

# Morphological Description, DNA Barcoding, and Taxonomic Review of Five Nudibranch Species (Gastropoda) from South Korea

Jina Park<sup>†</sup>, Damin Lee<sup>†</sup>, Eggy Triana Putri, Haelim Kil, Joong-Ki Park<sup>\*</sup>

Division of Ecoscience, Ewha Womans University, Seoul 03760, Korea

## ABSTRACT

The nudibranch is one of the most colorful gastropod species found in oceans worldwide. Unlike many other gastropod groups, the nudibranch loses an external shell in the adult stage, but instead develops various chemical defense systems. More than 2,500 nudibranch species have been reported worldwide, and 73 species are currently recorded in Korean waters. In this study, we present morphological descriptions, DNA barcode information of mtDNA *cox1* sequence, and taxonomic review for five nudibranch species: *Apata pricei* (MacFarland, 1966), *Doto rosacea* Baba, 1949, *Janolus toyamensis* Baba and Abe, 1970, *Polycera abei* (Baba, 1960), and *Trinchesia sibogae* (Bergh, 1905). Of these, we also provide in-depth discussion of taxonomic issue of *A. pricei* that was previously subdivided into two subspecies, *A. pricei pricei* and *A. pricei komandorica*. Our morphological examination and molecular analyses of the mtDNA *cox1* sequences indicate that these two subspecies are not taxonomically warranted. The phylogenetic information for the other nudibranch species from mtDNA *cox1* sequence analysis is also included, providing a molecular basis for species identification and inferring their local phylogenies within each of the species groups discussed herein.

**Keywords:** Mollusca, Nudibranchia, morphology, DNA barcode analysis, Korea

## INTRODUCTION

The Nudibranchia Cuvier, 1817 is an order of marine gastropods that are readily distinguished from other mollusks by having beautiful color patterns, a bilaterally symmetrical body, naked gills, and no shell in adult stage. This order is divided into two suborders: Cladobranchia and Doridina. In the former, various kinds of cerata are found with the anus positioned on the right side of body, while the latter is characterized by the presence of feather-like (or flower-like) branchial gills and a median dorsal anus (Willan and Morton, 1984; Bouchet et al., 2017).

This colorful nudibranch comprises more than 2,558 species worldwide (MolluscaBase, 2023). They are widely distributed in marine environments, from intertidal to a water depth up to 2,300 m (Ekimova et al., 2015; Gosliner et al., 2018; Valdés et al., 2018). The majority of nudibranch are known to be carnivorous that feeds on various animals such as sponges, hydroids, bryozoans, and ascidians (Nybakken

and McDonald, 1981; Folino, 1997; Winters et al., 2018). It has developed diverse defense systems instead of having an external shell for protecting themselves from predators. These include camouflages to resemble their surroundings (Marín and Ros, 1991), or showing aposematism to warn potential predators with its colors (Aguado and Marín, 2007; Winters et al., 2018). Some nudibranch species also use intact or recombinant chemicals for defense systems from ingested organisms, or newly synthesized defense chemicals (Aguado and Marín, 2007; Winters et al., 2018).

To date, a total of 73 nudibranch species has been recorded in Korean waters (National Marine Biodiversity Institute of Korea, 2022), but morphological diagnosis and DNA barcode sequence information are not fully characterized. In this study, five nudibranch species were identified based on morphological examination and molecular analyses of DNA barcode information of the mtDNA *cox1* sequences for nudibranch collections by SCUBA diving in Korean waters: *Apata pricei* (MacFarland, 1966), *Doto rosacea* Baba, 1949,

© This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/3.0/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

<sup>†</sup>These authors contributed equally to this work.  
<sup>\*</sup>To whom correspondence should be addressed  
Tel: 82-2-3277-5948, Fax: 82-2-3277-2385  
E-mail: jkpark@ewha.ac.kr

*Janolus toyamensis* Baba and Abe, 1970, *Polycera abei* (Baba, 1960), and *Trinchesia sibogae* (Bergh, 1905). Here, we provide morphological descriptions, color images, DNA barcode sequence information, and taxonomic review of the five Korean nudibranch species that can be useful for species identification and inferring their local phylogenies within each of the species groups discussed herein.

## MATERIALS AND METHODS

### Sample collection and morphological analysis

Nudibranch samples were collected by SCUBA diving in Korean waters and preserved 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 of the specimens were examined under a stereoscopic dissecting microscope (Leica M205C, Germany), and color images were taken using a digital camera (TG-6, Olympus, Japan) when they were alive.

### DNA extraction, PCR-amplification, and Sequence analysis

Genomic DNA was extracted from foot tissue using a QIAamp DNA Micro Kit (QIAGEN, Germany) following the manufacturer's instructions. The mtDNA *cox1* sequences were PCR-amplified using the LCO1490 and HCO2198 primer set (Folmer et al., 1994) in a total of 25  $\mu$ L reaction mixture containing 17.375  $\mu$ L of distilled waters, 2.5  $\mu$ L of 10 $\times$  Ex Taq buffer, 2  $\mu$ L of dNTP, 1  $\mu$ L of each primer, 0.125  $\mu$ L of TaKaRa Ex Taq (TaKaRa Bio, Japan), and 1  $\mu$ L of template DNA. The PCR condition consisted of an initial denaturation at 94°C for 4 min, followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 42°C for 30 s, elongation at 72°C for 1 min, and 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 by Geneious Prime v.2023.0.4 (Biomatters, New Zealand).

### Phylogenetic analysis

The nucleotide sequences of the partial fragment of mtDNA *cox1* were aligned with homologous gene sequences obtained from NCBI database using the MAFFT (Katoh and Standley, 2013) in Geneious software with default parameters (Table 1). Genetic distances between and within species were calculated using MEGA X (Stecher et al., 2020) as uncorrected *p*-distance (Collins et al., 2012; Srivathsan and

Meier, 2012). The best-fit substitution models were estimated using the Akaike Information Criterion (AIC) in jModelTest (Darriba et al., 2012) for phylogenetic analyses. Phylogenetic relationships were inferred using maximum likelihood approach with RAxML v.8.2.12 (Stamatakis, 2014), and branch supports were calculated from bootstrap analysis with 1,000 iterations.

## SYSTEMATIC ACCOUNTS

Phylum Mollusca Linnaeus, 1758  
Class Gastropoda Cuvier, 1795  
Order Nudibranchia Cuvier, 1817  
Suborder Cladobranchia  
1\*Family Apataidae Korshunova et al., 2017a

**Type species.** *Coryphella pricei* MacFarland, 1966

**Diagnosis.** Body elongated, slender, laterally compressed. Rhinophores perfoliated. Cerata dorso-laterally raised in several rows. Oral tentacles smooth, longer than rhinophores. Anterior foot corners rather long and pointed. Metapodium elongate and tapered.

2\*Genus *Apata* Korshunova et al., 2017a

3\*1. *Apata pricei* (MacFarland, 1966) (Fig. 1A–D)

*Coryphella pricei* MacFarland, 1966: 313–315, pl. 58, fig. 6, pl. 65, figs. 9–13, pl. 66, figs. 8, 9.

*Flabellina pricei*: Debelius and Kuitert, 2007: 315.

*Apata pricei komandorica*: Korshunova et al., 2017a: 65, 66, fig. 48.

*Apata pricei pricei*: Korshunova et al., 2017a: 64, 66.

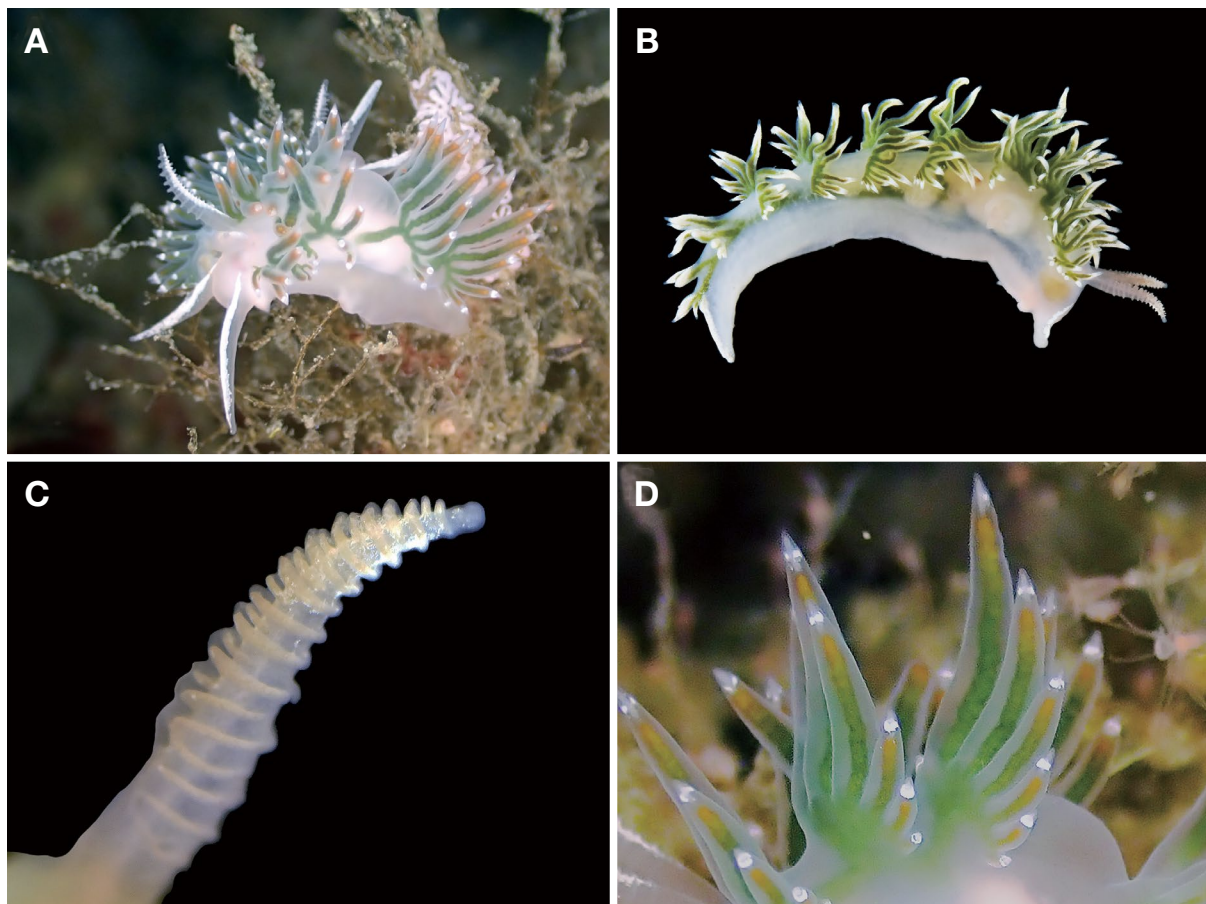
**Material examined.** 3 individuals (MO00184329, MMRBK7719, 7720), Munamjin-ri, Jugwang-myeon, Goseong-gun, Gangwon-do (38°18'03.2"N, 128°34'16.4"E), collected by SCUBA diving at depth of 30 m, 30 Mar 2022; 8 individuals (MMRBK7721–7728), Munamjin-ri, Jugwang-myeon, Goseong-gun, Gangwon-do (38°18'03.3"N, 128°34'16.0"E), collected by SCUBA diving at depth of 29 m, 10 Apr 2023.

