



A description of *Dendronotus shpataki* sp. nov. (Gastropoda: Nudibranchia) from the Sea of Japan: a contribution of citizen science to marine zoology

Описание *Dendronotus shpataki* sp. nov. (Gastropoda: Nudibranchia) из Японского моря: вклад научного волонтерства в морскую зоологию


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Abstract. The nudibranch genus *Dendronotus* Alder et Hancock, 1845 is a common component of boreal and arctic ecosystems, which has recently received a considerable attention due to its high cryptic diversity. Here we describe a new species *Dendronotus shpataki* sp. nov. from the northwestern Sea of Japan, using the material and observations provided by Andrey Shpatak, a local citizen, diver and underwater photographer. We studied morphological features of the new species, including external morphology, coloration, jaw and radular morphology, and configuration of the reproductive system, as well as its ecological traits including possible diet preferences. We obtained DNA sequences and reconstructed the phylogeny by Bayesian Inference and Maximum Likelihood approaches using four molecular markers (mitochondrial COI and 16S rRNA, and nuclear histone H3 and 28S rRNA), and tested the boundaries between the species by calculating the uncorrected *p*-distances and automatic species delimitation methods ABGD and GMYC. Our results show that *D. shpataki* sp. nov. differs both morphologically and genetically from all other *Dendronotus* species. The new species possibly represents a unique example of local endemism, being found in a single locality, while other local *Dendronotus* species demonstrate wide distribution in the North-West Pacific. We also report on a considerable wearing of the radular teeth during feeding, which is a remarkable case for the *Dendronotus*.

Резюме. Голожаберные моллюски рода *Dendronotus* Alder et Hancock, 1845 представляют собой обычный компонент бореальных и арктических экосистем и в последнее время стали предметом детального изучения ввиду их высокого криптического разнообразия. В данной статье мы описываем новый вид *Dendronotus shpataki* sp. nov. из северо-западной части Японского моря, используя материал и результаты наблюдений, предоставленные местным жителем, дайвером и подводным фотографом Андреем Шпатаком. Мы изучили морфологические особенности нового вида, включая внешнюю морфологию, окраску, морфологию челюстей и радулы, строение половой системы, а также его экологические особенности, в том числе возможные пищевые предпочтения. По результатам секвенирования ДНК, мы получили данные о последовательностях митохондриальных (COI и 16S рРНК) и ядерных (гистон H3 и 28S рРНК) генов,

реконструировали филогенетические отношения с использованием Байесовского метода и метода максимального правдоподобия и определили видовые границы путем подсчета нескорректированных *p*-дистанций и автоматических методов разделения видов ABGD и GMYC. Наши результаты показывают, что *D. shpataki* sp. nov. отличается от всех остальных видов рода *Dendronotus* морфологически и генетически. Предположительно, *D. shpataki* sp. nov. представляет собой уникальный пример локального эндемизма, поскольку этот вид найден только в типовом местонахождении, в то время как другие виды рода, обитающие в данном регионе, имеют широкое распространение в северо-западной части Тихого океана. Кроме того, мы обнаружили значительное истирание зубов радулы в ходе питания, что является крайне необычной чертой для представителей рода *Dendronotus*.

Keywords: North-West Pacific, biodiversity, morphology, radula, molecular markers, phylogeny, Nudibranchia, Dendronotidae, *Dendronotus*, new species

Ключевые слова: Северо-Западная Пацифика, биоразнообразие, морфология, радула, молекулярные маркеры, филогения, Nudibranchia, Dendronotidae, *Dendronotus*, новый вид

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Introduction

Citizen science is an emerging movement contributing to various research fields in zoological and botanical science (ElQadi et al., 2017; Jarić et al., 2020). It is often associated with popular and well-known activities such as birdwatching (Callaghan et al., 2021) and wildlife sighting report programs (Zhang, 2019). Marine habitats, with exception of the upper intertidal zone, are less accessible for the average biology enthusiast, and citizen science initiatives in the field of marine biology develop slower (Garcia-Soto et al., 2017). In recent years, special programs and initiatives focusing on marine ecosystems and biodiversity have been implemented (Giovos et al., 2019). As with terrestrial fauna, marine projects involving visually attractive and large animals like molluscs, crustaceans and corals are often much more successful and may become a powerful tool for ecological monitoring and description of new taxa (Garcia-Soto et al., 2021; Turicchia et al., 2021). For example, iNaturalist (2021) is one of the best-known and widespread citizen science programs, which also includes many marine taxa and largely contributes photos and unique data on species distribution via Global Biodiversity Information Facility (GBIF) (Matheson, 2014). As another particular example, the project “Sea slugs of southern Norway” united more than 135 active citizen members, who contributed to research of the sea

slug diversity on 8000 km coastline of southern Norway, and resulted in registration of more than 90 species, including several ones potentially new for science (Rauch & Malaquias, 2019).

Nudibranch biodiversity studies in Russia have received much attention in recent years and yielded discoveries of many new taxa at different taxonomic levels (Martynov et al., 2009, 2015, 2016, 2020b; Ekimova et al., 2015, 2019a; Chichvarhin, 2016; Chichvarhin et al., 2016, 2018; Korshunova et al., 2016a, 2016b, 2017a, 2018, 2020b; Korshunova & Martynov, 2020; and many others). A noteworthy example is the nudibranch genus *Dendronotus* Alder et Hancock, 1845, which is a common component of the boreal and arctic fouling communities (Martynov & Korshunova, 2011). Until recently, only three species were known from the boreal and Arctic coast of Russia (Martynov & Korshunova, 2011), however this number has been increased to 18 (Ekimova et al., 2019b; Korshunova et al., 2020a; Martynov et al., 2020b) as many new species were described or reported for the first time from previously poorly studied regions. Nevertheless, in many cases the Russian boreal and arctic biodiversity remains poorly studied due to high fieldwork expenses and undeveloped network of research marine biological stations in remote regions. Therefore, comprehensive sampling in such regions with help of local citizens may contribute to the further research of nudibranch diversity and discovery of new taxa.

