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Two New Moray Eels of Genera *Diaphenchelys* and *Gymnothorax* (Anguilliformes: Muraenidae) from Taiwan and the Philippines

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Two new moray eels of the genera *Diaphenchelys* and *Gymnothorax* from Taiwan and the Philippines are described. *Diaphenchelys laimospila* sp. nov. is described based on two specimens that represent the third species and a new geographic record of the genus. It can be distinguished from the other two congeners by the number of cephalic sensory pores, vertebral formula, morphometric measurements, and the coloration pattern. *Gymnothorax pseudokidako* sp. nov. is a muraenid with a dark brown body covered by pale snowflake-like blotches. It differs from the most similar species *Gymnothorax kidako* (Temminck and Schlegel) by having a relatively short tail (50.5–53.0% vs. 52.9–56.4% of TL), more dentary teeth (17–26 vs. 16–20), fewer total vertebrae (134–139 vs. 137–143), and the absence of white margin on anal fin (vs. prominent white margin). These two new species were also confirmed by molecular analyses, the mitochondrial *COI* gene (593 bp) for *D. laimospila*, and the nuclear *EGR3* gene (767 bp) for *G. pseudokidako*.

Key words: Elopomorpha, Muraeninae, Muraenoidei, New species, Western Pacific.

BACKGROUND

Diaphenchelys McCosker and Randall, 2007 is a muraenid genus characterized by body elongated and mottled, tail laterally compressed and much longer than the remaining part of the body, snout blunt, eyes placed well anteriorly, maxillary teeth biserial, and dentary teeth mostly uniserial with a few large teeth on inner row. To date, two species of *Diaphenchelys* have been described, viz. *Diaphenchelys dalmatian* Hibino, Satapoomin and Kimura, 2017, and *Diaphenchelys pelonates* McCosker and Randall, 2007. *Diaphenchelys pelonates* is only known from the Maumere Bay of Indonesia, while *D. dalmatian* is distributed in a wider range from type localities in the Andaman Sea and the Gulf of Thailand, and has been recently recorded in the Bay of Bengal along the Indian coast (Mohanty and Mohapatra 2020). In the present study, a third species of *Diaphenchelys* is described based on two specimens from Taiwan and the Philippines, representing a new geographic distribution of this genus.

The second undescribed species in this paper belongs to the genus *Gymnothorax* Bloch, 1795 with a coloration pattern of many pale snowflake-like blotches on head, body, and fins, which is commonly present in small to medium-sized morays. The arrangement of pale blotches can be quite variable intraspecifically, sometimes resulting in taxonomic confusion. For instance, *Gymnothorax kidako* (Temminck and Schlegel, 1846), one of the most common morays

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in the northwestern Pacific Ocean, used to comprise several synonyms and possible synonyms, including *Muraena similis* Richardson, 1848, *Gymnothorax mucifer* Snyder, 1904, and *Gymnothorax niphostigmus* Chen, Shao and Chen, 1996 (Böhlke and Smith 2002). However, validities of *G. mucifer* and *G. niphostigmus* have been subsequently supported by morphological and molecular characters (Huang et al. 2018 2019). The second undescribed species herein is morphologically similar to *G. kidako*. Both species have a dark brown body covered by pale snowflake-like blotches, but the prominent white margin of anal fin, an important diagnostic character of *G. kidako*, is not observed in the new species. We herein describe this new species based on 15 specimens from Taiwan and the Philippines.

MATERIALS AND METHODS

All specimens were collected from fish markets and fish landing sites, where morays were caught by bottom longline, eel tube, or bottom trawl in nearshore regions. Fresh specimens were photographed and measured; a piece of muscle tissue was cut, preserved in 95% ethanol, and stored in a -20°C freezer until DNA extraction. Voucher specimens were fixed in 10% formalin, and transferred to 50% isopropyl alcohol solution or 70% ethanol solution for permanent preservation. Morphometric measurements followed Böhlke et al. (1989), presented as percentage of total length (TL) or head length (HL). Counts of vertebral formula (VF) followed the terminology of Böhlke (1982), expressed as predorsal-preanal-total vertebrae. Teeth and cephalic sensory pores were counted under a stereomicroscope and their terminologies followed Smith et al. (2019). Teeth counts included the sockets of missing teeth. Specimens were deposited in the Museum of the Biodiversity Research Center, Academia Sinica, Taipei (ASIZP), National Museum of Marine Biology and Aquarium, Pingtung (NMMB-P); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Eastern Marine Biology Research Center, Fishery Research Institute, Taitung (FRIP); Laboratory of Aquatic Ecology, Department of Aquaculture, National Taiwan Ocean University, Keelung (TOU-AE); and Department of Oceanography, National Sun Yat-sen University, Kaohsiung (DOS).

DNA extraction was conducted using a GeneMark DNA Purification Kit (GMbiolab, Taichung, Taiwan). A fragment of the mitochondrial cytochrome oxidase subunit I (*COI*) gene was amplified by polymerase chain reaction (PCR) using primers FishF2 (5′-TCG ACT AAT CAT AAA GAT ATC GGC AC-3′) and FishR2 (5′-ACT TCA GGG TGA CCG AAG AAT CAG AA-3′) (Ward et al. 2005). Additionally, a fragment of nuclear early growth response 3 (*EGR3*) gene was amplified from holotype and two paratypes of *G. pseudokidako* and closely-related species of *Gymnothorax* to clarify the phylogenetic relationship due to a lack of reciprocal monophyly between *G. pseudokidako* and *G. kidako* in the *COI* analysis. The amplification of *EGR3* was conducted by nested PCR using following primers: E3 179F (5′-ATG GGA AGT GAA AAR GGC ACT-3′) and E3 1136R (5′-GGY TTC TTG TCC TTC TGT TTS AG-3′); E3 254F (5′-GTC ACC TAY YTG GGS AAG TTT-3′) and E3 1068R (5′-GTC CRC AGA ACT CGC ARG AGA-3′) (Chen et al. 2008 2013 2014). The thermal cycling profile was identical for all PCRs, with an initial denaturation at 95°C for 5 min, following by 35 cycles of amplification (denaturing at 95°C for 40 s, annealing at 50°C for 40 s, and extension at 72°C for 1 min), and a final extension at 72°C for 8 min. PCR products were purified using a SAP-Exo purification kit (Jena Bioscience, Jena) and sequenced by an ABI 3730 XL automated sequencer (Genomics BioSci. & Tech.). Sequences were edited and aligned manually using MEGA X (Kumar et al. 2018) and submitted to GenBank (accession numbers in Table 1).

Owing to the close relationships and morphological similarities with *D. laimospila*, *COI* sequences of *D. dalmatian*, *Gymnothorax melanosomatus* Loh, Shao and Chen, 2011, *Gymnothorax prolatus* Sasaki and Amaoka, 1991, *Strophidon dorsalis* (Seale, 1917), *Strophidon sathete* (Hamilton, 1822), *Strophidon tetraporus* Huang et al., 2020, and *Strophidon ui* Tanaka, 1918 were obtained for genetic tree reconstruction (Huang et al. 2020). Meanwhile, for *G. pseudokidako*, *COI* and *EGR3* sequences of the closely related species *G. kidako*, *G. mucifer*, and *G. niphostigmus* were used to reconstruct mitochondrial and nuclear genetic trees (Huang et al. 2019; Smith et al. 2019) (Table 1). Maximum likelihood (ML) trees were built using MEGA X based on the best selected substitution models suggested by jModelTest (Darriba et al. 2012) and bootstrap probability analyses with 1000 replicates (Felsenstein 1985). *Uropterygius macrocephalus* (Bleeker, 1864) was used as the outgroup for all ML trees.

RESULTS

Diaphenchelys laimospila Huang, Smith and Liao sp. nov.

Common name: Spotted-throat moray
(Table 2; Figs. 1–4, 10)
urn:lsid:zoobank.org:act:8B55EF56-7513-43C7-9100-D8099D6E1C6A

Holotype: NMMB-P26218 (290 mm TL, male), Donggang, Pingtung County, southwestern Taiwan, bottom trawl, depth unknown, 16 Jun. 2017, coll. H.C. Ho.

Paratype: USNM 407544 (525 mm TL, sex unknown), Sitio Pasiquit, San Vicente, Cagayan, Philippines, 4 Jun. 2012, coll. J.T. Williams, K.E. Carpenter, A. Lizano & T. Potenciana.

Etymology: From Greek words *laimos* (throat) and *spilos* (spot), in reference to the dense whitish spots on the throat of this moray. A noun in apposition.

