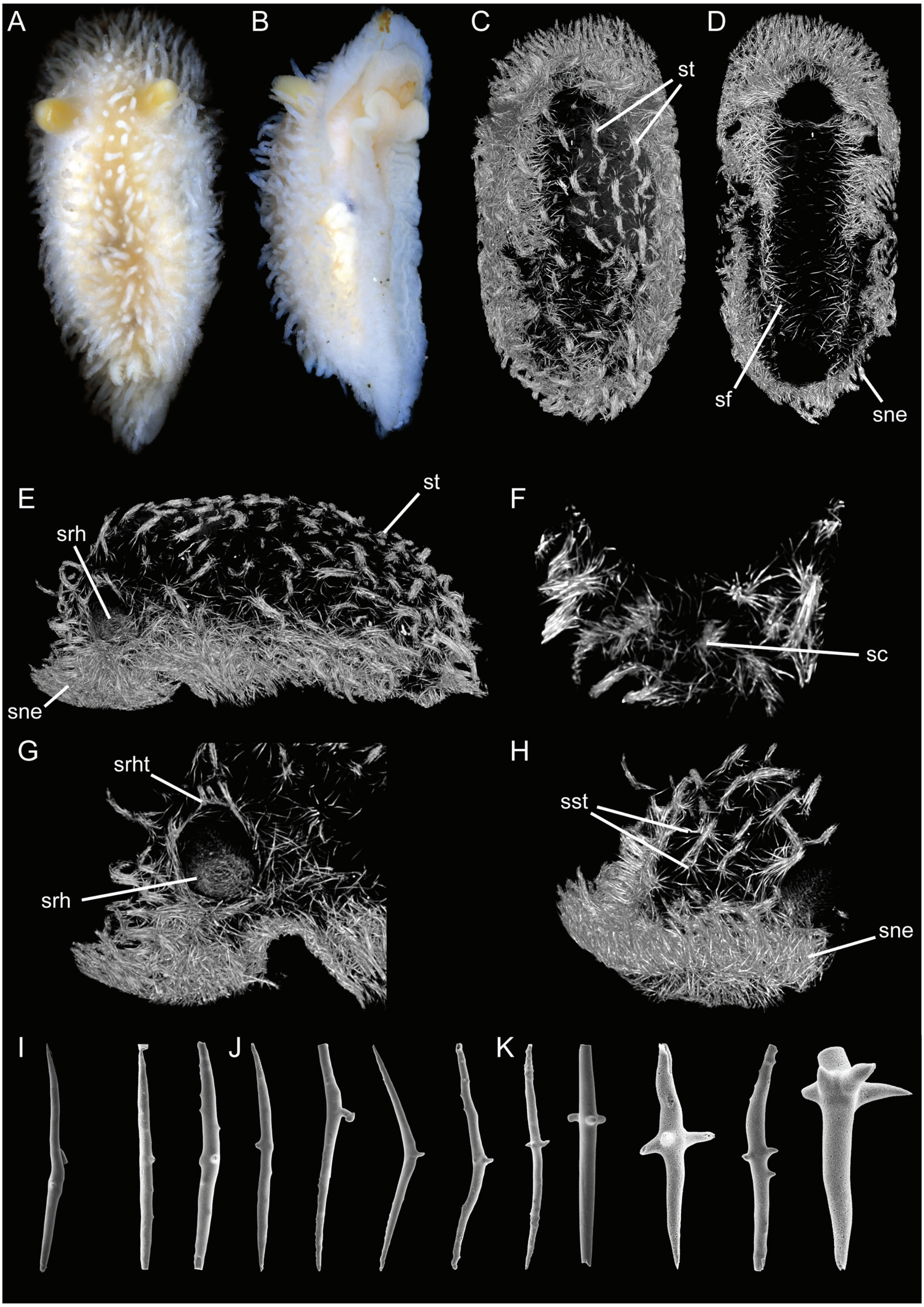

FIG. 4. External morphology and spicular complex of *Adalaria* ***boussoleana*** sp. nov, holotype MIMB48047. **A.** Living specimen, dorsal view. **B.** Living specimen, lateral view from right. **C, D, E.** Spicular complex, (**C**) dorsal view, (**D**) ventral view, (**E**) lateral view. **F.** Spicules of ctenidia. **G.** Spicules of rhinophore in the front part of the body, lateral view. **H.** Spicules of the stellular tract at the tubercle base, front part of the body. **H.** Monoaxone spicules. **J.** Diaxone spicules. **K.** Multiaxone spicules. Abbreviation: sc = spicules of ctenidia; sf = spicules of foot; sne = spicules of notum edge; srh = spicules of rhinophore; srht = spicules of tubercles on rhinophoral sheath; sst = spicule of stellular tract. Photo credits: **A, B.** Anastassya Maiorova.

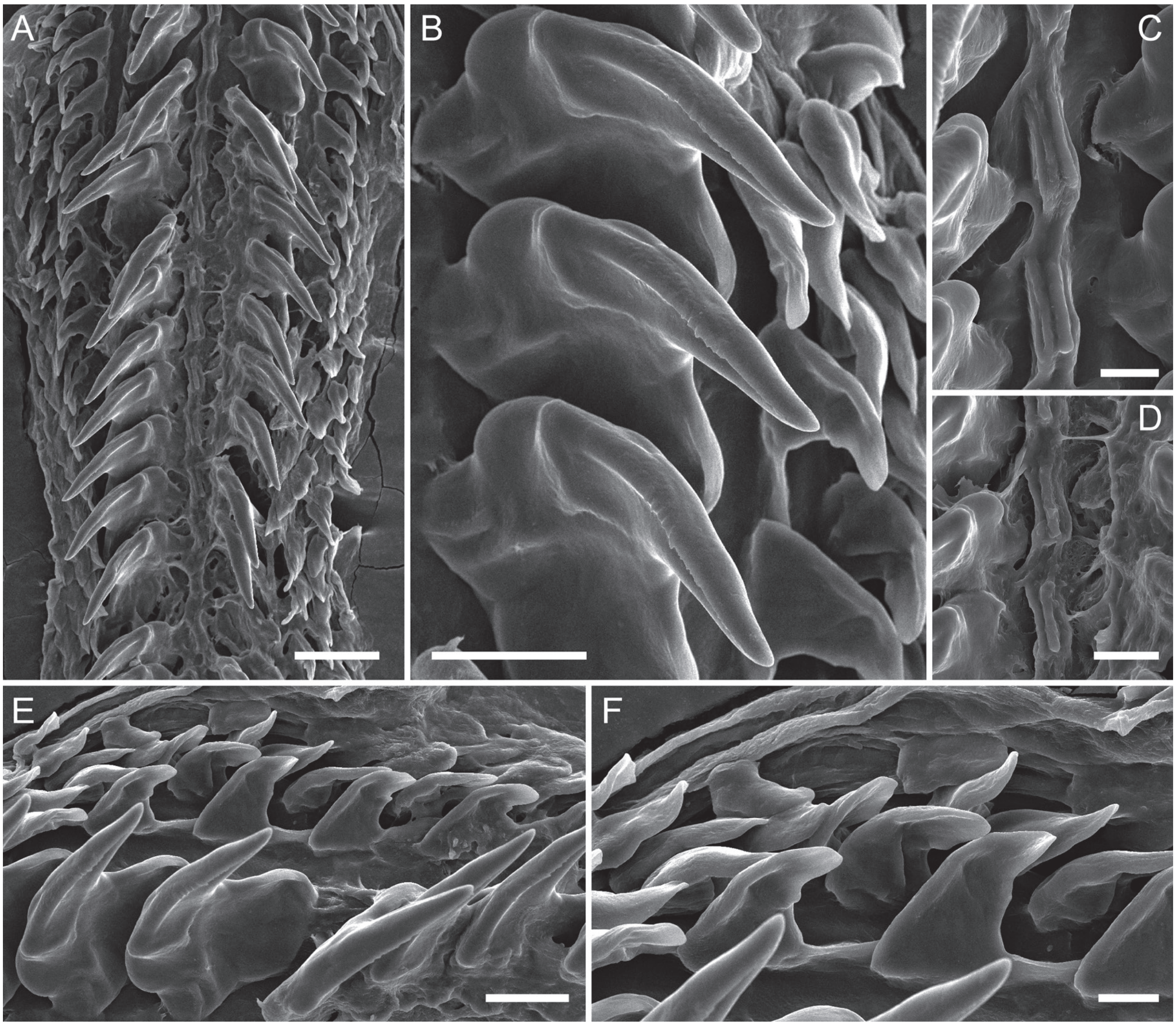

FIG. 5. Radular morphology of *Adalaria* ***boussoleana*** sp. nov., holotype MIMB48047 (SEM). **A.** Median and anterior radular portion. **B.** Lateral and inner marginal teeth. **C, D.** Rachidian teeth. **E.** Lateral and marginal teeth, posterior radular portion. **F.** Marginal teeth. Scale bars: A = 100 μm; B, E = 50 μm; C, D, F = 20 μm.