In this article, we describe a new species of the genus *Dendronotus* from the northwestern Sea of Japan, based on integrative approach combining morphological, molecular and ecological data, using the material and observations provided by a diver and a wildlife photographer Andrey Shpatak.

Material and methods

Material

The material was collected from a single site in the North-West Pacific, the Sea of Japan (Rudnaya Bay, Senkina Shapka dive site, 44°19.891'N 135°50.732'E; Electronic supplementary material 1, see the section “Addenda”), in October–November 2020 by Andrey Shpatak and in May 2021 by A. Shpatak and authors of this contribution. Several specimens were photographed underwater. Each specimen collected in May 2021 was photographed in the lab. All material was fixed in 96% ethanol for morphological and molecular analyses. Type specimens are deposited in the collection of the Museum of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch of Russian Academy of Sciences (MIMB); collection numbers of the type specimens are indicated below.

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from a tissue sample of each collected specimen (Electronic supplementary material 2, see the section “Addenda”), following the invertebrate protocol of the Canadian Center for DNA Barcoding (Ivanova et al., 2006). Extracted DNA was used as a template for amplification of partial mitochondrial cytochrome c oxidase subunit I and 16S rRNA, and nuclear histone *H3*, 28S rRNA and 18S rRNA. Reaction conditions and primers are available in Table 1. Polymerase chain reactions were performed with an “HS Taq” kit (Eurogen Lab, Russia), following the manufacturer’s protocol. For sequencing, 2 µL of amplicons were purified by ammonium acetate precipitation with ethanol (Osterburg et al., 1975) and used as a template for the sequencing reactions with a Big-Dye Terminator v3.1 sequencing kit by Applied Biosystems. Sequencing reactions were analysed using an ABI 3500 Genetic Analyzer (Applied Biosystems). All novel sequences were submitted to NCBI GenBank (Electronic supplementary material 3, see the section “Addenda”).

Data processing and phylogenetic reconstruction

Raw reads from forward and reverse primers 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, datasets obtained in previous studies on the genus *Dendronotus* (Korshunova et al., 2017b, 2020b; Ekimova et al., 2019b) were incorporated in the analysis. Representatives of the families Tritoniidae (Tritonioidea), Dotidae, Scyllaeidae (both Dendronotoidea) and the genus *Janolus* Bergh, 1884 (Janolidae, Proctonotoidea) with the data available in the GenBank were chosen as outgroups, considering that these families are the closest to the family Dendronotidae. Members of the same families were used as outgroups for *Dendronotus* in previous studies (Korshunova et al., 2017b, 2020b; Ekimova et al., 2019b). For the full list of species used, see Electronic supplementary material 3.

The original data and publicly available sequences were aligned with the MUSCLE algorithm (Edgar, 2004) in MEGA7 (Kumar et al., 2016). Additionally, all protein-coding sequences were translated into amino acids to verify reading frames and check for stop-codons. 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 reconstructions were conducted for the concatenated multi-gene partitioned datasets. The best-fit nucleotide evolution models were tested in the MEGA7 toolkit based on the Bayesian Information Criterion (BIC) for each partition. 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). Markov chains were sampled at intervals of 500 generations. The analysis was initiated with a random starting tree and ran for 10⁷ 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. 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.

Species delimitation based on COI sequences

The phylogenetic reconstruction was accompanied by the species delimitation tests: ABGD, GMYC and an analysis of intra- and interspecific COI *p*-distances. COI alignment was used for computational species delimitations methods; *p*-distances were calculated using MEGA7 software (Kumar et al., 2016). The ABGD analysis (Puillandre et al., 2012) was run on the online version of the program (<https://bioinfo.mnhn.fr/abi/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. Additionally, we performed a GMYC test proposed by Pons (Pons et al., 2006) and implemented by Fujisawa & Barraclough (2013).

COI-based ultrametric tree was calculated using BEAST 2.6.4 (Bouckaert et al., 2019) with 10⁷ generations and then analysed in the *R* environment (package *splits*), following instructions by Fujisawa & Barraclough (2013).

Morphological methods

All collected specimens were used for the examination of their external morphology (coloration, body texture, number and morphology of appendages, oral tentacles, rhinophores, location of anus and genital aperture, etc.) under a stereomicroscope. The internal morphology of one juvenile and five adult 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 two hours at 60 °C to dissolve connective and muscle tissues. The radula and the jaws were rinsed in distilled water, air-dried, mounted on an aluminium stub, and sputter-coated with gold for visualisation under a JEOL JSM 6380 scanning electron microscope (SEM). Features of the jaws were examined by optical stereomicroscopy and SEM. For study of the reproductive system, specimens were dissected from the dorsal side along the midline and examined under a stereomicroscope.

Table 1. Amplification and sequencing primers and PCR conditions.

| Marker | Primers | PCR conditions | References |
|--------------------------------|---|---|---|
| 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 – 94 °C, 35× [15 s – 95 °C, 45 s – 45 °C, 1 min – 72 °C], 7 min – 72 °C | Folmer et al. (1994) |
| 16S rRNA | 16Sar-L CGC CTG TTT ATC AAA AAC AT 16S R CCG RTY TGA ACT CAG CTC ACG | 5 min – 94 °C, 35× [20 s – 95 °C, 30 s – 52 °C, 45 s – 72 °C], 7 min – 72 °C | Palumbi (1996), Puslednik & Serb (2008) |
| Histone H3 | H3AF ATG GCT CGT ACC AAG CAG ACV GC H3AR ATA TCC TTR GGC ATR ATR GTG AC | 5 min – 94 °C, 35× [15 s – 94 °C, 30 s – 50 °C, 45 s – 72 °C], 7 min – 72 °C | Colgan et al. (1998) |
| 28S rRNA | 28SC1 ACC CGC TGA ATT TAA GCA T 28SC2 TGA ACT CTC TCT TCA AAG TTC TTT TC | 5 min – 94 °C, 35× [15 s – 94 °C, 30 s – 50 °C, 45 s – 72 °C], 7 min – 72 °C | Lê et al. (1993) |