**Description.** Body elongated (body length 7.3 mm; live specimen), slender, laterally compressed, notum high and arched. Ground color translucent white (Fig. 1A, B). Rhinophores annulated; each annulation in spiral structure, winding around central axis about 1.5 turns (Fig. 1C). Eyes black spots on base of rhinophores. Cerata 9–13 pairs of comb-like clusters, arranged in transverse rows dorso-laterally. Ceratal clusters typically comprised four to ten slender fusi-

Korean name: 1\*빛살갯민숭이과 (신칭), 2\*빛살갯민숭이속 (신칭), 3\*빛살갯민숭이 (신칭)

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

Family	Species	NCBI No.	Reference	Family	Species	NCBI No.	Reference
Apataidae	<i>Apata cf. pricei</i>	KY129060.1	Cella et al. (2016)	Pinufiidae	<i>Pinufius rebus</i>	HM162744.1	Pola and Gosliner (2010)
	<i>Apata pricei_01</i>	OQ919368	This study		<i>Gymnodoris brunnea</i>	KJ396778.1	Knutson and Gosliner (2014)
	<i>Apata pricei_02</i>	OQ919369	This study		<i>Gymnodoris striata</i>	HQ987955.1	Unpublished
	<i>Apata pricei_03</i>	OQ919370	This study		<i>Lecithophorus capensis</i>	MZ382782.1	Knutson and Gosliner (2022)
	<i>Apata pricei komanadorica</i>	MF523386.1	Korshunova et al. (2017a)		<i>Pallo dubia</i>	MZ382786.1	Knutson and Gosliner (2022)
	<i>Apata pricei pricei</i>	KY129052.1	Cella et al. (2016)		<i>Polycera abei_01</i>	OQ919374	This study
	<i>Doto africonata</i>	HM162734.1	Pola and Gosliner (2010)		<i>Polycera abei_02</i>	OQ919375	This study
	<i>Doto amyra</i>	KJ486701.1	Shipman and Gosliner (2015)		<i>Polycera faeroensis</i>	MZ425339.1	Korshunova et al. (2021)
	<i>Doto antarctica</i>	KJ486705.1	Shipman and Gosliner (2015)		<i>Polycera kernoensis</i>	MZ425390.1	Korshunova et al. (2021)
	<i>Doto columbiana</i>	GQ292026.1	Shields (2009)		<i>Polycerella emertoni</i>	OQ323052.1	Unpublished
	<i>Doto coronata</i>	AF249794.1	Wollscheid-Lengeling et al. (2001)		<i>Tambja abdere</i>	DQ230995.1	Pola et al. (2006)
	<i>Doto dunnei</i>	KJ486725.1	Shipman and Gosliner (2015)		<i>Tambja morosa</i>	DQ230997.1	Pola et al. (2006)
	<i>Doto floridicola</i>	AF249820.1	Wollscheid-Lengeling et al. (2001)		<i>Thecacera pennigera</i>	JX274094.1	Palomar et al. (2014)
<i>Doto fragilis</i>	KJ486735.1	Shipman and Gosliner (2015)	<i>Thecacera picta</i>	KP871652.1	Mahguib and Valdés (2015)		
<i>Doto from A</i>	KJ486704.1	Shipman and Gosliner (2015)	<i>Luisella babai_01</i>	HQ616754.1	Carmona et al. (2011)		
<i>Doto greenamyeri</i>	KJ486715.1	Shipman and Gosliner (2015)	<i>Luisella babai_02</i>	MK091274.1	Goodheart et al. (2018)		
<i>Doto koeneckeri</i>	AF249797.1	Wollscheid-Lengeling et al. (2001)	<i>Samla bicolor</i>	MF523383.1	Korshunova et al. (2017a)		
<i>Doto lemchei</i>	KJ486727.1	Shipman and Gosliner (2015)	<i>Samla bilas</i>	KY129051.1	Cella et al. (2016)		
<i>Doto millibayana</i>	KJ486726.1	Shipman and Gosliner (2015)	<i>Samla takashigei</i>	MF523384.1	Korshunova et al. (2017a)		
<i>Doto pinnatifida</i>	AF249793.1	Wollscheid-Lengeling et al. (2001)	<i>Catirona aurantia</i>	KY985467.1	Korshunova et al. (2018b)		
<i>Doto rosacea</i>	OQ919371	This study	<i>Catirona gymnota</i>	KY128907.1	Cella et al. (2016)		
<i>Doto sp. 2</i>	HM162737.1	Pola and Gosliner (2010)	<i>Diaphoreolis lagunae</i>	KY128956.1	Cella et al. (2016)		
<i>Doto sp. 7</i>	HM162738.1	Pola and Gosliner (2010)	<i>Diaphoreolis viridis</i>	MG266028.1	Korshunova et al. (2018b)		
<i>Doto sp. A</i>	KJ486724.1	Shipman and Gosliner (2015)	<i>Phestilla lugubris</i>	KY129075.1	Cella et al. (2016)		
<i>Doto sp. B</i>	HM162735.1	Pola and Gosliner (2010)	<i>Phestilla sibogae_01</i>	KY128975.1	Cella et al. (2016)		
<i>Doto sp. H</i>	HM162740.1	Pola and Gosliner (2010)	<i>Phestilla sibogae_02</i>	DQ417287.1	Fauci et al. (2007)		
<i>Doto sp. I</i>	HM162742.1	Pola and Gosliner (2010)	<i>Phestilla sibogae_03</i>	DQ417288.1	Fauci et al. (2007)		
<i>Doto sp. J</i>	HM162742.1	Pola and Gosliner (2010)	<i>Rubramoena amoena</i>	KY128904.1	Cella et al. (2016)		
<i>Doto sp. K</i>	HM162743.1	Pola and Gosliner (2010)	<i>Rubramoena rubescens</i>	KY128916.1	Cella et al. (2016)		
<i>Doto tuberculata</i>	KJ486734.1	Shipman and Gosliner (2015)	<i>Tenellia adspersa_01</i>	KY129085.1	Cella et al. (2016)		
<i>Doto ussi</i>	HM162736.1	Pola and Gosliner (2010)	<i>Tenellia adspersa_02</i>	KY129084.1	Cella et al. (2016)		
<i>Kabeiro phasmida</i>	HM162739.1	Pola and Gosliner (2010)	<i>Trinchesia caerulea</i>	MG266024.1	Korshunova et al. (2018b)		
<i>Kabeiro rubroreticulata</i>	KJ486739.1	Shipman and Gosliner (2015)	<i>Trinchesia foliata</i>	KY128912.1	Cella et al. (2016)		
<i>Antipella barbarensis</i>	KX889737.1	Goodheart et al. (2017)	<i>Trinchesia lenkae</i>	MG242334.1	Korshunova et al. (2018a)		
<i>Antipella fusca</i>	MH24281.1	Unpublished	<i>Trinchesia ornata</i>	KY128967.1	Cella et al. (2016)		
<i>Bonisa nakaza_01</i>	HM162746.1	Pola and Gosliner (2010)	<i>Trinchesia sibogae</i>	OQ919376	This study		
<i>Bonisa nakaza_02</i>	MH781055.1	Pola et al. (2019)	<i>Trinchesia speciosa</i>	KY128996.1	Cella et al. (2016)		
<i>Janolus flavoanulatus</i>	MH781070.1	Pola et al. (2019)	<i>Zelentia fulgens</i>	KY128951.1	Cella et al. (2016)		
<i>Janolus tricellariodes</i>	MH781074.1	Pola et al. (2019)	<i>Zelentia ninel</i>	KY952178.1	Korshunova et al. (2017b)		
<i>Janolus toyamensis_01</i>	OQ919372	This study	<i>Tritonia antarctica</i>	HM162718.1	Pola and Gosliner (2010)		
<i>Janolus toyamensis_02</i>	OQ919373	This study	<i>Tritonia challengeriana</i>	MW444250.1	Moles et al. (2021)		
<i>Madrella ferruginosa</i>	MH781053.1	Pola et al. (2019)	<i>Tritonia plebeia</i>	KR084480.1	Barco et al. (2016)		



**Fig. 1.** Images of *Apata pricei* (MacFarland, 1966) collected in Goseong-gun, Korea. A, Live specimens on hydroids with pale pink egg coils; B, A specimen in lateral view; C, Details of a rhinophore; D, Details of cerata.

form cerata, with innermost ceras largest and size decreasing towards outside, and fewer cerata at both distal clusters. Apex of cerata translucent white, with elongated white cnidosac (Fig. 1D). Subapical cerata with opaque white band. Digestive gland diverticulum about half thickness of ceras, greenish at base and yellowish-orange to brick reddish in color towards apex. Oral tentacles smooth, long, and tapered with blunt tips. Rhinophores and oral tentacles with scattered opaque white dots forming longitudinal lines from base to distal end on upper side. Foot narrow, tapering toward posterior. Anterior foot corner relatively long, curved backward. Metapodium elongated and pointed; white lines speckled, below both cerata, arranged from 7th ceratal clusters to end, merged in posterior part.