Diagnosis: A moderately sized, elongate moray. Tail very long, more than twice trunk length, compressed posteriorly, tip of tail pointed. Snout blunt, nasal cavity somewhat enlarged. Eyes well anteriorly placed, closer to tip of snout than corner of mouth. Three supraorbital pores, three infraorbital pores, six preoperculo-mandibular pores. Maxillary teeth biserial, dentary teeth uniserial or biserial anteriorly. Ground color of body pale brown, with whitish spots scattered on head, body, and dorsal fin, scarcely perceptible on snout, anal fin and posterior part of tail. Caudal fin semi-transparent, fins on posterior part of tail with dark brown margin. Predorsal vertebrae 4, preanal vertebrae 45, and total vertebrae 125–131.

Description: Proportions in percent of TL: tail length of holotype 63.8 (of paratype 63.2), trunk length 24.8 (25.4), head length 11.4 (11.3), predorsal length 6.9 (7.0), depth at gill opening 3.9 (5.4), depth at anus 3.7 (3.8). Proportions in percent of HL: predorsal length 60.6 (62.2), length of jaws 35.2 (39.5), interorbital width 9.0, snout length 11.5 (12.4), eye diameter 7.8 (6.7).

Body slender, anus well anterior to mid-body. Tail very long, more than twice trunk length, compressed posteriorly, tip of tail pointed. Dorsal and anal fin low and inconspicuous, caudal fin relatively long. Origin of dorsal fin anterior to gill opening and branchial pores. Origin of anal fin immediately behind anus (Fig. 1). Gill opening oval, below lateral midline of body, equal to eye in diameter. Eyes moderate in size and well anteriorly placed, posterior margin of eye anterior to middle of mouth gape, snout/upper jaw length 0.33 (0.31). Snout short and blunt, nasal cavity somewhat enlarged. Jaws not arched, subequal in holotype, upper jaw slightly longer than lower jaw in paratype, teeth

Table 1. Accession numbers and catalogue numbers of voucher specimens used in this study

Species	Voucher number	Accession number	
		COI	*EGR3*
Diaphenchelys dalmatian	**PMBC 27945**	LC189004	na
Diaphenchelys laimospila sp. nov.	**NMMB-P26218**	*MW354732*	na
Gymnothorax kidako	DOS 03540	MF774817	*MW355581*
	DOS 06258	MH400959	*MW355582*
	DOS 06259	MH400960	*MW355583*
Gymnothorax melanosomatus	**TOU-AE 1991**	*MW354733*	na
	TOU-AE 5095	*MW354734*	na
Gymnothorax mucifer	DOS 06265	MH400955	*MW355584*
	DOS 06267	MH400957	*MW355585*
Gymnothorax niphostigmus	DOS 03536	MF774815	*MW355586*
	DOS 03537	MF774816	*MW355587*
Gymnothorax prolatus	DOS 03171-1	*MW354735*	na
	DOS 07225	MT318342	na
Gymnothorax pseudokidako sp. nov.	**ASIZP0080920**	*MW354729*	*MW355578*
	ASIZP0080923	*MW354730*	*MW355579*
	NMMB-P34697	*MW354731*	*MW355580*
Strophidon dorsalis	DOS 07224-2	MT318347	na
	DOS 07224-4	MT318349	na
Strophidon sathete	DOS 07222	MT318373	na
	DOS 07264	MT318374	na
Strophidon tetraporus	**ASIZP0080910**	MT318378	na
	ASIZP0080913	MT318381	na
Strophidon ui	DOS 07245-1	MT318391	na
	DOS 07343-3	MT318404	na
Uropterygius macrocephalus	DOS 06260	MH400961	*MW355588*

Voucher numbers in bold represent the holotype; accession numbers in italic represent sequences newly generated in this study.

not visible when mouth closed. Anterior nostril at tip of snout, tubular and short, its length about half of eye diameter. Posterior nostril as a hole opening in caudal direction, located above anterior margin of eye with slightly raised rim (Fig. 2). Three supraorbital pores, first on tip of snout below level of anterior nostril, second anterior to base of anterior nostril, third along margin of snout at about same level of middle of eye. Three infraorbital pores, first immediately below base of anterior nostril, second located at midpoint between anterior nostril and anterior margin of eye, third below and slightly anterior to middle of eye. Six preoperculo-mandibular pores, all along lower jaw anterior to the corner of mouth. For branchial pores, holotype with two on each side of head, paratype with two on left side and four on right side, all pores on posterior-dorsal area of head, posterior to origin of dorsal-fin and anterior to gill opening (Fig. 2). Predorsal vertebrae 4 (4), preanal vertebrae 45 (45), total vertebrae 131 (125).

Dentition (Fig. 3): Teeth pointed and somewhat retrorse, edge smooth. Peripheral intermaxillary teeth uniserial, 6 (3) on each side, increasing in size posteriorly. Median intermaxillary teeth 3 (2) in uniserial, large, slender and somewhat depressible, teeth larger posteriorly. Maxillary teeth biserial, 33–35 (17) small, retrorse teeth on outer row, anteriormost and posteriormost teeth very small, equal-sized centrally; inner row with 8–10 (2) tall, straight and

Table 2. Morphometric measurements and meristic counts of *Diaphenchelys dalmatian*, *D. laimospila* sp. nov., and *D. pelonates*

Source	*D. dalmatian*[a, b]	*D. laimospila* sp. nov.		*D. pelonates*[c]
		holotype	paratype	
TL (mm)	290–503	290	525	121–465
As % of TL				
Tail length	62.0–64.6	63.8	63.2	59.6–61.5
Preanal length	35.4–38.0	36.2	36.8	38.5–40.4
Trunk length	23.9–27.6	24.8	25.4	29.1*
Head length	10.3–11.5	11.4	11.3	9.4–10.0
Predorsal length	7.4–8.6	6.9	7.0	6.5–7.1
Body depth at gill opening	3.7–4.1	3.9	5.4	3.3–3.5
Body depth at anus	3.0–3.7	3.7	3.8	3.2*
As % of HL				
Predorsal length	-	60.6	62.2	69.3*
Length of upper jaw	35.4–41.1	35.2	39.5	36.3–37.3
Length of lower jaw	-	35.2	-	36.2*
Snout length	11.4–14.2	11.5	12.4	11.3–15.0
Interorbital width	6.6–8.2	9.0	-	9.6*
Eye diameter	5.4–7.6	7.8	6.7	6.9–8.2
Snout/upper jaw length	-	0.33	0.31	0.33–0.34
Teeth				
Peripheral intermaxillary	5–8	6	3	7
Median intermaxillary	1–3	3	2	3
Maxillary outer	23–24	33–35	17	30
Maxillary inner	4–7	8–10	2	7–8
Vomerine	6–10	8	4	5–6
Dentary outer	22–25	34	17	25–26
Dentary inner	1–2	1	0	5
Cephalic sensory pores				
supraorbital	3	3	3	3
infraorbital	3	3	3	4–5
preoperculo-mandibular	5	6	6	6–7
branchial	2	2	2–4	2
Vertebrae				
Predorsal	6–9	4	4	4–6
Preanal	43–47	45	45	55–58
Total	126–132	131	125	153–155

[a], Hibino et al., 2017; [b], Mohanty & Mohapatra, 2020; [c], McCosker & Randall, 2007; *data only from the holotype.

well-spaced teeth originating adjacent to third outer tooth, not extending to end of outer row. Vomerine teeth 8 (4) uniserial, stout but pointed, decreasing in size posteriorly, anteriormost teeth about size of peripheral intermaxillary teeth. Dentary teeth biserial in holotype, with 3 large teeth plus 31 smaller, equal-sized teeth on each side, one pair of large teeth on inner row; dentary teeth uniserial in paratype, 17 on each side of lower jaw.

Coloration (Fig. 1): Pale brown ground color, with whitish spots scattered on head, body, and dorsal fin. Whitish spots densest on lower jaw and ventral part of head, somewhat gathering into worm-like marking; spots getting sparser posteriorly, scarcely perceptible on anal fin, posterior part of tail, and snout. Fins on

Fig. 1. *Diaphenchelys laimospila* sp. nov.. (A) NMMB-P26218, holotype, 290 mm TL, male, fresh coloration, photo by HC Ho; (B) preserved coloration of holotype; (C) USNM 407544, paratype, 525 mm TL, sex unknown, fresh coloration, photo by JT Williams.

posterior part of tail with dark brown margin. Caudal fin semi-transparent. Cephalic sensory pores without dark edge. Throat grooves, gill opening, and corner of mouth not darkish. Color of oral cavity pale brown. Iris of eyes yellowish. Preserved color slightly paler than fresh (Fig. 1B).

