

Discovery of Trans-Arctic Nudibranch Species, *Coryphella amabilis* and *Dendronotus zakuro* (Mollusca: Gastropoda) in Korean Waters

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ABSTRACT

The Nudibranchia Cuvier, 1817 is a group of soft-bodied, marine gastropod order (often called sea slugs) belonging to the subclass Heterobranchia Burmeister, 1837. This order comprises more than 2,600 species worldwide, but only a relatively small fraction of nudibranch species diversity—89 species—has been reported in Korean waters to date, awaiting further investigation in faunal studies in Korea. During our field survey of nudibranch fauna in Korea, we discovered two trans-Arctic species *Coryphella amabilis* and *Dendronotus zakuro* from Gangwon-do province in the East Sea of Korea. In this study, we present detailed morphological descriptions of the body and radula characters of the two newly discovered species and compare them with their close relatives based on molecular analysis as well. The morphological and molecular data presented in this study will contribute to the accurate identification of nudibranch species and provide diagnostic morphological traits and genetic information that help differentiate them from closely related congeneric species.

Keywords: *Coryphella*, *Dendronotus*, allopatric speciation, morphological variation, species delineation, DNA barcode information

INTRODUCTION

The Nudibranchia Cuvier, 1817 is a group of soft-bodied, marine gastropod order (often called as sea slugs) belonging to the subclass Heterobranchia Burmeister, 1837. Unlike many other gastropod groups, nudibranch species is characterized by its beautiful colored, intricate body patterns that completely lack an external shell at the adult stage. This order comprises more than 2,600 species worldwide that are found at varying depths in seawater environments, ranging from the intertidal zone to the subtidal zone, up to nearly 2,300 m in water depth (Ekimova et al., 2015; Gosliner et al., 2018; Valdés et al., 2018; MolluscaBase, 2024). Many nudibranch species are known to prey on various animals, including sponges, hydroids, bryozoans, ascidians, or other nudibranchs (Nybakken and McDonald, 1981; Folino, 1997; Nakano et al., 2007; Winters et al., 2018). Compared to global species diversity, only a relatively small fraction of nudibranch species—89 species—has been reported in Korean waters to date (National Marine Biodiversity Insti-

tute of Korea, 2023). Recent explorations of nudibranchs in Korean waters have led to the first discoveries of species that had not been previously recorded in the Korean fauna (Park et al., 2023). From our field survey of nudibranch fauna in Korea, two species belonging to the genera *Coryphella* and *Dendronotus* were discovered for the first time. In this study we present detailed morphological descriptions of the body and radula characters of the two newly discovered nudibranch species. Additionally, we performed phylogenetic analysis to confirm species identification and assess their relationships within each of their respective families using mtDNA *cox1* sequences, one of the most commonly employed genetic markers for species identification.

MATERIALS AND METHODS

Sample collection and morphological analysis

Nudibranch samples were collected at Gangwon-do province in Korean waters (Fig. 1) by SCUBA diving and pre-

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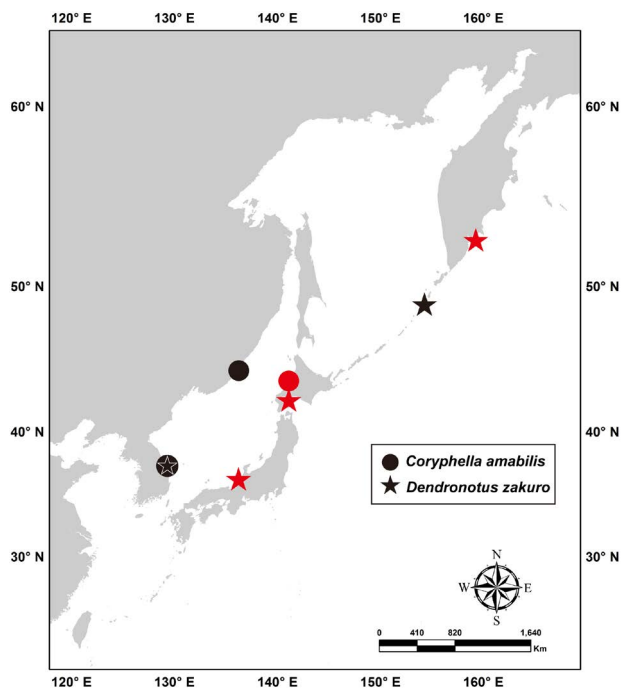


Fig. 1. Collection site of *Coryphella amabilis* and *Dendronotus zakuro* in Korea and their world-wide distribution records. Circles and stars indicate collection sites of *C. amabilis* and *D. zakuro*, respectively. Red-colored symbols indicate their type localities.

served in 95% ethanol solution. The voucher specimens were deposited in both the Marine Mollusk Resource Bank of Korea (MMRBK), and the National Marine Biodiversity Institute of Korea (MABIK). Morphological characters were examined under a stereomicroscope (Nikon SMZ1500, Japan). For jaw and radula observation, the buccal mass was extracted and soaked in 180 µL of ATL buffer and 20 µL of proteinase K (QIAGEN, Germany) overnight to dissolve the tissues. After dissolving the tissue, remaining jaw and radula were rinsed with distilled water and ethanol solution. The microstructures of the jaw and radula were observed using a scanning electron microscope (JEOL JSM-6390LV, Japan). Images of the external morphology were captured using a DSLR camera (Nikon D810) and a waterproof camera (Olympus TG6, Japan).

DNA extraction, PCR-amplification and barcode sequence analysis

Genomic DNA was extracted from the foot tissue using a QIAamp DNA Micro Kit (QIAGEN) following the manufacturer’s instructions. The mtDNA *coxI* sequences were PCR-amplified using the LCO1490 and HCO2198 primer

set (Folmer et al., 1994) in a total of 50 µL reaction mixture containing 37.75 µL of distilled water, 5 µL of 10 × Ex Taq buffer, 4 µL of dNTP, 1 µL of each primer, 0.25 µL of TaKaRa Ex Taq (TaKaRa Bio, Japan), and 1 µL of 1/100 diluted template DNA. The PCR conditions included an initial denaturation at 94°C for 4 min, followed by 40 cycles consisting of denaturation at 94°C for 30 s, annealing at 42°C for 30 s and elongation at 72°C for 1 min, and concluded with a final extension at 72°C for 10 min. The PCR-amplified target fragments were sequenced using an ABI PRISM 3700 DNA analyzer (Applied Biosystems, USA), and analyzed with Geneious Prime v.2023.0.4 (Biomatters, New Zealand). The nucleotide sequences of the partial fragment of mtDNA *coxI* were aligned with homologous gene sequences obtained from NCBI database using MAFFT (Katoh et al., 2002) in the Geneious software with default parameters (Appendix 1). Genetic distances among species were calculated using MEGA X (Stecher et al., 2020) as uncorrected *p*-distance (Collins et al., 2012; Srivathsan and Meier, 2012). Finding a best-fit substitution model and inferring phylogenetic tree were performed with IQTREE (Nguyen et al., 2015). The phylogenetic relationships were inferred using the maximum likelihood (ML) approach, and branch supports for each node were estimated from standard bootstrap analysis with 1,000 iterations.

SYSTEMATIC ACCOUNTS

- Phylum Mollusca Linnaeus, 1758
- Class Gastropoda Cuvier, 1795
- Order Nudibranchia Cuvier, 1817
- Family Coryphellidae Bergh, 1889
- Genus *Coryphella* J. E. Gray, 1850

^{1*}*Coryphella amabilis* (Hirano and Kuzirian, 1991) (Figs. 2, 3)

- Flabellina amabilis* Hirano and Kuzirian, 1991: 48–55, figs. 1–7; Behrens, 2004: 47.
- Microchlamyella amabilis*: Korshunova et al., 2017a: 40.
- Coryphella amabilis*: Ekimova et al., 2022: 231, figs. 8F, 10, 11D–G, 12C–F.