**GenBank accession number.** OQ919368–OQ919370.

**Distribution.** Korea, Russia (Commander Islands), USA (Alaska, California).

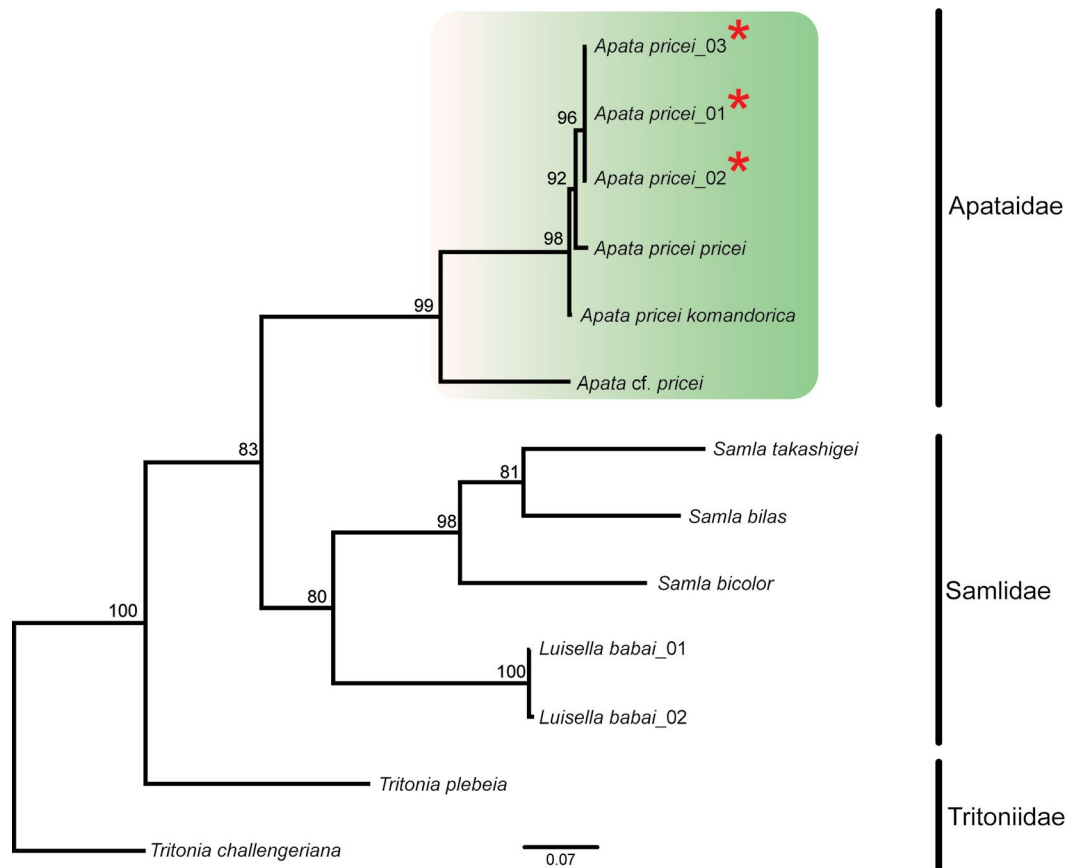
**Habitat.** Intertidal to 30 m depth on stony and soft bottom, or hydroids.

**Remarks.** This species is found mostly in cold waters from the Russian Far East to California, USA including Alaska. In Korea, it is only found near the Gangwon-do province, where the seawater temperature is low (3–6°C) in winter season. The color patterns of the body, cerata, and rhinophores correspond well to the original description (MacFarland, 1966), but the number of cerata per row (4-7-7-7-8-8-10-9-7-8-6-4-3) is slightly different from the original description, showing individual variation within the range of 1–3 in their number (Fig. 1B). Therefore, the number of cerata per row is considered variable.

Korshunova et al. (2017a) divided this species into two subspecies, *A. pricei pricei* (found in the northeastern Pacific from Alaska to California) and *A. pricei komandorica* (found in the northwestern Pacific: Commander Islands), distinguished by having different number of cerata rows (9–12 or more in *A. pricei* [MacFarland, 1966] and up to 10 in *A. p. komandorica* [Korshunova et al., 2017a]), and a low genetic distance of the mtDNA *cox1* sequences (*p*-distance of 1.8%).

**Table 2.** Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among *Apata* species

	<i>A. pricei_01</i>	<i>A. pricei_02</i>	<i>A. pricei_03</i>	<i>A. p. pricei</i>	<i>A. p. komandorica</i>
<i>A. pricei_01</i>					
<i>A. pricei_02</i>	0.3				
<i>A. pricei_03</i>	0.3	0.3			
<i>A. p. komandorica</i>	1.5	1.5	1.5		
<i>A. p. pricei</i>	2.0	2.0	2.0	1.8	
<i>Apata cf. pricei</i>	13.4	13.6	13.7	13.0	13.4

**Fig. 2.** Phylogenetic relationships among Apataidae species inferred from maximum likelihood method for the mtDNA *cox1* sequences. Node supporting values are indicated as bootstrap percentage over 50. Sequences used in this study are denoted by red asterisks (\*).

We revisited the taxonomic status of these two subspecies based on the morphological examination and molecular analyses of the mtDNA *cox1* sequences for collected samples from Korea. Our samples (11 individuals) show individual variations ranging from 9 to 13 in the number of cerata rows, but a very low *p*-distance of 0.3% among the sequenced individuals. Sequence comparison among these three geographic representatives also shows *p*-distances of 1.5% (between Korean samples and *A. p. komandorica*) and 2.0% (between

Korean samples and *A. p. pricei*), respectively (Table 2). Our phylogenetic tree of the mtDNA *cox1* sequences reveals that the Korean samples (denoted by *Apata pricei\_01*~*03*) are closely related to *A. p. pricei* than *A. p. komandorica* with a high bootstrap support value (Fig. 2). By comparing both morphological and molecular analyses, we conclude that the number of cerata rows that were used for discriminating the two subspecies by Korshunova et al. (2017a) is not useful for discriminating these two subspecies. In addition, sequence

divergences among *A. p. komandorica*, *A. p. pricei*, and Korean samples (ranging from 1.5% to 2.0%) can be regarded as individual variations, not representing a “DNA barcode gap” for subspecies delimitation of *A. pricei* that is widely distributed in the northern Pacific. Since the subspecies concept proposed by Korshunova et al. (2017a) does not satisfy the criteria for morphological and genetic evidences (Wilson and Brown, 1953; Mallet, 2007), the two subspecies, *A. p. pricei* and *A. p. komandorica*, should be lumped together under the valid name of *Apata pricei* (MacFarland, 1966), and this species is newly reported from Korean waters.

Family Dotidae Gray, 1853

Genus *Doto* Oken, 1815

**1\*2. *Doto rosacea* Baba, 1949 (Fig. 3A, B)**

*Doto (Doto) rosacea* Baba, 1949: 95, 172, pl. 39, fig. 139, text-fig. 119; Okutani, 2000: 799, 800.

*Doto rosacea*: Debelius and Kuitert, 2007: 302.

*Kabeiro rosacea*: Kil et al., 2020: 104, 105.

**Material examined.** 1 individual (MO00184330), northeastern Habaekdo Islet, Samsan-myeon, Yeosu-si, Jeollanam-do (34°02'14.9"N, 127°36'24.7"E), collected by SCUBA diving at depth of 23 m, 20 Jul 2022.

**Description.** Body elongated (body length 5.2 mm; preserved specimen) with laterally compressed dorsum, yellowish orange to bright rose in ground color (Fig. 3A). Rhinophores long and smooth, covered by rhinophore sheaths at one-third of base (Fig. 3B). Rhinophore sheaths margin irregularly wide and undulated, sometimes with a few lobules. Cerata seven pairs with blunt-tipped papillae, arranged dorso-laterally; last cerata smallest. Each cerata consisting of two to three circlets (circle rows); circlets bearing three to four elongated, globose tubercles. Oral veil bilobed and slightly extended on each side. Foot narrow; metapodium triangular.

**GenBank accession number.** OQ919371.

**Distribution.** Korea, Japan, Hong Kong.

**Remarks.** This species is morphologically similar to *D. japonica* Odhner, 1936 and *D. bella* Baba, 1938, but differs from them by having elongated papillar-shaped cerata that lack white or dark spots on their tips (Fig. 3B). Kil et al. (2020) assigned this species to the genus *Kabeiro* based on the characteristics of an elongated body. However, the genus *Kabeiro* is characterized by irregularly arranged cerata and tubercles, and a swollen pericardium, making it difficult to assign this species to the genus *Kabeiro* (Shipman and Gosliner, 2015).