Distribution: Currently, only known from southwestern Taiwan and Luzon of the northern Philippines (Fig. 4). The holotype was collected by bottom trawl thus this species might prefer to inhabit

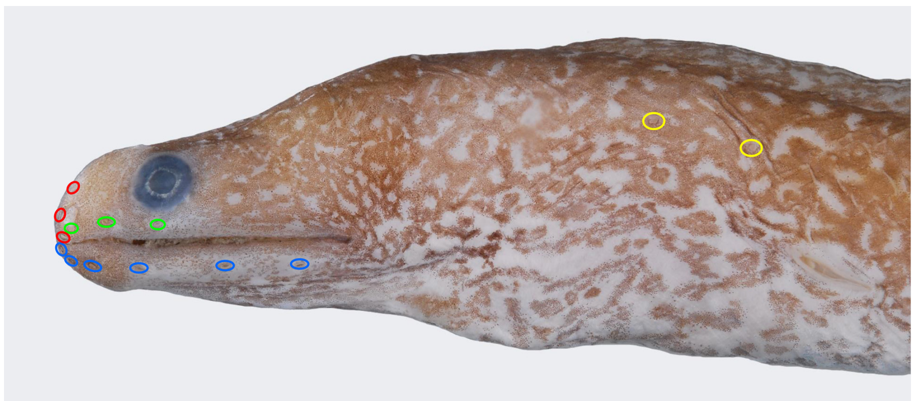

Fig. 2. *Diaphenchelys laimospila* sp. nov., lateral view of head marks with cephalic sensory pores: red for supraorbital pores; green for infraorbital pores; blue for preoperculo-mandibular pores; yellow for branchial pores. Photo of NMMB-P26218, holotype, 290 mm TL.

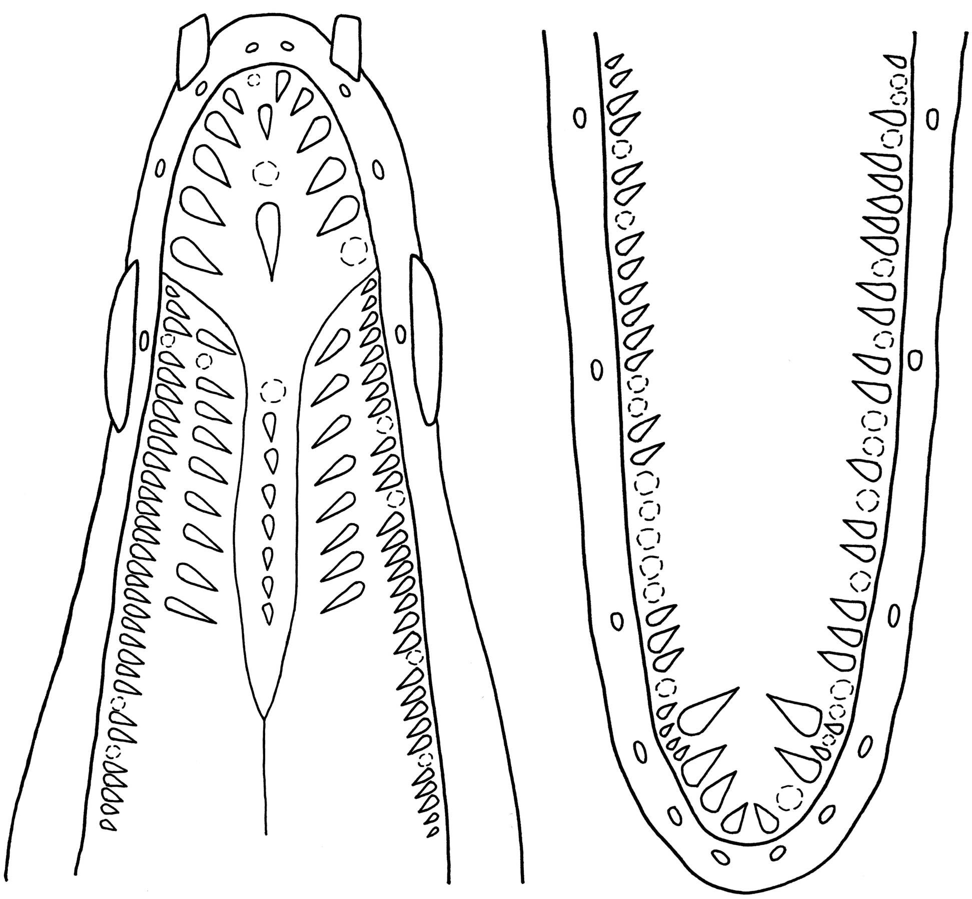

Fig. 3. Dentition of *Diaphenchelys laimospila* sp. nov., NMMB-P26218, holotype, 290 mm TL, male. Dotted lines represent the sockets of missing teeth. Upper jaw (left) and lower jaw (right).

sandy or muddy substrate. The paratype was purchased in a market.

Key to species of *Diaphenchelys*

1a. Tail length 59.6–61.5% of TL; infraorbital pores 4–5; preanal vertebrae 55–58, total vertebrae 153–155; anterior region of head dark brown .... *Diaphenchelys pelonates*
1b. Tail length 62.0–64.6% of TL; infraorbital pores 3; preanal vertebrae 43–47, total vertebrae 125–132; anterior region of head not dark 2
2a. Predorsal length 7.4–8.6% of TL; preoperculo-mandibular pores 5; predorsal vertebrae 6–9; white or yellowish white ground color with brown spots .... *Diaphenchelys dalmatian*
2b. Predorsal length 6.9–7.0% of TL; preoperculo-mandibular pores 6; predorsal vertebrae 4; pale brown ground color with whitish spots .... *Diaphenchelys laimospila* sp. nov.

Gymnothorax pseudokidako Huang, Loh and Liao sp. nov.

Common name: False kidako moray
(Table 3; Figs. 5–9, 11–12)
urn:lsid:zoobank.org:act:EC25B7CA-A401-4A18-8ECE-F6CC5404D04C

Holotype: ASIZP0080920 (801 mm TL, female), Fugang, Taitung County, eastern Taiwan, bottom longline, depth unknown, 09 May. 2020, coll. W.C. Huang.

Paratypes: 14 specimens (608–1041 mm TL). *Philippines*: USNM 438035 (618 mm, sex unknown), Dumaguete, Negros Oriental, 11 May. 2015, coll. A. Bucol. *Taiwan*: ASIZP0080923 (648 mm, male), Kanziding, Keelung City, 10 Aug. 2018, coll. W.C. Jhuang; ASIZP0080924 (913 mm, male), DOS 07906 (725 mm, male), DOS 07910 (821+ mm, male), NMMB-P33700 (794 mm, female), NMMB-P33701 (883 mm, female), collected with the holotype; ASIZP0080929 (608 mm, female), DOS 07961 (651+ mm, female), NMMB-P34698 (815 mm, male), Fugang, Taitung County, 08 Jul. 2020, coll. W.C. Huang; DOS 07940 (1041 mm, male), Fugang, Taitung County, 05 Jun. 2020, coll. W.C. Huang; FRIP21962 (757 mm, female), Chenggong, Taitung County, 14 Sept. 2006, coll. W.C Chiang; TOU-AE 5146 (641 mm, female), Heping Island, Keelung City, 02 Apr. 2009, coll. K.H. Loh; NMMB-P34697 (822 mm TL, female), Kanziding, Keelung City, 10 Aug. 2018, coll. W.C. Jhuang.

Etymology: Name from the Greek word *pseudēs* (false) and the species name *kidako*, in reference to the highly morphological similarity to *G. kidako*. A noun in