Material examined. Korea: 1 ind. (MMRBK7859), Gangwon-do: Goseong-gun, Jukwang-myeon, Munamjin-ri, Geumgangsán point, 38°18'04.6"N 128°34'08.3"E, collected by SCUBA diving at depth of 26.4 m, 8°C, 18 Mar 2024, collectors: Lee D, Park J, Kim Y, Ra S, Song G; 1 ind. (MMRBK7860 [MO00186629]), same locality to MMR

Korean name: ^{1*}민무늬흰점박이도롱이갯민숭이 (신칭)

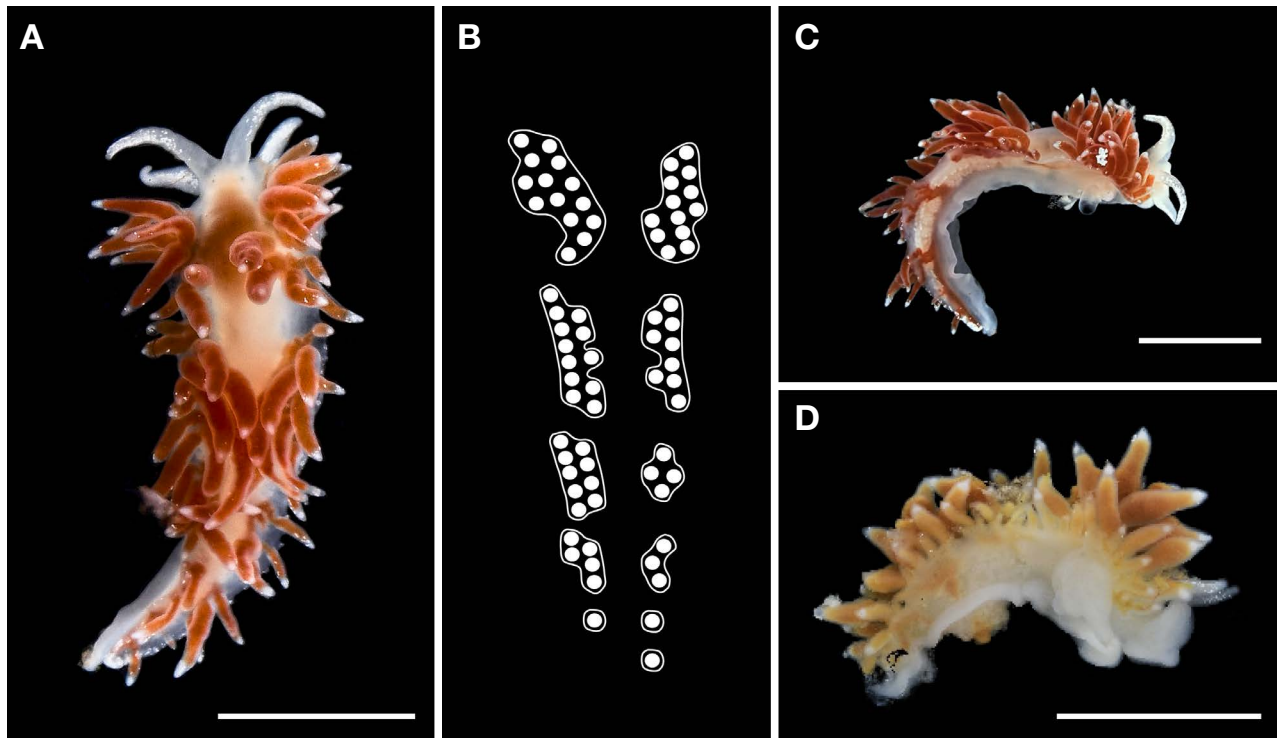


Fig. 2. *Coryphella amabilis* collected from Goseong-gun (Gangwon-do province), Korea. A, The specimen (MMRBK7860) in dorsal view; B, A symbolic presentation for cerata pattern per clusters; C, The specimen (MMRBK7860) in dorsolateral view; D, The specimen (MMRBK7859) in lateral view. Scale bars: A, C, D=5 mm.

BK7859, collected by SCUBA diving at depth of 23.2 m, 6°C, 11 Apr 2024, collectors: Lee D, Kim Y, Ra S, Song G.

Description. External morphology: Body elongated, laterally compressed, tapering posteriorly (body length up to 15 mm in live specimens) (Fig. 2A).

Oral tentacle smooth, about 2/3 length of rhinophore. Rhinophore slightly wrinkled. Eyes cloudy-black, present at base of rhinophore. Notal edge continuous (Fig. 2A).

Cerata fusiform or digitiform, arranged in six clusters dorsolaterally (Fig. 2A). Ceratal clusters separated from each other, consisting of numerous cerata following number of 14-12-9-5-1-0 on left side and 14-9-4-3-1-1 on right side (Fig. 2B, C); cerata size large on middle of body, decreasing toward notal edge. Cnidosac distinct, elongated.

Foot narrow, with flared margin, bluntly rounded anteriorly, tapering posteriorly (Fig. 2D).

Anus pleuroproctic, positioned below third row of second ceratal cluster. Reproductive opening placed laterally on right side, below middle of first ceratal cluster (Fig. 2C, D).

Coloration: Body pale white to light gray (Fig. 2A, D). White band gathered by white dots on dorsal surface of oral tentacle and distal 2/3 length of dorsal surface on rhinophore. Notal

edge with sparse white dots, having V-shaped white line gathered by white dots on posterior margin. Digestive gland diverticula inside cerata reddish brown to orange. Cerata with few white dots on distal margin, having white cnidosac.

Internal morphology: Jaw triangular plate, convex, with masticatory border bearing 4–8 rows of denticles (Fig. 3A, B). Radula formula 15–18 × 1.1.1 (Fig. 3C). Rachidian tooth pentagon-shaped with central cusp, bearing 7–10 lateral denticles on each side (Fig. 3D, E). Central cusp elongated conical shaped, 1.5–2 times length of lateral denticles. Lateral teeth triangular, having inner-curved, elongated cusp, bearing 7–9 denticles on inner side, with attenuated basal process; denticle seldomly bifurcated (Fig. 3D).

Distribution. Northwestern Pacific: Japan (Hokkaido [Hirano and Kuzirian 1991]), Russia (Primorsky Krai, 7–20 m in depth [Ekimova et al., 2022]), South Korea (Gangwon-do [present study]) (Fig. 1).