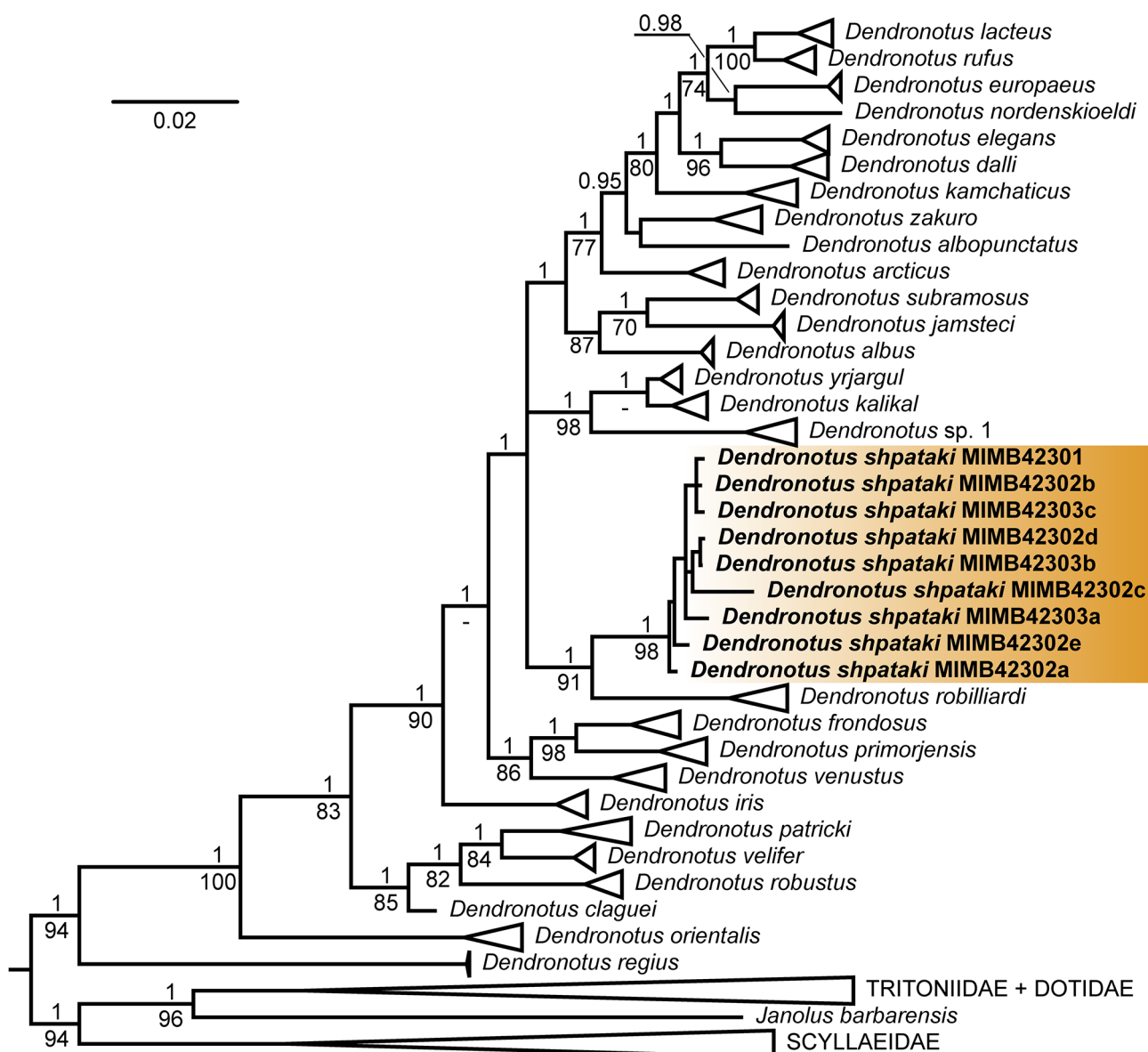


Fig. 1. Bayesian phylogenetic hypothesis of the genus *Dendronotus*, based on the concatenated dataset of four molecular markers (COI, 16S, H3, 28S). Species-level clades and outgroups are collapsed to a single branch, except target species. Numbers above branches indicate posterior probabilities from Bayesian Inference, numbers below branches, bootstrap support from Maximum Likelihood.

Results

Molecular phylogeny

Single-gene phylogenetic trees (Electronic supplementary material 2, see the section “Addenda”) were poorly supported, and most interspecific relationships were not resolved. Maximum Likelihood and Bayesian trees based on the concatenated dataset of four markers yielded

the same topology for supported monophyletic groups (Fig. 1; both unedited trees available in Electronic supplementary material 2). The genus *Dendronotus* was monophyletic [posterior probability of Bayesian Inference (PP) = 1; bootstrap support from Maximum Likelihood (ML) = 94], with *D. regius* Pola et Stout, 2008 representing sister relationships to the rest of the genus. Two large monophyletic groups were represented

by (1) deep-water *Dendronotus* (PP = 1; ML = 85), including the *D. robustus* species–group and the recently described *D. claguei* Valdés, Lundsten et Wilson, 2018 (Valdés et al., 2018), and (2) the shallow-water boreal and arctic species of *Dendronotus* (PP = 1, ML = 90). Our specimens from the Sea of Japan belong to the latter clade. All specimens formed a monophyletic supported group (PP = 1, ML = 98), which was recovered sister to *D. robilliardi* Korshunova et al., 2016 (PP = 1, ML = 91). The relationships of these two species with other shallow-water species of *Dendronotus* were unresolved. Each species of *Dendronotus* formed a monophyletic highly supported clade (PP = 1, ML > 90) (Electronic supplementary material 2), except *D. kalikal* Ekimova et al., 2015, *D. yrjargul* Korshunova et al., 2020 and *Dendronotus* sp. 1, which formed a polytomy in the Maximum Likelihood analysis, but each represented a highly supported clade in the Bayesian Inference analysis.