РИС. 5. Морфология радулы *Adalaria* ***boussoleana*** sp. nov., голотип MIMB48047 (СЭМ). **A.** Средняя и передняя часть радулы. **B.** Латеральные и внутренние маргинальные зубы. **C, D.** Центральные зубы. **E.** Латеральные и маргинальные зубы, задняя часть радулы. **F.** Маргинальные зубы. Масштабные линейки: A = 100 μm; B, E = 50 μm; C, D, F = 20 μm.

other Onchidorididae genera: (1) *Adalaria evincta* Millen, 2006, which recovered sister to the genus *Onchidoris* (PP = 1, BS = 100), (2) *Adalaria slavi* Martynov *et al.*, 2009 and *A.* ***boussoleana*** sp. nov. clade (PP = 1; BS = 85), (3) *Adalaria loveni* (Alder et Hancock, 1862), *A. proxima* and *A. rossica* Martynov et Korshunova, 2017 clade (PP = 1; BS = 91), (4) *Adalaria jannae* Millen, 1987.

Distribution: This species is known only from the type locality.

Remarks: Although our analysis shows that the genus *Adalaria* is likely polyphyletic (Fig. 6), we have chosen to designate the new species as a member of the genus *Adalaria* for several reasons. Firstly, the genus is currently accepted as valid with *Adalaria loveni* as the type species [Furfaro *et al.*, 2022]. Secondly, *Adalaria* ***boussoleana*** sp. nov. clearly fits the diagnosis of this genus according to the most recent revision of the family Onchidorididae [Furfaro *et al.*, 2022]: it has rachidian teeth, a large number of marginal teeth, and a boreal distribution. Additionally, the nodal support for deep relationships of *Adalaria* in our phylogenetic trees is low (Fig. 6), suggesting that the polyphyly of the genus may not be entirely fully justified. Lastly, our analysis does not include several species of the genus *Adalaria,* which were recently described from the North-West Pacific (*Adalaria olgae* Martynov *et al*., 2009*, Adalaria ultima* Martynov et Korshunova, 2017*, Adalaria neptuni* Martynov et Korshunova, 2022*, Adalaria sergeii* Martynov et Korshunova, 2022). Therefore, we tentatively designate *Adalaria* ***boussoleana*** sp. nov. as a member of the genus *Adalaria*, recognizing that a comprehensive revision of the genus is war-

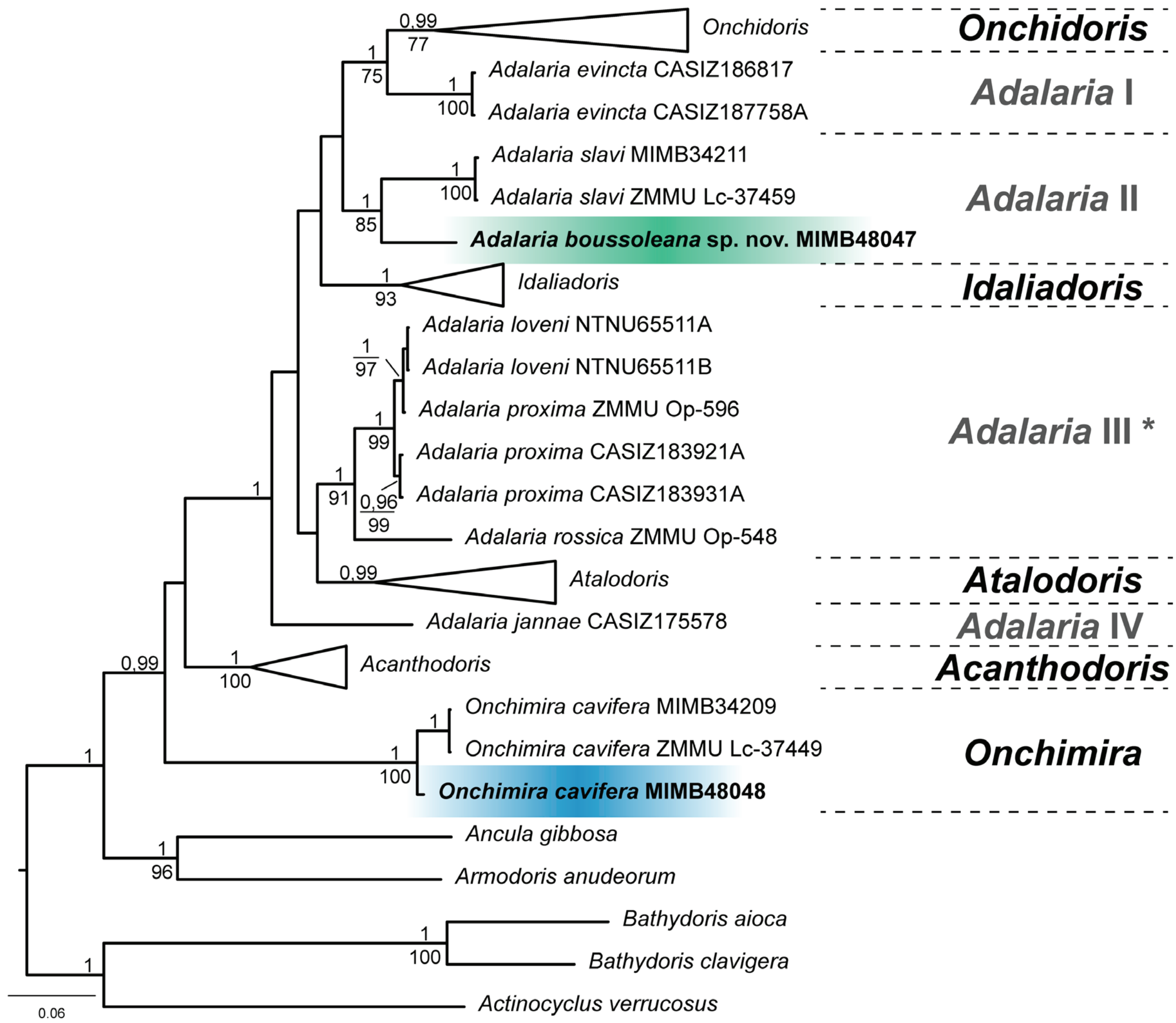

FIG. 6. Molecular phylogenetic hypothesis of the family Onchidorididae, Bayesian Inference, concatenated dataset of three markers (COI + 16S + H3), species-level clades and genera are collapsed to a single branch, except the genus *Adalaria.* Asterisk indicates a clade containing type species of the genus *Adalaria.* Numbers above branches indicate posterior probabilities from Bayesian Inference (values higher than 0.9 are shown), numbers below branches – bootstrap support from Maximum Likelihood (in %, values higher than 60% are shown).

РИС. 6. Молекулярно-филогенетическое дерево для семейства Onchidorididae, основании комбинированного датасета (COI + 16S + H3) при помощи байесовского анализа, клады видового уровня сколлапсированы, кроме клад изучаемых видов с о. Сахалин. Звездочкой обозначена клада с типовым видом рода *Adalaria.* Значения над ветвями обозначают апостериорные вероятности (показаны значения более 0.9). Значения под ветвями обозначают поддержки бутстрепа (в %, показаны значения более 60%).

ranted with the inclusion of extensive molecular data and increased sampling efforts.