Shipman and Gosliner (2015) conducted systematic studies

of the genus *Doto* using both morphological examination and molecular sequences of the mtDNA (*cox1* and 16S rDNA) and the nuclear histone H3. They divided this genus into four clades based on a combination of body morphology and geographic region, i.e., Short-bodied/north Atlantic clade, Short-bodied/Indo-Pacific clade, Short-bodied/eastern Pacific and south Atlantic clade, and Elongate/Indo-Pacific clade. A phylogenetic tree for the mtDNA *cox1* sequences including a new *D. rosacea* sequence from this study generally agrees with the previous analysis (Fig. 4), but *Doto* sp. I and J are grouped as basal members in the Short-bodied/Indo-Pacific clade (95% bootstrap support value), differing from the result of Shipman and Gosliner (2015).

In general, *Kabeiro* species belong to the Elongate/Indo-Pacific clade based on their elongated body and distribution in the Indo-Pacific, and this clade is distinguished from the Short-bodied/Indo-Pacific clade (Shipman and Gosliner, 2015). Unexpectedly, our phylogenetic tree of the mtDNA *cox1* sequence data including *D. rosacea* sequence reveals that *D. rosacea* species is positioned as the most basal among Dotidae species (with 100% bootstrap support value), not sister to any of short-bodied or elongated-bodied Dotidae clade distributed in the Indo-Pacific. The *p*-distances between *D. rosacea* and other species of *Doto* and *Kabeiro* range from 13.1% to 18.6% (Table 3). Interestingly, the distribution range of *D. rosacea* is generally restricted to the northwestern Pacific (e.g., Korea, Japan, and Hong Kong). Taken together, the non-overlapping distribution range of *D. rosacea* species and their independent phylogenetic position within the mtDNA *cox1* gene tree cast doubt on their taxonomic position, i.e., belonging to the genus *Doto* Baba, 1949, awaiting further validation based on in-depth morphological and molecular analyses for extensive taxon sampling.

Family Janolidae Pruvot-Fol, 1933

Genus *Janolus* Bergh, 1884

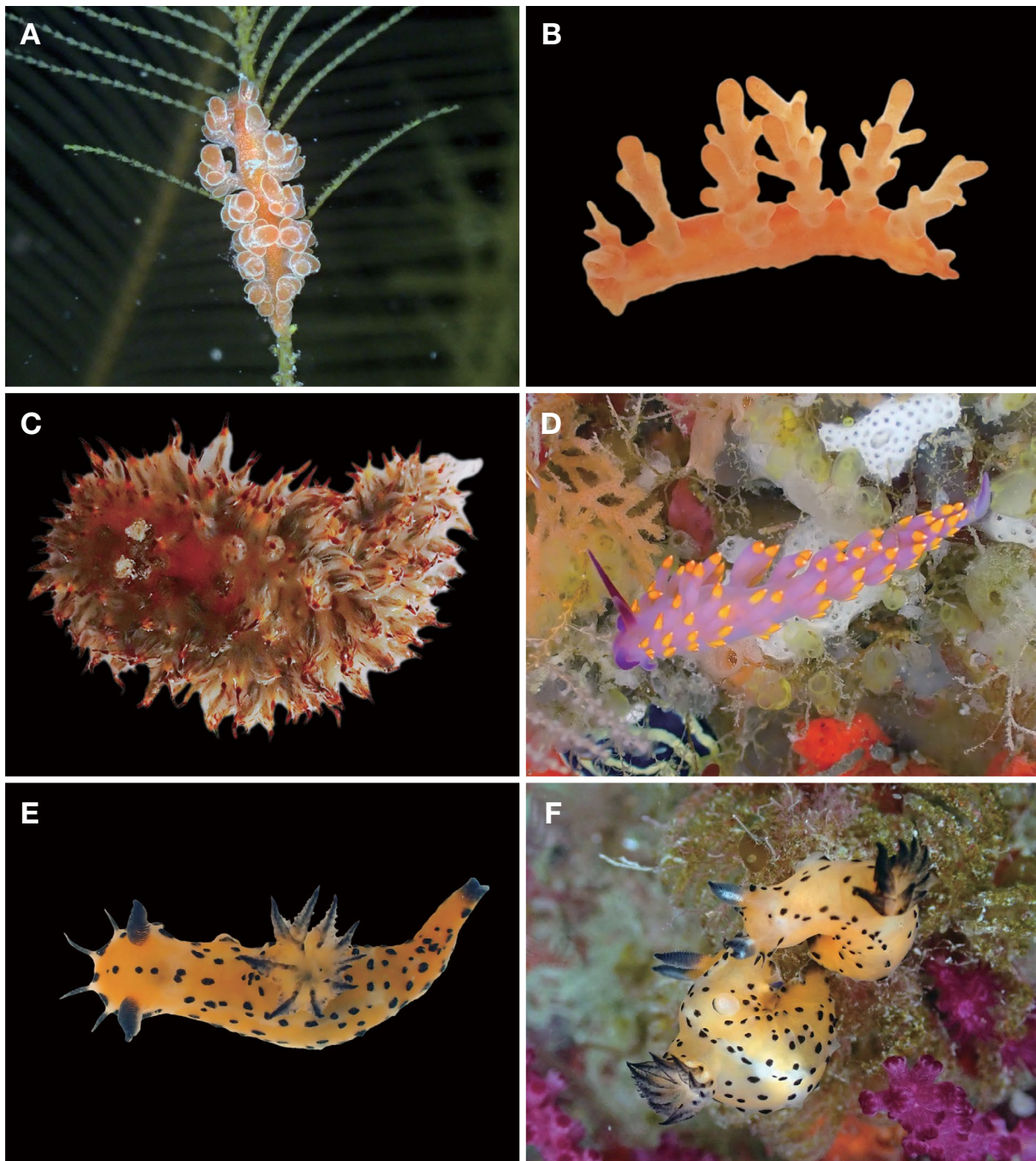
**2\*3. *Janolus toyamensis* Baba and Abe, 1970 (Fig. 3C)**

*Janolus toyamensis* Baba and Abe, 1970: 63–65, fig. 1; Gosliner, 1981: 2, 28, 31–34, tables 1, 2, figs. 26C, 27E; Baba, 1986: 183, 184, figs. 1, 2; Debelius and Kuitert, 2007: 284; Gosliner et al., 2018: 242; Kil et al., 2020: 136, 137; Vadher et al., 2021: 120, 121, fig. 3.

**Material examined.** 3 individuals (MO00184331, MMRBK 7731, 7732), Damuraemi Islet, Daeseo-ri, Chuja-myeon, Jeju-si, Jeju-do (33°58'14.08"N, 126°17'00.04"E), collected by SCUBA diving at depth of 16 m, 1 Sep 2021.

**Description.** Body elongated (length 27.4 mm; live speci-

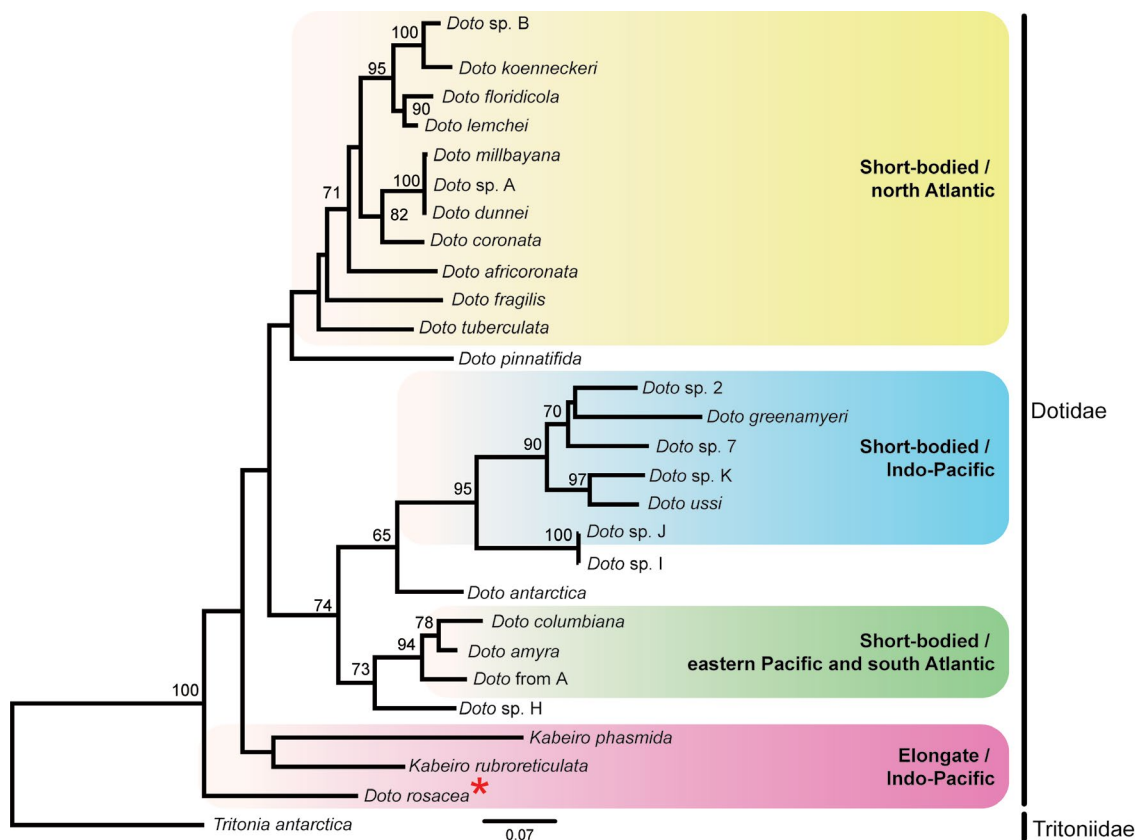
Korean name: <sup>1\*</sup>분홍술방울갯민숭이, <sup>2\*</sup>금빛버들잎갯민숭이



**Fig. 3.** Images of four Nudibranchia species in Korea. A, A live specimen of *Doto rosacea* on hydroids in nature; B, A specimen of *D. rosacea* in lateral view; C, A specimen of *Janolus toyamensis* in dorsal view; D, A live specimen of *Trinchisia sibogae*; E, A specimen of *Polycera abei* in dorsal view; F, Live specimens of *Po. abei*.

men), translucent ash-brown in ground color, with white longitudinal lines scattered throughout whole body. Rhinophores weakly papillate, having whitish markings on upper side; rhinophore stalk stout; caruncle between rhinophores. Dorsal cerata fusiform, with sparse nodules, extremely thin and elon-

gated toward tip; apex reddish brown; subapical bands yellow (Fig. 3C). Digestive gland in cerata dark green to brown. Cerata covering whole body irregularly except center of dorsal side. Oral tentacles short and slender. Foot broad; anterior corner rounded; metapodium elongated and tapering.



