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A new species of *Muraenichthys* (Anguilliformes: Ophichthidae) from Taiwan, with redescription of *Muraenichthys thompsoni* Jordan & Richardson, 1908

YUSUKE HIBINO^{1*}, HSUAN-CHING HO^{2,3} & JOHN E. MCCOSKER⁴

¹Kitakyushu Museum of Natural History and Human History, 2-4-1 Higashida, Yahatahigashi-ku, Kitakyushu, Fukuoka 805-0071, Japan

²National Museum of Marine Biology & Aquarium, Pingtung, Taiwan

³Institute of Marine Biology, National Dong Hwa University, Pingtung, Taiwan

⁴California Academy of Sciences, San Francisco, CA 94118, USA

*Corresponding author. E-mail: yusukeelology@gmail.com

Abstract

Muraenichthys longirostris **sp. nov.** is described based on a single specimen 206 mm total length (TL) collected from off Dong-gang, southwestern Taiwan. The species is characterized by a long and slender snout (18% of head length), unique within the genus. It is also characterized by its position of the dorsal-fin origin (positioned at 2/5 of trunk; horizontal distance from the origin to a vertical through mid-anus 113% of head length), long tail (67% TL), and vertebrae 23-41-131. In addition, *Muraenichthys thompsoni* Jordan & Richardson, 1908 is redescribed based on the holotype and 63 specimens from Fiji to Madagascar, north to Japan. *Muraenichthys malabonensis* Herre, 1923 is recognized as a junior synonym of *M. thompsoni*.

Key words: Taxonomy, Myrophinae, Muraenichthys, Muraenichthys malabonensis, worm eel

Introduction

The ophichthid eel genus *Muraenichthys* Bleeker, 1853, subfamily Myrophinae, has contained as many as 19 heterogenous species (McCosker 1970). Castle & McCosker (1999) divided *Muraenichthys* into two genera, *Muraenichthys* and *Scolecenchelys* Ogilby, 1897. Hibino & Kimura (2015) recently revised *Muraenichthys* and recognized eight valid species. They defined *Muraenichthys* based on the following combination of characters: eye located anterior to mid-jaw; inner hole of posterior nostril above upper lip, outer hole usually outside of mouth, with a prominent but short projected flap anteriorly; a single sensory pore between anterior and posterior nostrils; three preopercular pores; teeth on jaws, vomer, and intermaxillary area; tooth shape variable, blunt to pointed but not distinctly recurved and tooth length equal or less than half of eye diameter; teeth on jaws and vomer arranged in one to five rows; gill opening constricted, its height < 1.7 times eye diameter; and pectoral fins absent. Formerly the genus was characterized by the tooth shape, which is blunt and granular, forming a tooth band. However, most congeners have pointed teeth and three species (*Muraenichthys philippinensis* Schultz & Woods, 1949, *Muraenichthys sibogae* Weber & de Beaufort, 1916, and *Muraenichthys thompsoni* Jordan & Richardson, 1908) have uniserial teeth on jaws and/or vomer (Hibino & Kimura 2015).

During a collecting survey in southwestern Taiwan by the team in the National Museum of Marine Biology & Aquarium, many eel species were found, including *M. thompsoni* and a unique undescribed *Muraenichthys*. Here we describe the new species and modify the partial diagnostic characters of the genus. In addition, *M. thompsoni* is redescribed and recognized as a senior synonym of *Muraenichthys malabonensis* Herre, 1923.

Materials and methods

All methods follow Hibino & Kimura (2015). Measurements of total length were made either with a 300 mm or 600 mm ruler to the nearest 0.1 mm or with a digital caliper to the nearest 0.01 mm for all other measurements. In

the case of large specimens, preanal length and tail length were measured by a ruler. Total and head lengths are abbreviated as TL and HL, respectively. Institutional abbreviations follow Fricke & Eschmeyer (2019) and KMNH is abbreviation of the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan.

Result

Taxonomy

Muraenichthys longirostris sp. nov.