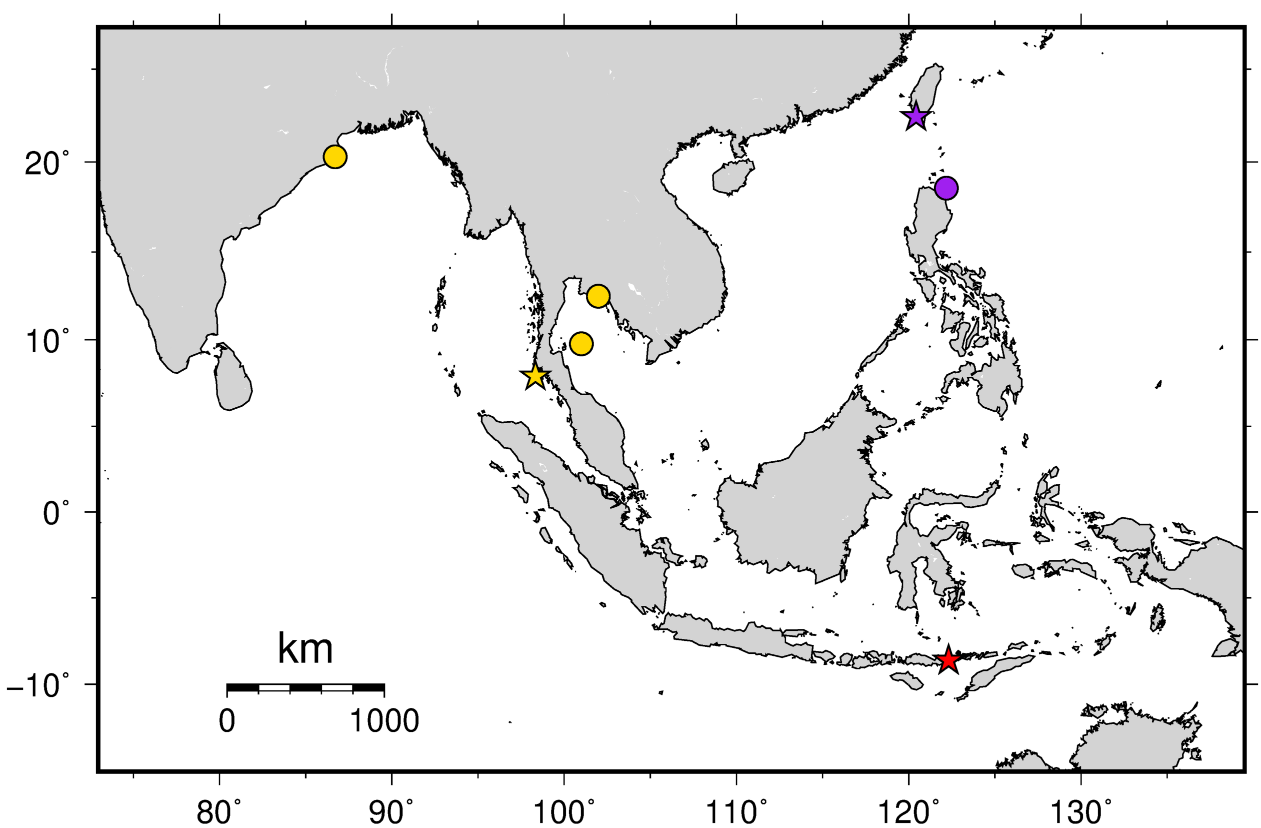

Fig. 4. Distribution of species in the genus *Diaphenchelys*. Yellow for *D. dalmatian*; purple for *D. laimospila* sp. nov.; red for *D. pelonates*. Star represents the type locality of each species.

apposition.

Diagnosis: A moderately sized moray, body stout, anus slightly anterior to mid-body. Teeth mostly uniserial, smaller individuals with an additional inner row of maxillary teeth, vomerine teeth sometimes in a staggered row. Color dark brown covered by pale spots. Spots usually gathering into snowflake-like blotches on trunk, tail, fins, and posterior part of head, scattered evenly on snout and lips. A conspicuous saddle-like marking of ground color on top of head between eyes and origin of dorsal fin. Fins without pale margin. Throat grooves, gill opening, and corner of mouth darkish. Iris of eyes yellowish or reddish brown. Predorsal vertebrae 4–7, preanal vertebrae 53–57, and total vertebrae 134–139.

Description: Proportions in percent of TL: tail length 51.7 of holotype (of paratypes 50.5–53.0), trunk length 35.2 (33.3–35.9), head length 13.0 (12.6–14.3), predorsal length 10.0 (8.4–11.2), depth at gill opening 9.3 (7.5–10.6), depth at anus 7.5 (5.6–7.9). Proportions in percent of HL: predorsal length 76.9 (66.4–81.8), length of upper jaw 45.7 (39.1–51.0), length of lower jaw 44.2 (40.9–49.3), interorbital width 12.2 (10.8–13.9), snout length 22.2 (19.8–22.8), eye diameter 8.7 (7.2–9.7).

A moderately sized moray with typical muraenid shape, body stout, anus slightly anterior to mid-body. Dorsal fin moderately high, originating anterior to gill opening. Anal fin shallow and the origin immediately behind anus (Fig. 5). Gill opening as a hole below lateral midline, smaller than eye in diameter. Eyes above mid-jaw. Snout acute and moderately elongate. Jaws subequal and not arched, teeth not visible when mouth closed. Anterior nostril at tip of snout, elongate and

Table 3. Morphometric measurements and meristic counts of *Gymnothorax kidako*, *G. mucifer*, *G. niphostigmus*, and *G. pseudokidako* sp. nov.. The means of morphometric measurements and number of vertebrae are given in parentheses

	G. kidako	*G. mucifer*	*G. niphostigmus*	*G. pseudokidako* sp. nov.	
	n = 15	*n* = 23	*n* = 12	holotype ASIZP0080920	Total *n* = 15
TL (mm)	572–840	221–666	635–950	801	608–1041
As % of TL					
Tail length	52.9–56.4 (54.1)	51.0–58.4 (54.9)[b]	52.4–55.1 (53.7)[c]	51.7	50.5–53.0 (51.7)[e]
Preanal length	44.2–47.3 (46.1)	41.6–48.4 (45.0)[b]	45.5–48.2 (46.7)[c]	48.3	47.0–49.5 (48.2)[e]
Trunk length	31.5–34.6 (33.2)	28.6–35.1 (32.3)[b]	31.4–35.3 (33.4)[c]	35.2	33.3–35.9 (34.6)[e]
Head length	12.0–14.0 (12.9)	11.5–13.7 (12.6)[b]	12.2–14.1 (13.3)[c]	13.0	12.6–14.3 (13.7)[e]
Predorsal length	8.1–10.5 (9.1)	8.4–10.5 (9.5)[b]	8.1–10.2 (9.4)[c]	10.0	8.4–11.2 (10.1)[e]
Body depth at gill opening	6.8–10.0 (7.9)	3.7–7.6 (5.4)[b]	5.7–8.8 (7.4)[c]	9.3	7.5–10.6 (9.4)[e]
Body depth at anus	5.2–7.6 (6.3)	3.5–5.9 (4.7)[b]	5.1–6.7 (5.9)[c]	7.5	5.6–7.9 (6.9)[e]
As % of HL					
Predorsal length	61.0–85.4 (71.0)	66.1–87.0 (75.8)	61.7–82.6 (71.8)	76.9	66.4–81.8 (74.4)
Length of upper jaw	39.5–49.8 (43.5)	38.2–53.2 (44.3)	39.9–48.1 (43.6)	45.7	39.1–51.0 (44.9)
Length of lower jaw	38.7–49.3 (42.8)	37.6–50.8 (43.6)	38.7–47.6 (42.4)	44.2	40.9–49.3 (44.7)
Snout length	18.5–22.2 (20.5)	16.9–22.5 (19.5)	17.2–20.9 (19.1)	22.2	19.8–22.8 (21.4)
Interorbital width	9.5–14.8 (12.4)	8.6–11.2 (10.2)	10.1–15.6 (11.6)	12.2	10.8–13.9 (12.3)
Eye diameter	7.1–9.4 (8.0)	8.5–12.2 (10.2)	7.3–10.2 (8.5)	8.7	7.2–9.7 (8.4)
Teeth					
Peripheral intermaxillary	5–7[a]	5–7	6–7[d]	6–7	5–8
Median intermaxillary	2–4[a]	2–4	1–3[d]	3	2–3
Maxillary	10–16[a]	10–18	10–17[d]	15–16	12–17
Vomerine	7–13[a]	5–20	2–14[d]	14	6–18
Dentary	16–20[a]	17–27	17–25[d]	25	17–26
Vertebrae					
Predorsal	4–6 (5)	4–6 (5)	4–6 (5)	5	4–7 (5)
Preanal	52–57 (56)	51–55 (53)	53–57 (55)	55	53–57 (55)
Total	137–143 (140)	130–141 (137)[b]	140–146 (144)[c]	139	134–139 (137)[e]
White margin of anal fin	Yes	Yes	Yes	No	No

[a]dentition counts from 12 specimens, not including TOU-AE 4828, 4829, and 4830. [b]data from 18 specimens, not including DOS 06261, 06262, 06265, 06268, and TOU-AE 4163, due to damage of their tails. [c]data from nine specimens, not including TOU-AE 5606, ASIZP056941, and TFRI-TT063, due to damage of their tails. [d]dentition counts from seven specimens, not including TOU-AE 0238, 4981, 4982, 5582, and 5606. [e]data from 13 specimens, not including DOS 07910 and DOS 07961, due to damage of their tails.

tubular, shorter than eye diameter in length. Posterior nostril above the anterior margin of eye, as an oval pore with slightly raised rim (Fig. 6). Number of head pores typical within muraenids (Fig. 6). Three supraorbital pores, first at tip of snout below level of anterior nostril, second just above base of anterior nostril, third on margin of snout above level of middle of eye, paratype TOU-AE 5146 with a fourth pore immediately behind third pore on right side of snout. Four infraorbital pores, first immediately below and posterior to base of anterior nostril, second about at anterior two fifths of distance between anterior nostril and anterior margin of eye, third below anterior margin of eye, fourth below posterior margin of eye. Six preoperculo-mandibular pores along lower jaw before corner of mouth; in paratype FRIP21962, right side of lower jaw without first pore, but presence of an additional pore between the fourth and fifth pores amounting the same number of pores

Fig. 5. *Gymnothorax pseudokidako* sp. nov., ASIZP0080920, holotype, 801 mm TL, female, fresh coloration.