**Fig. 4.** Phylogenetic relationships among Dotidae species inferred from maximum likelihood method for the mtDNA *cox1* sequences. Four clades (Short-bodied/north Atlantic, Short-bodied/Indo-Pacific, Short-bodied/eastern Pacific and south Atlantic, and Elongate/Indo-Pacific) were proposed by Shipman and Gosliner (2015). Node supporting values are indicated as bootstrap percentage over 50. A sequence used in this study is denoted by a red asterisk (\*).

**GenBank accession number.** OQ919372, OQ919373.

**Distribution.** Korea, Indo-Pacific, Japan, Hawaii, India.

**Remarks.** This species is morphologically similar to *J. indicus* (Eliot, 1909), but can be distinguished by the presence of short white longitudinal lines on its body instead of reddish-brown dots (Eliot, 1909; Baba and Abe, 1970; Baba, 1986). However, some previous studies have synonymized *J. indicus* to *J. toyamensis* due to their overlapping geographic distribution in India and the lack of detailed descriptions of color patterns and reproductive system in Eliot’s description (Vishal and Deepak, 2013; Vadher et al., 2020, 2021). Therefore, a re-examination of their morphological features by comparing with the type specimen is necessary to confirm the taxonomic validity of *J. indicus*.

The phylogenetic tree shows that the three genera of the Janolidae (*Antiopella*, *Bonisa*, and *Janolus*) are reciprocally monophyletic, with *J. toyamensis* comprising a sister group

with other congeneric species (Fig. 5A). The *p*-distances among *Janolus* species range from 9.7% to 14.1% (Table 4). The minimum distance is found between *J. flavoanulatus* Pola and Gosliner, 2019 and *J. tricellariodes* Pola and Gosliner, 2019, while the maximum distance is found between *J. flavoanulatus* and *J. toyamensis*. The maximum *p*-distance within Janolidae is found between *Antiopella fusca* (O’Donoghue, 1924) and *J. tricellariodes* (21.9%).

Family Trinchesiidae F. Nordsieck, 1972  
Genus *Trinchesia* Ihering, 1879

**1\*4. *Trinchesia sibogae* (Bergh, 1905) (Fig. 3D)**

*Hervia sibogae* Bergh, 1905: 231, 232, taf. 2, fig. 17, taf. 20, figs. 1–3.

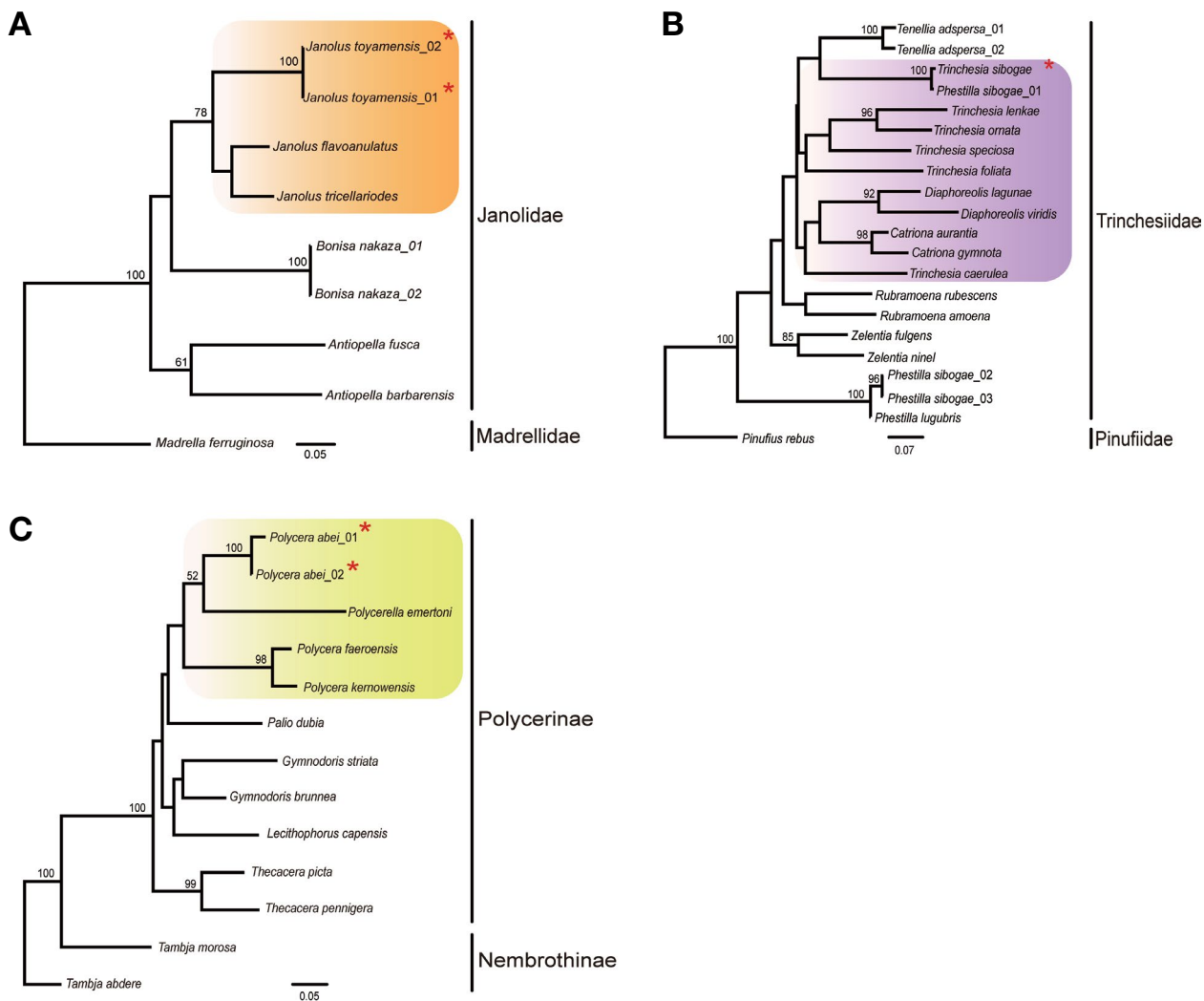
*Trinchesia sibogae*: Debelius and Kuitert, 2007: 351; Kil et al., 2020: 128, 129.