(Slender-snout worm eel) (長吻蟲鰻)

Holotype. NMMB-P24388, 206 mm TL, off Dong-gang, Pingtung, southwestern Taiwan, 24 August 2016, bottom trawl, collected by H.-C. Ho from a fish landing ground.

Diagnosis. A species of *Muraenichthys* having a slender snout, its length 18% HL, with the following combination of characters: head 11% TL, tail 67% TL; dorsal-fin origin anterior to a vertical through mid-anus, horizontal distance from the vertical to the origin 113% HL; teeth relatively slender, uniserial on maxilla and vomer; predorsal vertebrae 23, preanal 41 and total 131.

Description. Counts and measurements (in mm) of the holotype: predorsal vertebrae 23; preanal vertebrae 41; total vertebrae 131; preanal lateral-line pores 42. Total length 206; head length 23.3; trunk length 45.5; tail length 137.3; predorsal length 40.9; body depth at gill opening 6.6; body depth at mid-anus 6.7; body width at gill opening 5.8; body width at mid-anus 5.9; dorsal-fin origin to anus 26.1; upper-jaw length 10.3; length of mouth gape 9.4; snout length 4.2; snout tip to tip of lower jaw 1.3; eye diameter 1.9; interorbital width 2.3; gill-opening length 1.6. Body long, subcylindrical, its depth at gill opening 31.2 in TL (Fig. 1); tail compressed posteriorly, its depth weakly reduced gradually.



FIGURE 1. Preserved condition of *Muraenichthys longirostris* **sp. nov.**, NMMB-P24388, holotype, 206 mm TL, Dong-gang, Pingtung, southern Taiwan.

Head moderately large, branchial basket slightly expanded; head 8.8, and head and trunk 3.0 in TL; snout relatively long and slender, tip relatively acute, its length more than twice eye diameter; ventral groove on snout absent; lower jaw included in upper jaw, its tip beyond anterior base of anterior-nostril tube; mouth large, rictus well behind a vertical from posterior margin of eye and slightly behind a vertical through last infraorbital pore, along with a groove reaching to end of jaw; eye moderate in size, 5.4 in upper jaw and 12.3 in HL, covered by a transparent skin; mid-eye located above mid-jaw (mid-point between tip of snout and end of maxilla); anterior nostril a simple ventrally projected tube, its length half of eye diameter, its opening with a very low rim; inner opening of posterior nostril above upper lip, and outer opening oblique and outside the mouth; rim of outer opening projected ventrally; lips mostly smooth with scattered papillae on upper lip; interorbital region smooth, slightly convex; gill opening constricted, located ventrolaterally.

Dorsal and anal fins low, slightly elevated in posterior region of tail, ending confluent with caudal fin; dorsal fin originating at about 2/5 of trunk; caudal fin prominent and tip rounded; pectoral fin absent.

Head pores small but obvious; arrangement of sensory pores on head as follows (Fig. 2A): one + four on supraorbital; three + two on infraorbital, one between anterior and posterior nostrils; six on mandible and three on preopercle; midtemporal and interorbital pores present.



FIGURE 2. Line drawings of *Muraenichthys longirostris* **sp. nov.** A, lateral view of head with sensory pores; B, teeth on maxilla and palatal area; C, teeth on mandible. IPN, inner opening of posterior nostril [inner hole in Hibino & Kimura (2015)]; OPN, outer opening of posterior nostril [outer hole in Hibino & Kimura (2015)]. Arrows indicate first mandibular (left), frontal (middle) and mid-temporal (right) pores.

Lateral-line developed, sensory canal reaching middle portion of tail, 11 in branchial basket, 23 anterior to dorsal-fin origin, 42 anterior to anus, and 80 in total.

Teeth (Fig. 2B, C) moderate in size, conical, pointed, relatively slender; teeth on maxilla and vomer uniserial; teeth on mandible mostly uniserial with an additional tooth at each inner side around the symphysis; seven plus three intermaxillary teeth form an oval cluster, the anterior margin arranged in a circular pattern.