The new species clearly differs from most of species of the genus *Adalaria* in external morphology due to the presence of narrow and elongated notal tubercles. *Adalaria ultima* was recently described from Sakhalinsky Bay (Northwestern Sakhalin, the Sea of Okhotsk) and possesses a similar external morphology with elongated narrow spicular tubercles [Martynov, Korshunova, 2017]. *Adalaria* ***boussoleana*** sp. nov. differs from *A. ultima* by the radular morphology: the former has 5 triangle and smooth marginal teeth on each side (Fig. 5E, F), while the latter has up to 10 elongated marginals bearing curved hooked cusps [Martynov, Korshunova, 2017]. Also, the lateral teeth of *A. ultima* are smooth, but in *A.* ***boussoleana*** sp. nov. they possess a single row of reduced denticles (Fig. 5B). *Adalaria tschuktchica* Krause, 1885 and *A. rossica* from the Chukchi Sea and Franz Josef Land respectively, also possess elongated tubercles, but have more marginal teeth than *A.* ***boussoleana*** sp. nov.: up to 8 in *A. tschuktchica* and up to 10 in *A. rossica.* From the latter species *A.* ***boussoleana*** sp. nov. is considerably different in molecular data as these species are placed in different supported clades (Fig. 6). *Adalaria* ***boussoleana*** sp.

nov. radular morphology is similar to *"Lamellidoris" spiculoides* Volodchenko, 1941, which was described from the tidal areas of the Bering Sea [Bering Is., see Volodchenko, 1941b] and subsequently transferred to the genus *Adalaria* [Martynov, 2006]. *Adalaria spiculoides* has 5 triangle marginals and possesses a single row of denticles on the lateral teeth [Volodchenko, 1941b]. Externally *A. spiculoides* has spiculate elongate and narrow tubercles and thus show many similarities with *A.* ***boussoleana*** sp. nov. However, the reproductive system of *A. spiculoides* has not been described. Martynov [2006], Millen [2006] and Martynov *et al.* [2009] suggested *A. spiculoides* to be a *nomen dubium:* Martynov [2006] highlighted that specimens from ZIN labelled as "*Archidoris spiculoides* (sic!)" collected from the type locality of the species and identified by Volodchenko, belong in fact to the genus *Onchidoris.* The type material of this species is lost [Martynov, 2006]. Also, it should be noted that *A. spiculoides* was described from the intertidal areas and has much smaller body size (up to 11 mm in length), while *Adalaria* ***boussoleana*** sp. nov. was collected from 209–240 m in depth. Finally, in external morphology *Adalaria* ***boussoleana*** sp. nov. possesses well-expressed elongate tubercles on rhinophoral sheaths (similarly to *A. tschuktchica*) (Fig. 4A, E, G), which are absent in *A. spiculoides.* Thus, we follow the suggestion by Martynov [2006] and Millen [2006] and consider *A. spiculoides* as *nomen dubium* and support *A.* ***boussoleana*** sp. nov. as distinct species. From phylogenetically close *A. slavi* the new species differs in both external morphology (shape of tubercles) and internal morphology (*A. slavi* has up to nine marginal teeth and well-expressed denticles on the lateral teeth).

Etymology: This species is named after French ship "Boussole" commanded by Jean-François de Galaup, Comte de Lapérouse, famous French explorer and leader of the scientific expedition around the world. The Comte de Lapérouse was the first European explorer reaching the northwestern coast of the Sea of Japan (Tataria), western and southern parts of Sakhalin Island. On the 15–16 August 1787 his expedition reached the same locality as the type locality of the new species to the south from the Gulf of Patience.

Onchimira cavifera Martynov, Korshunova, N. Sanamyan et K. Sanamyan, 2009
(Fig. 7A)

Material studied: MIMB48048, 1 specimen, dissected, the Sea of Okhotsk, Severny Bay, 54°31.5'N, 140°44.7'E, 80–82 m in depth, 31.07.2019, coll. A. Mayorova.

Diagnosis: Length 16 mm. Notum semitransparent white, rounded in front and posteriorly. Notum wrinkled, soft, with slight elevations and low tubercles. Eight rhinophoral lamellae, rhinophoral sheath lacking tubercles. 13 branchial leaves surrounded by low gill cavity. Radular formula: 24 x 6.1.6. Rachidian tooth subulate, smooth. Lateral teeth large beak-shaped, smooth. Marginal teeth elongated plates. Reproductive system was not study due to bad fixation.

Molecular data: A BLAST-n search of COI sequence resulted 97.12% identical to 2 sequences of *Onchimira cavifera* from GenBank (including the paratype ZMMU:Lc-37449, MN224073). On the phylogenetic tree (Fig. 6) our specimen also forms a single clade with *O. cavifera* from GenBank (PP = 1; ML = 100).

Distribution: This species was described from the North-West Pacific, Starichkov Is., Kamchatka, 18–26 m in depth [Martynov *et al.*, 2009], and subsequently reported from the same locality [Hallas *et al.*, 2017]. Its discovery off Sakhalin Is. expands its known geographic and bathymetric range to the southwestern Sea of Okhotsk at 82 m in depth, suggesting this species could be found in other localities of this sea.

Remarks: Although the external and internal morphology of our specimen matches the original description of *O. cavifera* [Martynov *et al.*, 2009], genetic data show slight differences (*p*-distance = 2.7%) in the COI marker between specimens from the Sea of Okhotsk and Kamchatka, suggesting restricted geneflow between these localities. Further studies are needed to test species limits across the geographical range of *O. cavifera.*

Suborder Cladobranchia Willan et Morton, 1984

Superfamily Dendronotoidea Allman, 1845
Family Dendronotidae Allman, 1845

Dendronotus dalli Bergh, 1879
(Fig. 7B, F, G)

Material studied: MIMB42234, 8 specimens, Sea of Okhotsk, NE Sakhalin Is., 52°12′4″N, 144°26′8″E, depth 218–192 m, 30 July 2019, coll. A. Mayorova. MIMB48049, 1 specimen, Sea of Okhotsk, NE Sakhalin Is., 52°12'4"N, 144°26'48.0"E, depth 165-168 m, 30 July 2019, coll. A. Mayorova. MIMB48050–MIMB48053, 4 specimens, Sea of Okhotsk, Sakhalin Is., Severny Bay, 54°27'9"N, 142°14'18.0"E, 38 m depth, 31 July 2019, coll. A. Mayorova. MIMB48054, 1 specimen, Sea of Okhotsk, Sakhalin Is., Severny Bay, 54°29'8"N, 141°16'54.0"E, 58–59 m depth, 31 July 2019, coll. A. Mayorova. MIMB48055, 1 specimen, Sea of Okhotsk, Sakhalin Is., Aniva Bay, Moguchi River, Hirano ridge, 46°04.978'N, 142°13.021'E, 15–18 m depth, 19 August 2023, coll. A. Plaksin, A. Semenov. MIMB48056–MIMB48060, 5 specimens, Sea of Okhotsk, Sakhalin Is., Aniva Bay, Moguchi River, Hirano ridge, 46°05.372'N, 142°13.612'E, 20 m depth, 20 August 2023, coll. A. Plaksin, A. Semenov. MIMB48061–MIMB48066, 6 specimens, Sea of Okhotsk, Sakhalin Is., Aniva Bay, Moguchi River, Hirano ridge, 46°04.826'N, 142°12.985'E, 13 m depth, 23 August 2023, coll. A. Plaksin, A. Semenov.

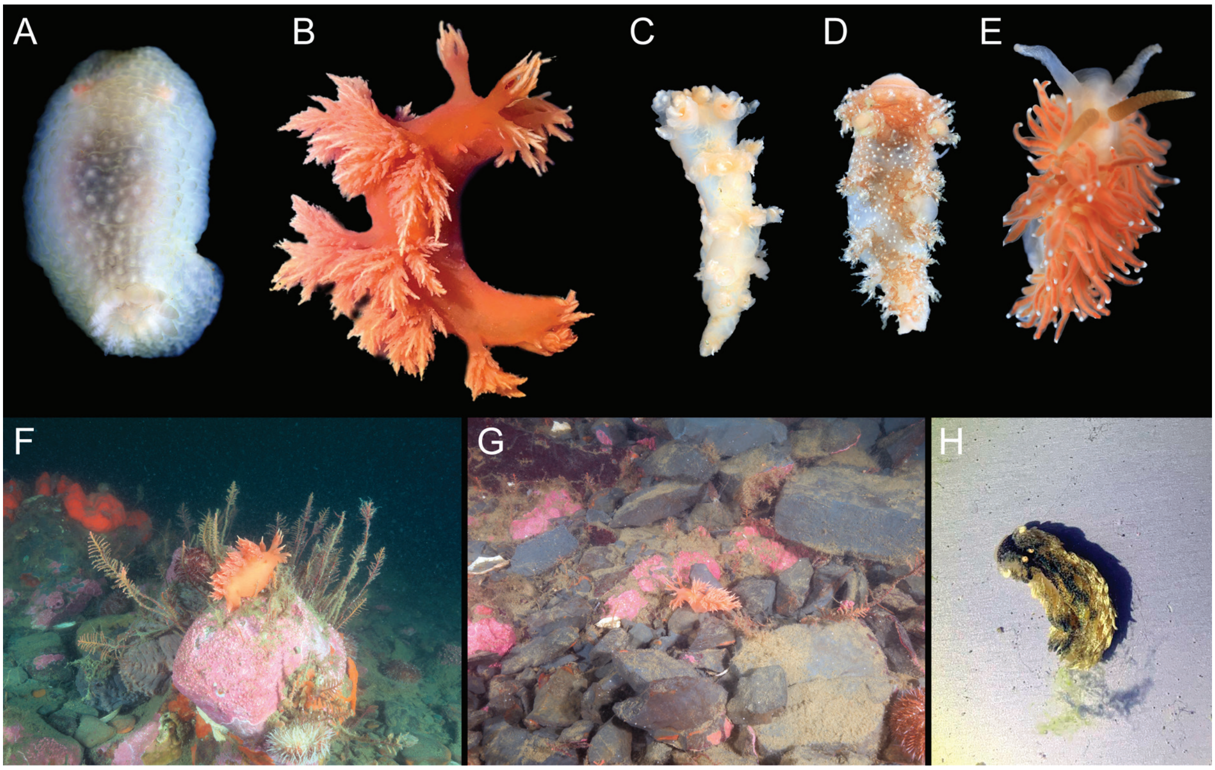

FIG. 7. Living photos of dorid and cladobranch nudibranchs found in Sakhalin Is. coastal waters. **A.** *Onchimira cavifera* MIMB48048 (Onchidorididae). **B.** *Dendronotus dalli* MIMB48057 (Dendronotidae). **C.** *Dendronotus pseudodalli* MIMB44620 (Dendronotidae). **D.** *Dendronotus patricki* MIMB42240 (Dendronotidae). **E.** *Coryphella nobilis* MIMB40022 (Coryphellidae). **F. G.** underwater photos of *Dendronotus dalli* in Aniva Bay, Hirano ridge. **H.** *Aeolidia papillosa* MIMB48078 (Aeolidiidae). Photo credits: **A, C–E.** Anastassya Mayorova; **B, H.** Anton Plaksin; **F, G.** Alexander Semenov.

