Zootaxa 4747 (3): 495–513
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4747.3.4
http://zoobank.org/urn:lsid:zoobank.org:pub:357D0749-89D1-4DE4-8BDE-A32F40C4EF38

Three new species of the genus *Dendronotus* from Japan and Russia (Mollusca, Nudibranchia)

ALEXANDER MARTYNOV[1,7], YOSHIHIRO FUJIWARA[2], SHINJI TSUCHIDA[2], RIE NAKANO[3], NADEZHDA SANAMYAN[4], KAREN SANAMYAN[4], KARIN FLETCHER[5] & TATIANA KORSHUNOVA[1,6]
[1]*Zoological Museum, Moscow State University, Bolshaya Nikitskaya Str. 6, 125009 Moscow, Russia*
[2]*Japan Agency for Marine-Earth Science & Technology, 2-15 Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan*
[3]*Kuroshio Biological Research Foundation, 560-I, Nishidomari, Otsuki, Hata-Gun, Kochi, 788-0333 Japan*
[4]*Kamchatka Branch of Pacific Geographical Institute FEB RAS, Partizanskaya Str. 6, 683000 Petropavlovsk-Kamchatsky Russia*
[5]*Milltech Marine, Port Orchard Washington, 98366, USA*
[6]*Koltzov Institute of Developmental Biology RAS, 26 Vavilova Str., 119334 Moscow, Russia*
[7]*Corresponding author. E-mail: martynov@zmmu.msu.ru*

Abstract

Three new species of the genus *Dendronotus* are described from the North Pacific waters of Japan and Russia. For the first time since 1949, three new species, ***D. jamsteci*** **sp. nov.**, ***D. zakuro*** **sp. nov.** and *D.* ***bathyvela*** **sp. nov.** are described from the waters of the Japanese Islands. ***D. zakuro*** **sp. nov.** was also discovered in the waters of Russia (Kamchatka). The descriptions of the new species ***D. jamsteci*** **sp. nov.** and ***D. zakuro*** **sp. nov.** are based on morphological and molecular data; *D.* ***bathyvela*** **sp. nov.** morphologically belongs to the group of *D. robustus*, *D. velifer* and *D. patricki*. This study revises our knowledge of North Pacific species of the genus *Dendronotus*, considerably expands the number of species worldwide and contributes to the multilevel fine-scale diversity concept.

Key words: morphological data, molecular phylogeny, multilevel fine-scale diversity, new species, North Pacific Ocean, taxonomy

Introduction

The genus *Dendronotus* is a common nudibranch taxon in the northern waters of the Atlantic and Pacific oceans. While North Pacific species, including Russian and North American fauna, have had a long history of investigations (e.g. MacFarland 1966; Robilliard 1969, 1970, 1972, 1975; Roginskaya 1987, 1997; Martynov & Korshunova 2011) and have recently received considerable attention (e.g. Martynov *et al.* 2015a,b; Ekimova *et al.* 2015; Korshunova *et al.* 2016a,b, 2017; Lundin *et al.*, 2017; Valdés *et al.* 2018; Korshunova *et al.* 2019a), the Japanese species of the genus *Dendronotus* are rarely visited and insufficiently studied. Because of its abundance and diversity, the genus *Dendronotus* is a good model group to study various taxonomic, phylogenetic and biogeographic problems (Martynov & Korshunova 2011; Korshunova *et al.* 2016a; Lundin *et al.* 2017). Furthermore, is the first genus of nudibranchs to which principles of a previously outlined ontogenetic taxonomy (Martynov 2012; Martynov *et al.* 2015) were applied at the species level in the work by Ekimova *et al.* (2015) according to the original idea by A.V. Martynov.

There are 26 currently recognized species in the genus *Dendronotus* (MolluscaBase 2019). However, *Dendronotus* species diversity is still insufficiently known, despite the recent progress. In the Northern part of the Japanese Islands, only a single species has been recorded (Baba 1993). In 2018, several *Dendronotus* species known from other Pacific locations were recorded in Japan (Nakano 2018) and confirmed using molecular and morphological data (Korshunova *et al.* 2019a). Since 1949, when *D. gracilis* was described (Baba 1949), no new *Dendronotus* species have been described from the Japanese Islands despite the region being the subject of numerous taxonomic studies and new nudibranch descriptions. For the first time, during the present study deep-sea samples were collected not only by dredging operations, but also by using special bio-tracking base stations with remotely controlled manipulators, a method that currently is employed by the Japan Agency for Marine-Earth Science & Technology (e.g. Jamstec 2013), to reveal the diversity of the genus *Dendronotus* in Japan. To further study the composition of the *Dendronotus* genus, we have examined new materials encompassing both sides of the North Pacific waters of the Japanese, Russian and North American coasts (with a focus on the NW Pacific fauna) and describe three new species of the genus *Dendronotus*, which belong to three different clades of the genus.

Materials and methods

Collecting data. Shallow-water species were collected in Usujiri (North West Pacific, Hokkaido, Japan), Starichkov Islands (North West Pacific, Kamchatka, Russia), and Port Orchard (North East Pacific, Washington, USA) by SCUBA diving and stored in the Zoological Museum Moscow State University (ZMMU) and the Natural History Museum, Kishiwada City (KSNHM). Deep-sea species off Sanriku, the northern part of Honshu (Japan), were collected during surveys by the Japan Agency for Marine-Earth Science & Technology (JAMSTEC) from long-term bio-tracking base stations using remotely controlled manipulators, and by the National Museum of Nature and Science (NSMT) during dredging operations. Specimens are stored in each institution and museum respectively. All specimens were preserved in 80–95% EtOH, except those collected by NSMT, which were preserved in formalin.

Molecular analysis. Seven specimens of the genus *Dendronotus* were sequenced for the mitochondrial genes cytochrome c oxidase subunit I (COI) and 16S rRNA, and the nuclear genes 28S rRNA (C1-C2 domain). Small pieces of tissue were used for DNA extraction with Diatom™ DNA Prep 100 kit by Isogene Lab, according to the producer's protocols. Standard PCR amplifications and sequencing were applied (for details, see Korshunova *et al.* 2018). COI sequences were translated into amino acids to verify coding regions and avoid improper base-calling. All new sequences were deposited in GenBank (Table 1, highlighted in bold). Publicly available sequences of *Dendronotus* species plus several outgroup taxa (*Tritonia*, *Marionia*, and *Notobryon*) were also included in the molecular analysis. Phylogenetic analysis was performed using forty-seven specimens of the genus *Dendronotus*, and six outgroup specimens (Table 1). Sequences were aligned with the MAFFT algorithm (Katoh *et al.* 2002). Separate analyses were conducted for COI (658 bp), 16S (466 bp), 28S (347 bp), and the concatenated dataset (1471 bp). The GTR+I+G model was chosen for the concatenated datasets using MrModelTest 2.3 (Nylander *et al.* 2004). Two different phylogenetic methods, Bayesian inference (BI) and Maximum Likelihood (ML), were used to infer evolutionary relationships. Bayesian estimation of posterior probability was performed in MrBayes 3.2 (Ronquist *et al.* 2012). Four Markov chains were sampled at intervals of 1000 generations; a 25% majority rule consensus tree (contype = halfcompat) was calculated. Analysis was started with random starting trees and 10^7 generations. Maximum Likelihood based phylogeny inference was performed in GARLI 2.0 (Zwickl, 2006) with bootstrap in 1000 pseudo-replications. Final phylogenetic tree images were rendered in FigTree 1.4.2. Nodes in the phylogenetic trees with Bayesian posterior values > 0.96% and bootstrap values > 90% were considered 'highly' supported, nodes with 0.90–0.95% and 80–89% accordingly were considered 'moderately' supported (lower support values were considered not significant, Korshunova *et al.* 2018). The program MEGA7 (Kumar *et al.* 2016) was used to calculate the uncorrected p-distances between all the sequences and for revealing the maximum intra- and minimum interspecific genetic distances. Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2012) was used to estimate *Dendronotus* species (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html). Alignment from the COI markers were submitted and processed in ABGD using the Jukes-Cantor (JC69) and Kimura (K80) models and the following settings: a prior for the maximum value of intraspecific divergence between 0.001 and 0.1, 10 recursive steps.

Morphological analysis. All specimens were examined with a stereomicroscope (MBS-9) and photographed using Nikon D-90, D-600 and D-810 digital cameras with a set of extension rings. The reproductive systems were investigated under stereomicroscope. The pharynxes were removed and processed with a weak solution of domestic bleach (NaClO). The jaws and radulae were examined under a scanning electron microscope (JSM and CamScan Series II) at the National Museum of Nature and Science (Japan, Tsukuba) and the electron microscopy laboratory of the Biological Facility of Moscow State University.

TABLE 1. List of specimens used for the molecular analyses.

Species name	Voucher	Locality	COI	16S	28S
Dendronotus albus MacFarland, 1966	ZMMU:Op-566	USA: Washington	KX788135	KX788123	KX788114
Dendronotus albus MacFarland, 1966	LACM:2004-2.2	USA: California	KX058081	KX058121	KX058093
Dendronotus arcticus Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016	ZMMU:Op-561	Russia: Laptev Sea	KX788140	KX788129	KX788118
Dendronotus arcticus Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016	ZMMU:Op-562	Russia: Laptev Sea	KX788141	KX788130	KX788119
Dendronotus dalli Bergh, 1879	ZMMU:Op-330	Russia: Kamchatka	KM396999	KM397081	KM397040
Dendronotus dalli Bergh, 1879	ZMMU:Op-331	Russia: Kamchatka	KM397000	KM397082	KM397041
Dendronotus frondosus (Ascanius, 1774)	ZMMU:Op-380	Norway	KM396976	KM397056	KM397017
Dendronotus frondosus (Ascanius, 1774)	ZMMU:Op-588	Norway	KY391832	KY391852	KY391870
Dendronotus europaeus Korshunova, Martynov, Bakken & Picton, 2017	ZMMU:Op-554	Norway	KY391823	KY391842	KY391860
Dendronotus europaeus Korshunova, Martynov, Bakken & Picton, 2017	ZMMU:Op-581	UK: Irish Sea	KY391826	KY391845	KY391863
Dendronotus iris J. G. Cooper, 1863	CASIZ:174471	USA: Washington	KX058083	HM162631	KX058096
Dendronotus iris J. G. Cooper, 1863	LACM:174194	USA: Washington	KX058082	GU339188	KX058095
Dendronotus jamsteci **sp. nov.**	JAMSTEC No. 1160047463	Japan	**MN808558**	**MN811023**	**MN811017**
Dendronotus jamsteci **sp. nov.**	JAMSTEC No. 1160047475	Japan	**MN808559**	**MN811024**	-
Dendronotus kalikal Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-657	Russia: Matua	MK302458	MK302453	MK302465
Dendronotus kalikal Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-349	Russia: Kamchatka	KM396987	KM397069	KM397028
Dendronotus kamchaticus Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-245	Russia: Kamchatka	KC660032	KC611288	KC660016
Dendronotus kamchaticus Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-565	USA: Washington	KX788144	KX788111	KX788121
Dendronotus lacteus (W. Thompson, 1840)	ZMMU:Op-584	Norway	KY391830	KY391849	KY391867
Dendronotus lacteus (W. Thompson, 1840)	ZMMU:Op-587	Russia: Franz Josef Land	KY391838	KY391851	KY391869
Dendronotus niveus Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-269	Russia: White sea	KM396996	KM397078	KM397037
Dendronotus niveus Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015	ZMMU:Op-279	Russia: Barents Sea	KM396995	KM397077	KM397036
Dendronotus patricki Stout, Wilson & Valdés, 2011	SIO-BIC M12133	USA: California	HQ225828	HQ225829	-