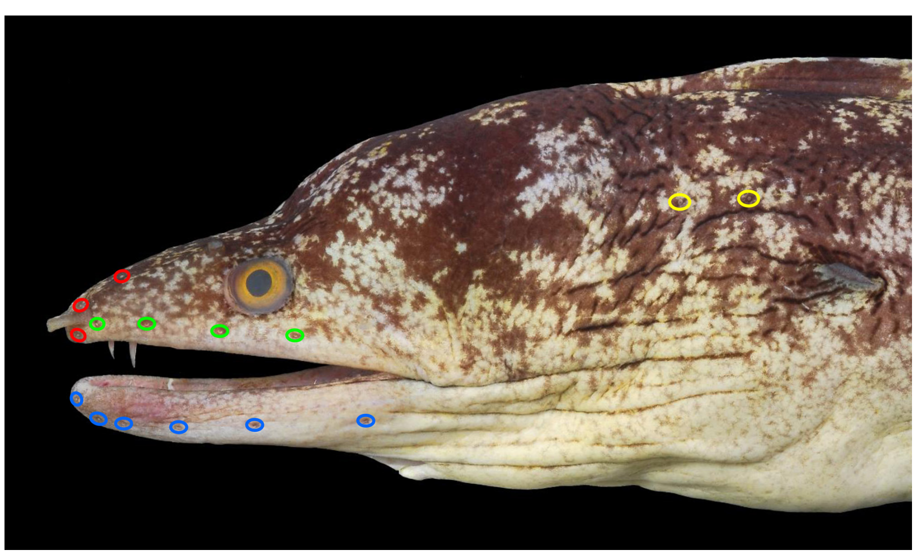

Fig. 6. *Gymnothorax pseudokidako* sp. nov.. lateral view of head marks with cephalic sensory pores: red for supraorbital pores; green for infraorbital pores; blue for preoperculo-mandibular pores; yellow for branchial pores. Photo of DOS 07961, paratype, 651+ mm TL.

on left side (Fig. 7); in paratype NMMB-P33700, an additional pore immediately behind third pore on right side of lower jaw. Two branchial pores on posterior-dorsal head, posterior to origin of dorsal-fin and anterior to gill opening. Predorsal vertebrae 5 (4–7), preanal vertebrae 55 (53–57), total vertebrae 139 (134–139).

Dentition (Fig. 7): Teeth slender, sharp, slightly retrorse, with smooth margin. Peripheral intermaxillary teeth uniserial, with 6–7 (5–8) canines on each side, teeth larger posteriorly. Median intermaxillary teeth uniserial, with 3 (2–3) tall, spaced, and depressible teeth, longest posteriorly. Maxillary teeth uniserial in most specimens, with 15–16 (12–17) triangular and recurved teeth on each side, the most anterior 1–5 teeth sometimes very small, and sharply increasing to about size of peripheral intermaxillary teeth, then gradually decreasing in size, smallest at posterior end; smallest paratype (ASIZP0080929, 608 mm TL) with additional two inner maxillary teeth on each side of upper jaw, teeth tall, straight, and anteriorly placed. Vomerine teeth 14 (6–18), uniserial; teeth small, short, and stout, sometimes in a staggered row; paratype TOU-AE 5146 with biserial teeth centrally. Dentary teeth uniserial, with 25 (17–26) teeth on each side, most anterior 4–5 pairs of teeth obviously larger, about size of peripheral intermaxillary teeth, remaining teeth smaller, subequal in size centrally, and gradually decreasing posteriorly. Some small teeth in space between larger teeth on peripheral intermaxillary and anterior dentary.

Coloration (Figs. 5, 8, 9): brown to dark brown in ground color, covered with small, yellowish spots on head, body, and fins. Spots usually gathering into snowflake-like blotches on trunk, tail, fins, and head region posterior to eyes, scattered evenly on snout and lips, and scarcely perceptible on lower jaw and throat. Pale snowflake-like blotches often making dark background visually like dendritic or vermicular markings on body (Fig. 8). On head region, blotches usually smaller and densely scattered behind eyes, making ground color a conspicuous saddle-like marking on top of head between eyes and origin of dorsal fin (Fig. 9E). Blotches more separated on posterior tail and sometimes blurred (Fig. 8B). Ventral parts of head and trunk usually paler and yellowish, palest at throat. Fins without pale margin. Throat grooves, gill opening, and corner of mouth darkish. Color of oral cavity slightly darker or identical to head, sometimes with blurred pale spots. Iris of eyes yellowish or reddish brown.

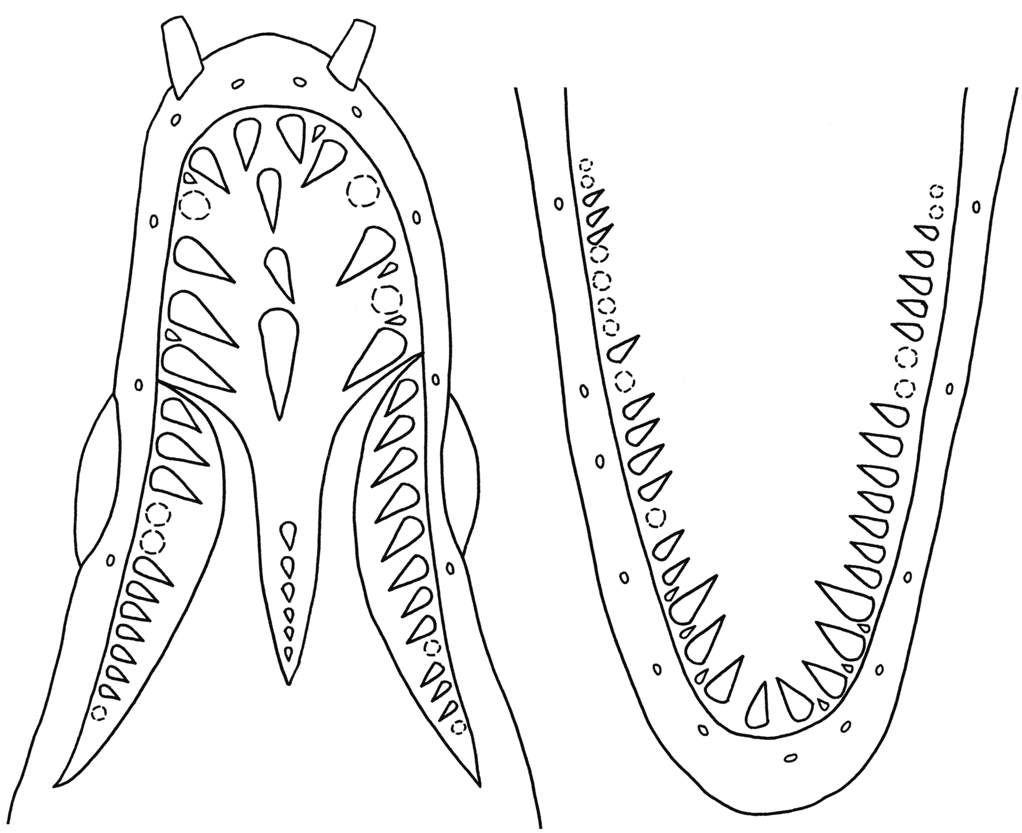

Fig. 7. Dentition of *Gymnothorax pseudokidako* sp. nov., FRIP21962, paratype, 757 mm TL, female. Dotted lines represent the sockets of missing teeth. The aberrant distribution of preoperculo-mandibular pores is shown on the right side of lower jaw. Upper jaw (left) and lower jaw (right).

Distribution: This species is currently known based on types collected from northern and eastern Taiwan and Negros Oriental of the Philippines, caught by bottom longlines and eel tubes in nearshore areas at the depth ca. less than 100 m.