Species delimitation based on COI sequences

The ABGD test revealed 26 [prior intraspecific divergence (P) = 0.0010–0.0129] or 25 groups (P = 0.0215) in the initial partition (Electronic supplementary material 4, see the section “Addenda”). In the case of 26 groups, the species identity of all species was supported except *Dendronotus yrjargul* and *D. kalikal*, which were recovered in a single group. Same is true for *D. lacteus* (W. Thompson, 1840) and *D. rufus* O’Donoghue, 1921 that were united in a single group with P = 0.0215. All studied specimens from the Sea of Japan formed a single group in the initial partition, in all iterations.

The same results were obtained in GMYC analysis (Electronic supplementary material 5, see the section “Addenda”) except for *Dendronotus arcticus* Korshunova et al., 2016, *D. patricki* Stout et al., 2011, *D. robilliardi* and *D. venustus* MacFarland, 1966, where several separated groups were found, suggesting possible over-splitting. However, the identity of most species, including *D. shpataki* sp. nov., was supported in this analysis.

The maximum intraspecific p -distance within the new species in COI marker was 0.92%. The minimum uncorrected interspecific p -distances

in COI marker between the new species and the rest *Dendronotus* diversity are displayed in Table 2. The lowest interspecific distance was observed between the new species and *D. subramosus* MacFarland, 1966 (8.8%).

As a conclusion, our results support the high level of molecular divergence between the studied specimens and other species of the genus *Dendronotus*, therefore we propose it represents a new species for science, described below.

Table 2. Uncorrected minimal p -distances in COI marker between *Dendronotus shpataki* sp. nov. and other species of the genus *Dendronotus* (in %).

| Species | Distance value |
|---|----------------|
| <i>D. albopunctatus</i> Robilliard, 1972 | 10.6 |
| <i>D. albus</i> MacFarland, 1966 | 12.4 |
| <i>D. arcticus</i> Korshunova et al., 2016 | 10.8 |
| <i>D. dalli</i> Bergh, 1879 | 12.9 |
| <i>D. elegans</i> Verrill, 1880 | 10.4 |
| <i>D. europaeus</i> Korshunova et al., 2017 | 10.6 |
| <i>D. frondosus</i> (Ascanius, 1774) | 9.0 |
| <i>D. iris</i> Cooper, 1863 | 10.4 |
| <i>D. jamsteci</i> Martynov et al., 2020 | 9.2 |
| <i>D. kalikal</i> Ekimova et al., 2015 | 9.9 |
| <i>D. kamchaticus</i> Ekimova et al., 2015 | 12.2 |
| <i>D. lacteus</i> (Thompson, 1840) | 11.5 |
| <i>D. nordenskiöldi</i> Korshunova et al., 2020 | 10.8 |
| <i>D. orientalis</i> (Baba, 1932) | 15.9 |
| <i>D. patricki</i> Stout, Wilson et Valdés, 2011 | 11.8 |
| <i>D. primorjensis</i> Martynov, Sanamyan et Korshunova, 2015 | 10.8 |
| <i>D. regius</i> Pola et Stout, 2008 | 15.0 |
| <i>D. robilliardi</i> Korshunova et al., 2016 | 10.1 |
| <i>D. robustus</i> Verrill, 1870 | 13.4 |
| <i>D. rufus</i> O’Donoghue, 1921 | 10.6 |
| <i>D. subramosus</i> MacFarland, 1966 | 8.8 |
| <i>D. velifer</i> Sars, 1878 | 12.9 |
| <i>D. venustus</i> MacFarland, 1966 | 10.4 |
| <i>D. yrjargul</i> Korshunova et al., 2020 | 9.9 |
| <i>D. zakuro</i> Martynov et al., 2020 | 9.7 |

Description of the new species

Order **Nudibranchia** de Blainville, 1814

Suborder **Cladobranchia** William et Morton, 1984

Superfamily **Dendronotoidea** Allman, 1845

Family **Dendronotidae** Allman, 1845

Genus ***Dendronotus*** Alder et Hancock, 1845

***Dendronotus shpataki* sp. nov.**

(Figs 2–5)

Holotype. Adult specimen, **Russia**, *Primorie Terr., Sea of Japan*, Rudnaya Bay, 44°19.891'N 135°50.732'E, depth 16–20 m, 18.V.2021, coll. A. Shpatak (MIMB42304).

Paratypes. **Russia**, *Primorie Terr., Sea of Japan*, same site as for holotype, depth 16–20 m: 4 adult specimens, 16.V.2021, coll. T. Antokhina & A. Mikhlina (MIMB42305, MIMB42307, MIMB42308, MIMB42309); 1 juvenile specimen, same date and collectors (MIMB42306); 1 adult specimen, 17.V.2021, coll. A. Shpatak (MIMB42310); 1 adult specimen, 3.X.2020, coll. A. Shpatak (MIMB42301); 5 adult specimens, 6.XI.2020, coll. A. Shpatak (MIMB42302); 3 adult specimens, 7.XI.2020, coll. A. Shpatak (MIMB42303).

Description. External morphology (Figs 2, 3). Body length up to 25 mm. Body slender, narrowing towards posterior end. Anterior foot portion wider than body, narrowing posteriorly. No lip papillae. Up to eight long, secondarily branched oral appendages. Rhinophoral sheath with five secondary branched crown appendages; posterior appendage longer than four anterior ones. Lateral papilla tiny, unbranched, in some specimens (MIMB42305) of same size as body tubercles. Up to seven dorsolateral processes on low elevations, with extensive secondary branching; first appendages with few tertiary branches. In juveniles (including exemplars photographed in nature but not collected), five secondary branched appendages. Size of appendages decreasing to posterior end. Anal opening dorsolateral, on right side between second and third appendages. Reproductive opening lateral, on right side under second appendages.