Family Dendronotidae Allman, 1856

Genus *Dendronotus* Alder & Hancock, 1845

¹**Dendronotus zakuro* Martynov et al., 2020 (Figs. 4–6)

Korean name: ¹*팔색긴수지갯민숭이 (신칭)

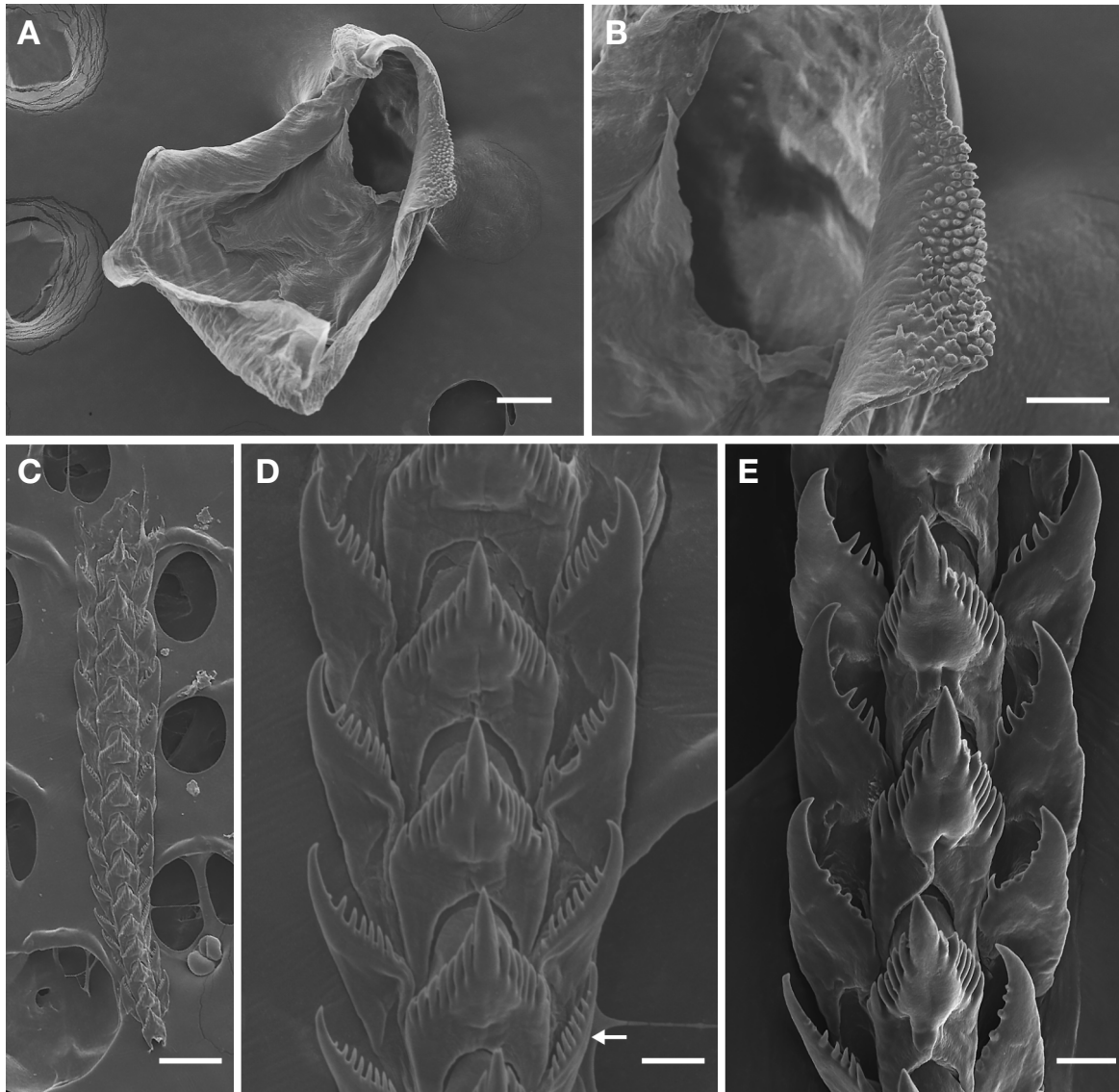


Fig. 3. Scanning electron microscope images of buccal mass of *Coryphella amabilis*. A, Left jaw (MMRBK7859); B, Denticles on masticatory border (MMRBK7859); C, Radula (MMRBK7859); D, Posterior part of the radula (MMRBK7859), arrow indicating bifurcation; E, Posterior part of the radula (MMRBK7860). Scale bars: A, C=100 μ m, B=50 μ m, D, E=20 μ m.

Dendronotus zakuro Martynov et al., 2020: 505–507, figs. 3, 5B; Ekimova et al., 2021: 768–770, fig. 11; Korshunova et al., 2021: 131, 132, fig. 7.

Material examined. Korea: 1 ind. (MMRBK7853), Gangwon-do: Goseong-gun, Jukwang-myeon, Munamjin-ri, Geumgangsan point, 38°18'04.5"N 128°34'08.4"E, collected by SCUBA diving at depth of 29 m, 11°C, 6 May 2021, collectors: Lee Y, Lee D, Park J, Ra S, Song G; 1 ind. (MMRBK7854), same locality to MMRBK7853, collected by SCUBA diving at depth of 25.6 m, 5°C, 29 Mar 2022, collectors: Lee D, Park J; 1 ind. (MMRBK7855), same local-

ity to MMRBK7853, collected by SCUBA diving at depth of 26.4 m, 8°C, 18 Mar 2024, collectors: Lee D, Park J, Kim Y, Ra S, Song G; 1 ind. (MMRBK7856 [MO00186628]), same locality to MMRBK7853, collected by SCUBA diving at depth of 24.8 m, 6°C, 19 Mar 2024, collectors: Lee D, Park J, Kim Y, Ra S, Song G; 1 ind. (MMRBK7857), Goseong-gun, Jukwang-myeon, Munamjin-ri, Maisan point, 38°18'02.9"N 128°34'15.9"E, collected by SCUBA diving at depth of 30.5 m, 6°C, 19 Mar 2024, collectors: Lee D, Park J, Kim Y, Ra S, Song G; 1 ind. (MMRBK7858), same locality to MMRBK7843, collected by SCUBA diving at depth of 24.7 m, 10°C, 21 Mar 2024, collectors: Lee D, Park J, Kim Y,