FIG. 7. Прижизненные фотографии дорид и голожаберных моллюсков-кладобранхий, обнаруженных в прибрежных водах о. Сахалин. **A.** *Onchimira cavifera* MIMB48048 (Onchidorididae). **B.** *Dendronotus dalli* MIMB48057 (Dendronotidae). **C.** *Dendronotus pseudodalli* MIMB44620 (Dendronotidae). **D.** *Dendronotus patricki* MIMB42240 (Dendronotidae). **E.** *Coryphella nobilis* MIMB40022 (Coryphellidae). **F, G.** подводные фотографии *Dendronotus dalli* в заливе Анива, камни Хирано. **H.** *Aeolidia papillosa* MIMB48078 (Aeolidiidae). Авторство фотографий: **A, C–E.** Анастасия Майорова; **B, H.** Антон Плаксин; **F, G.** Александр Семенов.

Diagnosis: Body elongated, up to 80 mm in length, uniform milky-white to pink and salmon. Large oral veil with up to 10 branched oral appendages, rhinophoral sheath with up to five branched appendages, lateral papilla present, up to six pairs of dorsolateral appendages with extensive secondary and tertiary branching, terminal branches with opaque white pigmentation. Jaws elongate with slightly curved masticatory border bearing single row of blunt denticles. Radular formula 36 × 11–12.1.11–12. Triangular smooth rachidian tooth. Lateral teeth elongated, narrow, with large cusp and 3–4 small denticles. Ampulla large, folded. Prostate with few alveolar glands. Penis slightly curved.

Molecular data: The intraspecific *p*-distance in COI marker was 1,7%. A BLAST-n search of COI sequences resulted in up to 99% identity to sequences of *D. dalli* from GenBank thus confirming distinctness of studied specimens.

Distribution: This species is widely distributed in the North-West Pacific, including Kamchatka [Ekimova *et al.*, 2015], the Kurile Islands [Ekimova *et al.*, 2021a], the Commander Islands [Martynov, 2006], Sakhalin Is. [Chichvarkhin, 2016, this study], the Sea of Japan [Korshunova *et al.*, 2020c]. It was also found in the Chuckchi Sea [Ekimova *et al.*, 2019]. In the North-East Pacific this species is known from Alaska to Washington [Robilliard, 1970]. This species has a wide bathymetric range, being found from 5 to 227 m in depth [Ekimova *et al.*, 2021a; this study].

Dendronotus pseudodalli Ekimova, Mikhlina, Stanovova, Krupitskaya, Chichvarkhina et Schepetov, 2023
(Fig. 7C)

Material studied: MIMB44619, 1 specimen, Sea of Okhotsk, Sakhalin Is., 52°12’4”N, 144°26’8”E, depth 192–218 m, 30 July 2019, coll. A. Mayorova. MIMB44620, 1 specimen, Sea of Okhotsk, Sakhalin Is., 54°27’9”N, 142°14’3”E, depth 38 m, 31 July 2019, coll. A. Mayorova. MIMB44621, 1 specimen, same locality and collection date.

Diagnosis: Body elongated, up to 27 mm in length, uniform milky-white to pale pink. Large oral veil with up to six simple secondary branched appendages, rhinophoral sheath with up to five branched appendages, lateral papilla present, five pairs of dorsolateral appendages with secondary and tertiary branching, tips with opaque white pigment. Jaws elongate with slightly curved masticatory border bearing single row of small blunt denticles. Radular formula 46 × 8–10.1.8–10. Triangular rachidian tooth with up to 11 large denticles on both sides. Lateral teeth with sharp elongated cusp and 2–5 small denticles. Ampulla S-shaped. Prostate with 18 alveolar glands, arranged in double ring. Penis curved.

Distribution: Known only from Sakhalin Island, from two localities: off northeastern Sakhalin coast (192–218 m depth) and from Severny Bay (38 m depth) [Ekimova *et al.*, 2023a].

Remarks: This species performs identical external morphology with sympatrically living *D. dalli* but is considerably different from this species in both internal morphology and on the molecular level [see Ekimova *et al.*, 2023a for details].

Dendronotus patricki Stout, Wilson et Valdés, 2010 (Fig. 7D)

Material studied: MIMB42239, 1 specimen, Sea of Okhotsk, Sakhalin Is., Bay of Patience, 49°10′4″N, 145°03′1″E, depth 262–266 m, 29 July 2019, coll. A. Mayorova. MIMB42240, 1 specimen, Sea of Okhotsk, Sakhalin Is., Bay of Patience, 49°10′4″N, 145°03′1″E, depth 262–266 m, 29 July 2019, coll. A. Mayorova. MIMB42241, 1 specimen, Sea of Okhotsk, NE Sakhalin Is., 52°45′0″N, 144°24′3″E, depth 261–282 m, 30 July 2019, coll. A. Mayorova.

Diagnosis: Body broad, up to 41 mm in length, light pink to brownish with opaque white dots. Large oral veil with up to nine small appendages, poorly defined rhinophoral sheath with up to six appendages, lateral papilla absent, up to six pairs of dorsolateral appendages. Jaws oval, with slightly curved masticatory border bearing at least three rows of small conical denticles. Radular formula 30 × 12.1.12. Triangular rachidian tooth, central cusp strong, conical, 9-14 denticles on each side of cusp. Lateral teeth triangle smooth blades. Large convoluted ampulla. Prostate with 22 alveolar glands. Penis elongated.

Distribution: This species has a wide range, encompassing bathyal and abyssal areas of the Arctic, the NE Pacific and the North-West Pacific [Ekimova *et al.*, 2021a]. In Sakhalin Island it was found in the Bay of Patience (262–266 m depth) and off the northeastern Sakhalin coast (depth 261–282 m).

Superfamily Fionoidea Gray, 1857
Family Coryphellidae Bergh, 1889

Coryphella nobilis A. E. Verrill, 1880 (Fig. 7E)

Material studied: MIMB40022, MIMB40023, 2 specimens, Sea of Okhotsk, Severny Bay, 54°27’9”N, 142°14’18.0”E, 38 m depth, 31 July 2019, coll. A. Mayorova.

Diagnosis: Body wide, narrowing posteriorly, up to 19 mm in length, translucent white. Rhinophores wrinkled, orange to light brown with white tips. Cerata orange to red, arranged in continuous rows. Jaws oval-shaped with 9–12 rows of small conical denticles on slightly curved masticatory border. Radular formula 18 × 1.1.1. Triangular rachidian tooth, small conical cusp non-compressed by adjacent denticles, and 6–7 denticles on each side. Lateral teeth broad, triangular, with 11–13 denticles. Ampulla coiled, narrow. Vas deferens slightly curved, short, widened. Penis lobe-shaped.

Distribution: This species has a wide distribution in boreal Atlantic and Arctic waters, having been recorded from different localities of the North Atlantic, subarctic and Arctic waters [Ekimova *et al.*, 2022a]. It was recently discovered on Sakhalin Island [Ekimova *et al.*, 2022a].

Family Fionidae Gray, 1857 [*sensu* Cella *et al.*, 2016]

Eubranchus alexeii (Martynov, 1998) (Fig. 8A, H)

Material studied: MIMB48067, 1 specimen, dissected, Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05’06.5”N, 142°12’39.4”E, 0.1–1 m in depth, on *Zostera* sp. with *Obelia longissima* colonies, 7 August 2023, coll. I. Ekimova, D. Grishina.