Coloration (Figs 2, 3). Background colour greyish beige. Body wall semitransparent; digestive gland mass and diverticula brownish orange. Tips of oral, rhinophoral and dorsolateral appendages orange, with opaque-white pigment under

body wall. Low tubercles of different size, with bright opaque white pigment. Rhinophoral clavus bright white on its anterior side.

Anatomy (Figs 4, 5). Jaws as elongate plates with strong dorsal process and slightly curved masticatory border (Fig. 4A), bearing a single row of denticles (Fig. 4B). Radular formula in four adult specimens examined 32–38 × 8–9.1.8–9 (Fig. 4C). Rachidian tooth triangular, central cusp reduced; in posterior radular part (radular sac) up to 40 small (1 μm) denticles on each side, with distinct remains of furrows on tooth surface (Fig. 4D, E, K); in anterior radular portion (working plane) rachidian teeth devoid of denticles (Fig. 4F, H, L), with remains of furrows. Lateral teeth as elongate narrow plates, slightly curved, with large sharp cusp and 6–8 small denticles in middle part of tooth (Fig. 4D, I, J). Cusp length maximal in middle lateral teeth. Innermost teeth thin, curved, highly denticulated. Outermost teeth plate-like.

Reproductive system triaulic (Fig. 5). Ampulla muscular, folded twice. Proximal part of vas deferens short; prostate very small, surrounding vas deferens as a ring. Alveolar glands four (in 18-mm specimen) to five (in 25-mm specimen). Distal part of vas deferens long, widened proximally, gradually narrowing into curved penis with flattened tip. Muscular bursa copulatrix rounded; bursal duct making a loop around near connection to vaginal portion. Small receptaculum seminis near proximal part of vagina.

Comparison. *Dendronotus shpataki* sp. nov. has several diagnostic characters clearly differentiating this new species from other species of the genus *Dendronotus*. Externally, no other species possess such a small indistinct lateral papilla on the rhinophoral sheath. In other *Dendronotus*, the lateral papillae are either distinct and branched or completely absent (Ekimova et al., 2019b; Korshunova et al., 2020a). Another diagnostic character of *D. shpataki* sp. nov. is the rhinophoral clavus and bases of the lamellae that are covered by opaque-white pigment (Figs 2, 3). Finally, configuration of the reproductive system is unique (Fig. 5), as no other *Dendronotus* species has such a small number of alveolar prostatic glands (Fig. 4).

The new species shares some similarities in the internal and external morphology with its sister

species, *D. robilliardi*: both species have specific orange-brown pigment in the subapical areas of appendages, the process of outer rhinophoral sheath longer than the other four processes, they possess up to seven branched appendages, both have a similar radular type (so-called “albus” radular type; see Ekimova et al., 2019b) and have an overall similar configuration of the reproductive system (Ekimova et al., 2016b; Martynov et al., 2020a). However, in *D. robilliardi* the lateral papilla is also simple, but longer and usually branched. Also *D. shpataki* sp. nov. differs from *D. robilliardi* in the details of coloration: *D. robilliardi* in general has milky-white background colour with lines of opaque-white pigment on the rhinophoral and dorsolateral processes, while *D. shpataki* sp. nov. is translucent greyish beige in colour, with numerous opaque dots on the low tubercles or on the appendage tips. Some differences were observed in radular characters: *D. robilliardi* has less denticles on the rachidian tooth. The arctic species *D. arcticus* shares some similarities in coloration with *D. shpataki* sp. nov., having rhinophoral clavi with opaque-white tips (Korshunova et al., 2016b), a general brownish appearance, and white pigment on the appendage tips of the low tubercles. However, *D. arcticus* considerably differs from *D. shpataki* sp. nov. in a combination of external characters (swollen primary appendages with extensive secondary branching, lateral rhinophoral papilla with secondary branches, moderately wide body) and internal characters (S-shaped lateral teeth, furrows on rachidian tooth lacking, prostate consisting of 30 alveolar glands, distal vas deferens short).

Distribution. This species is known only from the type locality (Electronic supplementary material 1, see the section “Addenda”). Specimens of this coloration were never reported from other regions of the Sea of Japan or the North-West Pacific.

Bionomics. Spawning season is unknown. Egg masses are unknown. Specimens collected in October and May were fully mature; juvenile specimens were also observed during both seasons. Feeding on *Abietinaria filicula* (Ellis et Solander, 1786) was observed (Fig. 3).

Etymology. The new species is named in honour of Andrey Shpatak, diver and underwater photographer, the first discoverer of this species. Andrey Shpatak dives and photographs nudibranch

molluscs in the Rudnaya Bay, the Sea of Japan, for many years, and his contribution to the knowledge on biology and local diversity of nudibranchs and other marine animals is highly acknowledged.

Discussion

Dendronotus shpataki sp. nov. is clearly distinct from other species of *Dendronotus* as supported by the morphological and molecular data presented here. According to both the Bayesian Interference and Maximum Likelihood analyses, *Dendronotus shpataki* sp. nov. is closely related to the North Pacific species *D. robilliardi* (Fig. 1), as also demonstrated by several similarities in external and internal morphology (Figs 2, 3; see Ekimova et al., 2016b; Korshunova et al., 2016b). Both species are found on similar hydroids of the genus *Abietinaria* Kirchenpauer, 1884 and possess similar radular configuration with small denticles along the edge of the rachidian tooth and with reduced thin furrows (Ekimova et al., 2016b, 2019b; Korshunova et al., 2016b, 2020a; Martynov et al., 2020a). This implies it is unlikely that ecological specialisation was the main driven force of the speciation in these two species, as was suggested for other shallow-water *Dendronotus* occurring sympatrically in the North Pacific region (Ekimova et al., 2019b). The same situation was recently demonstrated for *D. primorjensis* Martynov, Sanamyan et Korshunova, 2015 and *D. frondosus* (Ascanius, 1774), which are sister species and possess high similarities in the external appearance and radular morphology, and even have overlapping ranges in the North-West Pacific (Ekimova et al., 2016a, 2019b). Possibly, these cases could be explained by a process of allopatric speciation when ancestral populations were isolated following Plio- and Pleistocene glaciations and thus established permanent reproductive barriers (Hallas et al., 2016; Lindsay et al., 2016; Lindsay & Valdés, 2016; Ekimova et al., 2019b; Jung et al., 2020). However, to test this hypothesis, more data on the ecology and distribution of these molluscs on both sides of the North Pacific are needed.