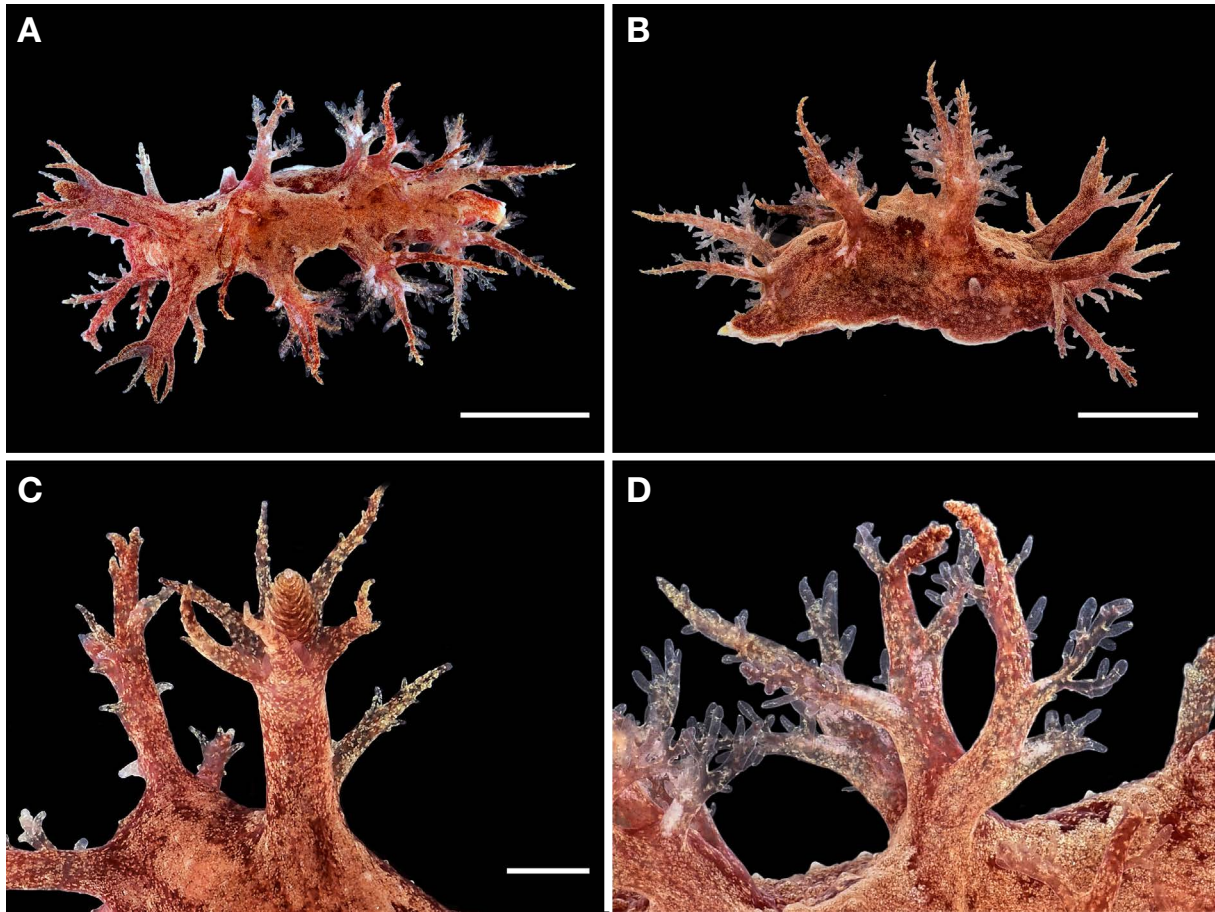


Fig. 4. *Dendronotus zakuro* collected from Goseong-gun (Gangwon-do province), Korea (MMRBK7858). A, The specimen in dorsal view; B, The specimen in lateral view; C, Rhinophore; D, Left dorsolateral appendage of first pair. Scale bars: A, B=10 mm, C=2 mm.

Ra S, Song G.

Description. External morphology: Body (Fig. 4A) elongated, laterally compressed (body length in live specimens: 5.8 mm [MMRBK7855]; 23.6 mm [MMRBK7856]; 13.7 mm [MMRBK7857]; 30.1 mm [MMRBK7858]).

Oral veil with about 25 lip papillae and 6–7 branched appendages; two median appendages longest, 0.5–0.7 times of rhinophore length, having bifurcated primary stalks (Fig. 4A, B). Rhinophoral sheath with long stalk and 5–6 branched appendages (Fig. 4C). Lateral papilla branched, about 1/3 times of rhinophore length, placed on outer basal surface. Clavus consisting of 11 lamellae.

Dorsolateral appendages consisting of 4–7 pairs, branched up to tertiary branches (Fig. 4B). First and second appendages consisting of bifid or trifid stalks with dichotomy near base; inner stalk larger than other stalks (Fig. 4D). Subsequent appendages smaller and less branched toward posterior. Last appendages atrophied.

Foot narrow, rounded anteriorly, tapering posteriorly, with yellowish-white line on edge (Fig. 4B).

Anus pleuroproct, positioned between first and second dorsolateral appendages. Reproductive opening placed laterally on right side, near first dorsolateral appendage (Fig. 4B).

Coloration: In nature, broad color range observed. Body brown to reddish brown in ground color, covered with scattered tiny light-yellowish dots especially on dorsal surface, having large dark brown spots among rhinophore and dorsolateral appendages, and small white dots on lateral surface (MMRBK7858) (Fig. 5A); body light-pink in ground color, covered with scattered tiny brown to reddish brown dots especially on dorsal surface, having yellow spotted lines among rhinophore and dorsolateral appendages, and small white dots on lateral surface (MMRBK7855) (Fig. 5B); body orange in ground color with dark brown spots among rhinophore and dorsolateral appendages (MMRBK7856) (Fig.

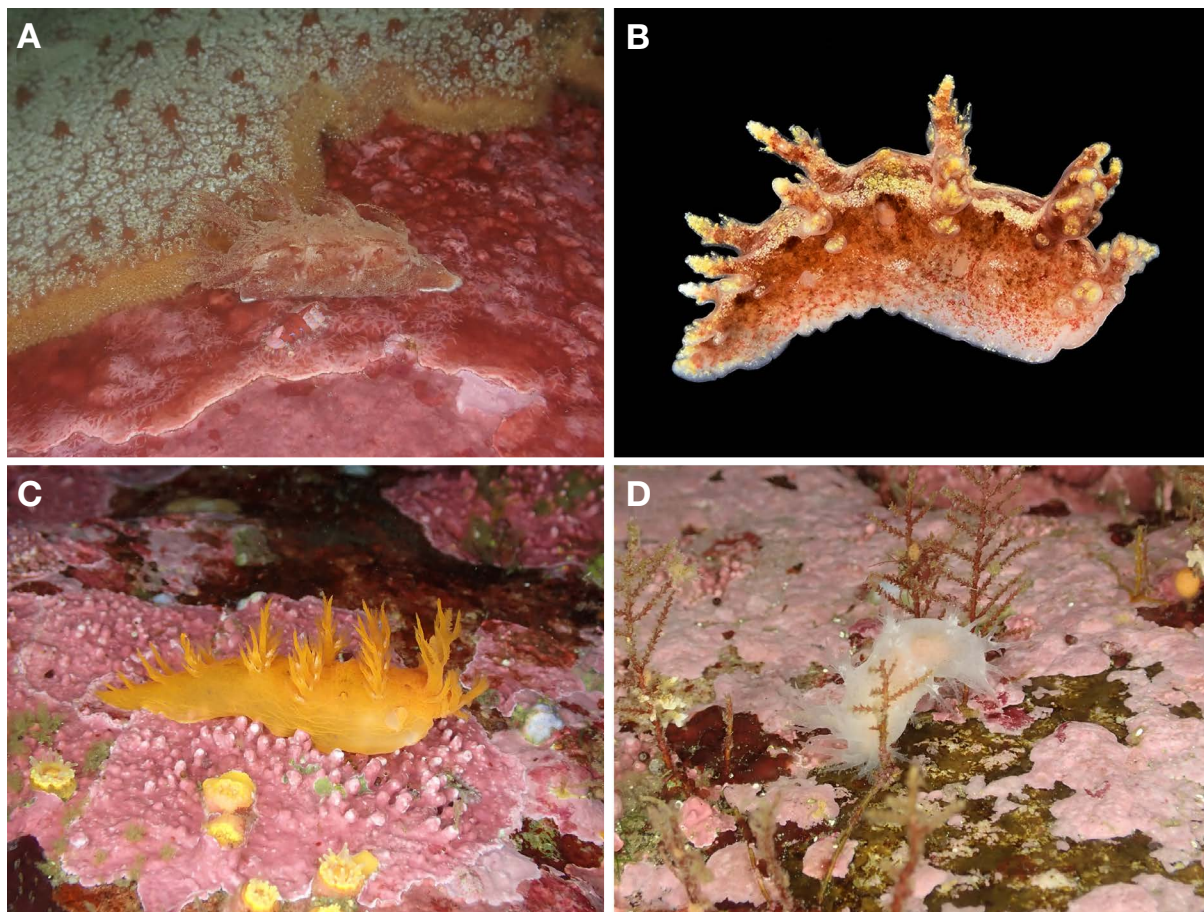


Fig. 5. Broad range of color variations in *Dendronotus zakuro*. A, Live specimen in nature (MMRBK7858); B, Live specimen photographed in laboratory (MMRBK7855); C, Live specimen in nature (MMRBK7856); D, Live specimen in nature (MMRBK7857).

5C); body white in ground color, covered with scattered tiny white dots, having dark brown broken lines among rhinophore and dorsolateral appendages (MMRBK7857) (Fig. 5D).