......continued on the next page

TABLE 1. (Continued)

Species name	Voucher	Locality	COI	16S	28S
Dendronotus primorjensis Martynov, Sanamyan & Korshunova, 2015	ZMMU:Op-419	Russia: Sea of Japan	KX672010	KX672008	KX672006
Dendronotus primorjensis Martynov, Sanamyan & Korshunova, 2015	ZMMU:Op-420	Russia: Sea of Japan	KX672011	KX672009	KX672007
Dendronotus primorjensis Martynov, Sanamyan & Korshunova, 2015	ZMMU:Op-639	Japan	MK302456	MK302451	MK302463
Dendronotus primorjensis Martynov, Sanamyan & Korshunova, 2015	ZMMU:Op-640	Japan	MK302457	MK302452	MK302464
Dendronotus primorjensis Martynov, Sanamyan & Korshunova, 2015	KSNHM:OP0485	Japan	**MN808560**	**MN811025**	-
Dendronotus regius Pola & Stout, 2008	CASIZ:179492	Philippines	HM162708	HM162629	-
Dendronotus regius Pola & Stout, 2008	CASIZ:179493	Philippines	JN869451	JN869407	-
Dendronotus robilliardi Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016	ZMMU:Op-567	Russia: Kamchatka	KX788136	KX788124	KX788115
Dendronotus robilliardi Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016	ZMMU:Op-447	Russia: Kamchatka	KX788139	KX788127	KX788117
Dendronotus robilliardi Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016	ZMMU:Op-659	USA: Washington	MK302459	MK302454	MK302466
Dendronotus robustus A. E. Verrill, 1870	ZMMU:Op-343	Russia: Barents Sea	KM397002	KM397084	KM397043
Dendronotus robustus A. E. Verrill, 1870	ZMMU:Op-390-5	Russia: Barents Sea	KM396968	KM397051	KM397009
Dendronotus rufus O'Donoghue, 1921	LACM:174861	USA: Alaska	KX058084	GU339191	KX058097
Dendronotus rufus O'Donoghue, 1921	LACM:174863	USA: Alaska	KX058085	KX058122	KX058098
Dendronotus subramosus MacFarland, 1966	ZMMU:Op-699	USA: Washington	**MN808564**	**MN811029**	**MN811020**
Dendronotus subramosus MacFarland, 1966	LACM:174192	USA: California	-	GU339192	KX058100
Dendronotus subramosus MacFarland, 1966	LACM:174868	USA: California	-	KX058123	KX058099
Dendronotus velifer G. O. Sars, 1878	ZMMU:Op-348	Russia: Kara Sea	MF685027	KY996407	MK302461
Dendronotus velifer G. O. Sars, 1878	ZMMU:Op-546	Russia: Laptev Sea	KY996409	KY996405	MK302462
Dendronotus venustus MacFarland, 1966	ZMMU:Op-660	USA: Washington	MK302460	MK302455	MK302467
Dendronotus venustus MacFarland, 1966	LACM:174850	USA: California	HM162709	HM162630	-
Dendronotus zakuro **sp. nov.**	KSNHM: OP0485	Japan	**MN808562**	**MN811027**	**MN811019**
Dendronotus zakuro **sp. nov.**	KSNHM:OP0485	Japan	**MN808563**	**MN811028**	-
Dendronotus zakuro **sp. nov.**	ZMMU:Op-700	Russia: Kamchatka	**MN808561**	**MN811026**	**MN811018**
Marionia arborescens Bergh, 1890	CASIZ:177578	Philippines	HM162722	HM162646	-
Marionia blainvillea (Risso, 1818)	CASIZ:176812	Portugal	HM162721	HM162645	-
Notobryon thompsoni Pola, Camacho-Garcia & Gosliner, 2012	CASIZ:176362	South Africa	JN869456	JN869413	-
Notobryon wardi Odhner, 1936	CASIZ:177540	Philippines	JN869454	JN869411	-
Tritonia nilsodhneri Marcus Ev., 1983	CASIZ:176219	South Africa	HM162716	HM162641	-
Tritonia plebeia Johnston, 1828	ZMMU:Op-572	Norway	KX788134	KX788122	KX788132

Results

Molecular phylogeny

Bayesian Inference (BI) and Maximum Likelihood (ML) analyses based on the combined dataset for the mitochondrial COI and 16S and the nuclear 28S genes yielded similar results (Fig. 1). Unresolved polytomies in the BI tree correspond to lower supported clades in the ML tree (Fig S1). All *Dendronotus* constitute a highly supported clade (PP = 1, BS = 99). (Fig 1.) Twenty-one species of the genus *Dendronotus* form maximal or highly supported separate clades.

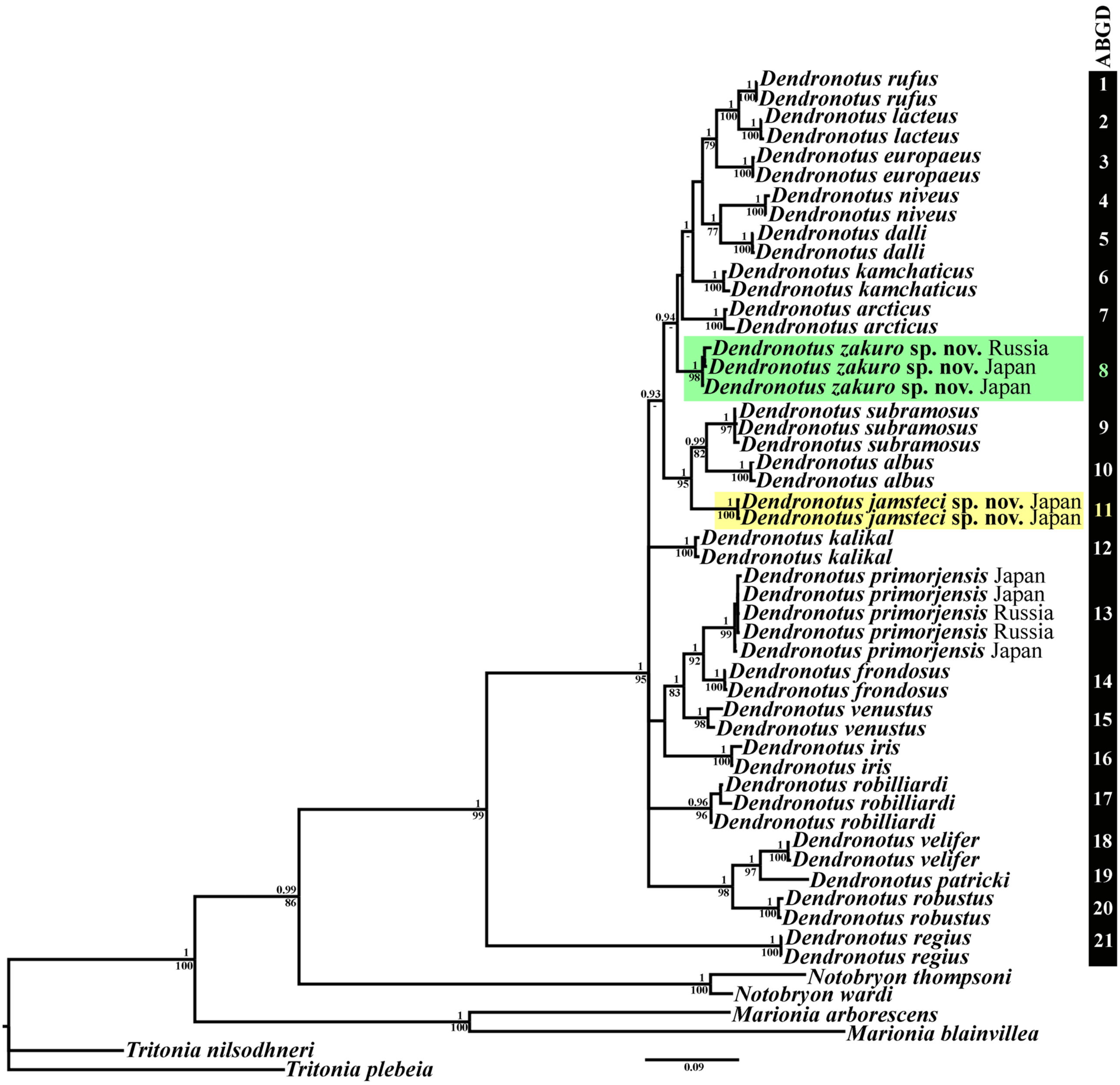

FIGURE 1. Phylogenetic relationships of the species of the genus *Dendronotus* based on COI + 16S + 28S concatenated dataset inferred by Bayesian inference (BI). Numbers above branches represent posterior probabilities from BI; numbers below branches indicate bootstrap values for Maximum Likelihood. Summary of species delimitation results are noted by numbered, clusters from the ABGD analyses for the COI dataset.