As it has been shown in several recent studies, the radular morphology in all *Dendronotus* species undergoes significant changes during the post-larval ontogenesis (Ekimova et al., 2015, 2019b;



Fig. 2. *Dendronotus shpataki* sp. nov., general appearance of living specimens. Holotype: dorsal view (A), lateral view (B) and ventral view (C). Paratypes, dorsal view: adult specimens MIMB42309 (D), MIMB42308 (E), MIMB42305 (F) and juvenile MIMB42306 (G). Scale bar: 5 mm.

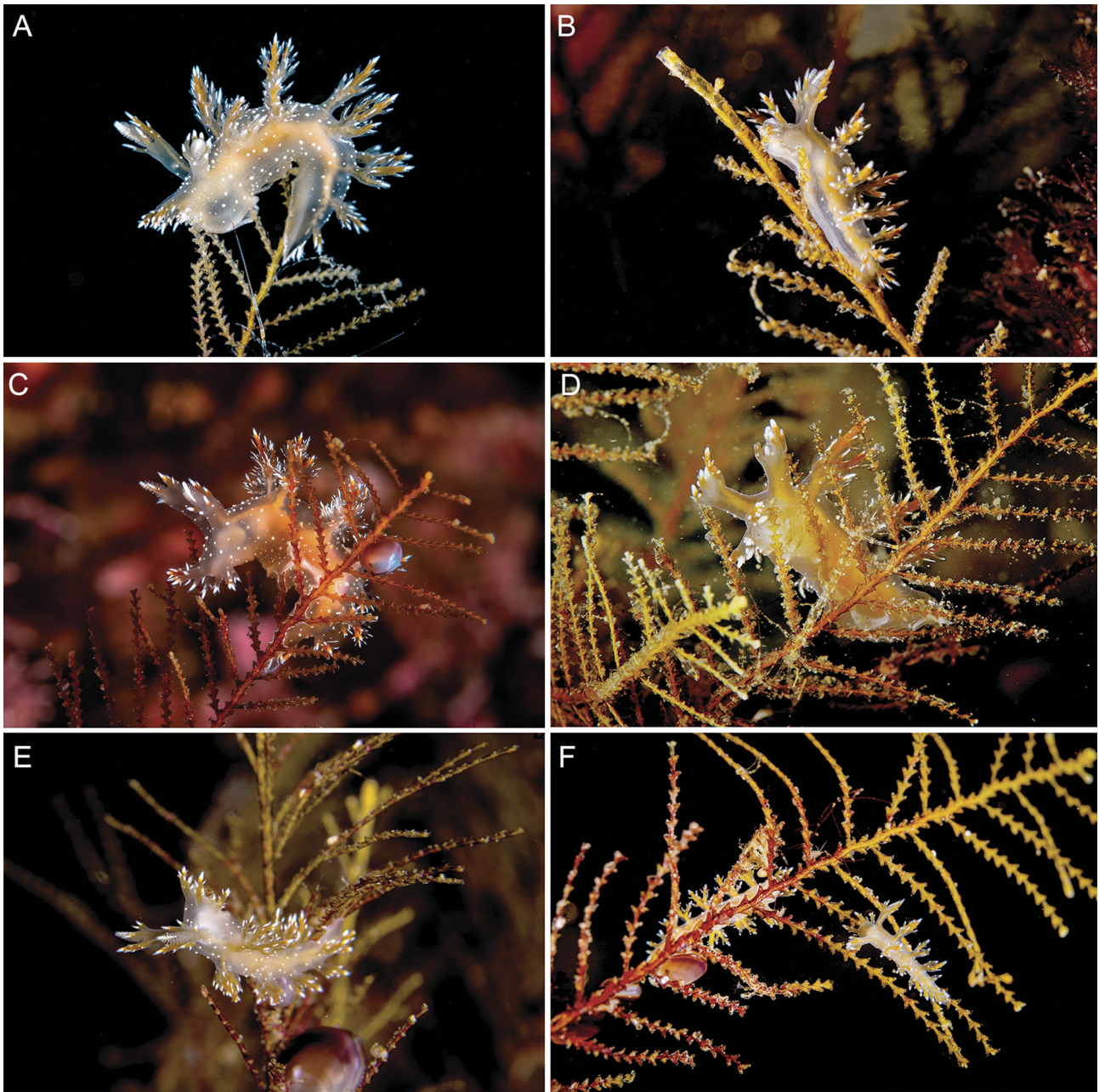
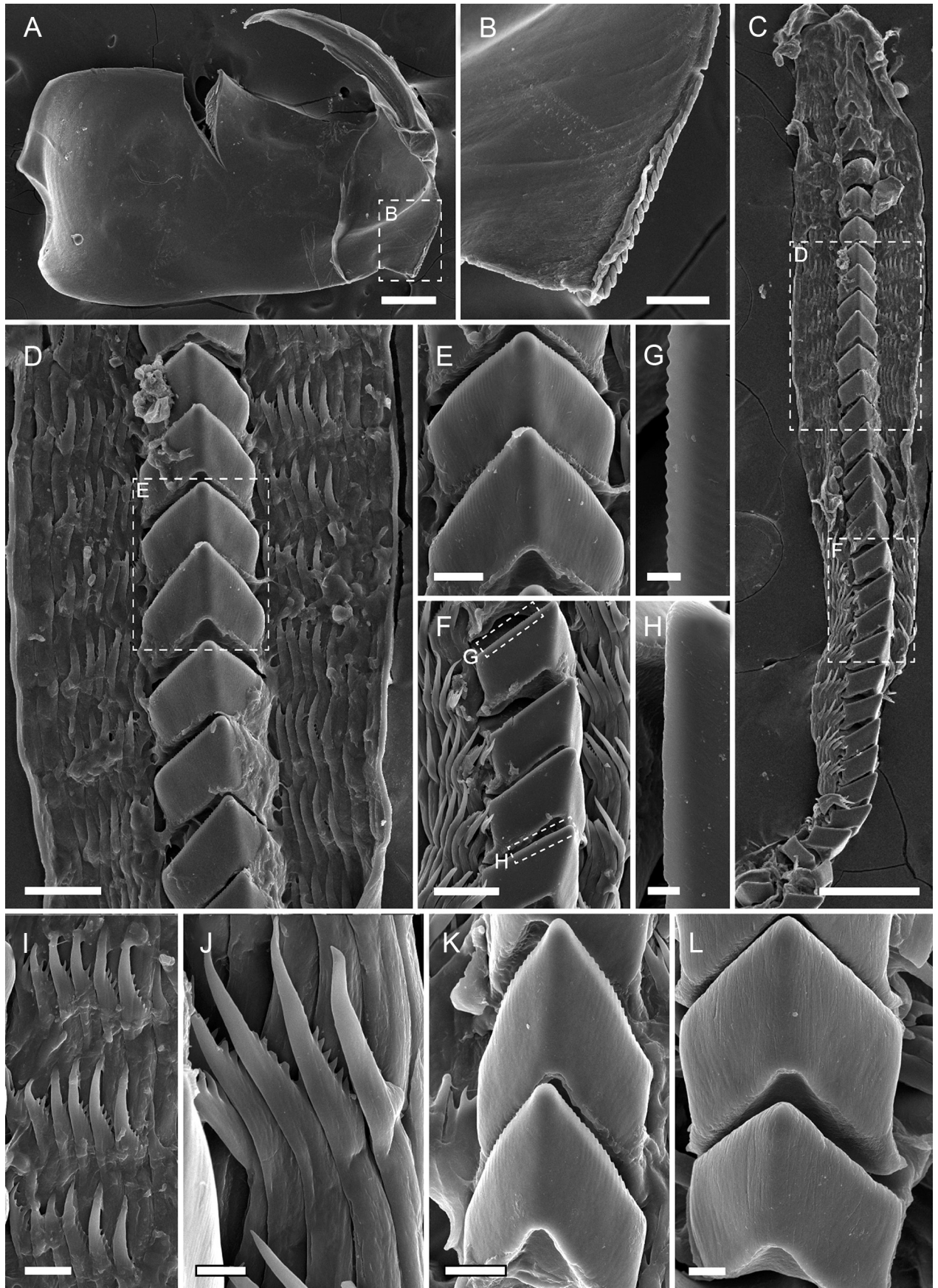