Korean name: 1\*불꽃도롱이갯민숭이



**Table 3.** Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among *Doto* and *Kabeiro* species

	<i>D. africanata</i>	<i>D. amyra</i>	<i>D. antarctica</i>	<i>D. columbiana</i>	<i>D. coronata</i>	<i>D. dunnei</i>	<i>D. floridicola</i>	<i>D. fragilis</i>	<i>Doto from A</i>	<i>D. greenamyeri</i>	<i>D. koenaeckeri</i>	<i>D. lemchei</i>	<i>D. millbayana</i>	<i>D. pinatifida</i>	<i>D. rosacea</i>	<i>Doto sp. 2</i>	<i>Doto sp. 7</i>	<i>Doto sp. J</i>	<i>Doto sp. A</i>	<i>Doto sp. B</i>	<i>Doto sp. H</i>	<i>Doto sp. I</i>	<i>Doto sp. K</i>	<i>D. tuberculata</i>	<i>D. ussi</i>	<i>K. phasmida</i>	<i>K. rubroreticulata</i>	
<i>D. africanata</i>																												
<i>D. amyra</i>	14.3																											
<i>D. antarctica</i>	15.7	11.0																										
<i>D. columbiana</i>	14.9	4.3	11.4																									
<i>D. coronata</i>	9.6	15.3	14.3	14.9																								
<i>D. dunnei</i>	9.4	15.5	14.5	14.9	5.9																							
<i>D. floridicola</i>	10.2	15.5	14.3	15.7	7.6	8.2																						
<i>D. fragilis</i>	11.6	14.1	14.9	14.5	12.0	11.8	11.4																					
<i>Doto from A</i>	14.9	4.7	11.2	5.7	15.5	14.3	15.5	16.1																				
<i>D. greenamyeri</i>	14.3	17.6	17.3	18.0	16.1	16.1	16.3	16.3	17.8																			
<i>D. koenaeckeri</i>	9.8	13.3	14.1	13.7	8.6	9.4	6.9	12.7	14.1	15.5																		
<i>D. lemchei</i>	9.2	14.5	14.1	15.1	7.1	7.3	3.3	10.0	14.9	15.7	5.5																	
<i>D. millbayana</i>	9.2	15.3	14.3	14.7	5.7	0.2	8.0	11.6	14.1	15.9	9.2	7.1																
<i>D. pinatifida</i>	14.3	14.7	14.1	15.1	12.4	12.4	13.1	15.1	15.5	17.6	14.5	12.7	12.4															
<i>D. rosacea</i>	13.1	16.1	15.9	16.9	14.1	14.1	14.5	15.7	16.5	18.6	13.9	13.7	13.9	15.5														
<i>Doto sp. 2</i>	15.3	14.1	12.5	15.1	16.7	15.7	13.7	14.9	13.9	11.8	14.9	12.9	15.5	15.1	17.3													
<i>Doto sp. 7</i>	16.3	16.3	14.7	16.5	16.9	16.7	16.3	16.5	14.9	11.8	16.1	15.3	16.9	16.9	17.6	9.8												
<i>Doto sp. J</i>	13.9	14.1	12.7	15.1	17.1	15.9	16.9	15.9	14.1	12.7	16.9	16.7	15.7	18.4	17.1	12.9	13.5											
<i>Doto sp. A</i>	9.2	15.3	14.3	14.7	5.7	0.2	8.0	11.6	14.1	15.9	9.2	7.1	0.0	12.4	13.9	15.5	16.9	15.7										
<i>Doto sp. B</i>	9.4	14.7	13.9	14.7	8.0	8.8	6.3	12.0	15.5	14.7	4.5	5.7	8.6	13.9	14.7	14.1	15.5	15.5	8.6									
<i>Doto sp. H</i>	15.9	9.6	11.2	9.2	14.7	13.7	15.5	15.3	9.4	17.8	13.3	14.7	13.5	14.3	16.9	15.9	15.3	15.1	13.5	14.1								
<i>Doto sp. I</i>	13.9	14.1	12.7	15.1	17.1	15.9	16.9	15.9	14.1	12.7	16.9	16.7	15.7	18.4	17.1	12.9	13.5	0.0	15.7	15.5	15.1							
<i>Doto sp. K</i>	13.7	15.3	14.3	16.5	17.5	15.9	14.9	16.3	15.5	13.7	15.7	14.7	16.1	16.9	16.9	9.2	10.4	13.5	16.1	15.7	16.3	13.5						
<i>D. tuberculata</i>	11.2	16.3	15.7	15.7	10.4	9.6	11.2	11.6	15.1	14.9	11.8	10.2	9.4	12.4	14.7	14.9	15.9	15.9	9.4	11.0	15.9	17.3						
<i>D. ussi</i>	15.3	15.1	14.3	16.7	17.5	17.3	15.9	15.1	15.3	13.9	16.9	14.9	17.1	17.8	17.3	10.8	11.6	13.3	17.1	15.1	17.6	13.3	7.1	17.5				
<i>K. phasmida</i>	17.3	17.8	18.2	18.4	16.9	18.0	17.3	15.9	19.2	20.2	16.5	16.1	17.8	19.8	16.9	19.4	19.4	18.4	17.8	16.5	18.0	18.4	20.8	17.1	19.6			
<i>K. rubroreticulata</i>	13.5	14.7	14.3	14.7	13.5	13.7	14.7	13.5	13.7	17.3	14.3	13.7	13.7	13.3	15.1	13.7	15.3	16.1	13.7	14.5	14.3	16.1	13.9	13.5	15.1	17.8		



**Fig. 5.** Phylogenetic relationships inferred from maximum likelihood method for the mtDNA *cox1* sequences. A, Janolidae species; B, Trinchesiidae species; C, Polycerinae species. Node supporting values are indicated as bootstrap percentage over 50. Sequences used in this study are denoted by red asterisks (\*).

**Table 4.** Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among Janolidae species

	<i>Antiopella barbarensis</i>	<i>A. fusca</i>	<i>Bonisa nakaza_01</i>	<i>B. nakaza_02</i>	<i>Janolus flavoanulatus</i>	<i>J. toyamensis_01</i>	<i>J. toyamensis_02</i>
<i>A. barbarensis</i>							
<i>A. fusca</i>	19.9						
<i>B. nakaza_01</i>	21.4	19.5					
<i>B. nakaza_02</i>	21.4	19.5	0.0				
<i>J. flavoanulatus</i>	17.5	20.5	18.1	18.1			
<i>J. toyamensis_01</i>	19.8	20.7	19.1	19.1	14.1		
<i>J. toyamensis_02</i>	19.6	20.7	19.0	19.0	14.0	0.2	
<i>J. tricellariodes</i>	19.1	21.9	17.9	17.9	9.7	14.0	13.8

**Material examined.** 1 individual (MO00184333), Seopseom Islet, Bomok-dong, Seogwipo-si, Jeju-do (33°13'47.04"N, 126°36'18.05"E), collected by SCUBA diving at depth of 23 m, 3 Dec 2022.

**Description.** Body elongated (length 7.1 mm; preserved specimen), slender, pale pink to violet in ground color (Fig. 3D). Rhinophores smooth and tapering towards tips, purple to deep violet in color. Cerata arranged laterally in 10–12 pairs of ceratal clusters, except mid-dorsum. Each ceratal cluster with mostly five to seven ceras, decreasing in number and size towards tail. Each ceras long and papillary in shape, tapered at top, pink to reddish purple with bright yellow tips. Oral tentacles similar in shape and color to rhinophores, but slenderer and half in length. Foot narrow; anterior corners resembling oral tentacles in shape, length and color; metapodium elongated and pointed.

**GenBank accession number.** OQ919376.

**Distribution.** Korea, Japan, Indonesia, Indo-West Pacific.

**Remarks.** This species shows color variations according to their food source such as *Sertularella* hydroid (Debelius and Kuitert, 2007).

The phylogenetic tree from the mtDNA *cox1* sequences groups *Trinchesia sibogae* with the *cox1* sequence of *Phestilla sibogae\_01*, separated from other *P. sibogae* haplotype sequences (*P. sibogae\_02*, 03) (Fig. 5B, Table 5). *Phestilla sibogae\_01* haplotype was nested within *Trinchesia* species showing a very low *p*-distance of 1.2% from *T. sibogae* which is often encountered as within the range of intraspecific variation. Based on this sequence information, it is likely that the *cox1* sequence labelled as *P. sibogae\_01* is actually the same species with *T. sibogae*, as mentioned in Korshunova et al. (2018a). Morphologically, *Phestilla* and *Trinchesia* are readily distinguished by the presence of an anterior foot corner and cnidosacs (Korshunova et al., 2017b). In addition, the color pattern of *T. sibogae* includes a reddish-purple body with yellowish-tipped cerata, whereas *P. sibogae* has a bright milky-white body with white-tipped, brownish-grey cerata of which color is associated with feeding on hard corals.

In our phylogenetic tree, all genera belonging to the family Trinchesiidae are monophyletic except *Trinchesia* of which species members are not monophyletic and split into different clades (Fig. 5B). The *p*-distances within the genus *Trinchesia* range from 13.4% (between *T. lenkai* Martynov, 2002 and *T. ornata* [Baba, 1937]) to 19.4% (between *T. foliata* [Forbes and Goodsir, 1839] and *T. sibogae*) (Table 5). Non-monophyly of this genus is also observed in the previous phylogenetic analyses based on the combined dataset of mtDNA *cox1*, 16S rDNA, and histone H3, awaiting further evidences for resolving taxonomic ambiguities of this genus (Hu et al., 2020; Mehrotra et al., 2020).

**Table 5.** Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among Trinchesiidae species

	<i>Catirona aurantia</i>	<i>C. gymnota</i>	<i>C. diaphora</i>	<i>C. lagunae</i>	<i>C. viridis</i>	<i>D. viridis</i>	<i>P. lugubris</i>	<i>P. sibogae_01</i>	<i>P. sibogae_02</i>	<i>P. sibogae_03</i>	<i>R. amoena</i>	<i>R. rubescens</i>	<i>Tenella adspersa_01</i>	<i>Te. adspersa_02</i>	<i>Trinchesia caerulea</i>	<i>Tr. foliata</i>	<i>Tr. lenkai</i>	<i>Tr. ornata</i>	<i>Tr. sibogae</i>	<i>Tr. speciosa</i>	<i>Z. fulgens</i>	<i>Z. nini</i>		
<i>C. aurantia</i>	7.3																							
<i>C. gymnota</i>	15.2	17.0																						
<i>D. lagunae</i>	17.5	17.7	12.5																					
<i>D. viridis</i>	18.7	20.0	18.7	12.5																				
<i>P. lugubris</i>	15.9	16.9	18.9	18.9	21.5																			
<i>P. sibogae_01</i>	19.7	20.7	18.9	19.2	21.4	2.3	20.9																	
<i>P. sibogae_02</i>	20.0	20.9	19.2	19.2	21.5	2.3	21.5	0.3																
<i>P. sibogae_03</i>	13.5	14.4	16.7	17.4	19.2	18.7	15.9	19.0	19.4															
<i>R. amoena</i>	15.2	16.2	17.4	16.4	19.5	19.4	17.4	19.5	19.5	19.5	11.5													
<i>R. rubescens</i>	15.4	15.7	16.4	16.4	19.5	19.4	15.9	21.7	21.7	21.7	14.9	14.5												
<i>Te. adspersa_01</i>	16.0	16.5	16.2	16.2	18.9	20.5	17.0	20.9	21.2	21.2	15.5	15.4	4.3											
<i>Te. adspersa_02</i>	16.0	16.4	15.7	15.7	19.2	18.9	17.4	19.2	19.5	19.5	15.9	18.5	16.5	16.4										
<i>Tr. caerulea</i>	17.5	18.0	18.2	18.2	18.9	20.2	19.4	20.2	20.5	20.5	15.2	14.7	17.4	17.9	18.5									
<i>Tr. foliata</i>	16.2	17.7	17.7	17.7	18.0	18.7	19.0	18.9	19.2	19.2	15.9	18.5	16.5	16.4	17.2	17.7								
<i>Tr. lenkai</i>	15.2	15.9	16.5	16.5	18.5	17.5	17.4	18.0	18.4	18.4	16.7	17.5	17.2	17.4	18.4	19.0	13.4							
<i>Tr. ornata</i>	16.2	16.9	18.9	18.9	21.7	21.2	1.2	21.4	21.5	21.5	15.0	17.0	16.2	16.9	17.5	19.4	18.9	17.4						
<i>Tr. sibogae</i>	13.2	15.0	18.4	18.4	18.5	18.7	16.7	18.9	19.2	19.2	15.0	14.9	15.7	16.2	15.9	17.2	16.2	14.9	16.7					
<i>Tr. speciosa</i>	14.0	15.0	18.0	18.4	18.4	18.7	17.5	19.2	19.0	19.0	13.5	14.7	14.4	14.9	18.7	17.2	17.7	16.5	18.2	13.5				
<i>Z. fulgens</i>	15.7	17.0	16.4	16.4	17.5	19.9	18.4	20.2	20.5	20.5	15.2	16.5	16.7	17.0	18.5	18.5	18.9	16.9	18.5	15.5	15.5			
<i>Z. nini</i>																								