D. regius Pola & Stout, 2008 forms a maximally supported separate clade, sister to a clade containing all other species of the genus *Dendronotus* analysed here. Three *D.* ***zakuro*** **sp. nov.** (see descriptions of the new species below) are clustered together (PP = 1, BS = 98). Clade *D.* ***zakuro*** **sp. nov.** has the closest position to the clades *D. arcticus*, *D. dalli*, *D. kamchaticus, D. niveus*, *D. lacteus*, *D. europaeus* and *D. rufus*, but with moderate/low support (PP = 0.94, BS = 61). Maximum intraspecific genetic distance amongst the *D.* ***zakuro*** **sp. nov.** clade is 1.1% for the COI marker (Table 2). The lowest COI interspecific distance of 5.33% is found between *D.* ***zakuro*** **sp. nov.** and *D. europaeus* Korshunova, Martynov, Bakken & Picton, 2017. *D.* ***jamsteci*** **sp. nov.** are clustered in a maximally supported clade (PP = 1, BS = 100) that is sister (PP = 1, BS = 95) to the clade containing *D. albus* MacFarland, 1966 and *D. subramosus* MacFarland, 1966 (PP = 0.99, BS = 82), which was successfully sequenced for the COI gene for the first time. Intraspecific genetic distance amongst the *D.* ***jamsteci*** **sp. nov.** clade is 0.47% for the COI marker. The lowest COI interspecific distance of 6.64% is found between *D.* ***jamsteci*** **sp. nov.** and *D. frondosus* (Ascanius, 1774). Unresolved evolutionary ties were revealed for *D. kalikal* Ekimova, Korshunova, Schepetov, Neretina, Sanamyan & Martynov, 2015 and *D. robilliardi* Korshunova, Sanamyan, Zimina, Fletcher & Martynov, 2016, and *D. iris* J. G. Cooper, 1863, whereas *D. velifer* G. O. Sars, 1878, *D. patricki* Stout, Wilson & Valdés, 2011, and *D. robustus* A. E. Verrill, 1870 show close evolutionary relationships, as well as another group *D. primorjensis*, *D. frondosus*, and *D. venustus* MacFarland, 1966. *D. robustus, D. patricki,* and *D. velifer* clustered together in a separate clade with the high support (PP = 1, BS = 98), that branched to three clades. *D. patricki* and *D. velifer* clustered in two distinct and separated sister clades (PP = 1, BS = 97) that formed the sister group to the *D. robustus* clade. *D. primorjensis*, *D. frondosus*, and *D. venustus* clustered together in another separate clade with moderate support (PP = 1, BS = 83), that branched to three clades. The first clade (PP = 1, BS = 98) includes *D. venustus.* This clade is sister to the clade divided into two subclades: *D. frondosus* and *D. primorjensis*. *D. primorjensis* Martynov, Sanamyan, Korshunova, 2015 from Japan are clustered in a highly supported clade (PP = 1, BS = 99) together with the type specimens of *D. primorjensis* from Russia.

The ABGD analysis of the COI data set run with two different models revealed twenty- one potential *Dendronotus* species. ABGD results are fully concordant with the clades in the molecular phylogenetic analysis (Fig. 1). Thereby, two new species of the genus *Dendronotus* were identified through clarification of their phylogenetic relationships.

Molecular genetic analysis supports recognition of two new species *D.* ***zakuro*** **sp. nov.** and *D.* ***jamsteci*** **sp. nov.** within the genus *Dendronotus*. Molecular data for *D* ***bathyvela*** **sp.nov.** is not available because of the formaline-based fixation of the material so a comparison was performed based on the morphological data.

Systematics

Family Dendronotidae

Dendronotus jamsteci **sp. nov.**
(Figures 1–2, 5A)
http://zoobank.org/B8DAC5AC-56F4-4C92-90EC-D48C5173772A

Type material. Holotype, JAMSTEC No. 1160047475, 17.5 mm long preserved, dissected, Cruise KS-16-J03, on board ID HPD #1952, Japan, Northern Honshu, off Otsuchi, 39° 18.5378' N 142° 17.82' E, 08 March 2016, depth—670 m, collector Shinji Tsuchida. One paratype, JAMSTEC No. 1160047461, Cruise KS-16-J03, on board ID HPD #1952-07, Dive No. HPD #1952, 21.5 mm long (preserved), Japan, Northern Honshu, off Otsuchi, 39° 18.4453' N 142° 18.0498' E, 08 March 2016, depth—761 m, collector Shinji Tsuchida. Five paratypes, JAMSTEC No. 1160047464, Cruise KS-16-J03, on board ID HPD #1952-10, Dive No. HPD #1952, 2–7 mm long (preserved), Japan, Northern Honshu, off Otsuchi, 39° 18.4453' N 142° 18.0498' E, 08 March 2016, depth—761 m, collector Shinji Tsuchida. Ca. 60 paratypes, JAMSTEC No. 1160047463, Cruise KS-16-J03, on board ID HPD #1952-09, Dive No. HPD #1952, 1.5–15 mm long (preserved), Japan, Northern Honshu, off Otsuchi, 39°18.4453' N 142°18.0498' E, 08 March 2016, depth—761 m, collector Shinji Tsuchida. Three paratypes, JAMSTEC No. 1160047392, Cruise KS-16-J03, on board ID HPD #1950-16, Dive No. HPD #1950, 11–11.5 mm long (preserved), Japan, Northern Honshu, off Otsuchi, 39° 18.7059' N 142° 18.0498' E, 05 March 2016, depth—684 m, collector Shinji Tsuchida. Nine paratypes, JAMSTEC No. 1160047475, Cruise KS-16-J03, on board ID HPD #1952, 2 –21 mm long, Japan, Northern Honshu, off Otsuchi, 39° 18.5378' N 142° 17.82' E, 08 March 2016, depth—670 m, collector Shinji Tsuchida. Three paratypes, JAMSTEC No. 1160047380, Cruise KS-16-J03, on board ID HPD #1950-

TABLE 2. Maximum intraspecific (highlighted in bold) and minimum interspecific genetic distances (%) for COI marker in *Dendronotus* species.

	D. jamsteci **sp. nov.**	***D. zakuro*** **sp. nov.**	***D. robilliardi***	***D. venustus***	***D. primorjensis***	***D. frondosus***	***D. subramosus***	***D. albus***	***D. kamchaticus***	***D. arcticus***
D. jamsteci **sp. nov.**	**0.47**	6.81	9.75	7.76	8.11	6.64	7.23	8.12	9.25	8.18
D. zakuro **sp. nov.**	6.81	**1.10**	8.64	7.16	7.36	7.18	7.02	6.62	5.47	5.50
D. robilliardi	9.75	8.64	**1.58**	10.31	8.71	9.47	10.79	10.18	9.25	9.25
D. venustus	7.76	7.16	10.31	**2.07**	5.71	5.34	8.43	7.60	8.42	8.12
D. primorjensis	8.11	7.36	8.71	5.71	**0.63**	4.23	7.99	8.70	9.06	9.63
D. frondosus	6.64	7.18	9.47	5.34	4.23	**0.16**	7.4	8.83	9.24	8.84
D. subramosus	7.23	7.02	10.79	8.43	7.99	7.4	-	6.42	8.32	9.10
D. albus	8.12	6.62	10.18	7.60	8.70	8.83	6.42	**0.78**	8.27	8.45
D. kamchaticus	9.25	5.47	9.25	8.42	9.06	9.24	8.32	8.27	**0.94**	7.46
D. arcticus	8.18	5.50	9.25	8.12	9.63	8.84	9.10	8.45	7.46	**1.1**
D. niveus	7.83	5.71	7.96	7.79	8.53	8.16	8.54	6.61	6.74	7.02
D. dalli	9.17	6.22	9.66	8.71	10.48	10.28	10.68	9.43	6.17	7.16
D. rufus	8.39	6.57	9.45	9.45	10.46	9.66	8.86	9.46	6.57	7.76
D. lacteus	9.31	6.56	9.82	9.07	10.44	9.29	9.23	10.01	7.47	8.11
D. europaeus	7.63	5.33	9.23	7.75	10.27	9.30	8.29	7.73	6.88	6.24
D. kalikal	8.50	7.10	8.65	9.21	7.78	8.31	8.68	7.71	9.73	7.11
D. iris	9.79	8.88	9.04	7.63	8.90	8.14	10.59	10.50	10.84	9.15
D. velifer	12.20	11.24	12.82	10.57	10.78	11.76	12.79	12.07	12.69	11.62
D. patricki	11.81	11.46	12.94	10.99	11.16	10.98	12.56	12.95	13.30	12.65
D. robustus	12.46	11.46	12.38	11.63	12.49	12.04	12.78	11.95	13.09	11.33
D. regius	15.35	13.34	14.13	14.43	13.31	14.76	13.54	14.60	15.50	14.21

......continued on the next page

TABLE 2. (Continued)

	D. niveus	*D. dalli*	*D. rufus*	*D. lacteus*	*D. europaeus*	*D. kalikal*	*D. iris*	*D. velifer*	*D. patricki*	*D. robustus*	*D. regius*
***D. jamsteci* sp. nov.**	7.83	9.17	8.39	9.31	7.63	8.50	9.79	12.20	11.81	12.46	15.35
***D. zakuro* sp. nov.**	5.71	6.22	6.57	6.56	5.33	7.10	8.88	11.24	11.46	11.46	13.34
D. robilliardi	7.96	9.66	9.45	9.82	9.23	8.65	9.04	12.82	12.94	12.38	14.13
D. venustus	7.79	8.71	9.45	9.07	7.75	9.21	7.63	10.57	10.99	11.63	14.43
D. primorjensis	8.53	10.48	10.46	10.44	10.27	7.78	8.90	10.78	11.16	12.49	13.31
D. frondosus	8.16	10.28	9.66	9.29	9.30	8.31	8.14	11.76	10.98	12.04	14.76
D. subramosus	8.54	10.68	8.86	9.23	8.29	8.68	10.59	12.79	12.56	12.78	13.54
D. albus	6.61	9.43	9.46	10.01	7.73	7.71	10.50	12.07	12.95	11.95	14.60
D. kamchaticus	6.74	6.17	6.57	7.47	6.88	9.73	10.84	12.69	13.30	13.09	15.50
D. arcticus	7.02	7.16	7.76	8.11	6.24	7.11	9.15	11.62	12.65	11.33	14.21
D. niveus	**0.16**	5.32	6.61	7.15	6.09	7.18	9.72	11.13	11.14	10.89	12.09
D. dalli	5.32	**0.16**	6.94	7.12	6.55	8.87	10.55	12.75	12.73	11.48	12.76
D. rufus	6.61	6.94	**0**	3.53	5.49	9.02	10.10	13.75	13.46	10.84	14.44
D. lacteus	7.15	7.12	3.53	**0.16**	6.36	9.37	10.85	14.11	13.62	10.63	14.24
D. europaeus	6.09	6.55	5.49	6.36	**0**	8.05	9.72	12.11	11.87	11.10	14.22
D. kalikal	7.18	8.87	9.02	9.37	8.05	**0.62**	7.63	11.45	11.07	12.30	12.67
D. iris	9.72	10.55	10.10	10.85	9.72	7.63	**0.31**	11.64	10.42	11.60	13.52
D. velifer	11.13	12.75	13.75	14.11	12.11	11.45	11.64	**0.31**	4.64	7.21	14.28
D. patricki	11.14	12.73	13.46	13.62	11.87	11.07	10.42	4.64	-	8.49	14.37
D. robustus	10.89	11.48	10.84	10.63	11.10	12.30	11.60	7.21	8.49	**0.78**	14.28
D. regius	12.09	12.76	14.44	14.24	14.22	12.67	13.52	14.28	14.37	14.28	**0**

4, 7–18 mm long (preserved), Japan, Northern Honshu, off Otsuchi, 39° 18.6579' N 142° 18.0498' E, 05 March 2016, depth—704 m, collector Shinji Tsuchida.