Fig. 3. *Dendronotus shpataki* sp. nov. in natural environment. Paratype MIMB42302 (A–C); the first documented finding of the new species in May 2015, the specimen was not collected (D); paratypes MIMB42303 (E, F). Photos by Andrey Shpatak.

Fig. 4. *Dendronotus shpataki* sp. nov., buccal armature. Paratype MIMB42309, left jaw plate (A); paratype MIMB42309, denticulation of masticatory border (B); paratype MIMB42309, radula (C); paratype MIMB42309, rachidian and lateral teeth, posterior radular portion (D); paratype MIMB42309, rachidian teeth, posterior radular portion (E); paratype MIMB42309, rachidian and lateral teeth, middle radular portion (F), paratype MIMB42309, denticulation of working plane in rachidian tooth of younger radular portion (G); paratype MIMB42309, lack of denticles on working plane in rachidian tooth of older radular portion (H); paratype MIMB42309, lateral teeth (I); paratype MIMB42309, lateral teeth denticulation (J); paratype MIMB42310, denticulated rachidian tooth in posterior radular portion (K); paratype MIMB42310, smooth rachidian tooth in anterior radular portion (L). Scale bars: 200 μ m (A, C), 50 μ m (B, D, F), 20 μ m (E, I, K), 5 μ m (G, H), 10 μ m (J, L). →