Diagnosis: Body elongate, up to 4 mm in length, yellowish semitransparent with reddish-brown round spots. Rhinophores and oral tentacles elongated, smooth. Cerata finger-shaped, bearing thickening in middle part with digestive gland bulging, arranged in 5 rows with 2–3 cerata per row. Jaws rectangular, with masticatory border bearing one row of small conical denticles. Radular formula 29 × 1.1.1. Triangular rachidian tooth, central cusp cylindrical, with pointed tip, 4–6 lateral denticles on each side of cusp, innermost denticles smallest. Lateral teeth two times wider than rachidian teeth, with rectangular base, triangular cusp. Penis absent, copulative apparatus formed by everting atrium with complex stylet system.

Molecular data: A BLAST-n search of COI sequences resulted in 99.17% identity to sequences of *Eubranchus alexeii* from GenBank thus confirming identification of the studied specimen.

Distribution: *Eubranchus alexeii* was described and further mentioned as an endemic species of the Peter the Great Bay, northern Sea of Japan [Martynov, 1998; Martynov *et al.*, 2015b]. Subsequent works suggested it has wider geographic range at least in the Sea of Japan [Chichvarkhin, 2016, as *Eubranchus misakiensis* Baba, 1960]. Its discovery in Aniva Bay support this view and extends the

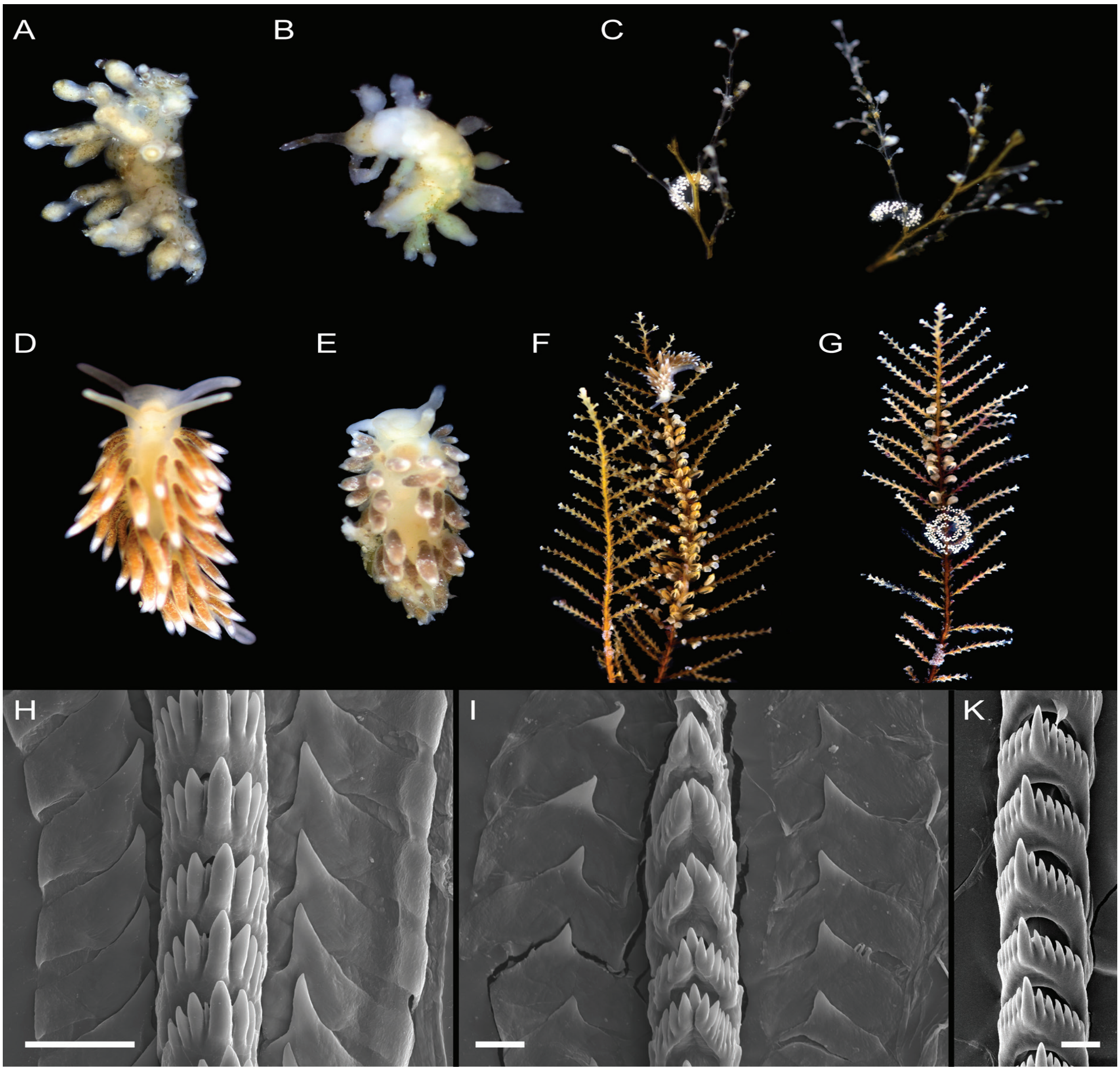

FIG. 8. External and internal morphology of studied representatives of the family Fionidae. **A.** *Eubranchus alexeii,* MIMB48067, living specimen. **B.** *Eubranchus rupium,* MIMB48068, living specimen. **C.** *Eubranchus rupium,* egg masses on *Obelia longissima* colonies. **D.** *Cuthonella soboli,* MIMB48071, living specimen. **E.** *Cuthonella soboli,* MIMB48073, living specimen. **F, G.** living specimen of *Cuthonella soboli* MIMB48071 (**F**) and its egg-mass (**G**) on *Sertularia* sp. colony. **H.** *Eubranchus alexeii,* MIMB48067, middle radular portion, SEM. **I.** *Eubranchus rupium,* MIMB48070, posterior radular portion, SEM. **K.** *Cuthonella soboli,* MIMB48073, anterior radular portion, SEM. Scale bars: H, K = 20 µm; I = 10 µm. Photo credits: **A–C, E.** Darya Grishina; **D, F, G.** Irina Ekimova.

РИС. 8. Внешняя и внутренняя морфология изученных представителей семейства Fionidae. **A.** *Eubranchus alexeii,* MIMB48067. **B.** *Eubranchus rupium,* MIMB48068. **C.** *Eubranchus rupium,* кладка на колонии *Obelia longissima*. **D.** *Cuthonella soboli,* MIMB48071. **E.** *Cuthonella soboli,* MIMB48073. **F, G.** *Cuthonella soboli* MIMB48071 (**F**) и ее кладка (**G**) на колонии *Sertularia* sp. **H.** *Eubranchus alexeii,* MIMB48067, средняя часть радулы, СЭМ. **I.** *Eubranchus rupium,* MIMB48070, задняя часть радулы, СЭМ. **K.** *Cuthonella soboli,* MIMB48073, передняя часть радулы, СЭМ. Масштабные линейки: H, K = 20 µm; I = 10 µm. Авторство фотографий: **A–C, E.** Дарья Гришина; **D, F, G.** Ирина Екимова.

known range of this species to southern parts of the Sea of Okhotsk.

Eubranchus rupium (Møller, 1842)
(Fig. 8B, C, I)

Material studied: MIMB48068– MIMB48070, 3 specimens, all dissected, Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05’06.5”N, 142°12’39.4”E, 0.1–1 m in depth, on *Zostera* sp. with *Obelia longissima* colonies, 7 August 2023, coll. I. Ekimova, D. Grishina.

Diagnosis: Body elongate, narrow, up to 5 mm in length, yellowish semitransparent with small reddish-brown spots. Rhinophores and oral tentacles elongated, smooth. Cerata finger-shaped, with pointed tips, bearing small thickening in upper part, arranged in 5–7 groups with 1–2 cerata per group. Jaws triangular-shaped with masticatory border bearing one row of small conical denticles. Radular formula 18–22 × 1.1.1. Triangular rachidian tooth with depressed central cusp and 6-7 lateral denticles on each side. Lateral teeth with rectangular base and triangular cusp. Ampulla small, bean-shaped. Vas deferens without prostatic part. Penis conical. Receptaculum seminis bent in middle part, expanded.

Molecular data: A BLAST-n search of COI sequences resulted in 99.57% identity to sequences of *E. rupium* from GenBank thus confirming distinctness of the studied specimens.

Distribution: This species has a wide distribution, having been recorded from Greenland [type locality, see Møller, 1842], Norway, Sweden, the Barents Sea, and the White Sea [Martynov, 1998; Cella *et al.*, 2016], the Sea of Japan [Martynov, 1998], Maine [Cella *et al.*, 2016]. This is the first record of this species from Sakhalin Is. (Aniva Bay), although it has been found from adjacent areas [Martynov, 2013].