Type locality. Japan, off the Pacific coast of Northern Honshu.

Etymology. In honour of the Japan Agency for Marine-Earth Science and Technology (JAMSTEC) which has made a considerable contribution to the understanding of deep-sea fauna in Japan and worldwide.

Diagnosis. Body elongate, 6–7 pairs dorsolateral appendages, colour whitish with brownish spots and streaks, central tooth with well-defined denticles and furrows, vas deferens moderate in length, penis conical, moderately narrow.

Description. Body elongate, up to 21.5 mm in length (Fig. 2A, B), 6–9 branched appendages of oral veil, 4–5 appendages of rhinophoral stalks, 12–15 rhinophoral lamellae, branched rhinophoral lateral papilla present, 6–7 pairs dorsolateral appendages, 20–25 lip papillae. Dorsolateral appendages with thickened primary stalk, moderately branched secondary branches, and blunted tertiary branches (Fig. 2A, C). Reproductive and anal openings placed laterally on right side. General colour whitish with scattered distinct opaque white dots on notum, tips of lateral appendages, oral appendages, lip papillae, and rhinophores (Fig. 2C).

The jaws are ovoid with strong dorsal processes, denticles present. Masticatory processes bear ca. 60 denticles (holotype, including simple triangular and broadly lamellated ones (Fig. 2D, E). Radula formula is 33 × 1–6.1.6–1 (paratype 7 mm), 34 × 3–8.1.8–3 (holotype), 38 × 3–8.1.8–3 (paratype 20 mm), 29 × 3–8.1.8–3 (paratype 21.5 mm). Central tooth strongly denticulated and bearing up to 17 distinct denticles (Fig. 2F) with well-defined furrows. Lateral teeth are short, slightly curved, bearing up to 9 long denticles (Fig. 2G).

Reproductive system triaulic (Fig. 5A), ampulla moderately thin, triple folded (Fig 5A, am), prostate consisting of 50–60 alveolar glands (Fig. 5A, pr), vas deferens moderate in length (Fig. 5A, vd) expanding to a narrow penial sheath (Fig. 5A, psh), penis short and conical (Fig. 5A, p), vagina long and twisted (Fig. 5A, vg), bursa copulatrix is medium-sized, rounded (Fig. 5A, bc) with small seminal receptaculum placed distally (Fig. 5A, rs).

Biology. On hydroids within sand and muddy substrates.

Distribution. Presently known only off the Pacific coast of Northern Honshu (Japan), at depths of 670–761 m.

Remarks. *Dendronotus* ***jamsteci*** **sp. nov.** is superficially similar to *D. frondosus* and *D. primorjensis*, but different in the details of 1) colouration: compared to *D. frondosus* and *D. primorjensis*, *D.* ***jamsteci*** **sp. nov.** has a weakly coloured whitish ground colour with dispersed brownish spots), 2) radula: *D.* ***jamsteci*** **sp. nov.** has different number of rows (up to 8 in *D.* ***jamsteci*** **sp. nov.**, up to 9 in *D. primorjensis*, up to 10 in *D. frondosus*) and denticles on the central (up to 17 denticles in *D.* ***jamsteci*** **sp. nov.** , up to 18 in *D. primorjensis*, up to 14 in *D. frondosus*) and lateral tooth (up to 9 denticles in *D.* ***jamsteci*** **sp. nov.** , up to 8 in *D. primorjensis*, up to 7 in *D. frondosus*), and 3) reproductive system: *D.* ***jamsteci*** **sp. nov.** considerably differs in the number of alveolar glands (50–60 in *D.* ***jamsteci*** **sp. nov.**, 12–19 in *D. primorjensis*, 16–30 in *D. frondosus*) as well as details in the patterns of the bursa and copulative organ arrangements. Importantly, according to the molecular phylogenetic data (Fig. 1), *D.* ***jamsteci*** **sp. nov.** doesn't belong to the clade comprised of *D. frondosus*, *D. primorjensis* and *D. venustus* (this species readily differs externally from *D.* ***jamsteci*** **sp. nov.** by its bright yellow markings or large amounts of opaque white pigment) (MacFarland 1966; Stout *et al.* 2010) but is sister to the clade that includes *D. subramosus* and *D. albus*. However, both the latter species are considerably different morphologically from *D.* ***jamsteci*** **sp. nov.**. Particularly, although *D. subramosus* externally shares a similar brownish colouration with *D.* ***jamsteci*** sp. nov. it lacks lateral rhinophoral papilla common in most species of the genus *Dendronotus* including *D.* ***jamsteci*** **sp. nov.** By this feature, it readily differ from *D.* ***jamsteci*** **sp. nov.**, whereas *D. albus* considerably differs from *D.* ***jamsteci*** **sp. nov.** by its uniform whitish or lilac colour and patterns of the radula and reproductive system. Such a discrepancy of molecular and morphological evolution is very interesting. From the NW Pacific species *D. kalikal*, *D.* ***jamsteci*** **sp. nov.** differs by the absence of subparallel brownish dorsal stripes, details of the radula and very significantly by the molecular data (Fig. 1). Two other NW Pacific species, *D. kamchaticus* and ***D. zakuro*** **sp. nov.**, are substantially different from *D.* ***jamsteci*** **sp. nov.** by their colouration and the smooth central teeth of their radula at the adult stage and in addition, they belong to a different molecular clade (Fig. 1). None of these species inhabit bathyal depths as *D.* ***jamsteci*** **sp. nov.** does, and their bathymetric distribution is restricted to shallow waters, not deeper than 60 m. Recently, a deep-sea species off the NE Pacific coast, *D. claguei*, was described (Valdés *et al.* 2018). For that species, only H3 gene data was provided in the cited publication, so the absence of COI and 16S data prevented its use here for molecular analysis

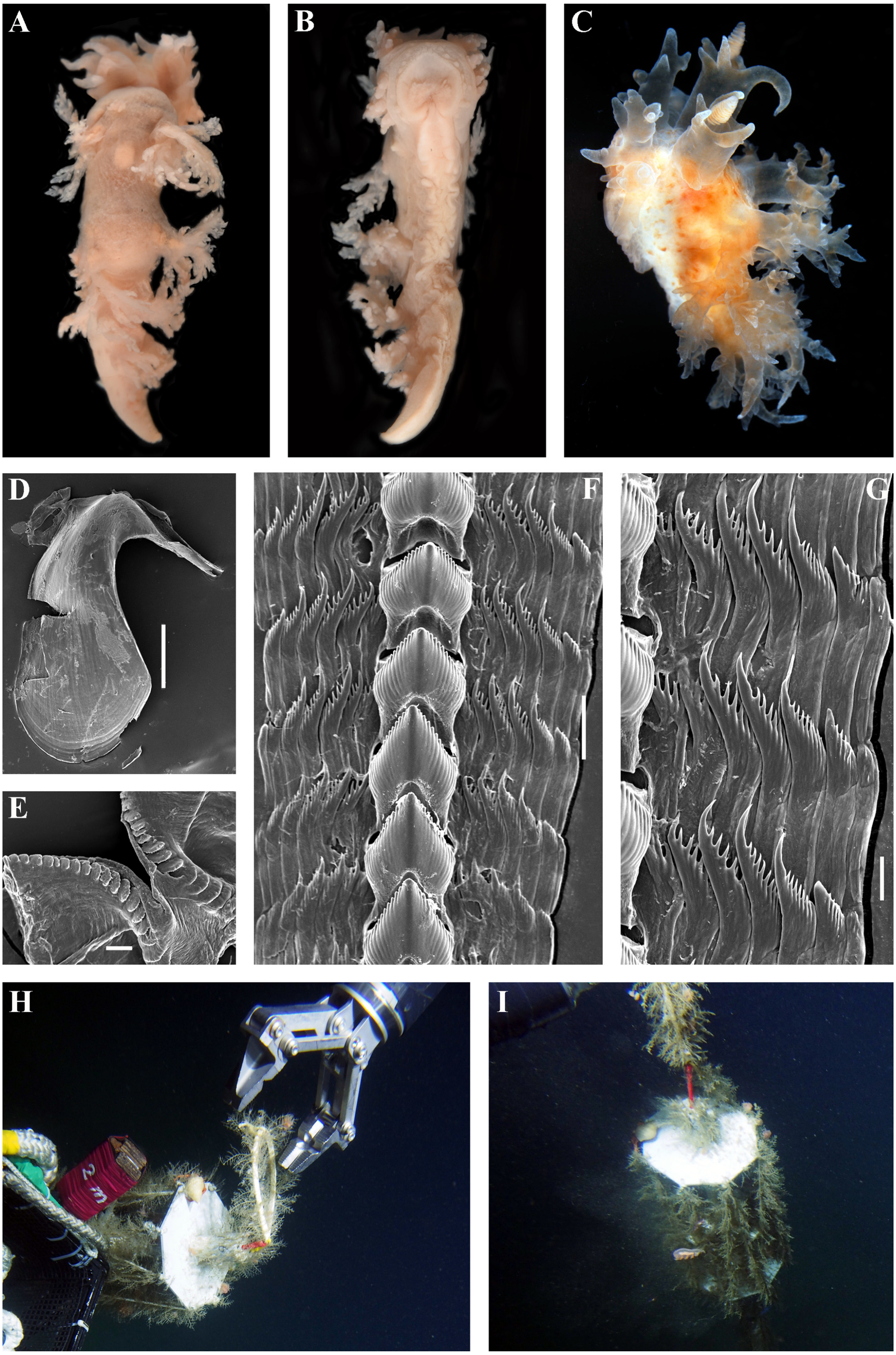

FIGURE 2. *Dendronotus* ***jamsteci*** **sp. nov.** Holotype, JAMSTEC No. 1160047475, 17.5 mm length (preserved), Northern Honshu, off Otsuchi, 670 m depth. **A, B**. Dorsal and ventral views respectively, preserved holotype. **C**. Live holotype. **D**. Jaws, SEM; **E**. Masticatory processes of jaws, SEM; **F**. Radula, posterior part; **G**. Lateral teeth, posterior part. **H**. Collecting of specimens in situ by remotely controlled manipulators. **I**. Overview of one of the bio-tracking base stations installed at the depth 761 m from which specimens were collected. Scale bars: D, 500 µm, E,G, 20 µm, F, 50 µm. Photos: Alexander Martynov (A,B, D–G), Yoshihiro Fujiwara (C, H, I).

because the H3 gene is almost identical for closely related species of the genus *Dendronotus*. *D. claguei* fundamentally differs from *D.* ***jamsteci*** **sp. nov.** by its uniform translucent white colour, radular details, and in addition *D. claguei* inhabits upper abyssal depths (2369 m) and not upper bathyal depths (670–761 m) as *D.* ***jamsteci*** **sp. nov.** does. Maximum intraspecific and minimum interspecific genetic distances for the COI marker in the species of the genus *Dendronotus* including ***D. jamsteci*** **sp. nov**. are presented in Table 2.