Internal morphology: Jaw ovoid plate, convex, having large dorsal process (Fig. 6A). Masticatory border curved, bearing a row of round denticles (Fig. 6B). Radula formula 37–41 × 8–10.1.8–10 (Fig. 6C). Rachidian tooth chevron-shaped, having faint furrows and/or longitudinal grain on surface, lacking denticle (Fig. 6D, F, G). Lateral teeth curved, elongated with pointing cusp, bearing less than nine denticles (Fig. 6E).

Distribution. Northwestern Pacific: Kuril Islands (285–300 m in depth [Ekimova et al., 2021]), Japan (Hokkaido and Honshu, 7.1–20 m in depth [Martynov et al., 2020]), Russia (Kamchatka, 12 m in depth [Martynov et al., 2020]), South Korea (Gangwon-do, 24.7–30.5 m in depth [present study]) (Fig. 1).

DISCUSSION

Coryphella amabilis (Hirano and Kuzirian, 1991)

Morphologically, the Korean specimens of *C. amabilis* correspond well to the original description, but minor differences are observed in the cerata and buccal mass. The number of ceratal clusters and cerata per cluster differ from the original description (originally described as left cerata: 15-12-6-6-2; right cerata: 15-12-7-5-2) (Fig. 2B). It is assumed that the Korean specimens were either damaged or that the difference in the number of cerata represents individual variation. Differences were observed in the number of denticle rows on the masticatory border (Fig. 3B), radula rows (Fig. 3C), and the denticles of the rachidian and lateral teeth (Fig. 3D, E), compared to the original description by Hirano and Kuzirian (1991). Since individual variation in radula characters has been continuously reported, radula morphology alone cannot reliably distinguish *C. amabilis* from other congeneric species, as these differences likely represent in-

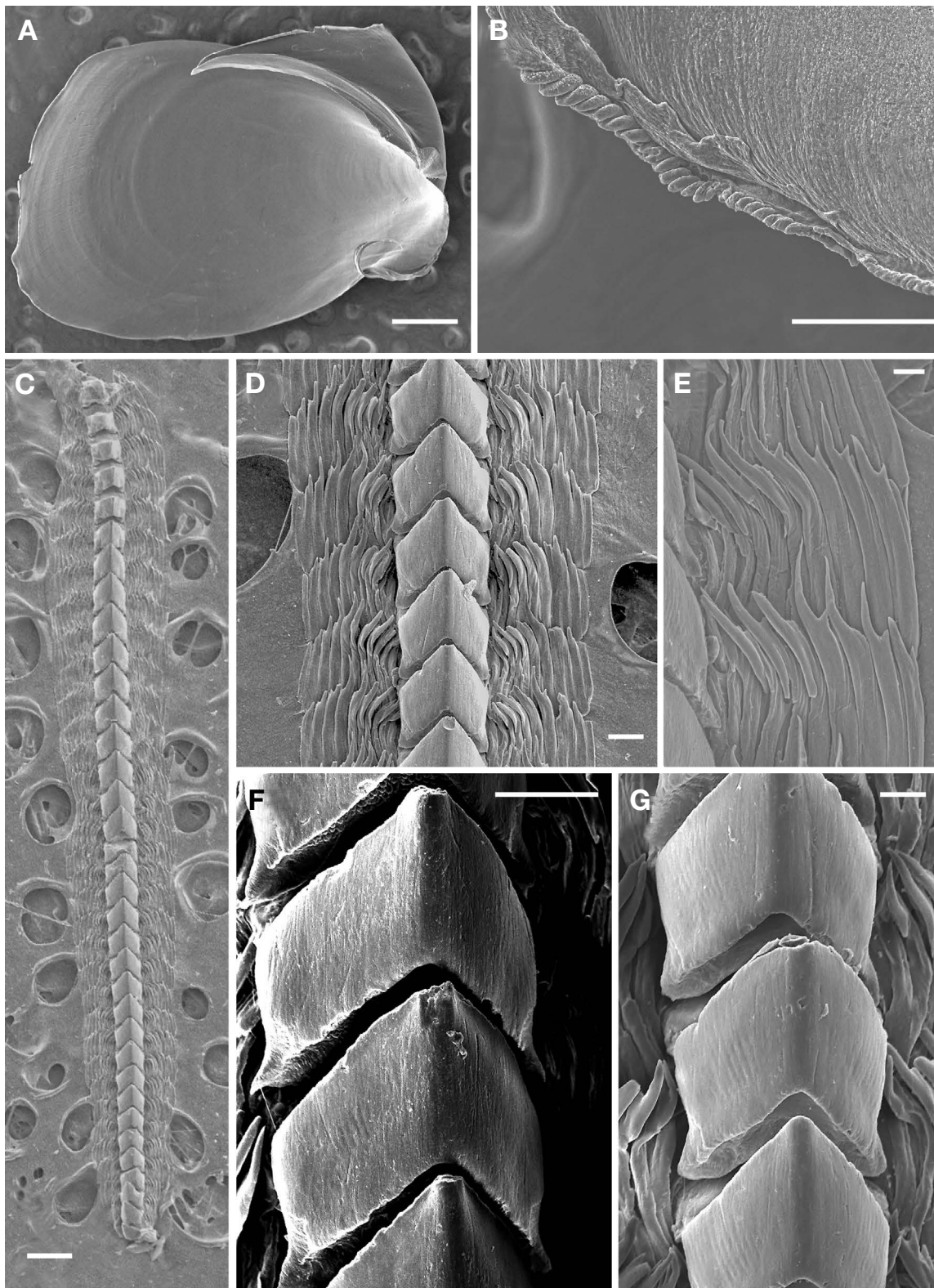


Fig. 6. Scanning electron microscope images of buccal mass of *Dendronotus zakuro*. A, Left jaw (MMRBK7858); B, Denticles on masticatory border (MMRBK7858); C, Radula (MMRBK7858); D, Posterior part of radula (MMRBK7858); E, Lateral teeth (MMRBK7856); F, Rachidian tooth (MMRBK7856); G, Rachidian tooth (MMRBK7857). Scale bars: A=500 μ m, B=100 μ m, C=200 μ m, D, F=50 μ m, E, G=20 μ m.

dividual variation (Ekimova et al., 2022).

The external morphology of *C. amabilis* is similar to *C. abei* Baba, 1987, *C. alexanderi* Ekimova, 2022, and *C. athadona* Bergh, 1875. However, it is distinguished by a combination of the following characteristics: the presence of white bands on the oral tentacle and the rhinophore, discontinuous ceratal clusters, and the absence of a Y-shaped band on the head (Hirano and Kuzirian, 1991; Ekimova, 2022). Nevertheless, *C. amabilis* and *C. gracilis* are so similar that they are indistinguishable by morphological analysis alone

Table 1. Comparison of minimum and maximum pairwise uncorrected *p*-distances (%) of the mtDNA *cox1* sequences of *Coryphella amabilis* with other *Coryphella* species

Species	Minimum	Maximum
<i>C. amabilis</i>	0.16	1.31
<i>C. alexanderi</i>	12.75	13.56
<i>C. athadona</i>	13.40	15.03
<i>C. borealis</i>	13.07	13.73
<i>C. browni</i>	11.60	11.93
<i>C. chriskaugei</i>	10.95	11.60
<i>C. falklandica</i>	15.52	16.18
<i>C. gracilis</i>	3.76	5.39
<i>C. lineata</i>	11.11	12.58
<i>C. monicae</i>	16.01	16.50
<i>C. nobilis</i>	13.07	14.38
<i>C. orjani</i>	14.48	14.87
<i>C. sanamyanae</i>	14.22	14.71
<i>C. trilineata</i>	12.42	13.56
<i>C. verrucosa</i>	14.22	15.03

(Ekimova et al., 2022).