Color (Fig. 1) (preserved in 50% isopropyl alcohol) of head and body brown, lower half of head to anterior tail

region relatively paler. Dorsal and anal fins pale whitish brown, becoming darker before tail tip; caudal fin dark brown.

Distribution. Known only from the holotype, from off southwestern Taiwan.

Etymology. From the Latin, *longirostris*, in reference to the snout shape.

Remarks. The new species can be easily distinguished from all congeners by its slender and long snout (18% HL vs. 8.4–15.5% HL). The snout shape is similar to that of members of the genus *Scolecenchelys* Ogilby, 1897. The position of the dorsal-fin origin overlaps with that of *M. thompsoni*. The former can be separated from the latter by the snout shape and length (vs. 9.5–14% HL) and its longer tail (67% TL vs. 57–64% TL).

Hibino & Kimura (2015) defined the eye of the congeners of *Muraenichthys* as located anterior to mid-jaw, but the position of the eye of the present species is just mid-jaw (mid-point between tip of the snout and end of maxilla). Except for these, our new species agrees well with all other diagnostic characters of *Muraenichthys*. In addition, the location of the orbit (from x-ray photo) corresponds with that of other *Muraenichthys*. Therefore, we recognized the new species as a species of *Muraenichthys*, and the character of the eye location is expanded from "eyes located anterior to mid-jaw" to "mid-eye located anterior to or just above mid-jaw" for the genus.

Muraenichthys thompsoni Jordan & Richardson, 1908

(English name: Thompson's Worm Eel) (New Japanese standard name: Shino-mimizu-anago) (Taiwanese name: 湯氏蟲鰻)

Muraenichthys thompsoni Jordan & Richardson, 1908: 237 (Manila Bay, Luzon, Philippines); Allen & Erdmann 2012: 106 (Manila Bay, Luzon, Philippines); McCosker 2014: 339 (Philippines); Ho et al. 2015: 169 (Taiwan); Hibino 2017: 31 (Panay Island, Philippines); Hibino 2018: 22 (Ha Long Bay, Vietnam).

Muraenichthys malabonensis Herre, 1923: 157 (Bañgos pond at Malabon, Rizal Province, Manila Bay, Philippines); McCosker 2014: 339 (Philippines; with question); Hibino & Kimura 2015: 63, table 1 (only key characters).



FIGURE 3. Fresh condition of *Muraenichthys thompsoni*, KMNH VR 100226, 209 mm TL, Dong-gang, Taiwan. A, whole body; B, enclosed view of head.

Material examined. 64 specimens, 48–267 mm TL: SU 20201, holotype, 96.5 mm TL, Manila Bay, Luzon, Philippines; BPBM 37185, 202 mm TL, Maumere Bay, Flores, Indonesia, depth 3–4 m; FRLM 4244, 48 mm TL, Zagashima island, Shima, Mie, Japan, depth 2–3 m (excluded from description because of the small body); KAUM-I.

69442, 69445, 69447, three specimens, 102–178 mm TL, Panay, Philippines; KMNH VR 100226, 209 mm TL, Dong-gang, Taiwan; MNHN 1965-340, 207 mm TL, southwestern coast of Madagascar; MUFS 43869, 267 mm TL, Kadogawa, Miyazaki, Japan; NMMB-P12488, 144 mm TL, Phen Thiet, Vietnam; NMMB-P17508, 175 mm TL, NMMB-P30619, 219 mm TL, Dong-gang, Taiwan; PMBC 20588, 166 mm TL, Ao Nambor, Phuket, Thailand; PMBC 21061, 189 mm TL, Lanta Yai Island, Krabi, Thailand; SU 60966, 19 specimens, 86–158 mm TL, Tolo Channel, Hong Kong, China; SU 61117, 4 specimens, 98–164 mm TL, Hong Kong, China; USNM 259666, 55 mm TL, Naqara Island, Fiji, depth 0.9 m; USNM 259672, 25 specimens, 63–151 mm TL, Naqara Island, Fiji, depth 0.9 m; Vietnam.