Dendronotus zakuro **sp. nov.**

(Figures 1, 3, 5B)

http://zoobank.org/ 3B54EB14-A55E-42C5-B962-82D6A40B9BF5

Type material. Holotype, ZMMU Op-700, 30 mm long live, 15 mm preserved, dissected, Russia, Kamchatka, Starichkov Island, 17.07.2015, depth—12 m, on stones, collector N.P. Sanamyan. Two paratypes, KSNHM-OP0485, Japan, Hokkaido, Usujiri, 10 and 12 mm long (preserved), 13.03.2016, depth 10–20 m, stones, collector Sho Kashio. One paratype, ZMMU Op-664, 25 mm long live, Japan, Honshu, Echizen Coast, Fukui Prefecture, 19.04.2018, depth 7.1 m, collector Chihiro Dairi.

Type locality. Russia (Kamchatka) and Japan (Hokkaido; Honshu: Sea of Japan).

Etymology. From *zakuro* (ザクロ, 石榴、柘榴), meaning in Japanese “pomegranate”, after a striking red to red-brownish colouration of the new species.

Diagnosis. Body elongate, 6–7 pairs dorsolateral appendages, colour bright reddish to reddish-brownish with opaque white spots, central tooth completely smooth (in adults), lacking denticles and furrows, vas deferens moderate in length, penis massive, long, twisted.

Description. Body elongate, up to 30 mm in length (Fig. 3A–E), 5–7 branched appendages of oral veil, ca. 5 appendages of rhinophoral stalks, 10–11 rhinophoral lamellae, branched rhinophoral lateral papilla present, 6–7 pairs dorsolateral appendages, 25–30 lip papillae. Dorsolateral appendages with elongate primary stalk, moderately relatively highly branched secondary branches, and attenuated tertiary branches (Fig. 3A–E). Reproductive and anal openings placed laterally on right side. General colour bright red to reddish-brownish with thin white broken lines between dorsolateral appendages, also scattered opaque white dots and speckles on dorsal and lateral sides, and on various appendages (Fig. 3 A, D, E).

The jaws are ovoid with strong dorsal processes, denticles present (Fig. 3F–G). Masticatory processes bear up to 120 denticles. Radula formula is 36 × 3–11.1.11–3 (holotype), 34 × 3–12.1.12–3 (paratype, 12 mm). Central tooth completely devoid of denticles and furrows in most parts of the radula (except for the anterior-most juvenile radula in some specimens) only faint traces of the furrows on the surface appear on some teeth in the holotype (Fig. 3H, J); the studied paratype possesses almost completely smooth central teeth throughout the whole radula. Lateral teeth are long, distinctly curved, bearing up to 7 long denticles (Fig. 3I, K).

Reproductive system triaulic (Fig. 5B), ampulla thin, twice folded (Fig. 5B, am), prostate consisting of ca. 25 alveolar glands (Fig. 5B, pr), vas deferens relatively long (Fig. 5B, vd) expanding to voluminous penial sheath (Fig. 5B, psh), penis long and twisted (Fig. 5B, p), vagina long and straight (Fig. 5B, vg), bursa copulatrix is large, rounded, and elongated (Fig. 5B, bc) with small seminal receptaculum placed distally (Fig. 5B, rs).

Biology. Inhabits stony and rocky substrates, 7–20 m.

Distribution. Presently known from three remote locations in the North Western Pacific, from Hokkaido Island and Echizen coast (Honshu) in Japan and Starichkov Island, Kamchatka in Russia. Further intermediate findings on the Kurile Islands between these two remote points are therefore expected.

Remarks. *D.* ***zakuro*** **sp. nov.** by combination of colouration, radular patterns and molecular phylogenetic data well differs from all previously described species of the genus *Dendronotus*. The almost smooth central teeth in adult radular morphology combined with the non-uniform, partly variegated external colouration of *D.* ***zakuro*** **sp. nov.** is only similar to *D. kamchaticus*. However, *D. kamchaticus* is phylogenetically distantly related to *D.* ***zakuro*** **sp. nov.** (Fig. 1). Furthermore, morphologically *D.* ***zakuro*** **sp. nov.** differs from *D. kamchaticus* by bright red to red-brownish colouration (the known range of colouration for *D. kamchaticus* is brownish to transparent greyish, see Korshunova *et al*., 2016a), larger number of rows of lateral teeth and patterns of their denticulations. *D. subramosus* with commonly brownish general colouration considerably differs from *D.* ***zakuro*** **sp. nov.** by the absence of lateral rhinophoral papillae and strongly denticulated central radular teeth. According to molecular phylogenetic analysis,

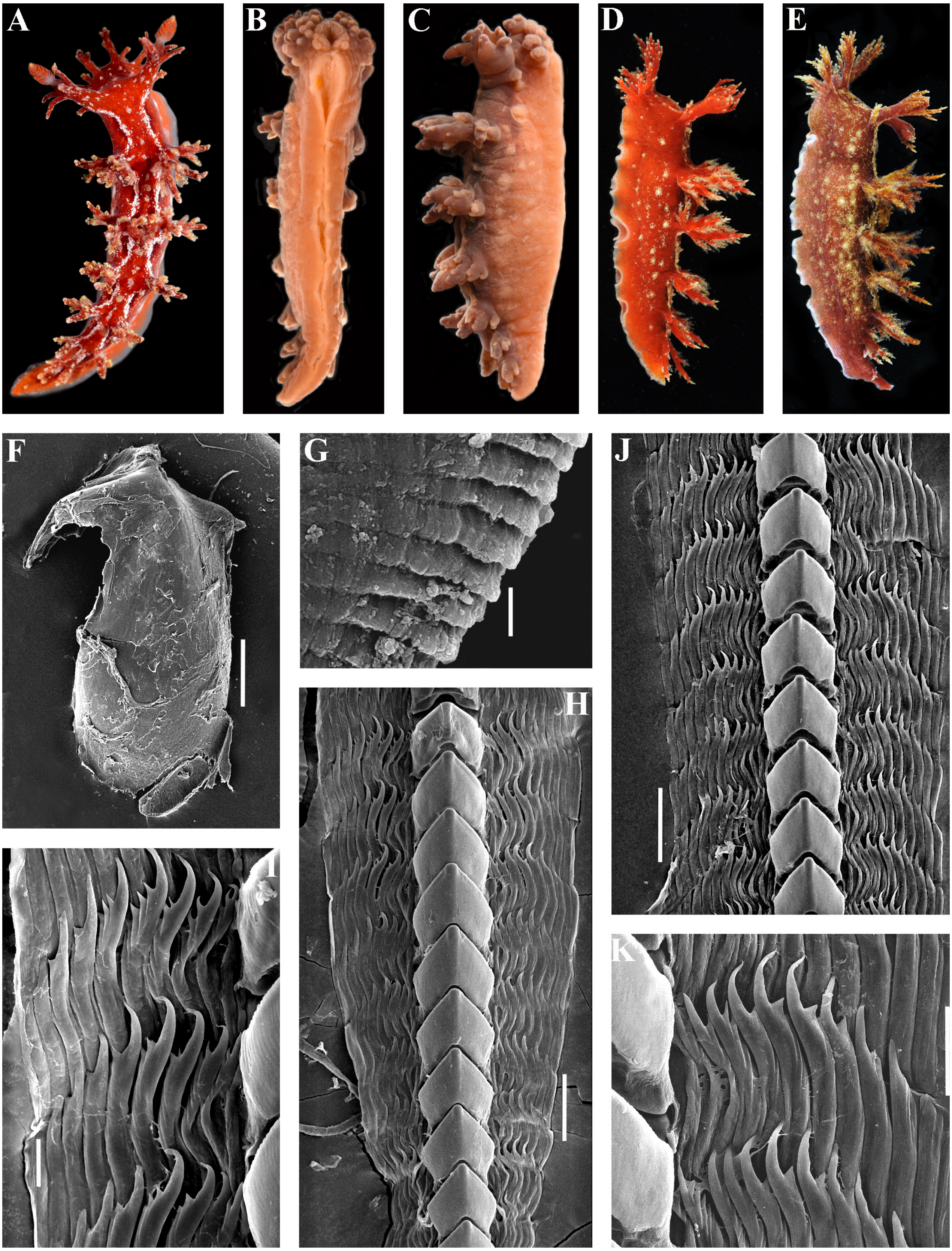

FIGURE 3. *Dendronotus* ***zakuro*** **sp. nov. A–C, F–I**. Holotype, ZMMU-700, Kamchatka, 12 m depth. **D, E, J, K**. Two paratypes KSNHM-OP0485, Hokkaido; **A**. Living animal, dorsal view, 30 mm length; **B-C**. Preserved holotype, ventral and lateral views respectively; **D-E**. Living animals, lateral views; **F**. Jaws, SEM; **G**. Masticatory processes of jaws, SEM; **H**. Radula, posterior part; **I**. Lateral teeth, posterior part. **J**. Radula, posterior part; **K**. Lateral teeth, posterior part. Scale bars: F, 500 µm, G, 10 µm, H, J,100 µm, I, 30 µm, K, 50 µm. Photos: Karen Sanamyan (A), Alexander Martynov (B,C, F–I, J, K), Sho Kashio (D, E).

evolutionary ties for *D. zakuro* **sp. nov.** are not fully clarified. Clade *D.* ***zakuro*** **sp. nov.** has the closest position to the clades *D. arcticus*, *D. dalli*, *D. kamchaticus, D. niveus*, *D. lacteus*, *D. europaeus* and *D. rufus* (Fig. 1), but none of these species (except *D. kamchaticus*) demonstrate any external or internal similarity to *D.* ***zakuro*** **sp. nov.** Maximum intraspecific and minimum interspecific genetic distances for the COI marker in the species of the genus *Dendronotus* including *D.* ***zakuro*** **sp. nov.** are presented in the Table 2.