Comparative material: *Gymnothorax kidako*: 15 specimens (572–840 mm TL). *Taiwan*: DOS 03540 (658 mm), Aodi, New Taipei City; DOS 06258 (631 mm), DOS 06259 (572 mm), DOS 06360 (676 mm), DOS 06361 (626 mm), DOS 08048-1 (840 mm), DOS 08048-2 (716 mm), TOU-AE 7575 (714 mm), TOU-AE 7576 (711 mm), Heping Island, Keelung City; DOS 07930-1 (732 mm), DOS 07930-2 (672 mm), Kanziding, Keelung City; DOS 07967 (702 mm), TOU-AE 4828 (633 mm), TOU-AE 4829 (595 mm), TOU-AE 4830 (666 mm), Daxi, Yilan County. *Gymnothorax mucifer*: 23 specimens (221–666 mm TL). *Taiwan*: DOS 06261 (552+ mm), DOS 06264 (592+ mm*), DOS 06265 (662+ mm), DOS 06266 (587+ mm*), DOS 06267 (666 mm), DOS 06268 (558+ mm), Heping Island, Keelung City; DOS 06262 (519+ mm), Aodi, New Taipei City; DOS 06263 (576 mm), Daxi, Yilan County; TOU-AE 1949 (314 mm), TOU-AE 1950 (270 mm), TOU-AE 2350 (246 mm), TOU-AE 3471 (290 mm), TOU-AE 3665 (331 mm), TOU-AE 3692 (332 mm), TOU-AE 3776 (339 mm), TOU-AE 3782 (431 mm), TOU-AE 3783 (402 mm), TOU-AE 4163 (272+ mm), Changbin, Taitung County. *Hawaiian Islands*: BPBM 29284 (314 mm), Hawaii; BPBM 28625 (221 mm), Molokai; BPBM 8511 (504 mm), BPBM 37046 (485 mm), BPBM 37047 (318 mm), Oahu. *Tail tip is damaged but hypural remains. *Gymnothorax niphostigmus*: 12 specimens (635–950 mm TL). *Taiwan*: ASIZP056940 (713 mm, holotype), DOS 03537 (842 mm), TOU-AE 5582 (820 mm), TOU-AE 5606 (745+ mm), Heping Island, Keelung City; ASIZP056941 (757+ mm, paratype), Aodi, New Taipei City; DOS 03536 (950 mm), Magong, Penghu County; DOS 07056 (899 mm), Qianzhen, Kaohsiung City; TFRI-TT 063 (737+ mm, paratype), Chenggong, Taitung County; TFRI-TT 071 (635 mm, paratype), TOU-AE 0238 (882 mm), TOU-AE 4981 (743 mm), TOU-AE 4982 (754 mm), Changbin, Taitung County.

Fig. 8. *Gymnothorax pseudokidako* sp. nov., variation of coloration patterns of fresh specimens. (A) ASIZP0080924, paratype, 913 mm TL, male; (B) ASIZP0080923, paratype, 648 mm TL, male; (C) DOS 07906, paratype, 725 mm TL, male; (D) NMMB-P34697, paratype, 822 mm TL, female.

Reconstructing the genetic tree

Seven *COI* (674–682 bp) and 11 *EGR3* (775–826 bp) sequences were newly amplified in this study (Table 1). After alignment, 593 bp and 666 bp of *COI* sequences were applied for ML tree reconstructions of *D. laimospila* and *G. pseudokidako*, respectively, and 767 bp of *EGR3* sequences were used for ML tree of *G. pseudokidako*. Substitution models GTR + Γ + I, HKY + I, and GTR + I were applied for *COI* of *D. laimospila*

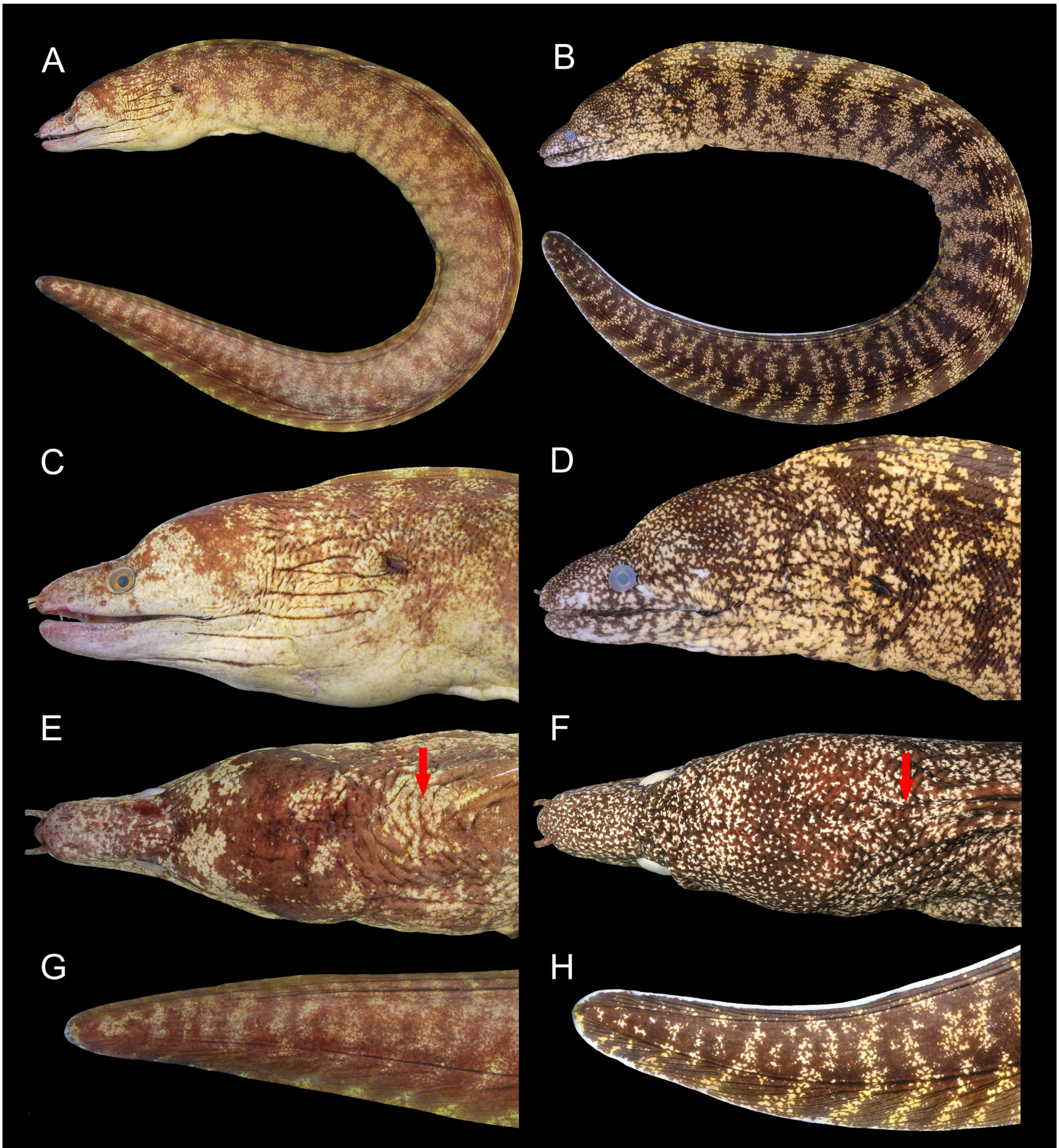

Fig. 9. Comparison of coloration patterns between (A, C, E, G) *Gymnothorax pseudokidako* sp. nov., and (B, D, F, H) *G. kidako*. (A–B) lateral view; (C–D) lateral view of head; (E–F) dorsal view of head; (G–H) lateral view of tail. Arrows point out the origin of dorsal fin. (A, C, G) ASIZP0080920, holotype, 801 mm TL; (E) ASIZP0080924, paratype, 913 mm TL; (B, D, H) DOS 06258, 631 mm TL; (F) DOS 08048-1, 840 mm TL.

and *G. pseudokidako*, and *EGR3* of *G. pseudokidako*, respectively (Hasegawa et al. 1985; Nei and Kumar 2000).

In the *COI* tree of *D. laimospila* (Fig. 10), *D. laimospila* is sister to *D. dalmatian* with a high bootstrap supporting value and a 10.8% K2P genetic distance (Kimura 1980), which far exceeds the intraspecific variation of muraenids (1.0–1.6% in average and maximum to 3.7%; Reece et al. 2011; Huang et al. 2018). Genera *Diaphenchelys* and *Strophidon* are sister groups, and they are sister to *G. melanosomatus* and *G. prolatus*. The mean K2P genetic distance between genera *Diaphenchelys* and *Strophidon* is 16.7%, larger than individually mean intrageneric distances (10.8% and 9.8%, respectively). The *COI* analysis genetically supported *D. laimospila* as a new species and revealed a reciprocal monophyly of genera *Diaphenchelys* and *Strophidon*.

In the *COI* tree of *G. pseudokidako* (Fig. 11A), *G. mucifer* and *G. niphostigmus* are reciprocally monophyletic and sister to *G. kidako* and *G. pseudokidako*. *Gymnothorax kidako* is monophyletic, but nested in the clade of *G. pseudokidako*, making the two species not reciprocally monophyletic. By contrast, monophyly of every species is supported by *EGR3* tree (Fig. 11B), advocating *G. kidako* and *G. pseudokidako* as well-separated sister groups.