Diagnosis. A species of the genus *Muraenichthys* with the following combination of characters: head 12–15% TL, tail 57–64% TL; dorsal-fin origin anterior to a vertical through mid-anus, horizontal distance from the origin to the vertical 42–64% of trunk length; eyes large, 6.6–10% HL; snout to interorbital region not concaved along dorsal midline; all teeth relatively slender and pointed, rows uniserial or biserial anteriorly and uniserial posteriorly; vomer relatively slender; predorsal vertebrae 24–32, preanal 42–46 and total 128–138; MVF 27-44-134.

Description. Counts and measurements are shown in Table 1. Body long, subcylindrical, its depth at gill opening 21.3–40.0 in TL (Figs. 3, 4); tail compressed posteriorly, its depth slightly reduced posteriorly.

	Holotype SU 20201	Syntypes of Muraenichthys malabonensis* (n=4)	Other specimens (<i>n</i> =63)
Total length (mm)	96	117–193	48–267 (134.1)
Counts			
Lateral-line pores before anus	-	-	42–46 (44.1, 27)
Predorsal vertebrae	29	-	24–32 (27.4, 56)
Preanal vertebrae	43	-	42–46 (43.9, 56)
Total vertebrae	131	-	128–138 (134.1, 56)
Measurements			
As % of total length			
Head length	15	13-15 (14.0)	12–15 (13.6, 33)
Trunk length	27	26	23–27 (24.7, 33)
Tail length	57	60-62 (60.3)	59–64 (61.5, 33)
Predorsal length	30	-	20–29 (26.0, 33)
Body depth at gill opening	3.8	-	2.5-4.7 (3.9, 27)
Body width at gill opening	2.6	-	1.5–3.4 (2.4, 27)
As % of trunk length			
Dorsal-fin origin to anus	46	ca. 50	42-64 (49.7, 33)
As % of head length			
Dorsal-fin origin to anus	82	-	72–116 (90.3, 33)
Upper-jaw length	-	-	35–46 (39.9, 33)
Length of mouth gape	26	29-38 (31.9)	24–33 (29.6, 33)
Snout length	11	-	9.5–15 (12.0, 33)
Eye diameter	10	7.1–9.1 (8.3)	6.6–9.9 (8.2, 33)
Interorbital width	7.5	-	5.0–11 (8.8, 33)
Gill-opening length	4.8	-	3.1–11 (6.2, 33)

TABLE 1. Counts and measurements of Muraenichthys thompsoni.

Figures in parentheses indicate mean values and sample size, respectively

*Data from Herre (1923)



FIGURE 4. Holotype of *Muraenichthys thompsoni*, SU 20201, 97 mm TL, Manila Bay, Luzon, Philippines. A, enclosed view of head; B, whole body.

Head large, branchial basket weakly expanded; head 6.5–8.3 and head and trunk 2.3–2.8 in TL; snout robust, rounded, its length equal to more than twice eye diameter; ventral groove on snout absent; lower jaw included in upper jaw, its tip beyond anterior base of anterior-nostril tube; mouth large, rictus well behind a vertical from posterior margin of eye and slightly behind a vertical through posteriormost infraorbital pore, along with a groove reaching to end of jaw; eye moderate in size, 10.1–15.2 in HL, covered by a transparent skin; mid-eye located anterior to above mid-jaw (mid-point between tip of snout and end of maxilla); anterior nostril tubular, its length slightly shorter than eye diameter, somewhat anteriorly directed; inner opening of posterior nostril above upper lip, and outer opening of posterior nostril located above upper lip, anteroventral to eye, a slit-like opening towards down side with a short flap anteriorly; lips smooth or with scattered small papillae; interorbital region smooth, convex but usually without a groove or an extremely shallow depression; gill opening constricted, located ventrolaterally.

Dorsal and anal fins low, slightly elevated in posterior tail region, ending confluent with caudal fin; dorsal fin originating about mid-trunk but variable, about 1/3 to 3/5 of trunk; caudal fin prominent, its tip rounded; pectoral fin absent.