Dendronotus bathyvela **sp. nov.**

(Figures 4, 5C)

http://zoobank.org/28A36F6D-C221-4C34-B40A-631E3129B943

Type material. Holotype, NSMT-Mo 94455, 45 mm long preserved, dissected, Japan, Tohoku, off Ofunato, Iwate Prefecture, 38° 53.5' N 142° 2.8' E, 18.10.2007, depth 303–307 m, collector K. Hasegawa, H. Komatsu. Three paratypes, NSMT-Mo 94450, 25, 26, 27 mm long (preserved), Japan, Tohoku, off Shimokita Peninsula, Aomori Prefecture, 41° 0.5' N 141° 2.0' E, 10.10.2006, depth 511–510 m, collector T. Kuramochi, T. Fujita. Paratype, NSMT-Mo 94452, 35 mm long (preserved), Japan, Tohoku, off Kinkazan, Miyagi Prefecture, 38° 23.2' N 141° 58.2' E, 04.11.2006, depth 305–309 m, collector H. Komatsu. Paratype, NSMT-Mo 93078, 35 mm long (preserved), Japan, Tohoku, off Kesennuma, Miyagi Prefecture, 38° 4.6' N 141° 55.3' E, 19.11.2005, depth 249 m, collector T. Fujita, H. Saito. Paratype, NSMT-Mo 93080, 21 mm long (preserved), Japan, Tohoku, off Kesennuma, Miyagi Prefecture, 38° 4.2' N 141° 58.9' E, 19.11.2005, depth 306–309 m, collector T. Fujita, H. Saito. Paratype, NSMT-Mo 93061, 14 mm long (preserved), Japan, Tohoku, off Kinkazan, Miyagi Prefecture, 38° 2.3' N 142° 2.1' E, 17.11.2005, depth 382–376 m, collector T. Fujita, H. Saito.

Type locality. Japan, off the Pacific coast of Northern Honshu.

Etymology. From Ancient Greek βάθος (deep sea) + velum (veil) in reference to the deepest record so far known of this wide-bodied *Dendronotus* species with a broad oral veil.

Diagnosis. Body broad, 6–7 pairs dorsolateral appendages, colour dull reddish-brownish with numerous white spots, central tooth with well-defined denticles and furrows, vas deferens moderate in length, penis long, very thin.

Description. Body broad, up to 45 mm in length (Fig. 4A–D), 10–15 long branched appendages of oral veil, 5 appendages of rhinophoral stalks, 15–25 rhinophoral lamellae, branched rhinophoral lateral papilla absent, 6–7 pairs dorsolateral appendages (including smallest posterior ones), ca. 50–70 lip papillae. Dorsolateral appendages with moderate primary stalk, moderately branched secondary branches, and elongated tertiary branches (Fig. 4 A–D). Reproductive and anal openings placed laterally on right side. General colour dull reddish-brownish with numerous distinct opaque white dots on notum, tips of lateral appendages, oral appendages (Fig. 4 D).

The jaws are ovoid with strong dorsal processes, denticles present (Fig. 4E–F). Masticatory processes apparently bear ca 60 denticles. Radula formula is 36 × 1–13.1.13–1 (paratype 21 mm), 41 × 1–12.1.12–1 (paratype 27 mm), 37 × 1–13.1.13–1 (paratype 35 mm), 36 × 1–14.1.14–1 (holotype 45 mm). Central tooth with broad, relatively low cusp, strongly denticulated and bearing up to over 30–35 distinct to small denticles (Fig. 4G). Lateral teeth are long, slightly curved, commonly completely smooth or bearing few (up to 2) weak denticles (Fig. 4H).

Reproductive system triaulic (Fig. 5C), ampulla folded several times (Fig. 5C, am), prostate consisting of 21–25 alveolar glands (Fig. 5C, pr), vas deferens long (Fig. 5C, vd) expanding to elongate penial sheath (Fig. 5C, psh), penis very long, thin (Fig. 5C, p), vagina very long and considerably twisted (Fig. 5C, vg), bursa copulatrix is large, rounded, and elongated (Fig. 5C, bc) with small seminal receptaculum placed distally (Fig. 5C, rs).

Biology. Inhabits sand and muddy substrates with stones.

Distribution. Presently known only off the Pacific coast of Northern Honshu (Japan), at depths of 249–510 m.

Remarks. According to the morphological data *Dendronotus* ***bathyvela*** **sp. nov.** clearly belongs to the group of wide-bodied *Dendronotus* species, which includes only a few species, i.e. *D. patricki, D. robustus* and *D. velifer.* Because all available *D.* ***bathyvela*** **sp. nov.** were formalin-fixed, this prevented us from including this species in the molecular phylogenetic analysis. However, the present morphological data are enough to distinguish *D.* ***bathyvela*** **sp. nov.** from all other wide-bodied species of the genus *Dendronotus*. The abyssal NE Pacific species, *D. patricki,* readily differs from the bathyal NW Pacific *D.* ***bathyvela*** **sp. nov.** by its uniform pinkish colouration (white pigment presents only on apices of dorsolateral and velar appendages, but not on the body) and details of the radula (Stout *et al.,* 2011). Particularly, in *D. patricki* the number of lateral teeth is up to eight, whereas in *D.* ***bathyvela*** **sp. nov.**—up to 14. The number of lateral denticles on the central teeth is about 20 in *D. patricki*, whereas in *D.* ***bathyvela*** **sp. nov.** there are over 30 denticles. Previously, *D. robustus* had been recorded from the Sea of Japan and the Pacific side of Honshu (Roginskaya 1997; Hasegawa 2009). However, the true *D. robustus* from the shallow waters of the North Atlantic (see Lundin *et al.* 2017) considerably differs from the North Pacific material in the details of colouration and the radula. For a long time, *D. velifer* from Northern Europe and the Arctic was also confused with *D. robustus*, however recently it was shown that this is a distinct species, according to both morphological and molecular data (Lundin *et al.* 2017). The following differences between *D. velifer* and *D.* ***bathyvela*** **sp. nov.** are: 1) Appendages of the oral veil in living specimens of *D. velifer* are distinctly shorter than in living *D.* ***bathyvela*** **sp. nov.** (Fig. 4A–D); 2) Large specimens of *D. velifer* commonly bear not more than four main dorsolateral appendages (an exceptionally large specimen was reported as having up to five main appendages plus a sixth smaller one),

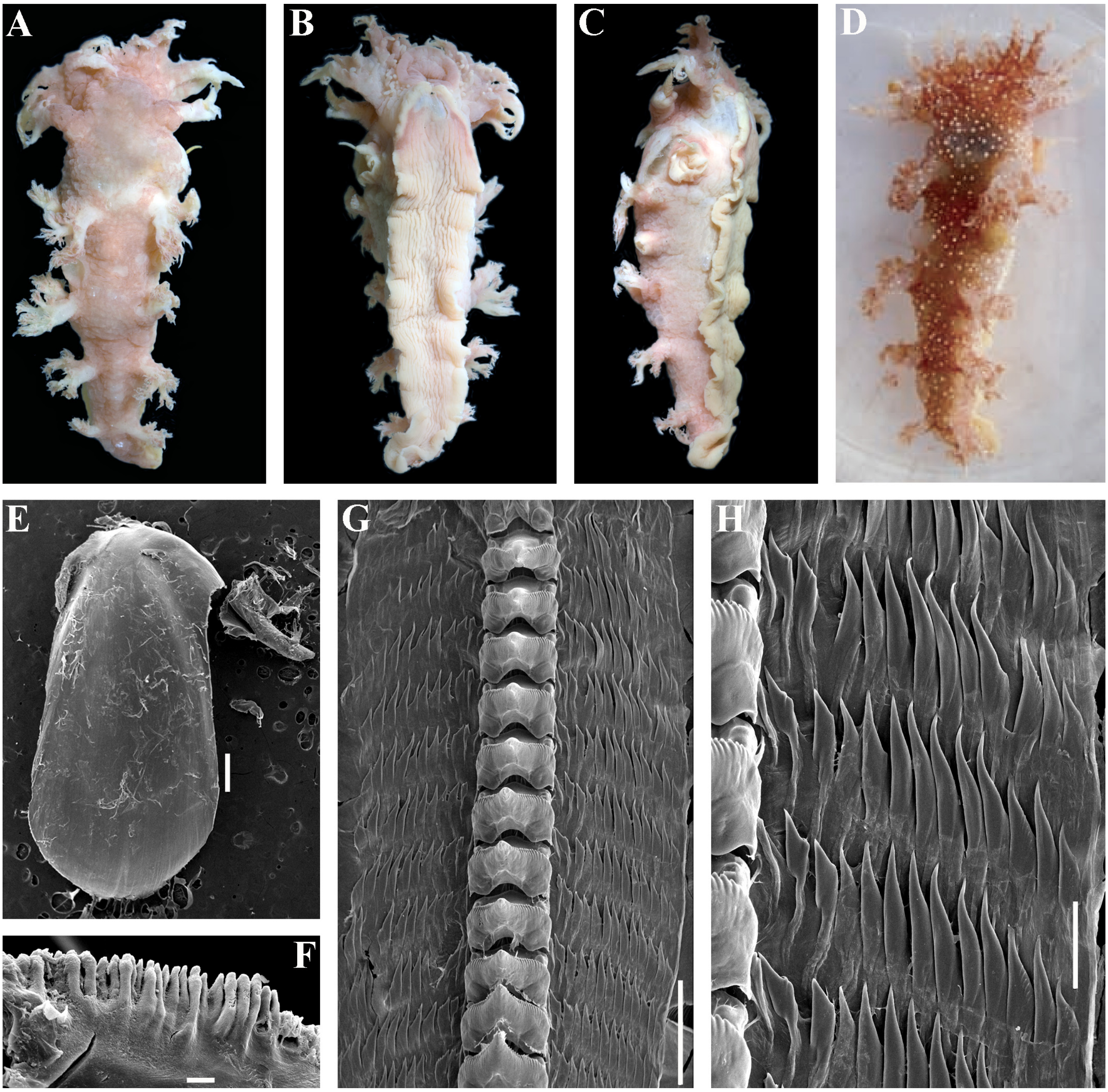

FIGURE 4. *Dendronotus* ***bathyvela*** **sp. nov.** Holotype, NSMT-Mo 94455, length 45 mm (preserved), Tohoku, off Ofunato, 307 m. **A–C**. Dorsal, ventral and lateral views respectively, preserved holotype. **D**. Live holotype. **E**. Jaws, SEM; **F**. Masticatory processes of jaws, SEM; **G**. Radula, posterior part; **H**. Lateral teeth, posterior part. Scale bars: E, 1000 mm, F, 30 µm, G, 300 µm, H, 100 µm. Photos: Alexander Martynov (A–C, E–H); D, from Hasegawa (2009: fig. 444A) with permission.