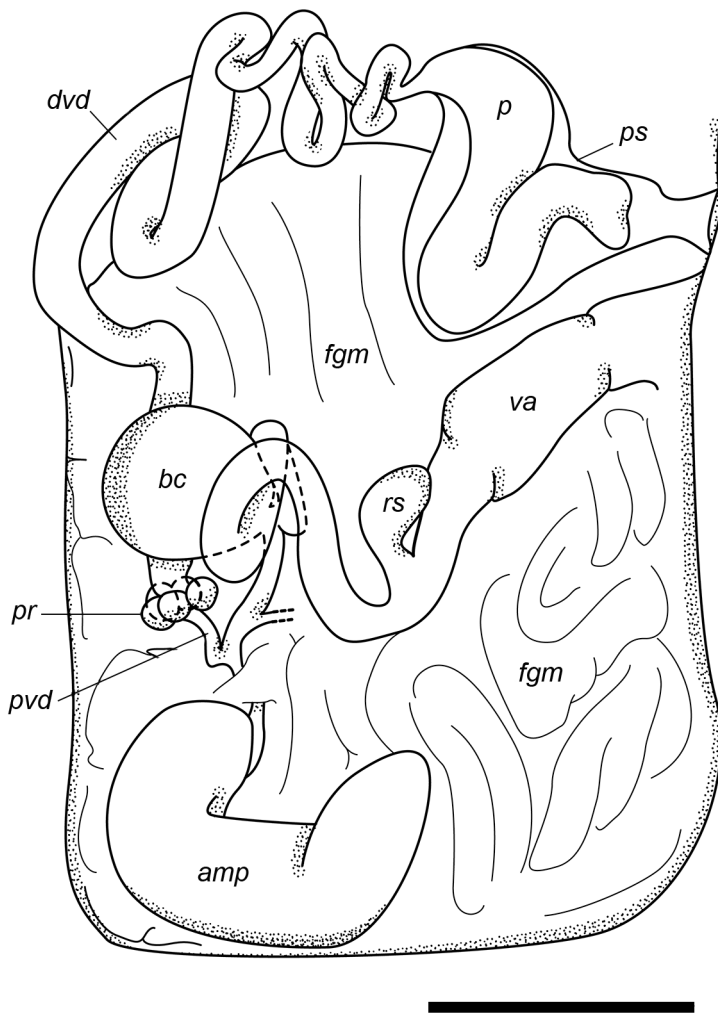


Fig. 5. *Dendronotus shpataki* sp. nov. Reproductive system, based on dissection of two paratypes (MIMB42309 and MIMB42303). Abbreviations: *amp* – ampulla, *bc* – bursa copulatrix, *dvd* – distal vas deferens, *fgm* – female gland mass, *p* – penis, *pr* – prostate, *ps* – penial sheath, *pvd* – proximal vas deferens, *rs* – receptaculum seminis, *va* – vagina, *vd* – vas deferens. Scale bar: 1 mm.

ble abrasive scrapes (Fig. 2E–H, K, L). According to the observation made by Andrey Shpatak, *Dendronotus shpataki* sp. nov. grabs hydrants of *Abietinaria*, which are covered by chitinous operculum. It should be also noted that species feeding on the same hydrozoans usually possess a smooth rachidian tooth (i.e. *D. dalli* Bergh, 1879 and *D. elegans* A.E. Verrill, 1880; see Ekimova et al., 2019b) and thus they likely have a similar feeding mechanism. Radular wear during feeding is a quite common feature for gastropods feeding on rough substrates by grazing or rasping (Franz, 1990; Ukmar-Godec et al., 2015; Krings & Gorb, 2021; Krings et al., 2021) and for specialised caenogastropod predators like drillers of bivalves and sea urchins (Carriker et al., 1974).

Ekimova & Malakhov, 2016; Korshunova et al., 2020a). Juvenile radula (anterior radular portion) is always highly denticulated, with deep furrows on the tooth surface from the juvenile to the sub-adult stage. At the same time, the posterior radular portion (newly developed teeth) have much smaller denticles in larger numbers and thinner furrows or complete smooth rachidian tooth, depending on species (Ekimova et al., 2019b). Therefore, these changes do not appear to be related to feeding on rough substrate and to teeth wear but reflect ontogenetic changes and may help tracing evolutionary patterns (Ekimova et al., 2019b). Here we report on a unique case of teeth wear during feeding for *Dendronotus*. While in adult specimens the rachidian tooth possess small but distinct denticles in the radular sac, the teeth on the working plane are smooth with remains of denticles on the outer edges of the tooth, and the surface has visi-

The diversity of the genus *Dendronotus* in the northwestern Sea of Japan is not as high as in the neighbouring areas such as Kamchatka, the Kuril Islands and the Japanese coastal waters, where several new species have been described recently (Ekimova et al., 2015, 2016a, 2019b; Korshunova et al., 2016b, 2019, 2020a; Martynov et al., 2015, 2020a). Only four species were confirmed to inhabit the northern parts of the Sea of Japan: *Dendronotus kamchaticus* Ekimova et al., 2015, *D. frondosus*, *D. primorjensis* and the enigmatic *D. orientalis* (Baba, 1932) (Martynov et al., 2015; Chichvarkhin, 2016; Ekimova et al., 2016a); the records of two other species, *D. dalli* and *D. albopunctatus* Robilliard, 1972 (Chichvarkhin, 2016), still need verification with integrative morphological and molecular approaches. All *Dendronotus* species in the Sea of Japan except *D. shpataki* sp. nov. display wide distributional

ranges, i.e. *D. frondosus* is an amphiboreal species (Ekimova et al., 2019b), *D. orientalis* inhabits temperate and subtropical areas along the Pacific coast of Asia (Martynov et al., 2015; Korshunova et al., 2020a), *D. kamchaticus* is found on both northwestern and northeastern Pacific coasts (Ekimova et al., 2015, 2016a, 2019b; Korshunova et al., 2016b), and *D. primorjensis* has been recently found in Japanese waters (Korshunova et al., 2019). In all these extensive studies of different localities in the North Pacific, no nudibranchs morphologically similar to *D. shpataki* sp. nov. were found, suggesting that the latter species may be a unique example of local endemism.

Addenda

Electronic supplementary material 1.

Map of the North-West Pacific showing a single collection locality in the Sea of Japan. File format: JPEG.

Electronic supplementary material 2.

Unedited concatenated Bayesian and Maximum Likelihood trees (COI + 16S + H3 + 28S) and single-gene trees of each marker from Maximum Likelihood inference. File format: TRE, six files as 7Z archive.

Electronic supplementary material 3.

List of specimens used in this study with voucher numbers, collection localities and GenBank accession numbers. Specimens sequenced for the present study are given in bold. File format: XLSX.

Electronic supplementary material 4.

Results of ABGD analysis, simple distance method. Histogram of pairwise distances is given on the upper left diagram, note barcode gap between 0.03 and 0.04 distance value. Number of species applying different Prior intraspecific divergence (P) is shown on the lower diagram. The results from initial partition are indicated as yellow dots, those from recursive partition, as red dots. File format: JPEG.

Electronic supplementary material 5.

Results of GMYC analysis showing a COI ultrametric non-calibrated tree of the genus *Dendronotus* that was produced with BEAST and analysed applying *splits* package in R environment. Respective voucher numbers for each specimen

are given after species names; for full list, see Electronic supplementary material 3. Red branches indicate intraspecific diversity, black branches, interspecific relationships. File format: PDF.

All these materials are available from: <https://doi.org/10.31610/zsr/2022.31.1.3>

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