Head pores small but obvious; arrangement of sensory pores on head as follows: one + four on supraorbital; three + two on infraorbital, one between anterior and posterior nostrils; six on mandible and three on preopercle; midtemporal and interorbital pores present.

Lateral-line pores developed to posterior tail, 11–13 in branchial basket, 23–26 anterior to dorsal-fin origin, 42–46 anterior to anus, and 84–110 in total, generally smaller specimens less developed than larger.

All teeth relatively slender and pointed; teeth on jaws generally uniserial (including holotype), rarely biserial anteriorly (Fig. 5C, D); vomerine teeth uniserial or biserial anteriorly, one to three teeth uniserial posteriorly (including holotype); intermaxillary teeth slightly larger than others, arranged in a semicircular rosette of five teeth (in holotype) or a tooth patch.



FIGURE 5. Teeth arrangement on maxilla and palatal areas of *Muraenichthys gymnopterus* (A, B) and *M. thompsoni* (C, D). A, USNM 243005, 222 mm TL, Batanta Island, Indonesia; B, KAUM-I. 20909, 147 mm TL, western Bengal; C, MNHN 1965-340, 207 mm TL, southwestern coast of Madagascar; BPBM 37185, 202 mm TL, Maumere Bay, Flores, Indonesia.

Color of head and body of fresh specimens (Fig. 3) brown to pale brown, darker and yellowish in posterior tail. Dorsal and anal fins pale whitish brown but becoming darker and yellowish before tip of tail; caudal fin yellowish dark brown. Color (once preserved in 50% isopropyl alcohol or 70% ethanol) of head and body dark brown to pale brown, with numerous dark melanophores on dorsal surface, lower half of head to anterior tail portion weakly paler. Fin coloration mostly the same as when fresh but yellowish color is faded.

Distribution and ecological note. Widely distributed in Indo-Pacific, known from Madagascar, western coast of Thailand, Vietnam, Philippines, Indonesia (Flores Sea), Hong Kong, Taiwan, Japan, and Fiji Islands. It is a shallow water species, found in rocky tide pools or shallow sandy and muddy bottoms usually <100 m.

Remarks. *Muraenichthys thompsoni* and *M. malabonensis* were described based on specimens collected from Manila Bay, Philippines. All syntypes of *M. malabonensis* were deposited at the Department of Agriculture, Bureau of Science, Manila, Philippines, and were destroyed during World War II (Fricke *et al.* 2019). Therefore the taxonomic status of *M. malabonensis* has been uncertain (McCosker 2014). Herre (1923) provided the key to Philippine species of *Muraenichthys* and stated that *M. thompsoni* and *M. malabonensis* can be distinguished by their arrangement of vomerine teeth ("vomer with two rows of teeth" vs. "vomer with teeth in one row, imperfectly two rowed or forming a Y") and the proportional length of eye diameter in head length ("eye 18 in head" vs. "eye 11 to 14 in head"). In the present examination, the holotype of *M. thompsoni* has small biserial teeth on the vomer anteriorly, but uniserial posteriorly. Moreover, the proportion of the eye diameter based on McCosker's measurement is 9.8 in HL. The holotype of *M. thompsoni*, and the range of *M. gymnopterus* which is the most similar species is also very wide. Consequently, these morphological differences between two nominal species can be regarded as intraspecific variation, and we conclude that *M. malabonensis* is a junior synonym of *M. thompsoni*.

Most of the present specimens identified as *M. thompsoni* were formerly identified as *Muraenichthys* sp. or *M. gymnopterus*. Although *M. thompsoni* and *M. gymnopterus* resemble each other, the former differs from the latter in the position of the dorsal-fin origin (horizontal distance from the origin to a vertical through mid-anus 42–64% of trunk length vs. 29–48%), eye diameter (6.6–10% HL vs. 3.2–7.1%), tooth rows on the maxilla (one or two anteriorly and one posteriorly vs. two or more; Fig. 5), and the shape of the vomerine teeth (pointed and relatively

slender vs. blunt and robust). Although *M. thompsoni* has been hitherto known only from the holotype collected in the Philippines, we now expand its range to Madagascar to Fiji, and north to Japan.