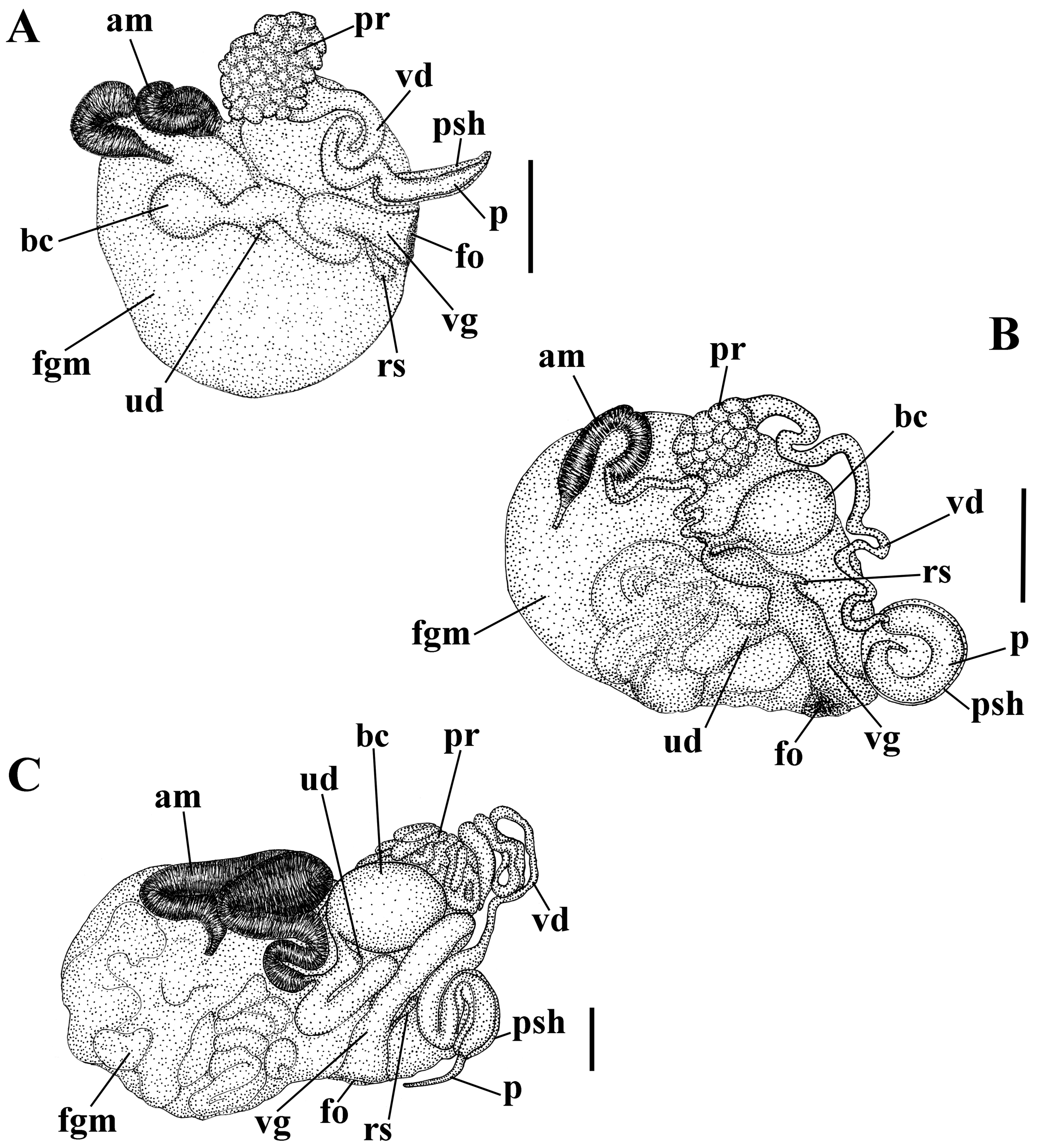

FIGURE 5. Reproductive systems. **A**. *Dendronotus* ***jamsteci*** **sp. nov. B**. *Dendronotus* ***zakuro*** **sp. nov. C**. *Dendronotus* ***bathyvela*** **sp. nov.** Abbreviations: am, ampulla; bc, bursa copulatrix; fgm, female gland mass; fo, female opening; p, penis; pr, prostate; psh, penial sheath; rs, receptaculum seminis; ud, uterine duct; vd, vas deferens; vg, vaginal duct. Scale bars: 1mm.

whereas even moderately sized *D.* ***bathyvela*** **sp. nov**. possess up to six main dorsolateral appendages (plus a seventh smaller one); 3) Colouration of living specimens of *D. velifer* is bright reddish, whereas *D.* ***bathyvela*** **sp. nov.** is dull reddish-brownish (Fig. 4D); 4) Number of denticles on the central teeth of *D. velifer* is commonly less than 30, whereas in *D.* ***bathyvela*** **sp. nov**. it reaches over 30; 5) Number of radular rows in *D. velifer* is up to 36, whereas in *D.* ***bathyvela*** **sp. nov**. the number of rows is up to 41 and more. It is remarkable that the North Atlantic shallow-water species *D. robustus* has up to seven dorsolateral appendages, like the NW Pacific shelf to bathyal new species *D.* ***bathyvela*** **sp. nov.**, but not like the true predominantly Arctic shelf species *D. velifer*, which commonly has only four dorsolateral appendages. This feature readily distinguishes *D.* ***bathyvela*** **sp. nov.** from *D. velifer*. At the same time, *D.* ***bathyvela*** **sp. nov.** is well-distinguished from *D. robustus* by the shape of the central radula and external colouration. Bathymetrically *D. velifer* is known from relatively shallow waters with a range commonly ca. 15–230 m, whereas *D.* ***bathyvela*** **sp. nov.** inhabits the low part of the continental shelf (not shallower than 249 m) to upper bathyal (510 m) depths. True North Atlantic *D. robustus* is in turn exclusively a shallow water species and was not recorded deeper than 20–30 m (see Lundin *et al.* 2017). This set of several complex morphological and ecological features allow us to distinguish *D.* ***bathyvela*** **sp. nov**. from *D. velifer*. Recently a deep-sea (but not wide-bodied) species, *D. claguei,* was described (Valdés *et al.* 2018) off the NE Pacific coast. *D. claguei* fundamentally differs from *D.* ***bathyvela*** **sp. nov.** by its uniform translucent white colour, elongate body shape, radular details, and in addition *D. claguei* inhabits upper abyssal depths (2369 m) and not shelf to upper bathyal depths (249–510 m) as *D.* ***bathyvela*** **sp. nov.** does. In addition, the NE Pacific shallow-water species *D. albopunctatus* Robilliard, 1972 is somewhat similar to the wide-bodied species group of the genus *Dendronotus*, but has fewer, and longer, oral veil appendages, lacks lip papilla and considerably differs by the presence of distinct denticulation on the lateral teeth of the radula (Robilliard, 1972).

Discussion

The present study provides significant contributions to the understanding of the taxonomy, phylogeny and biogeography of the genus *Dendronotus*. The main goal of this phylogenetic analysis is to reveal evolutionary ties between species of the genus *Dendronotus*, including new species. Phylogenetic trees constructed for a maximally large number of *Dendronotus* species based on several gene markers revealed lower supported values for certain nodes. To highlight this resolved and unresolved topology, a phylogeny was estimated using the 'halfcompat' majority rule consensus tree option for BI. While our present paper was under review, a prepublication by Ekimova *et al.* (2019) appeared with another attempt to investigate *Dendronotus* phylogeny. In this prepublication the species "*D. albus*" is wrongly identified under the invalid name "*D. diversicolor*" (see Korshunova *et al.* 2016a), whereas for the valid species *D. robilliardi,* the name "*D. albus*" was incorrectly applied. Also, *D. robilliardi* is not listed in the phylogenetic tree in Ekimova *et al.* (2019), yet Ekimova claims to have the most complete *Dendronotus* phylogeny. Thus, to persist in using these notable mistakes in future analysis only serves to further confuse modern knowledge of the genus *Dendronotus*.

Up to the present, deep-sea representatives of the genus *Dendronotus* were known only among wide-bodied species, such as *D. velifer* and *D. patricki*, or as a highly aberrant example without available molecular data, like *D. comteti*. Here, for the first time, we present evidence that a species, *D.* ***jamsteci*** **sp. nov.**, that is related to the exclusively shallow-water clades successfully colonized upper bathyal deep-sea waters and is present in this zone in large quantities. Further, in this study, we discovered one more species from the shallow waters of the NW Pacific, *D.* ***zakuro*** **sp. nov.**, which by radular features is very similar to *D. kamchaticus*, but by colouration and molecular data differs from it, thus contributing to the 'cryptic' species problem (see Korshunova *et al.* 2017a). Because instead of attempting to find putative distinctions between 'cryptic' and 'non-cryptic' species we recently have proposed the concept of a fine-scale multilevel diversity (Korshunova *et al.* 2019b) where morphological and molecular differences represent a complicated multilevel mosaic. The case of *D.* ***zakuro*** **sp. nov.** well agrees with such a general proposal. According to the morphology of the central teeth, *D.* ***zakuro*** **sp. nov.** is difficult to distinguish from *D. kamchaticus*, but according to the combination of lateral teeth numbers and patterns of external colouration and molecular data (Fig. 1), *D.* ***zakuro*** **sp. nov.** is an undoubtedly a separate species. In the case of *D.* ***bathyvela*** **sp. nov**., details of morphological features instead demonstrate a range that is different between *D.* ***bathyvela*** **sp. nov**., *D. velifer, D.patricki*, and *D. robustus.* In addition, biogeographical and bathymetrical patterns of *D.* ***bathyvela*** **sp. nov**. also diverge from the North Atlantic and Arctic *D. velifer* and the North Atlantic *D. robustus*, which makes *D.* ***bathyvela*** **sp. nov**. the southernmost and relatively the deepest representative among these related species, partially linking it to the NE Pacific abyssal *D. patricki.*

Another interesting feature, according to the present molecular phylogenetic analysis (Fig. 1), is the sister placement of *D.* ***jamsteci*** **sp. nov.** to a clade that comprises such morphologically different species as *D. subramosus* and *D. albus*. Whereas *D.* ***zakuro*** **sp. nov.** is most closely related to a clade that comprises such a variety of species as *D. kamchaticus*, *D. arcticus*, *D. dalli*, *D. lacteus, D. europaeus*, *D. niveus,* and *D. rufus.* The most striking feature that unites *D.* ***zakuro*** **sp. nov.** with several of these species is the tendency to form smooth central teeth in the adult state. From this list *D. lacteus* and *D. europaeus* commonly preserve some denticulation at the adult stage, and *D.*

arcticus and *D. rufus* have invariably denticulated central teeth, whereas *D. kamchaticus, D. dalli* and, *D. niveus*, like *D.* ***zakuro*** **sp. nov.** possess smooth central teeth at the adult stage. Thus, in that case we are dealing with the mosaic distribution of fine-scale multilevel diversity (both morphological and molecular) of various *Dendronotus* species. In summation, three new species of the genus *Dendronotus* from the NW Pacific are described here for the first time which thus further contributes to the understanding of the taxonomic, phylogenetic and biogeographic patterns of the worldwide diversity of the genus *Dendronotus*.