DISCUSSION

Diaphenchelys laimospila

Strophidon McClelland, 1844 is another muraenid genus that morphologically resembles *Diaphenchelys*, with an elongated body, anteriorly placed eyes, and biserial maxillary and dentary teeth. The close, but reciprocally monophyletic relationship of the two genera was supported in the present study (Fig. 10). Despite the high similarity and close systematic position of *Diaphenchelys* and *Strophidon*, Huang et al. (2020) proposed that the differences in the number of vertebral formulae (4–9, 43–58, 126–155 vs. 8–12, 59–84, 155–213) and the number of branchial pores (two, with the only exception from the paratype of *D. laimospila* vs. ranging from one to eight), based on *D. dalmatian*, *D. pelonates* and the five species of *Strophidon*, support the distinction of the two genera. The VF of *D. laimospila*

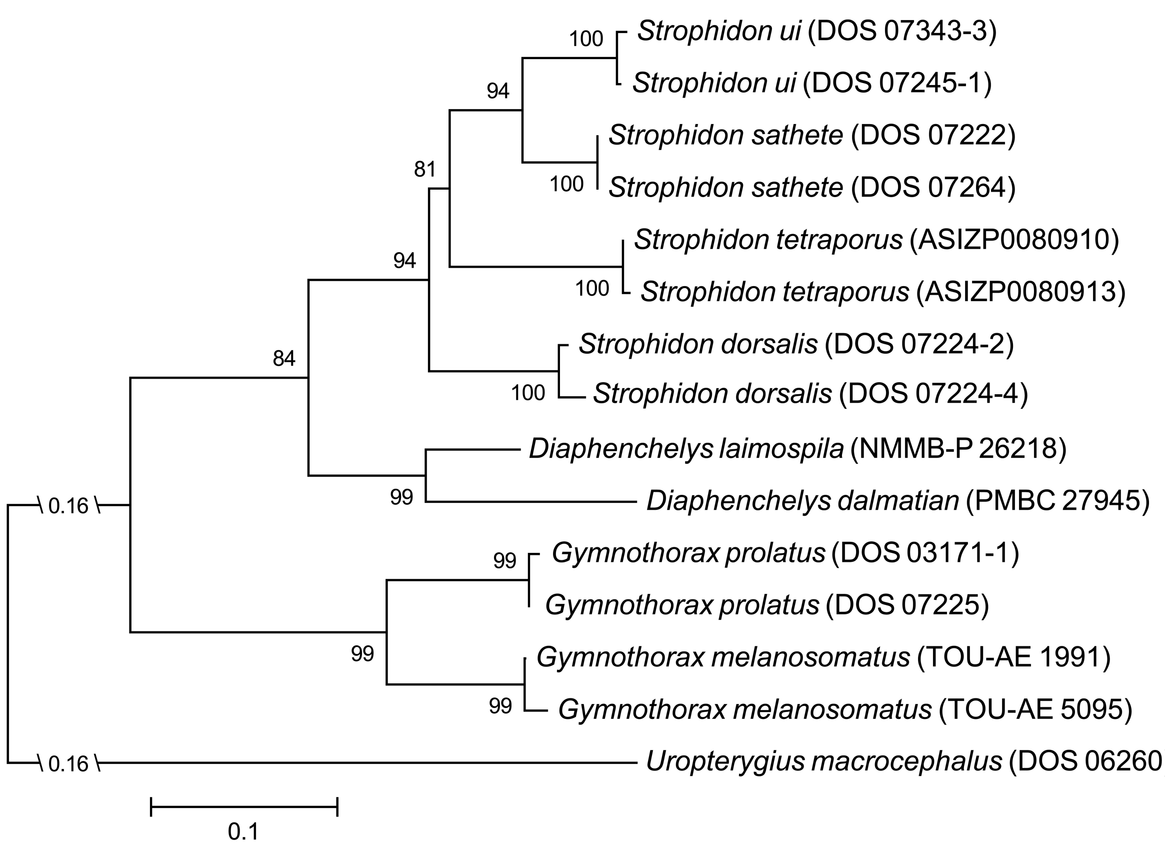

Fig. 10. The maximum likelihood tree of *Diaphenchelys laimospila* sp. nov. based on partial mitochondrial *COI* gene sequences (593 bp) and GTR + Γ + I model with *Uropterygius macrocephalus* as outgroup. Numerals beside the internal branches are bootstrap values.

falls into the range of *Diaphenchelys* and is significantly lower than species of *Strophidon*. Moreover, the number of branchial pores of *D. laimospila*, mostly two, also concurs with the character of *Diaphenchelys* except that the paratype has four on the left side of head. The additional branchial pores of paratype may be individual variation.

Diaphenchelys laimospila can be easily distinguished from *D. dalmatian* by having more anteriorly placed dorsal-fin origin (predorsal length 6.9–7.0% vs. 7.4–8.6% of TL; predorsal vertebrae 4 vs. 6–9), more preoperculo-mandibular pores (6 vs. 5), and pale brown of ground color with whitish spots (vs. white or yellowish white of ground color with brown spots) (Table 2; Hibino et al. 2017; Mohanty and Mohapatra 2020); and from *D. pelonates* by longer tail (63.2–63.8% vs. 59.6–61.5% of TL), longer head (11.3–11.4% vs. 9.4–10.0% of TL), shorter trunk (24.8–25.4% vs. 29.1% of TL), shorter predorsal length (60.6–62.2% vs. 69.3% of HL), fewer infraorbital pores (3 vs. 4–5), fewer vertebrae (4, 45, 125–131 vs. 4–6, 55–58, 153–155), and the coloration of anal fin (pale brown with dark margin vs. dark brown with pale margin) and lower jaw (pale brown with dense whitish spots vs. dark brown) (Table 2; McCosker and Randall 2007).

Gymnothorax pseudokidako

Gymnothorax pseudokidako might be confused with *G. kidako*, a morphologically similar species distributed in the North-West Pacific from Taiwan to Japan and sympatrically occurring with *G. pseudokidako* in northern Taiwan. The most important difference in the coloration pattern between the two species is that the white margin of anal fin is absent in *G. pseudokidako* but present in *G. kidako*. Moreover, the color of blotches on *G. pseudokidako* is creamy white, whereas the blotches are often bright-yellowish on *G. kidako*. The plainly colored lower jaw and throat is also a diagnostic character of *G. pseudokidako*, whereas *G. kidako* usually has a mottled lower jaw and throat (Fig. 9). In morphometric and meristic characters, *G. pseudokidako* can be distinguished from *G. kidako* by having a relatively short tail (50.5–53.0% vs. 52.9–56.4% of TL), more dentary teeth (17–26 vs. 16–20), and fewer total vertebrae (134–139 vs. 137–143) (Table 3 and Fig. 12). In molecular analysis, the reciprocal monophyly of *G. pseudokidako* and *G. kidako* is not

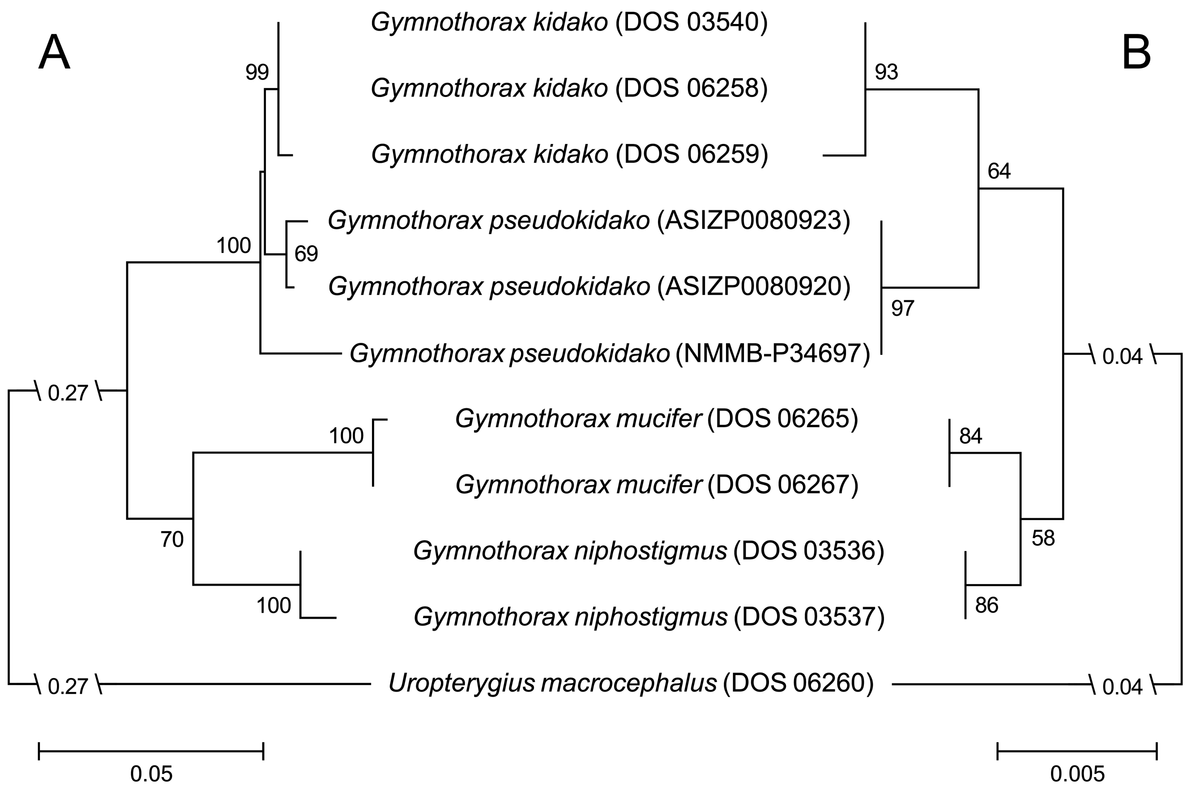

Fig. 11. Maximum likelihood trees of *Gymnothorax pseudokidako* sp. nov. and closely-related species, with *Uropterygius macrocephalus* as the outgroup. (A) partial mitochondrial *COI* gene sequences (666 bp) based on the HKY + I model; (B) partial nuclear *EGR3* gene sequences (767 bp) based on the GTR + I model. Numerals beside the internal branches are bootstrap values.