Cuthonella soboli Martynov, 1992
(Fig. 8D–G, K)

Material studied: MIMB48071, 1 specimen, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05’06.5”N, 142°12’39.4”E, 0.1–1 m in depth, on *Sertularia* sp. colonies, 7 August 2023, coll. I. Ekimova, D. Grishina. MIMB48072– MIMB48074, 3 specimens, two dissected, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05’06.5”N, 142°12’39.4”E, 0.1–1 m in depth, on *Sertularia* sp. colonies, 7 August 2023, coll. I. Ekimova, D. Grishina.

Diagnosis: Body elongated, narrow, up to 7 mm in length, yellowish semitransparent to light beige. Rhinophores and oral tentacles cylindrical, smooth, equal in size. Cerata cylindrical, with pointed tips, arranged in continuous rows. Cerata orange to light brown, with white speckles arranged in indistinct ring at upper midline. Jaws triangular-shaped with masticatory border bearing one row of small blunt denticles. Radular formula 21 × 0.1.0. Triangular rachidian tooth with strong, protracted, non-compressed conical cusp and 5–6 denticles on each side. Ampulla narrow, slightly convoluted. Vas deferens without prostatic part, supplementary gland long and narrow. Penis conical. Receptaculum seminis small, ovate, muscular.

Molecular data: A BLAST-n search of COI sequences resulted in 98.32–98.84% identity to sequences of *C. soboli* from GenBank thus confirming the distinctness of the studied specimens. At the same time, specimens of *C. soboli* do not form a monophyletic group on the phylogenetic trees (Fig. 10).

Distribution: This species is known from the northern part of the Sea of Japan [Korshunova *et al.*, 2020b]; these authors also suggested it may be found in the southern Kurile Islands and Hokkaido. This is the first confirmed record of this species in the Sea of Okhotsk.

Cuthonella ***anastasia*** sp. nov.
(Fig. 9)

Zoobank registration: urn:lsid:zoobank.org:act:C146AF09-1376-4C16-9FCB-FDE7143CFE64

Type material: MIMB48076, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°04.978’N, 142°13.021’E, 15–18 m in depth, 19 August 2023, coll. A. Plaksin, A. Semenov. Paratypes: MIMB48075, 1 specimen, dissected, same locality and collectors as holotype. MIMB48077, 1 specimen, partly dissected, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05.372’N, 142°13.612’E, 20 m in depth, 20 August 2023, coll. A. Plaksin, A. Semenov.

Type locality: The Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°04.978’N, 142°13.021’E, 15–18 m in depth.

External morphology (Fig. 9A, B): Body elongated, moderately wide, up to 5 mm in length (MIMB48077). Rhinophores and oral tentacles cylindrical, smooth, almost equal in size or rhinophores slightly shorter. Cerata cylindrical, with rounded tips, arranged in continuous rows. Anal opening cleioproctic. Reproductive opening on right side below first cerata groups.

Coloration (Fig. 9A, B): Background body color pale beige to light-orange. Rhinophores and oral tentacles with same color as body, with distinct opaque white spots arranged in discontinuous subapical band in rhinophores, or dorsal lines on oral tentacles. Opaque white spots on head region concentrated between eyes. Cerata reddish brown with distinct opaque white spots (commonly 5–10 on each ceras) and subapical ring of white speckles around cnidosac area.

Internal morphology (Fig. 9C, D): Jaws triangular-shaped with masticatory border bearing one row of small denticles. Radular formula 24 × 0.1.0. Triangular rachidian tooth with strong, protracted, non-compressed conical cusp and 5–7 denticles on each side. Reproductive system was not studied in detail because of very poor fixation of specimens.

Molecular data: Unfortunately, after numerous attempts we failed to amplify COI marker for this species using a large set of universal primers. Specimens of *C.* ***anastasia*** sp. nov. cluster together on the phylogenetic tree (Fig. 10; PP = 0.94, BS = 86). This species is recovered sister to *Cuthonella georgstelleri* Korshunova *et al.*, 2020 from Matua Is., middle Kurile Islands (PP = 0.89, BS = 65). The *p*-distance in 16S rRNA comprises 1.20%, which is in line with interspecific *p*-distance values within the genus *Cuthonella* [Korshunova *et al.*, 2020b].

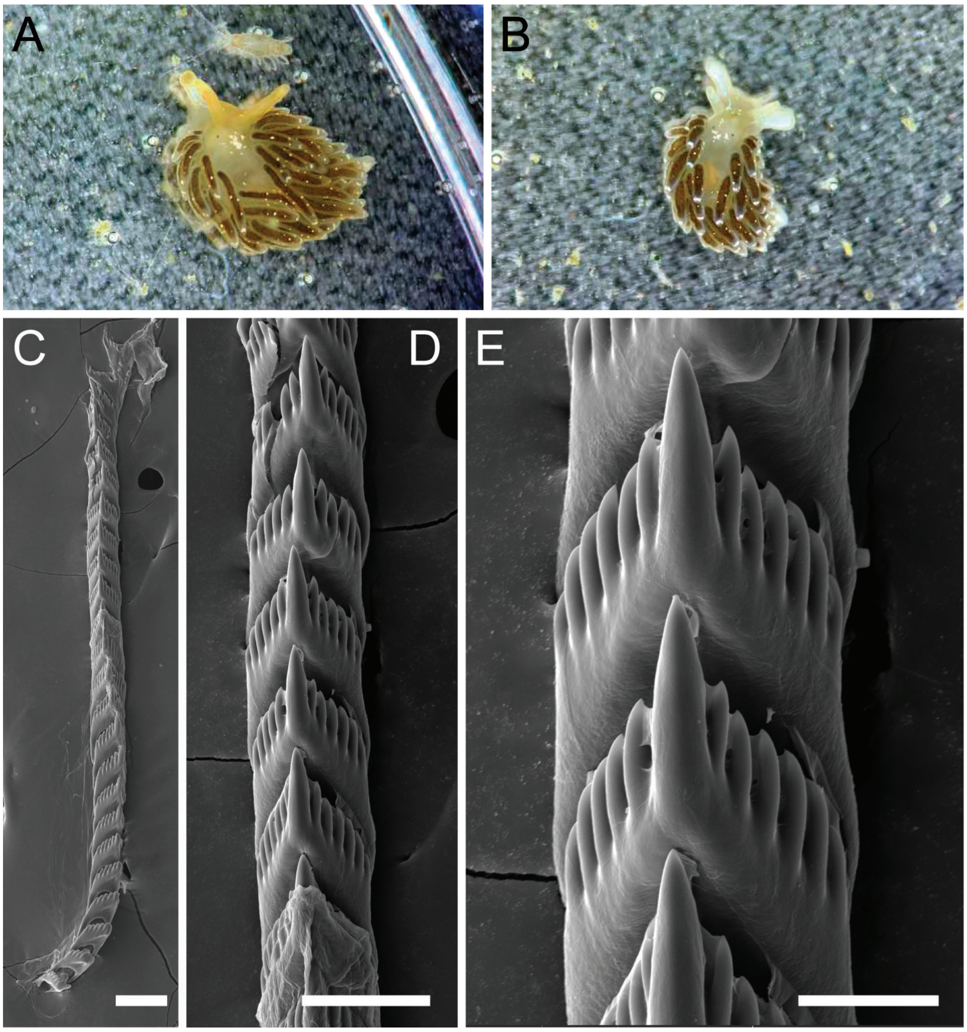

FIG. 9. External and internal morphology of *Cuthonella* ***anastasia*** sp. nov. **A.** Paratype MIMB48077, living photo. **B.** Holotype MIMB48076, living photo. **C**–**D.** MIMB48075, radula. Scale bars: C, D = 50 μm; E = 20 μm. Photo credits: **A, B.** Anton Plaksin.

РИС. 9. Внешняя и внутренняя морфология *Cuthonella* ***anastasia*** sp. nov. **A**. Паратип MIMB48077. **B.** Голотип MIMB48076. **C**–**D.** паратип MIMB48075, радула. Масштабные линейки: C, D = 50 μm, E = 20 μm. Авторство фотографий: **A, B.** Антон Плаксин.

Cuthonella ***anastasia*** sp. nov. and *C. georgstelleri* forms a large clade with other North-West Pacific *Cuthonella* species: *Cuthonella ainu* Korshunova *et al*., 2020*, Cuthonella benedykti* Korshunova *et al*., 2020*, C. soboli, Cuthonella osyoro* (Baba, 1940) (PP = 1; BS = 59).

Distribution: This species is known only from the type locality.