**Table 6.** Uncorrected *p*-distances (%) for the mtDNA *cox1* sequences among Polycerinae species

	<i>Gymnodoris brunnea</i>	<i>G. striata</i>	<i>Lecithophorus capensis</i>	<i>Palio dubia</i>	<i>Polycerella emertoni</i>	<i>Polycera abei_01</i>	<i>Po. abei_02</i>	<i>Po. faeroensis</i>	<i>Po. kernowensis</i>	<i>Po. pennigera</i>	<i>Thecacera pennigera</i>
<i>G. brunnea</i>											
<i>G. striata</i>	14.0										
<i>L. capensis</i>	12.3	15.7									
<i>Pa. dubia</i>	16.2	17.1	15.4								
<i>Pl. emertoni</i>	17.3	18.4	19.8	20.5							
<i>Po. abei_01</i>	13.2	17.0	13.4	15.2	17.4						
<i>Po. abei_02</i>	12.6	15.7	12.9	14.3	16.3	2.2					
<i>Po. faeroensis</i>	15.6	17.9	17.0	18.2	17.4	14.8	14.6				
<i>Po. kernowensis</i>	16.2	16.8	17.4	17.9	18.5	16.0	16.0	6.2			
<i>T. pennigera</i>	15.1	17.3	15.7	16.6	19.9	17.3	16.2	15.7	16.8		
<i>T. picta</i>	14.8	16.3	16.5	17.1	18.8	16.2	15.4	16.6	18.0	10.6	

Suborder Doridina

Family Polyceridae Alder and Hancock, 1845

Genus *Polycera* Cuvier, 1816

**<sup>1</sup>\*5. *Polycera abei* (Baba, 1960) (Fig. 3E, F)**

*Greilada abei* Baba, 1960: 75, 76, fig. 1A–D.

*Polycera abei*: Debelius and Kuitert, 2007: 35; Gosliner et al., 2018: 28; Kil et al., 2020: 264, 265.

**Material examined.** 2 individuals (MO00184332, MMR BK7734), northeastern Habaekdo Islet, Samsan-myeon, Yeosu-si, Jeollanam-do (34°02'14.9"N, 127°36'24.7"E), collected by SCUBA diving at depth of 23 m, 20 Jul 2022.

**Description.** Body elongated (length 14.3 mm; preserved specimen), slender, limaciform, translucent ash-white to yellow in ground color, with small black spots and sparse orange flecks scattered on dorsal surface of whole body (Fig. 3E, F). Velar tentacles six, tapered. Rhinophore bearing lamellate clubs; rhinophore stalks smooth. Gills seven to nine in number, simply pinnate, arranged in a circle around anus. Velar tentacles, rhinophores, gill with black tips. Foot narrow; anterior corners short, triangular; metapodium tapering with black tip.

**GenBank accession number.** OQ919374, OQ919375.

**Distribution.** Korea, Japan, Indo-Pacific.

**Remarks.** This species lacks exo-branchial appendages on each side of the gill, which distinguishes it from other congeneric species. It has been reported to have a wide range of variations in color patterns and spot sizes on the body.

The phylogenetic tree depicts the subfamily Polycerinae monophyletic where *Polycera abei* is a sister taxon to *Polycerella emertoni* A. E. Verrill, 1880 (Fig. 5C). Nevertheless,

relationships among species members within the subfamily including sister relationships between *Polycera abei* and *Polycerella emertoni* are not clearly resolved. The *p*-distances among the *Polycera* species range from 6.2% to 16.0% (Table 6). The minimum distance is found between *Po. faeroensis* Lemche, 1929 and *Po. kernowensis* Korshunova et al., 2021, while the maximum distance is found between *Po. abei* and *Po. kernowensis*. Within Polycerinae, the maximum *p*-distance is 20.5% between *Palio dubia* (M. Sars, 1829) and *Pl. emertoni*.

**ORCID**

Jina Park: <https://orcid.org/0000-0003-2220-4840>

Damin Lee: <https://orcid.org/0000-0002-7805-6050>

Eggy Triana Putri: <https://orcid.org/0000-0003-1197-6001>

Haelim Kil: <https://orcid.org/0009-0007-7130-3323>

Joong-Ki Park: <https://orcid.org/0000-0002-0607-3329>

**CONFLICTS OF INTEREST**

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

**ACKNOWLEDGMENTS**

Seung-Goo Ra (Ocean Research, Korea), Kwan-Young Song (PADI, Korea), and Yuchool Lee (Korea National Park Service, Korea) helped field survey. This work was supported

Korean name: <sup>1</sup>\*점토시능선갯민숭달팽이

by the management of Marine Fishery Bio-resources Center (2023) funded by the National Marine Biodiversity Institute of Korea (MABIK).

## REFERENCES

- Aguado F, Marin A, 2007. Warning coloration associated with nematocyst-based defences in aeolidioid nudibranchs. *Journal of Molluscan Studies*, 73:23-28. <https://doi.org/10.1093/mollus/eyl026>
- Baba K, 1949. Opisthobranchia of Sagami Bay collected by His Majesty the Emperor of Japan. Iwanami Shoten Press, Tokyo, pp. 1-207.
- Baba K, 1960. The genera *Polycera*, *Palio*, *Greilada* and *Thecacera* from Japan (Nudibranchia-Polyceridae). *Publications of the Seto Marine Biological Laboratory*, 8:75-78. <https://doi.org/10.5134/174699>
- Baba K, 1986. *Janolus* in Japan. *Shells and Sea Life*, 18:182-184.
- Baba K, Abe T, 1970. Two new species of Janolidae from Toyama Bay, Japan (Gastropoda: Nudibranchia). *The Veliger*, 13:63-66.
- Barco A, Raupach MJ, Laakmann S, Neumann H, Knebelberger T, 2016. Identification of North Sea molluscs with DNA barcoding. *Molecular Ecology Resources*, 16:288-297. <https://doi.org/10.1111/1755-0998.12440>
- Bergh R, 1905. Die Opisthobranchiata der Siboga-Expedition. *Buchhandlung und druckerei vormals EJ Brill Press*, Leiden, pp. 1-248.
- Bouchet P, Rocroi JP, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE, 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, 61:1-526. <https://doi.org/10.4002/040.061.0201>
- Carmona L, Gosliner TM, Pola M, Cervera JL, 2011. A molecular approach to the phylogenetic status of the aeolid genus *Babakina* Roller, 1973 (Nudibranchia). *Journal of Molluscan Studies*, 77:417-422. <https://doi.org/10.1093/mollus/eyr029>
- Cella K, Carmona L, Ekimova I, Chichvarkhin A, Schepetov D, Gosliner TM, 2016. A radical solution: the phylogeny of the nudibranch family Fionidae. *PLoS ONE*, 11:e0167800. <https://doi.org/10.1371/journal.pone.0167800>
- Collins RA, Boykin LM, Cruickshank RH, Armstrong KF, 2012. Barcoding's next top model: an evaluation of nucleotide substitution models for specimen identification. *Methods in Ecology and Evolution*, 3:457-465. <https://doi.org/10.1111/j.2041-210X.2011.00176.x>
- Darriba D, Taboada GL, Doallo R, Posada D, 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods*, 9:772.
- Debelius H, Kuitert RH, 2007. *Nudibranchs of the World*. IKAN-Unterwasserarchiv Press, Frankfurt, pp. 1-360.
- 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>
- Eliot C, 1909. Report on the nudibranchs collected by Mr. James Hornell at Okhamandal in Kattiarwar in 1905-6. Report to the Government of Baroda on the Marine Zoology of Okhamandal, 1:137-145.
- Faucci A, Toonen RJ, Hadfield MG, 2007. Host shift and speciation in a coral-feeding nudibranch. *Proceedings of the Royal Society B: Biological Sciences*, 274:111-119. <https://doi.org/10.1098/rspb.2006.3685>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R, 1994. DNA primers for amplification of mitochondrial cytochrome oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3:294-299.
- Folino NC, 1997. The role of prey mobility in the population ecology of the nudibranch *Cuthona nana* (Gastropoda: Opisthobranchia). *American Malacological Bulletin*, 14:17-25.
- Goodheart JA, Bazinet AL, Valdés Á, Collins AG, Cummings MP, 2017. Prey preference follows phylogeny: evolutionary dietary patterns within the marine gastropod group Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). *BMC Evolutionary Biology*, 17:221. <https://doi.org/10.1186/s12862-017-1066-0>
- Goodheart JA, Bleidißel S, Schillo D, Strong EE, Ayres DL, Preisfeld A, Collins AG, Cummings MP, Wägele H, 2018. Comparative morphology and evolution of the cnidosac in Cladobranchia (Gastropoda: Heterobranchia: Nudibranchia). *Frontiers in Zoology*, 15:43. <https://doi.org/10.1186/s12983-018-0289-2>
- Gosliner TM, 1981. The South African Janolidae (Mollusca: Nudibranchia) with a description of a new genus and two new species. *Annals of the South African Museum*, 86:1-42.
- Gosliner TM, Valdés Á, Behrens DW, 2018. *Nudibranch & sea slug identification. Indo-Pacific*. 2nd ed. New World Publications Press, Jacksonville, FL, pp. 1-452.
- Hu J, Zhang Y, Yiu SKF, Xie JY, Qiu JW, 2020. A new species of predatory nudibranch (Gastropoda: Trinchesiidae) of the scleractinian coral *Goniopora*. *Zoological Studies*, 59:e62. <https://doi.org/10.6620/ZS.2020.59-62>
- Katoh K, Standley DM, 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution*, 30:772-780. <https://doi.org/10.1093/molbev/mst010>
- Kil HJ, Jung DW, Nam E, Kim H, Valdés Á, 2020. Sea slugs of Korea. National Institute of Biological Resources Press, Incheon, pp. 1-313 (in Korean).
- Knutson VL, Gosliner TM, 2014. Three new species of *Gymnodoris* Stimpson, 1855 (Opisthobranchia: Nudibranchia)