Comparative materials. *Muraenichthys gymnopterus*: AMS I.4399, 184 mm TL, Luzon, Philippines; AMS I.39103-002, 236 mm TL, Viti Levu Island, Fiji; ASIZP 72203, Tainan, Taiwan; SU 38864, 148 mm TL, Dumaguete, Negros, Philippines; USNM 135156, 209 mm TL, Luzon, Philippines; USNM 135157, 181 mm TL, Luzon, Philippines; USNM 135158, 229 mm TL, Luzon, Philippines. Specimens of *M. gymnopterus* are those listed in Hibino & Kimura (2015).

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References

Allen, G.R. & Erdmann, M.V. (2012) Reef fishes of the East Indies. Vol. I. Tropical Reef Research, Perth, x + 424 pp.

- Castle, P.H.J. & McCosker, J.E. (1999) A new genus and two new species of Myrophine worm-eels, with comments on *Muraenichthys* and *Scolecenchelys* (Anguilliformes: Ophichthidae). *Records of the Australian Museum*, 51 (2–3), 113–122. https://doi.org/10.3853/j.0067-1975.51.1999.1300
- Fricke, R. & Eschmeyer, W.N. (2019) *Guide to fish collections. Electronic Version.* Available from: http://researcharchive. calacademy.org/research/ichthyology/catalog/collections.asp (accessed 10 January 2019)
- Fricke, R., Eschmeyer, W.N. & van der Laan, R. (Eds.) (2019) Catalog of fishes: Genera, species, references. Electronic Version. Available from: http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (accessed 10 January 2019)
- Herre, A.W.C.T. (1923) A review of the eels of the Philippine Archipelago. *Philippine Journal of Science*, 23, 123–236, pls. 1–11.
- Hibino, Y. (2017) Moriguidae, Muraenidae, Ophichthidae, Congridae, and Muraenesocidae. *In*: Motomura, H., Alama, U.B., Muto, N., Babaran, R.P. & Ishikawa, S. (Eds.), *Commercial and Bycatch Market Fishes of Panay Island, Republic of the Philippines*. The Kagoshima University Museum, Kagoshima, University of the Philippines Visayas, Iloilo, and Research Institute for Humanity and Nature, Kyoto, pp. 27–39.
- Hibino, Y. (2018) Muraenidae, Synaphobranchidae, Ophichthidae, Congridae, and Muraesocidae. *In*: Kimura, S., Imamura, H., Nguyen, V.Q. & Ha, P.H. (Eds.), *Fishes of Ha Long Bay, the natural world heritage site in northern Vietnam*. Fisheries Research Laboratory, Mie University, Shima, pp. 18–32.
- Hibino, Y. & Kimura, S. (2015) A new species of *Muraenichthys* (Anguilliformes: Ophichthidae) from the Indo-Pacific, with revised generic diagnosis. *Zootaxa*, 4060 (1), 62–70.
- Ho, H.-C., Smith, D.G., McCosker, J.E., Hibino, Y., Loh, K.-H., Tighe, K.A. & Shao, K.-T. (2015) Annotated checklist of eels (orders Anguilliformes and Saccopharyngiformes) from Taiwan. *Zootaxa*, 4060 (1), 140–189. https://doi.org/10.11646/zootaxa.4060.1.16
- Jordan, D.S. & Richardson, R.E. (1908) Fishes from islands of the Philippine Archipelago. *Bulletin of the Bureau of Fisheries*, 27, 233–287.
- McCosker, J.E. (1970) A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the descriptions of a new genus, *Schismorhynchus*, and a new species *Muraenichthys chilensis*. *Pacific Science*, 24 (4), 506–516.
- McCosker, J.E. (2014) A gigantic deepwater worm eel (Anguilliformes: Ophichthidae) from the Verde Island Passage, Philippine Archipelago. In: Williams, G.C. & Gosliner, T.M. (Eds.), The coral triangle. The 2011 Hearst Philippine Biodiversity Expedition. California Academy of Sciences, San Francisco, pp. 333–340.