Acknowledgements

Kazunori Hasegawa, Hiroshi Saito, Toshihiko Fujita (National Museum of Nature and Science, Tsukuba) Hiroyuki Yokooka (JAMSTEC), and Sho Kashio (Natural History Museum, Kishiwada City) are thanked for collecting and the loan of several materials. Torkild Bakken (NTNU University Museum) and the team of Gulen Dive Resort (Christian Skauge, Ørjan Sandnes, Monica Bakkeli and Guido Schmitz) are thanked for their generous help and support during fieldwork in Norway, as some of these specimens were used for comparative purposes in this study. Electron Microscopy Laboratory MSU is thanked for support with electron microscopy. This study was supported by the research project of MSU Zoological Museum (AAAA-A16-116021660077-3), and by the research project Tohoku Ecosystem-Associated Marine Sciences from the Ministry of Education, Culture, Sports, Science, and Technology. Finally, we would like to thank anonymous reviewers who suggested improvements to this paper.

References

Baba, K. (1949) *Opisthobranchia of Sagami Bay collected by His Majesty The Emperor of Japan*. Iwanami Shoten, Tokyo, 194 pp., 50 pls. [in Japanese and English]

Baba, K. (1993) A northern species of *Dendronotus* (Mollusca: Nudibranchia: Dendronotidae) from Sado Island, Sea of Japan. *Report of the Sado Marine Biological Station*, 23, 29–33.

Ekimova, I., Korshunova, T., Schepetov, D., Neretina, T., Sanamyan, N. & Martynov, A. (2015) Integrative systematics of northern and Arctic nudibranchs of the genus *Dendronotus* (Mollusca, Gastropoda), with descriptions of three new species. *Zoological Journal of the Linnean Society*, 173, 841–886. https://doi.org/10.1111/zoj.12214

Ekimova, I., Valdés, Á., Chichvarkhin, A., Antokhina, T., Lindsay, T. & Schepetov, D. (2019) Diet-driven ecological radiation and allopatric speciation result in high species diversity in a temperate-cold water marine genus *Dendronotus* (Gastropoda: Nudibranchia). *Molecular Phylogenetics and Evolution*, 141, 106609. https://doi.org/10.1016/j.ympev.2019.106609

Hasegawa, K. (2009) Upper Bathyal Gastropods of the Pacific Coast of Northern Honshu,

Japan, chiefly Collected by R/V Wakataka-maru. *In*: Fujita, T. (Ed.), *Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan.* National Museum of Nature and Science Monographs, No. 39, pp. 225–383.

Jamstec (2013) *JAMSTEC 2013 Annual report*. Japan Agency for Marine-Earth Science and Technology, Yokosuka-shi, Kanagawa-ken, 80 pp.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30, 3059–3066. https://doi.org/10.1093/nar/gkf436

Korshunova, T., Sanamyan, N., Zimina, O., Fletcher, K. & Martynov, A. (2016a) Two new species and a remarkable record of the genus *Dendronotus* from the North Pacific and Arctic oceans (Nudibranchia). *ZooKeys*, 630, 19–42. https://doi.org/10.3897/zookeys.630.10397

Korshunova, T.A., Sanamyan, N.P. & Martynov, A.V. (2016b) Morphological and molecular evidence indicate *Dendronotus primorjensis* is a valid species that has priority over *D. dudkai* (Nudibranchia). *ZooKeys*, 634, 15–28. https://doi.org/10.3897/zookeys.634.10231

Korshunova, T., Martynov, A., Bakken, T. & Picton, B. (2017a) External diversity is restrained by internal conservatism: New nudibranch mollusc contributes to the cryptic species problem. *Zoologica Scripta*, 46 (6), 683–692. https://doi.org/10.1111/zsc.12253

Korshunova, T.A., Martynov, A.V., Bakken, T., Evertsen, J., Fletcher, K., Mudianta, I.W., Saito, H., Lundin, K., Schrödl, M. & Picton, B. (2017b) Polyphyly of the traditional family Flabellinidae affects a major group of Nudibranchia: aeolidacean taxonomic reassessment with descriptions of several new families, genera, and species (Mollusca, Gastropoda). *ZooKeys*, 717, 1–139. https://doi.org/10.3897/zookeys.5555.21885.figure1

Korshunova, T.A., Lundin, K., Malmberg, K., Picton, B. & Martynov, A.V. (2018) First true brackish-water nudibranch mollusc

provides new insights for phylogeny and biogeography and reveals paedomorphosis-driven evolution. *PLOS ONE*, 13, e0192177.
https://doi.org/10.1371/journal.pone.0192177

Korshunova, T.A., Nakano, R., Fletcher, K., Sanamyan, N. & Martynov, A.V. (2019a) First molecular confirmation of the presence of *Dendronotus primorjensis* Martynov, Sanamyan & Korshunova, 2015 in Japan and new distributional records of *Dendronotus* species in the North Pacic (Nudibranchia: Dendronotidae). *Venus*, 77, 1–14.

Korshunova, T.A., Picton, B., Furfaro, G., Mariottini, P., Pontes, M., Prkić, J., Fletcher, K., Malmberg, K., Lundin, K. & Martynov, A.V. (2019b) Multilevel fine-scale diversity challenges the 'cryptic species' concept. *Scientific Reports*, 9, 1–23.
https://doi.org/10.1038/s41598-019-42297-5

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054

Lundin, K., Korshunova, T., Malmberg, K. & Martynov, A. (2017) Intersection of historical museum collections and modern systematics: a relict population of the Arctic nudibranch *Dendronotus velifer* G.O. Sars, 1878 in a Swedish fjord. *Contributions to Zoology*, 86 (4), 303–318.
https://doi.org/10.1163/18759866-08604004

MacFarland, F.M. (1966) Studies of opisthobranchiate mollusks of the Pacific coast of North America. *Memoirs of the California Academy of Sciences*, 6, 1–546.

Martynov, A.V. (2012) Ontogenetic systematics: The synthesis of taxonomy, phylogenetics, and evolutionary developmental biology. *Paleontological Journal*, 46, 833–864.
https://doi.org/10.1134/S0031030112080072

Martynov, A.V. & Korshunova, T.A. (2011) *Opisthobranch molluscs of the seas of Russia. A colour guide to their taxonomy and biology*. Fiton, Moscow, 231 pp.

Martynov, A., Ishida, Y., Irimura, S., Tajiri, R., O'Hara, T. & Fujita, T. (2015) When ontogeny matters: a new Japanese species of brittle star illustrates the importance of considering both adult and juvenile characters in taxonomic practice. *PLOS ONE*, 10, e0139463.
https://doi.org/10.1371/journal.pone.0139463

Martynov, A.V., Sanamyan, N.P. & Korshunova, T.A. (2015a) New data on the opisthobranch molluscs (Gastropoda: Opisthobranchia) of waters of Commander Islands and Far-Eastern seas of Russia. *Conservation of biodiversity of Kamchatka and coastal waters—Proceedings of XV international scientific conference Petropavlovsk-Kamchatsky*. Kamchat Press, Petropavlovsk-Kamchatsky, pp. 55–69.

Martynov, A.V., Sanamyan, N.P. & Korshunova, T.A. (2015b) Review of the opisthobranch mollusc fauna of Russian Far Eastern seas: Pleurobranchomorpha, Doridida and Nudibranchia. *Bulletin of Kamchatka State Technical University*, 34, 62–87.
https://doi.org/10.17217/2079-0333-2015-34-62-87

MolluscaBase. (2019) MolluscaBase. *Dendronotus* Alder & Hancock, 1845. Accessed through: World Register of Marine Species. Available from: http://www.marinespecies.org/aphia.php?p=taxdetails&id=137885 (accessed 12 July 201)

Nylander, J.A., Ronquist, F., Huelsenbeck, J.P. & Nieves-Aldrey, J.L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology*, 53, 47–67.
https://doi.org/10.1080/10635150490264699

Nakano, R. (2018) *Field Guide to Sea Slugs and Nudibranchs of Japan*. Bun-ichi Co., Ltd., Tokyo, 544 pp.

Puillandre, N., Lambert, A., Brouillet, S. & Achaz, G. (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, 21, 1864–1877.
https://doi.org/10.1111/j.1365-294X.2011.05239.x

Robilliard, G.A. (1969) Key to the species of *Dendronotus* of the Puget Sound Region in *Marine Fauna of the San Juan Archipelago*. Publication of the Puget Sound Biological Station.

Robilliard, G.A. (1970) The systematics and some aspects of the ecology of the genus *Dendronotus* (Gastropoda: Nudibranchia). *The Veliger*, 12, 433–479.

Robilliard, G.A. (1972) A new species of *Dendronotus* from the northeastern Pacific with notes on *Dendronotus nanus* and *Dendronotus robustus* (Molluscs: Opisthobranchia). *Canadian Journal of Zoology*, 50, 421–432.
https://doi.org/10.1139/z72-060

Robilliard, G.A. (1975) The nudibranch *Dendronotus frondosus*—One species or four? *The Festivus*, 6 (8), 44–47.

Roginskaya, I.S. (1987) Order Nudibranchia Blainville, 1814. *Molluscs of the White Sea*. *Keys to Fauna of USSR*, 151, 155–202.

Roginskaya, I.S. (1997) Predation by a nudibranch *Dendronotus robustus* from the Sea of Japan on Oweniid polychaetes. *Opisthobranch Newsletter*, 23, 21–23.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
https://doi.org/10.1093/sysbio/sys029

Stout, C.C., Pola, M. & Valdés, Á. (2010). Phylogenetic analysis of *Dendronotus* nudibranchs with emphasis on northeastern

Pacific species. *Journal of Molluscan Studies*, 76 (4), 367–375.

Stout, C.C., Wilson, N.G. & Valdés, Á. (2011) A new species of deep-sea *Dendronotus* Alder & Hancock (Mollusca: Nudibranchia) from California, with an expanded phylogeny of the genus. *Invertebrate Systematics*, 25, 60–69. https://doi.org/10.1071/IS10027

Valdés, Á., Lundsten, L. & Wilson, N.G. (2018) Five new deep-sea species of nudibranchs (Gastropoda: Heterobranchia: Cladobranchia) from the Northeast Pacific. *Zootaxa*, 4526 (4), 401–433. https://doi.org/10.11646/zootaxa.4526.4.1

Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. PhD dissertation. The University of Texas, Austin, Texas, 125 pp.