Remarks: Although we were not able to study the reproductive system of the new species due to improper preservation of a single mature specimen (paratype MIMB48077), *C.* ***anastasia*** sp. nov. is well characterized by a combination of available molecular and morphological data. In the phylogenetic trees, this species forms a monophyletic group, which is sister to *C. georgstelleri.* From the latter species, *C.* ***anastasia*** sp. nov. differs in external morphology: it has brown cerata with white spots and pale orange body, while *C. georgstelleri* has elongated orange-brownish to salmon brown cerata lacking additional pigmentation except white bands on tips, and whitish body with slight disperse white pigment [Korshunova *et al.*, 2020b]. *Cuthonella georgstelleri* has a larger body size than *C.* ***anastasia*** sp. nov. (14 mm vs 5 mm in length respectivelly). Finally, these species differ in radular characters: *C. georgstelleri* has more teeth (30) and more denticles on rachidian teeth (up to 10 on each side). No other described *Cuthonella* has numerous distinct opaque white spots on cerata [Korshunova *et al.*, 2020b]. *Cuthonella soboli* has similar radular morphology (Fig. 8K) but differs from *C.* ***anastasia*** sp. nov. in coloration, since *C. soboli* has orange to light brown cerata with white speckles arranged in indistinct ring at upper midline (Fig. 8D, E).

Etymology: The species name refers to the Cape

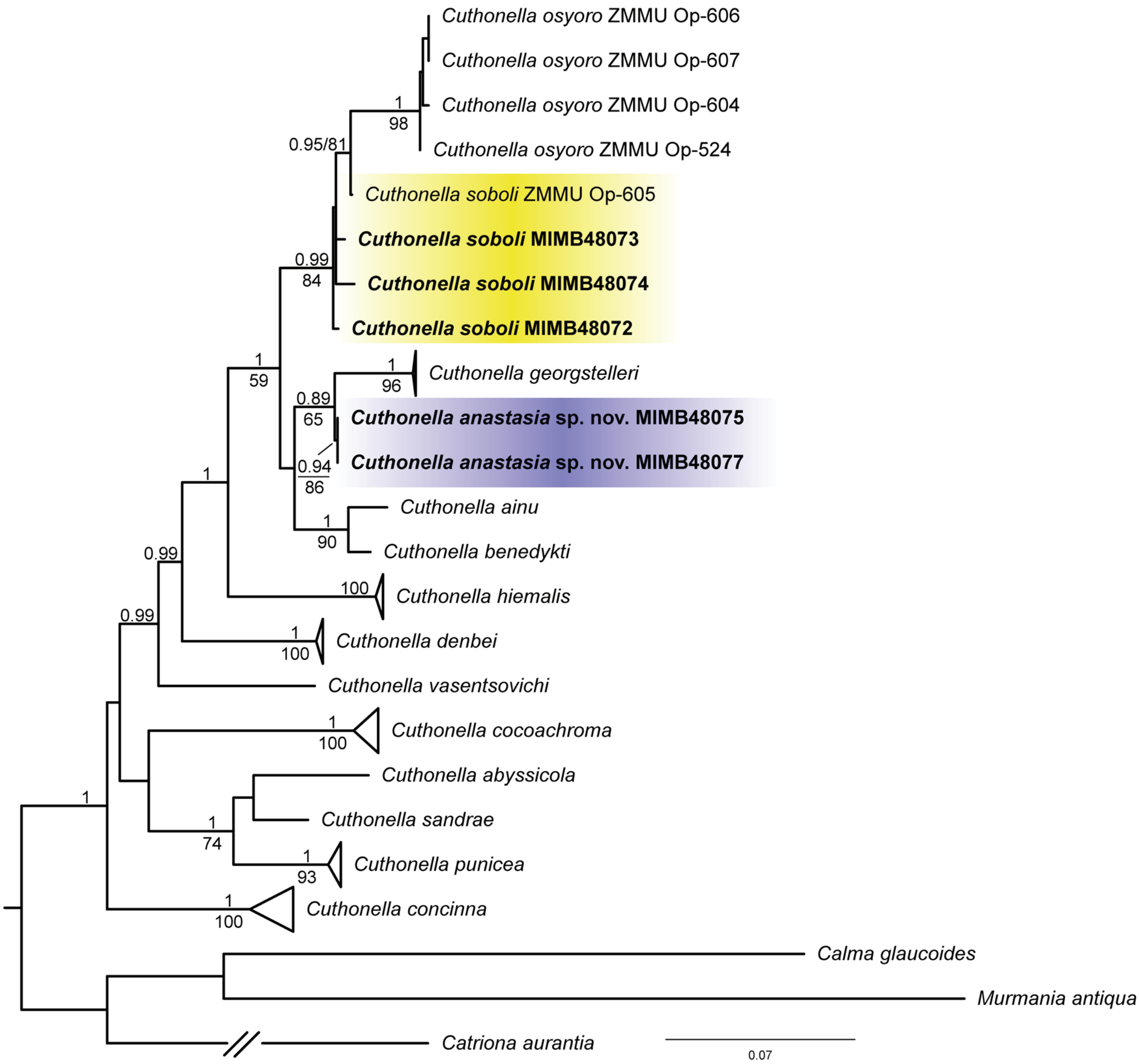

FIG. 10. Molecular phylogenetic hypothesis of genus *Cuthonella*, Maximum Likelihood, concatenated dataset of three markers (COI + 16S + H3), species-level clades and outgroups are collapsed to a single branch, except target species from Sakhalin Is. and *Cuthonella osyoro.* For *Cuthonella* ***anastasia*** sp. nov. only 16S and H3 data were available for analysis. Numbers above branches indicate posterior probabilities from Bayesian Inference (values higher than 0.9 are shown), numbers below branches – bootstrap support from Maximum Likelihood (in %, values higher than 60% are shown).

РИС. 10. Молекулярно-филогенетическое дерево для рода *Cuthonella*, построенное на основании комбинированного датасета при помощи метода максимального правдоподобия (COI + 16S + H3), клады видового уровня сколлапсированы, кроме клад изучаемых видов с о. Сахалин. Для *Cuthonella* ***anastasia*** sp. nov. только данные по маркерам 16S и H3 были доступны для анализа. Значения над ветвями обозначают апостериорные вероятности (показаны значения более 0.9). Значения под ветвями обозначают поддержки бутстрепа (в %, показаны значения более 60%).

Anastasia, the closest large cape in the Aniva Bay to the type locality of the new species.

Superfamily Aeolidioidea
Family Aeolidiidae

Aeolidia papillosa (Linnaeus, 1761)
(Fig. 7H)

Material studied: MIMB48078, 1 specimen, dissected, the Sea of Okhotsk, Aniva Bay, Moguchi River, Hirano ridge, 46°05.372’N, 142°13.612’E, 20 m in depth, 20.08.2013, coll. A. Plaksin, A. Semenov.

Diagnosis: Body large, wide, 30 mm in length, yellowish to brown with intensive dark brown to black pigmentation on dorsal side of anterior body parts and head. Body, rhinophores and tips of cerata intensively covered by opaque yellow and black speckles. Rhinophores conical, smooth. Cerata cylindrical, slightly flattened near base, arranged in continuous, densely packed rows. Jaws oval plates with smooth masticatory border. Radular formula 19

× 0.1.0. Wide rachidian tooth pectinate with 28–35 sharply pointed denticles. No central cusp visible. Ampulla narrow, convoluted. Vas deferens moderately long, widened near penial sheath. Penis conical. Receptaculum seminis ovate, muscular.

Molecular data: A BLAST-n search of COI sequence resulted 99.85% identical to sequences of *Aeolidia papillosa* from the North-East Pacific (JX087536, KF643410) thus confirming the species identity of our samples.

Distribution: This species has a wide distribution in the boreal regions of the North Pacific and North Atlantic and also occurs in Arctic waters [the White and the Barents seas, see Kienberger *et al.*, 2016]. Recent study highlighted that the presence of this species in Japan [Baba, 1935] needs further confirmation [Kienberger *et al.*, 2016]. Since Baba's specimens [1935] were also collected from Aniva Bay, our molecular results confirm the identity of this species in northwestern Pacific.

Discussion

Our integrative results revealed clear cases of unknown diversity within some groups of nudibranch molluscs from Sakhalin Island. Among the dorid nudibranchs, the new species *Adalaria* ***boussoleana*** sp. nov. has been discovered, which clearly differs from other species of the genus. The phylogenetic analyses place the new species as sister to another North Pacific species *A. slavi.* At the same time our phylogenetic analyses highlighted the polyphyly of the genus *Adalaria* (Fig. 6), which is in line with previous work on this group [Hallas, Gosliner, 2015; Furfaro *et al.*, 2022] and suggests this taxon requires modern taxonomical revision. Among specimens of the genus *Cadlina* we have detected two genetically distinct groups, one is close to *C. umiushi* and another species likely represents a new species for science (Fig. 3). Their morphology is similar to the diagnosis of *C. umiushi* (Fig. 1), and may represent a case of a true cryptic diversity. Similar discoveries have been made for cladobranch molluscs: our results revealed a new species of the genus *Cuthonella* described herein under the name *Cuthonella* ***anastasia*** sp. nov. Recent research has shown that the North-West Pacific represents a biodiversity hotspot for this nudibranch group [Korshunova *et al.*, 2020b] with numerous new species endemic in these waters. At the same time, another *Cuthonella* species found off Sakhalin Is., *C. soboli,* does not form a monophyletic group (Fig. 10), but instead it is included in a large polytomy along with samples of *C. osyoro* from the Sea of Japan. Taking into account this uncertainty in molecular phylogenetic data and considering the wide geographic range of *C. soboli* in the North-West Pacific, it is clear that additional research is needed to further determine the identity of the species in the *C. soboli / C. osyoro* clade.