- from Philippines. In: The Coral Triangle: The 2011 Hearst Philippine Biodiversity Expedition (Eds., Williams GC, Gosliner TM), pp. 129-143.
- Knutson VL, Gosliner TM, 2022. The first phylogenetic and species delimitation study of the nudibranch genus *Gymnodoris* reveals high species diversity (Gastropoda: Nudibranchia). *Molecular Phylogenetics and Evolution*, 171:107470. <https://doi.org/10.1016/j.ympev.2022.107470>
- Korshunova TA, Driessen FMF, Picton BE, Martynov AV, 2021. The multilevel organismal diversity approach decipherers difficult to distinguish nudibranch species complex. *Scientific Reports*, 11:18323. <https://doi.org/10.1038/s41598-021-94863-5>
- Korshunova T, Fujita T, Martynov A, 2018a. The first record of *Trinchesia lenkae* Martynov, 2002 from Japan: morphological and molecular comparison with the material from the type locality in Russia (Nudibranchia: Trinchesiidae). *Venus*, 76:19-28. [https://doi.org/10.18941/venus.76.1-4\\_19](https://doi.org/10.18941/venus.76.1-4_19)
- Korshunova T, Lundin K, Malmberg K, Picton B, Martynov A, 2018b. 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, Martynov A, Bakken T, Evertsen J, Fletcher K, Mudianta W, Saito H, Lundin K, Schrödl M, Picton B, 2017a. 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.717.21885>
- Korshunova T, Martynov A, Picton B, 2017b. Ontogeny as an important part of integrative taxonomy in tergipedit aeolidaceans (Gastropoda: Nudibranchia) with a description of a new genus and species from the Barents Sea. *Zootaxa*, 4324:1-22. <https://doi.org/10.11646/zootaxa.4324.1.1>
- MacFarland FM, 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North America. *Memoirs of the California Academy of Sciences*, 6:1-546.
- Mahguib J, Valdés Á, 2015. Molecular investigation of the phylogenetic position of the polar nudibranch *Doridoxa* (Mollusca, Gastropoda, Heterobranchia). *Polar Biology*, 38:1369-1377. <https://doi.org/10.1007/s00300-015-1700-5>
- Mallet J, 2007. Subspecies, semispecies, superspecies. *Encyclopedia of Biodiversity*, 5:523-526.
- Marín A, Ros J, 1991. Presence of intracellular zooxanthellae in Mediterranean nudibranchs. *Journal of Molluscan Studies*, 57 (Supplement Part 4):87-101. [https://doi.org/10.1093/mollus/57.Supplement\\_Part\\_4.87](https://doi.org/10.1093/mollus/57.Supplement_Part_4.87)
- Mehrotra R, Arnold S, Wang A, Chavanich S, Hoeksema BW, Caballer M, 2020. A new species of coral-feeding nudibranch (Mollusca: Gastropoda) from the Gulf of Thailand. *Marine Biodiversity*, 50:36. <https://doi.org/10.1007/s12526-020-01050-2>
- Moles J, Berning MI, Hooker Y, Padula V, Wilson NG, Schrödl M, 2021. Due South: the evolutionary history of Sub-Antarctic and Antarctic Tritoniidae nudibranchs. *Molecular Phylogenetics and Evolution*, 162:107209. <https://doi.org/10.1016/j.ympev.2021.107209>
- MolluscaBase, 2023. MolluscaBase [Internet]. Accessed 4 Mar 2023, <<https://www.molluscabase.org>>.
- National Marine Biodiversity Institute of Korea, 2022. National List of Marine Species, Vol. 2. Marine Invertebrate [Internet]. Accessed 4 Mar 2023, <[https://www.mabik.re.kr/prog/rsrchLtry/kor/sub03\\_02\\_04/view.do](https://www.mabik.re.kr/prog/rsrchLtry/kor/sub03_02_04/view.do)>.
- Nybakken J, McDonald G, 1981. Feeding mechanisms of west American nudibranchs feeding on Bryozoa, Cnidaria and Ascidiacea, with special respect to the radula. *Malacologia*, 20:439-449.
- Okutani T, 2000. Marine mollusks in Japan. Tokai University Press, Tokyo, pp. 1-1173.
- Palomar G, Pola M, Garcia-Vazquez E, 2014. First molecular phylogeny of the subfamily Polycerinae (Mollusca, Nudibranchia, Polyceridae). *Helgoland Marine Research*, 68:143-153. <https://doi.org/10.1007/s10152-013-0374-z>
- Pola M, Gosliner TM, 2010. The first molecular phylogeny of cladobranchian opisthobranchs (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution*, 56:931-941. <https://doi.org/10.1016/j.ympev.2010.05.003>
- Pola M, Hallas JM, Gosliner TM, 2019. Welcome back Janolidae and *Antiopella*: improving the understanding of Janolidae and Madrellidae (Cladobranchia, Heterobranchia) with description of four new species. *Journal of Zoological Systematics and Evolutionary Research*, 57:345-368. <https://doi.org/10.1111/jzs.12257>
- Pola M, Vallès Y, Cervera JL, Medina M, Gosliner TM, 2006. Taxonomic status of *Tambja abdere* and *Tambja fusca* based on morphological and molecular evidence, with comments on the phylogeny of the subfamily Nembrothinae (Nudibranchia, Polyceridae). *Annales Zoologici Fennici*, 43:52-64.
- Shields CC, 2009. Nudibranchs of the Ross Sea, Antarctica: phylogeny, diversity, and divergence. PhD dissertation, Clemson University, Clemson, SC, USA, pp. 1-92.
- Shipman C, Gosliner T, 2015. Molecular and morphological systematics of *Doto* Oken, 1851 (Gastropoda: Heterobranchia), with descriptions of five new species and a new genus. *Zootaxa*, 3973:57-101. <https://doi.org/10.11646/zootaxa.3973.1.2>
- Srivathsan A, Meier R, 2012. On the inappropriate use of Kimura-2-parameter (K2P) divergences in the DNA-barcoding literature. *Cladistics*, 28:190-194. <https://doi.org/10.1111/j.1096-0031.2011.00370.x>
- Stamatakis A, 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30:1312-1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stecher G, Tamura K, Kumar S, 2020. Molecular evolutionary genetics analysis (MEGA) for macOS. *Molecular Biology and Evolution*, 37:1237-1239. <https://doi.org/10.1093/molbev/msz312>

- Valdés Á, Lundsten L, Wilson NG, 2018. Five new deep-sea species of nudibranchs (Gastropoda: Heterobranchia: Cladobranchia) from the Northeast Pacific. *Zootaxa*, 4526:401-433. <https://doi.org/10.11646/zootaxa.4526.4.1>
- Vadher P, Kardani H, Beleem I, 2020. An annotated checklist of sea slug fauna of Gujarat coast, India. *Journal of Threatened Taxa*, 12:15835-15851. <https://doi.org/10.11609/jott.5278.12.8.15835-15851>
- Vadher P, Kardani HK, Beleem I, 2021. New distribution record of *Janolus flavoanulatus* Pola & Gosliner, 2019 (Nudibranchia: Janolidae) from India. *Journal of the Marine Biological Association of India*, 63:118-121. <https://doi.org/10.6024/jmbai.2021.63.2.2157-17>
- Vishal B, Deepak A, 2013. Current status of Indian opisthobranch fauna. In: Ecology and conservation of tropical marine faunal communities (Eds., Venkataraman K, Sivaperuman C, Raghunathan C). Springer, Berlin, pp. 63-79.
- Willan RC, Morton JE, 1984. Cape Rodney to Okakari Point Marine Reserve. Marine molluscs, Part 2. Opisthobranchia. Leigh Marine Laboratory Press, Leigh, pp. 1-106.
- Wilson EO, Brown WL Jr, 1953. The subspecies concept and its taxonomic application. *Systematic Biology*, 2:97-111. <https://doi.org/10.2307/2411818>
- Winters AE, White AM, Cheney KL, Garson MJ, 2018. Geographic variation in diterpene-based secondary metabolites and level of defence in an aposematic nudibranch, *Goniobranchus splendidus*. *Journal of Molluscan Studies*, 85:133-142. <https://doi.org/10.1093/mollus/eyy057>
- Wollscheid-Lengeling E, Boore J, Brown W, Wägele H, 2001. The phylogeny of Nudibranchia (Opisthobranchia, Gastropoda, Mollusca) reconstructed by three molecular markers. *Organisms Diversity and Evolution*, 1:241-256. <https://doi.org/10.1078/1439-6092-00022>

Received May 11, 2023  
 Revised June 2, 2023  
 Accepted June 12, 2023