supported by the topology of the *COI* tree. A similar phenomenon can be observed in a number of sibling muraenid species, *e.g.*, *Gymnothorax griseus* (Lacepède, 1803) vs. *Gymnothorax thyrsoideus* (Richardson, 1845), and *Gymnothorax margaritophorus* Bleeker, 1864 vs. *Gymnothorax pharaonis* Smith, Bogorodsky, Mal and Alpermann, 2019 (Smith et al. 2019). By contrast, the more conservative nuclear *EGR3* gene shows reciprocal monophyly between *G. pseudokidako* and *G. kidako* (Fig. 11B). Despite the mito-nuclear discordance, the more conservative, but separable *EGR3* gene highly supported *G. pseudokidako* as a separated species. Discordance between *COI* and other molecular markers is not a rare phenomenon in marine fishes. For instance, the eight tuna species of genus *Thunnus* can be well differentiated exclusively by the mitochondrial control

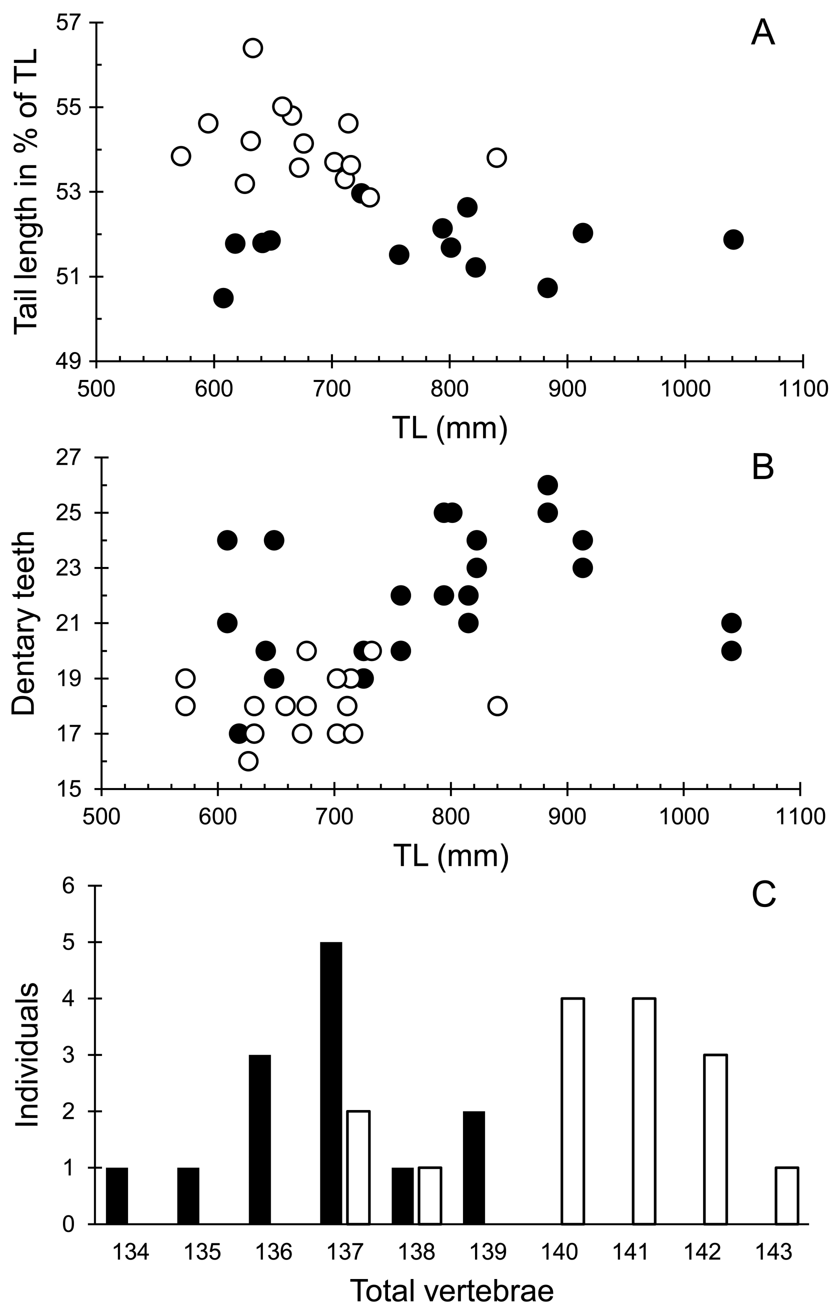

Fig. 12. Relationship of selected characteristics of *Gymnothorax pseudokidako* sp. nov. and *G. kidako*. (A) tail length in % of TL to TL; (B) number of dentary teeth to TL; (C) frequency distribution of total vertebrae. Black for *G. pseudokidako*; white for *G. kidako*. Teeth counted from each side of the jaw, two counts for each individual.

region (Viñas and Tudela 2009); damselfishes *Abudefduf sexfasciatus* and *A. vaigiensis* are indistinguishable in mitochondrial *COI* and cytochrome *b* genes but found to be distinct based on nuclear genes (*COI* sequences published on BoldSystems; Bertrand et al. 2017). The conflicting results between molecular markers may attribute to different evolutionary histories of genes.

Gymnothorax mucifer and *G. niphostigmus* are also sympatric species with *G. pseudokidako* in that they have similar coloration patterns and overlap in most of their morphometric measurements and meristic counts (Table 3). However, *G. pseudokidako* can be easily distinguished from both species by its lack of the white margin of the anal fin, and having a brown saddle-like marking on top of head (vs. dense pale spots on top of head). *Gymnothorax pseudokidako* further differs from *G. niphostigmus* in the number of total vertebrae (134–139 vs. 140–146). ML trees of *COI* and *EGR3* genes also support *G. pseudokidako* is a different species from *G. mucifer* and *G. niphostigmus* (Fig. 11). Lastly, *G. pseudokidako* is apparently different from *M. similis*, a synonym of *G. kidako*, by the lack of white margin on the anal fin, a shorter tail (50.5–53.0% vs. 54.5% of TL), a longer head (12.6–14.3% vs. 12.0% of TL), and more dentary teeth (17–26 vs. 13–14), although the vertebrae count is not available from the holotype of *M. similis* (Böhlke and Smith 2002). Based on morphological and molecular evidence, *G. pseudokidako* is clearly a new species well separated from *G. kidako* and other congeners.

Sexual dimorphism in the dentition, *e.g.*, females and immatures have an additional inner row of maxillary teeth but is lost in mature males, has been reported in several muraenids, including two pale-spotted species: *Gymnothorax baranesi* Smith, Brokovich and Einbinder, 2008 and *G. mucifer* (Smith et al. 2008; Huang et al. 2019). *Gymnothorax niphostigmus* was also reported to have 1–2 inner maxillary teeth in smaller individuals (Chen et al. 1996). However, the sexual dimorphism of dentition is not observed in *G. pseudokidako* or *G. kidako*. The inner row of maxillary teeth is absent in all mature males and females, except for the smallest paratype of *G. pseudokidako* (ASIZP0080929, a 608 mm female), which has two inner teeth on each side. Furthermore, the number of teeth is neither related to sex nor total length (data not shown, see Fig. 12B for example). Based on our observation, no dental change can be found in *G. kidako*; for *G. pseudokidako*, all small individuals might have an inner row of maxillary teeth and would be lost when growing larger regardless of sex. Thus the dental change in *G. pseudokidako* is more likely to be ontogeny-dependent rather than sex-dependent.

CONCLUSIONS

Two moray eels from Taiwan and the Philippines are new to science and are described in the present study. *Diaphenchelys* is a rarely known genus with only two species previously. We describe *Diaphenchelys laimospila* sp. nov., the third species and a new geographic record of the genus. A key to identify species of *Diaphenchelys* is also provided. *Gymnothorax pseudokidako* sp. nov. is a moray with pale snowflake-like blotches on the body, which is also present in several sympatric species. However, *G. pseudokidako* is significantly different from congeners by lacking the white margin of the anal fin. The present study expands the understanding of muraenid diversity in the western Pacific.

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