These discoveries are not exceptional, as previous integrative revisions of the nudibranch fauna in the North-West Pacific uncovered rich unknown biodiversity. During the last 5 years, more than 15 new species were described from the North-West Pacific [Korshunova *et al.*, 2020a,b; Ekimova, 2022; Korshunova, Martynov, 2022; 2023a,b; Martynov, Korshunova, 2022; Ekimova *et al.*, 2021a, b; 2023a], including two new species from Sakhalin waters: *Adalaria ultima* from Sakhalinsky Bay [Martynov, Korshunova, 2017], and *Dendronotus pseudodalli* from the eastern Sakhalin Is. [Ekimova *et al.*, 2023a]. Also, four species were recorded for Sakhalin Is. waters for the first time: *Cadlina umiushi, Onchimira cavifera, Eubranchus rupium* and *E. alexeii.* Considering the high biodiversity of nudibranchs occurring in the North-West Pacific [e.g. genera *Cadlina, Onchidoris, Adalaria, Dendronotus, Cuthonella* – see Korshunova *et al.*, 2020a,b; Martynov, Korshunova, 2022; Ekimova *et al.*, 2023a, b] further sampling activity in Sakhalin Is. may reveal new nudibranch taxa for science and local new faunistic findings.

Sakhalin Is. occupies a unique position in the North-West Pacific, this island is elongated in the meridional direction and extends 948 km from 45°54' N to 54°25' latitude, separating the Sea of Japan and the Sea of Okhotsk water basins. The different coasts of Sakhalin Is. are influenced by the warm Tsushima Current (southwestern side of Sakhalin), its branch, the Soya Current (southern side, including Cape Crillon), and the cold Eastern Sakhalin Current (northern and eastern side). These currents impose temperature limits for species distribution. Many researchers designate Sakhalin Is. as an important biogeographical boundary dividing temperate and boreal marine fauna: this boundary is located either between its southwestern/southeastern coasts or between Sakhalin Is. and Hokkaido Is. [Kussakin, 1979; Petryashev, 2005]. Although the nudibranch fauna of Sakhalin Is. is obviously understudied, available preliminary data shows different nudibranch assemblages on different coasts. The list of species from Sakhalin Is. includes 21 species (Table 2); among them, five species may be designated as endemics to Sakhalin, including: *Cadlina* sp., *Adalaria* ***boussoleana*** sp. nov., *A. ultima*, *Dendronotus pseudodalli*, *Cuthonella* ***anastasia*** sp. nov.; five species are distributed in temperate regions of the North-West Pacific, *e.g.* Sea of Japan and Pacific coast of Japan: *Cadlina umiushi*, *Dirona pellucida*, *Eubranchus alexeii*, *Cuthonella soboli, Diaulula odonoghuei* (Steinberg, 1963); four species are widely distributed in the boreal regions of the North-West Pacific (Kurile Islands, Kamchatka), and also in some cases in the North Pacific (the Bering Sea, Alaska): *Colga minichevi*, *Dendronotus dalli*, *Tritonia tetraquetra*,

Table 2. Species list of nudibranchs found in Sakhalin Island coastal waters. W – western Sakhalin Is., N – northern Sakhalin Is., E – eastern Sakhalin Is., S – southern Sakhalin Is.

Табл. 2. Список видов голожаберных моллюсков, обнаруженных в прибрежных водах острова Сахалин. W – западный Сахалин, N – северный Сахалин, E – восточный Сахалин, S – южный Сахалин.

	Species	Locality, Sakhalin Island	W	N	E	S	Reference
1	*Cadlina umiushi*	Aniva Bay, 20 m depth				+	This study
2	*Cadlina* sp.	Aniva Bay, 5-15 m depth				+	This study
3	*Colga minichevi*	Bay of Patience; Aniva Bay, 25-48 m depth			+	+	Martynov, Baranets, 2002
4	*Dialula odonoghue*	Western Sakhalin (Antonovo) (as *D. sandiegensis*)	+				Martynov, 1999
5	*Adalaria proxima*	Aniva Bay, 67 m depth	+			+	Martynov, 1999; 2006
6	*Adalaria* ***boussoleana*** sp. nov.	Bay of Patience, 209-240 m depth			+		This study
7	*Adalaria ultima*	Sakhalinsky Bay, 95 m depth		+			Martynov, Korshunova, 2017
8	*Onchidoris muricata*	Western Sakhalin, 4 m depth	+				Chichvarkhin *et al.*, 2018
9	*Onchimira cavifera*	Severny Bay, 80-82 m depth		+			This study
10	*Tritonia tetraquetra*	Western Sakhalin, Tatarsky Strait, 7-10 m depth	+	+			Baba, 1957 (as *Duvaucelia exsulans*), Martynov, 1999 Chichivarkhin, 2016
11	*Dirona pellucida*	Aniva Bay				+	Martynov, 1999
12	*Dendronotus dalli*	Common species, all coasts, 12-218 m depth	+	+	+	+	Martynov, 1999; Ekimova *et al.*, 2021a This study
13	*Dendronotus pseudodalli*	Severny Bay; NE Sakhalin; 38-218 m depth		+	+		Ekimova *et al.*, 2023a
14	*Dendronotus patricki*	Bay of Patience; NE Sakhalin; 261-282 m depth		+	+		Ekimova *et al.*, 2021a
15	*Coryphella verrucosa*	Southern Sakhalin; 25 m depth				+	Martynov, 1999;
16	*Coryphella nobilis*	Severny Bay; 58-59 m depth		+			Ekimova *et al.*, 2022a
17	*Eubranchus alexeii*	Aniva Bay; 0.1-1 m depth				+	This study
18	*Eubranchus rupium*	Aniva Bay; 0.1-1 m depth				+	This study
19	*Cuthonella soboli*	Western Sakhalin (Antonovo); Aniva Bay, 0.1-1 m depth (Aniva Bay)	+			+	Martynov, 1999; Korshunova *et al.*, 2020b; This study
20	*Cuthonella* ***anastasia*** *sp. nov.*	Aniva Bay, 15-20 m depth				+	This study
21	*Aeolidia papillosa*	Western Sakhalin (Antonovo), Aniva Bay, 0.5-20 m depth	+			+	Baba, 1937; Martynov, 1999; this study

Onchimira cavifera. Some of these species are also known for the northwestern coast of the Sea of Japan. Finally, seven species are trans-Arctic species, which are widely distributed in the North Pacific, Atlantic, and Arctic waters: *Adalaria proxima, Onchidoris muricata, Dendronotus patricki, Coryphella verrucosa, C. nobilis, Eubranchus rupium, Aeolidia papillosa.*

The spatial distribution of the species recorded for Sakhalin Is. shows several general trends. None of the endemic species have been found on the western coast of Sakhalin Is. (the Sea of Japan), all seven detected species are common in the Sea of Japan and widely distributed in its waters. These are the temperate *Diaulula odonoghue* and *Cuthonella soboli,* the boreal *Dendronotus dalli* and *Tritonia tetraquetra,* and the trans-Arctic *Adalaria proxima, Onchidoris muricata* and *Aeolidia papillosa* (see Table 2 for details). At the same time, none of the temperate species have been recorded on the northern and eastern coasts of Sakhalin Is. (Table 2). Most species (12) have been found in southern Sakhalin (Aniva Bay) and constitute either endemic, temperate, boreal, or trans-Arctic species. Although we have limited data on nudibranch species in Sakhalin waters due to low sampling, a comparison of the biogeographic affinity of species from different regions corresponds to the presence of a biogeographic boundary between northeastern and southwestern Sakhalin. In this regard, Aniva Bay is especially interesting, since it is influenced by branches of the warm Tsushima Current and by the cold waters of the Sea of Okhotsk, resulting in a diverse fauna containing both temperate and boreal elements, as well as endemic taxa.

In conclusion, this work reports 21 nudibranch species found in Sakhalin Is., however, it is evident that this number is likely underestimated drastically. It is recommended that additional inventories should be conducted, including thorough sampling in understudied areas, to further assess a potentially rich biodiversity present in the region.

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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.