In the molecular analyses of the mtDNA *cox1* sequences, the intraspecific genetic distances within *C. amabilis*, including Korean specimens, range from 0.16% to 1.31% (Table 1, Appendix 2). The interspecific genetic distances range from a minimum of 10.95% (compared with *C. chriskaugei*) to a maximum of 16.50% (compared with *C. monicae*). In contrast, the genetic distances between *C. amabilis* and *C. gracilis* are relatively low (3.76–5.39%), compared to the genetic distances among other congeneric species. Note that the phylogenetic analysis reveals that *C. gracilis* is nested within *C. amabilis* (Fig. 7). The integrative analysis of morphological and molecular data suggested that these two species were very closely related, but represented two separate species explained by allopatric speciation of the trans-Arctic clades (Ekimova et al., 2022). Further studies are required to confirm whether the genetic differentiation between these two species (3.76–5.39% in mtDNA *cox1* sequences) was caused by geographic barriers and/or limited gene flow between their populations. Nevertheless, it is interesting to note that the first discovery of this species from Goseong-gun, Gangwon-do (in the East Sea of Korea) extends its distribution range further south than previously documented.

Dendronotus zakuro Martynov et al., 2020

The specimens collected from Korean waters exhibit some differences in body color, the number of dorsolateral appendages, and radula morphology, compared to previous

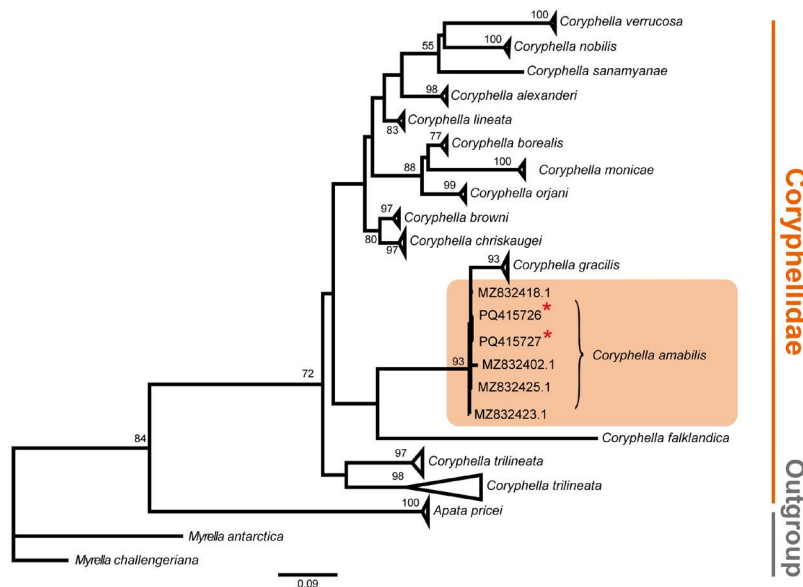
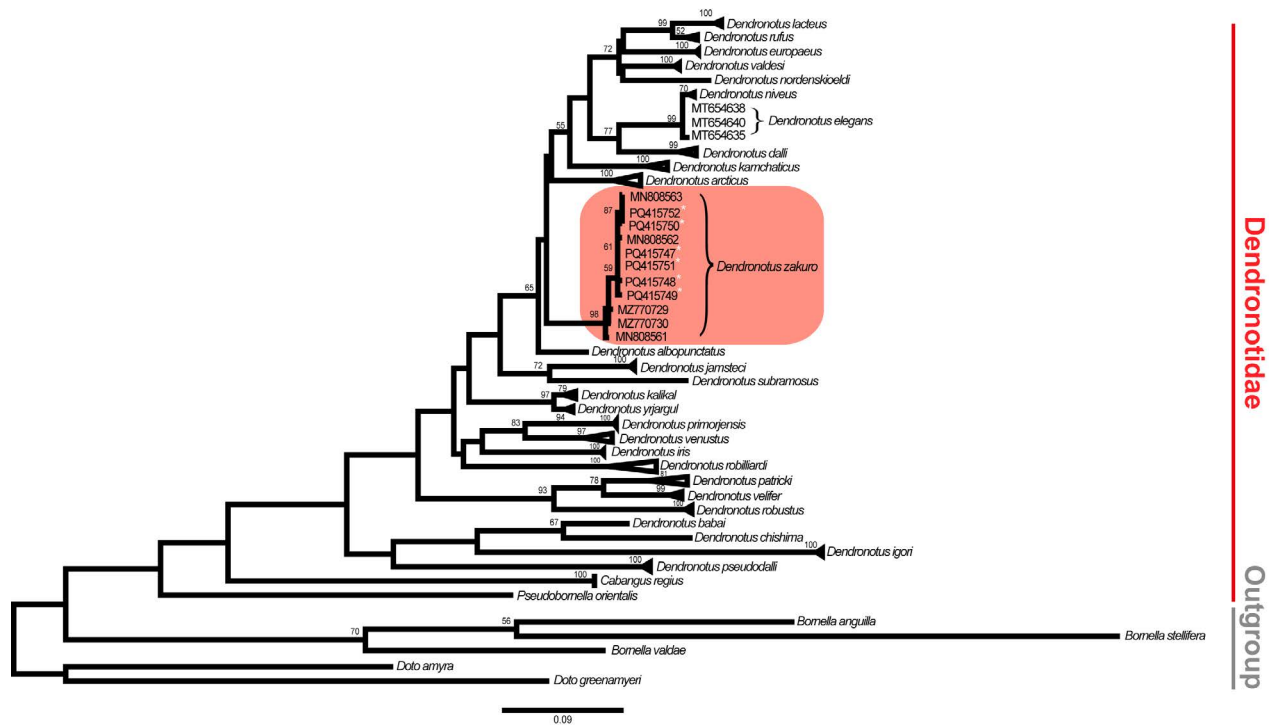


Fig. 7. Phylogenetic relationships among *Coryphella* species inferred from maximum likelihood method using the mtDNA *cox1* sequences. Branch supporting values are indicated as bootstrap percentage (≥ 50). Sequences determined in this study are denoted by asterisks (*).

Table 2. Comparison of minimum and maximum pairwise uncorrected *p*-distances (%) of the mtDNA *cox1* sequences of *Dendronotus zakuro* with other *Dendronotus* species

Species	Minimum	Maximum	Species	Minimum	Maximum
<i>D. zakuro</i>	0	1.63	<i>D. niveus</i>	7.99	8.71
<i>D. arcticus</i>	7.44	8.71	<i>D. nordenskiöldi</i>	8.71	9.26
<i>D. babai</i>	14.34	14.70	<i>D. patricki</i>	14.52	15.25
<i>D. chishima</i>	15.61	15.79	<i>D. primorjensis</i>	9.44	10.53
<i>D. dalli</i>	8.71	9.62	<i>D. pseudodalli</i>	14.34	15.06
<i>D. elegans</i>	7.99	8.53	<i>D. robilliardi</i>	11.07	12.34
<i>D. europaeus</i>	7.80	8.53	<i>D. robustus</i>	14.16	14.88
<i>D. igori</i>	15.43	16.15	<i>D. rufus</i>	8.53	9.98
<i>D. iris</i>	11.07	11.98	<i>D. subramosus</i>	9.44	9.80
<i>D. jamsteci</i>	9.80	10.71	<i>D. valdesi</i>	9.26	9.98
<i>D. kalikal</i>	8.89	10.16	<i>D. venustus</i>	9.07	9.80
<i>D. kamchaticus</i>	6.72	8.17	<i>D. velifer</i>	13.61	14.52
<i>D. lacteus</i>	8.89	9.98	<i>D. yrjargul</i>	9.26	9.80

**Fig. 8.** Phylogenetic relationships among *Dendronotus* species inferred from maximum likelihood method using the mtDNA *cox1* sequences. Branch supporting values are indicated as bootstrap percentage (≥ 50). Sequences determined in this study are denoted by asterisks (*).

descriptions. As the species name “zakuro” indicates, the reddish to reddish-brown body color is a distinctive feature of this species (Martynov et al., 2020). However, color variations, ranging from translucent milky-white with an orange tinge to variegated orange-brown, have previously been reported (Ekimova et al., 2022). In this study, additional color variations were also observed, including reddish brown,

light pink, orange, and even white, suggesting that the body color alone may not be a reliable feature for characterizing *D. zakuro* (Fig. 5). The original description documented 6–7 pairs of dorsolateral appendages in the type specimens, which was also observed as five pairs by subsequent study (Ekimova et al., 2021). Moreover, we found only four pairs of dorsolateral appendages (Fig. 4B), with the last append-

ages reduced to simple tubercles in one Korean specimen (MMRBK7858), indicating that individual variation in the number of dorsolateral appendages ranges from four to seven.

In terms of radula morphology, the number of radula rows in Korean specimens ranges from 37–41, which is higher than the previously reported range of 29–36 rows. The small-sized specimens exhibit shallow but distinct furrows on the rachidian tooth (Fig. 6G). On the other hand, the intermediate-sized specimen (MMRBK7856) shows a mixture of faint furrows and longitudinal grains (Fig. 6F), and the largest specimen (30.1 mm of body length in live, MMRBK7858) uniquely displays only longitudinal grains with no furrows (Fig. 6D). The presence or absence of these furrows has been observed in previous studies, and the heterogeneous patterns observed in this genus suggest that the radula morphology changes with their ontogenetic growth, ranging from denticulated form to spiniform, knife- or hook-shaped form (Ekimova et al., 2019).

Despite some morphological differences, *D. zakuro* closely resembles *D. kamchaticus* Ekimova et al., 2015, making it challenging to clearly distinguish the two species. The number of lip papillae in *D. zakuro* is typically about 25, whereas *D. kamchaticus* has fewer, ranging from 4–15. Additionally, *D. zakuro* possesses 10–11 lamellae, while *D. kamchaticus* shows a broader range of individual variation, with a clavus consisting of 5–25 lamellae. Regarding the jaw, the *D. zakuro* specimens have clearly defined denticles on the masticatory border, while in *D. kamchaticus*, the denticles on the masticatory border are absent in small specimens (Ekimova et al., 2015; 2016a) or fine-sized in a larger specimen (Korshunova et al., 2016b).

In our molecular analyses of the mtDNA *cox1* sequences, the intraspecific genetic distances for *D. zakuro*, including Korean specimens, range from 0% to 1.63% (Table 2, Appendix 3). The genetic distances between *D. zakuro* and other congeneric species range from a minimum of 6.72% (compared with *D. kamchaticus*) to a maximum of 16.15% (with *D. igori* Ekimova et al., 2023). The genetic distances between *D. zakuro* and *D. kamchaticus* (6.72–8.17%) are larger than the within-species distances in *D. zakuro*, and these two species are placed in different clades in the phylogenetic tree, indicating that the molecular analysis is highly effective in distinguishing them (Fig. 8).

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CONFLICTS OF INTEREST

No potential conflict of interest relevant to this article was reported.

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Appendix 1. Nucleotide sequences of mtDNA *cox1* gene used for the molecular analysis

Family	Species	Voucher No.	NCBI No.	References
Apataidae	<i>Apata pricei</i>	nu220303	OQ919370	Park et al. (2023)
Apataidae	<i>Apata pricei</i>	ZMMU:Op-533	MF523386	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella alexanderi</i>	MIMB42468	OL984252	Ekimova (2022)
Coryphellidae	<i>Coryphella alexanderi</i>	MIMB42469a	OL984251	Ekimova (2022)
Coryphellidae	<i>Coryphella alexanderi</i>	MIMB42469b	OL984250	Ekimova (2022)
Coryphellidae	<i>Coryphella amabilis</i>	WS14395	MZ832402	Ekimova et al. (2022)
Coryphellidae	<i>Coryphella amabilis</i>	WS14418	MZ832418	Ekimova et al. (2022)
Coryphellidae	<i>Coryphella amabilis</i>	WS14442	MZ832425	Ekimova et al. (2022)
Coryphellidae	<i>Coryphella amabilis</i>	WS14958	MZ832423	Ekimova et al. (2022)
Coryphellidae	<i>Coryphella amabilis</i>	MMRBK7859	PQ415726	This study
Coryphellidae	<i>Coryphella amabilis</i>	MMRBK7860	PQ415727	This study
Coryphellidae	<i>Coryphella athadona</i>		KT724949	Jung and Park (2015)
Coryphellidae	<i>Coryphella athadona</i>	WS14396	MZ832380	Ekimova et al. (2022)
Coryphellidae	<i>Coryphella athadona</i>	ZMMU:Op-498	MF523332	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella borealis</i>	GNM9417	MG452631	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella borealis</i>	MT09706	KR084560	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella borealis</i>	MT09694	KR084727	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella browni</i>	NTNU-VM:68800	MG452620	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella browni</i>	NTNU-VM:68801	MG452619	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella browni</i>	NTNU-VM:68802	MG452621	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella chriskaugei</i>	NTNU-VM:67131	MG452606	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella chriskaugei</i>	NTNU-VM:68804	MG452613	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella chriskaugei</i>	NTNU-VM:68807	MG452611	Barco et al. (2016)
Coryphellidae	<i>Coryphella falklandica</i>	ZSM Mol-20070592	MF523334	Barco et al. (2016)
Coryphellidae	<i>Coryphella gracilis</i>	NTNU-VM:68811	MG452628	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella gracilis</i>	ZMMU:Op-505	MF523340	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella gracilis</i>	ZMMU:Op-501	MF523336	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella lineata</i>	NTNU-VM:68815	MG452608	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella lineata</i>	ZMMU:Op-506	MF523343	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella lineata</i>	ZMMU:Op-507	MF523344	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella monicae</i>	NTNU-VM:68816	MG452609	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella monicae</i>	ZMMU:Op-408	MF523373	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella monicae</i>	ZMMU:Op-411	MF523370	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella nobilis</i>	ZMMU:Op-510	MF523347	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella nobilis</i>	ZMMU:Op-511	MF523348	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella orjani</i>	NTNU-VM:67091	MG452604	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella orjani</i>	ZMMU:Op-467	MF523361	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella orjani</i>	ZMMU:Op-468	MF523362	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella sanamyanae</i>	WS14394	MZ832430	Ekimova (2022)
Coryphellidae	<i>Coryphella trilineata</i>	CAS179466	KY129064	Cella et al. (2016)
Coryphellidae	<i>Coryphella trilineata</i>	BMBM-0139	MH242761	Unpublished
Coryphellidae	<i>Coryphella trilineata</i>	BMBM-0545	MH242762	Unpublished
Coryphellidae	<i>Coryphella verrucosa</i>	ZMMU:Op-527	MF523351	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella verrucosa</i>	ZMMU:Op-528	MF523352	Korshunova et al. (2017a)
Coryphellidae	<i>Coryphella verrucosa</i>	ZMMU:Op-529	MF523353	Korshunova et al. (2017a)
Dendronotidae	<i>Bornella anguilla</i>	SRR3726697	KX889723	Goodheart et al. (2017)
Dendronotidae	<i>Bornella stellifera</i>	USNM:1467443	MZ560289	Plaisance et al. (2021)
Dendronotidae	<i>Bornella valdae</i>	SAMA55952	JN869449	Pola et al. (2012)
Dendronotidae	<i>Cabangus regius</i>	CASIZ179492	HM162708	Unpublished
Dendronotidae	<i>Cabangus regius</i>	CASIZ179493	JN869451	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus albopunctatus</i>	-	GQ292064	Korshunova et al. (2016b)
Dendronotidae	<i>Dendronotus arcticus</i>	MIMB36291_2	MN138293	Korshunova et al. (2016b)
Dendronotidae	<i>Dendronotus arcticus</i>	ZMMU:Op-561	KX788140	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus arcticus</i>	ZMMU:Op-562	KX788141	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus babai</i>	25-003	OQ108630	Unpublished
Dendronotidae	<i>Dendronotus chishima</i>	AO220-018	OQ108629	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus dalli</i>	BMBM0953	MN138385	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus dalli</i>	ZMMU:Op295	KM397001	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus dalli</i>	ZMMU:Op330	KM396999	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus elegans</i>	ZMMU:Op-713	MT654640	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus elegans</i>	ZMMU:Op-715	MT654635	Korshunova et al. (2017b)
Dendronotidae	<i>Dendronotus elegans</i>	ZMMU:Op-716	MT654638	Korshunova et al. (2017b)
Dendronotidae	<i>Dendronotus europaeus</i>	ZMMU:Op-554	KY391823	Korshunova et al. (2017b)
Dendronotidae	<i>Dendronotus europaeus</i>	ZMMU:Op-555	KY391837	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus europaeus</i>	ZMMU:Op-578	KY391821	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus igori</i>	AO11-001	OQ108622	Unpublished
Dendronotidae	<i>Dendronotus igori</i>	AO25-12	OQ108623	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus iris</i>	BIOUG02303-D01	MG423495	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus iris</i>	CPIC00065	MN138305	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus iris</i>	CPIC00695	MN138306	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus jamsteci</i>	JAMSTEC-1160047463	MN808558	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus jamsteci</i>	JAMSTEC-1160047475	MN808559	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus kalikal</i>	ZMMU:Op349 clone 1	KM396986	Korshunova et al. (2019)
Dendronotidae	<i>Dendronotus kalikal</i>	ZMMU:Op349 clone 2	KM396987	Ekimova et al. (2016a)
Dendronotidae	<i>Dendronotus kalikal</i>	ZMMU:Op-657	MK302458	Ekimova et al. (2016a)
Dendronotidae	<i>Dendronotus kamchaticus</i>	W194_1	KT031822	Korshunova et al. (2016b)
Dendronotidae	<i>Dendronotus kamchaticus</i>	W194_2	KT031823	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus kamchaticus</i>	ZMMU:Op-565	KX788144	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus lacteus</i>	CPIC01186	MN138320	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus lacteus</i>	WS9133	MN138321	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus lacteus</i>	WS9134	MN138322	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus niveus</i>	ZMMU:Op269	KM396996	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus niveus</i>	ZMMU:Op270	KM396997	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus niveus</i>	ZMMU:Op279	KM396995	Stout et al. (2011)
Dendronotidae	<i>Dendronotus nordenskiöldi</i>	ZMMU:Op-665	MT654636	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus patricki</i>	SIO_BIC M12133	HQ225828	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus patricki</i>	WS9105	MN138336	Unpublished
Dendronotidae	<i>Dendronotus patricki</i>	WS9106	MN138337	Korshunova et al. (2016a)
Dendronotidae	<i>Dendronotus primorjensis</i>	-	OQ583563	Korshunova et al. (2016a)
Dendronotidae	<i>Dendronotus primorjensis</i>	ZMMU:Op-419	KX672010	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus primorjensis</i>	ZMMU:Op-420	KX672011	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus pseudodalli</i>	AO36-011	OQ108624	Pola and Gosliner (2010)
Dendronotidae	<i>Dendronotus pseudodalli</i>	AO41-004b	OQ108626	Pola et al. (2012)
Dendronotidae	<i>Dendronotus robillardi</i>	KM717	MN973970	Unpublished
Dendronotidae	<i>Dendronotus robillardi</i>	ZMMU:Op-447	KX788139	Korshunova et al. (2016b)
Dendronotidae	<i>Dendronotus robillardi</i>	ZMMU:Op-567	KX788136	Korshunova et al. (2016b)
Dendronotidae	<i>Dendronotus robustus</i>	ZMMU:Op343	KM397002	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus robustus</i>	ZMMU:Op344	KM397003	Ekimova et al. (2015)
Dendronotidae	<i>Dendronotus rufus</i>	LACM:174863	KX058085	Ekimova et al. (2016b)
Dendronotidae	<i>Dendronotus rufus</i>	MIMB36288	MN138344	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus rufus</i>	USNM:IZ:1524173	MZ580879	Unpublished
Dendronotidae	<i>Dendronotus subramosus</i>	ZMMU:Op-699	MN808564	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus valdesi</i>	AO25-002	OQ108619	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus valdesi</i>	AO83-008	OQ108621	Ekimova et al. (2023)
Dendronotidae	<i>Dendronotus velifer</i>	MIMB36293	MN138351	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus velifer</i>	IE182	MN138352	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus velifer</i>	WS9154	MN138353	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus venustus</i>	CPIC056	KX058087	Ekimova et al. (2016b)
Dendronotidae	<i>Dendronotus venustus</i>	CPIC059	KX058088	Ekimova et al. (2016b)
Dendronotidae	<i>Dendronotus venustus</i>	CPIC00417	MN138355	Ekimova et al. (2019)
Dendronotidae	<i>Dendronotus yrjargul</i>	NTNU-VM-76305	MT654645	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus yrjargul</i>	NTNU-VM-76306	MT654643	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus yrjargul</i>	NTNU-VM-76308	MT654644	Korshunova et al. (2021)
Dendronotidae	<i>Dendronotus zakuro</i>	KSNHM OP0485.1	MN808562	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus zakuro</i>	KSNHM OP0485.2	MN808563	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus zakuro</i>	MIMB42242	MZ770730	Ekimova et al. (2021)
Dendronotidae	<i>Dendronotus zakuro</i>	MIMB42244	MZ770729	Ekimova et al. (2021)
Dendronotidae	<i>Dendronotus zakuro</i>	ZMMU:Op-700	MN808561	Martynov et al. (2020)
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7853	PQ415747	This study
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7854	PQ415748	This study
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7855	PQ415749	This study
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7856	PQ415750	This study
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7857	PQ415751	This study
Dendronotidae	<i>Dendronotus zakuro</i>	MMRBK7858	PQ415752	This study
Dendronotidae	<i>Pseudobornella orientalis</i>	ZMMU:Op-664	MT654637	Korshunova et al. (2021)
Dotidae	<i>Doto amyra</i>	CASIZ179473a	KJ486701	Shipman and Gosliner (2015)
Dotidae	<i>Doto greenamyri</i>	CSIZ185101	KJ486715	Shipman and Gosliner (2015)
Tritoniidae	<i>Myrella antarctica</i>	CASIZ171177	HM162718	Pola and Gosliner (2010)
Tritoniidae	<i>Myrella challengeriana</i>	ZSM20061113	MW444250	Moles et al. (2021)

