Biodiversity and taxonomy of fishes in Taiwan and adjacent waters

Edited by
Hsuan-Ching Ho, Yusuke Hibino, Barry Russell, Mao-Ying Lee

PENSOFT

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Cover photo: Images of fresh specimens collected around Dongsha Island: *Diretmoides veriginae*, 157.03 mm SL; *Diretmus argenteus*, 51.84 mm SL; *Bregmaceros japonicus*, 82.38 mm SL; *Encheliophis* sp., 165.00 mm SL; *Beryx mollis*, 118.03 mm SL; *Hoplostethus melanopus*, 174.52 mm SL; *Hoplostethus roseus*, 110.34 mm SL; *Hoplostethus* sp., 107.77 mm SL; *Hoplostethus robustispinus*, 213.97 mm SL.

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Editorial

Biodiversity and taxonomy of fishes in Taiwan and adjacent waters

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Taiwan is situated in the northwestern Pacific Ocean and is surrounded by the South China Sea, the Okinawa Trough, the Philippine Sea and the Taiwan Strait. The region has a remarkably high fish diversity, comprising more than 3,400 species, which is approximately 1/10 of the world's total fish species. Over the past two decades, significant research efforts have been dedicated to the study of fish diversity and taxonomy in Taiwan, with a particular focus on Chondrichthyes, eels (Anguilliformes), and various deep-sea fish species. As a result, more than 200 new fish species have been described in Taiwan, and a few hundred new records have been added to the Taiwanese fish fauna. These findings have significantly enhanced our understanding of the fish species in Taiwan.

In this special issue, we invited all researchers who have been studying the fishes from Taiwan and adjacent areas to contribute their new findings. A total of seven species are described as new to science, including a new jawfish (Su and Ho 2024), a new beardfish (Fan et al. 2024), four snake eels (Hibino and Ho 2024; Hibino et al. 2024a, 2024b); and a new moray from Indo-west Pacific (Huang et al. 2024); all of which were collected from Taiwan. Lin and Han (2024) studied the species diversity of freshwater glass eel and increased the number of *Anguilla* species to seven. Ho and Kawai (2024) verified two barracudina species and settled two nominal species. Su et al. (2024) re-described a rare deep-sea beryciform fish from Taiwan. Koeda and Bessho-Uehara (2024) documented ten species in the genus *Pempheris* from Taiwan and Japan, five of which were found in Taiwan. Hibino and Ho (2024) documented two new recorded *Yirrkala* species from Taiwan. Finally, Ng et al. (2024) provide a remarkable checklist of fishes collected from Dongsha Island, which includes a list of 13 recently added species and 89 species recorded from Dongsha Island for the first time, with many of them being new to Taiwan; in addition, there are 35 species without a name, and many of them are likely undescribed.

With the publication of 11 valuable papers, we further improve the fish fauna of Taiwan. It is notable that the fish diversity in Taiwan is still rapidly increasing, and we may expect that more fishes will be found in the near future.

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Author contributions

The author solely contributed to this work.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Species diversity of freshwater glass eel (Anguilliformes, Anguillidae) of Yilan, Taiwan, with remark on two new records

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Abstract

Yilan, Taiwan is the first place in East Asia where freshwater glass eels, the juvenile stage of *Anguilla* species, arrive by ocean currents. We collected glass eels by fyke net in Lanyang River estuary twice a month from July 2010 to November 2023. By morphological examination and sequencing of the mitochondrial cytochrome b gene, we identified seven species of *Anguilla*. Most of the glass eels captured in Yilan belonged to the species *A. japonica*, *A. marmorata*, and *A. bicolor pacifica.* Only a few were *A. luzonensis*, and two *A. celebesensis* were recorded. In addition, two species were recorded for the time time from Taiwan; *A. interioris* and *A. borneensis* were confirmed by cytochrome b sequencing. Thus, we increase the number of *Anguilla* species in Taiwan from five to seven.

Key words: *Anguilla borneensis*, *Anguilla interioris*, glass eel, new records

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Introduction

The freshwater eel (*Anguilla* spp.) comprises 16 species and three subspecies (Arai 2016a). All *Anguilla* species are catadromous fish, meaning they migrate to the ocean to spawn (Arai and Chino 2012). The leaf-like larvae of *Anguilla* species, known as leptocephali, are carried by ocean currents and undergo metamorphosis into eel-like juveniles, which are known as glass eels (Tsukamoto et al. 2002; Hatakeyama et al. 2022). Glass-eel fishing is crucial for the eel aquaculture industry, as there are no artificial reproduction techniques for commercial purposes (Okamura et al. 2014). In Taiwan, the dispersal of glass eels is primarily influenced by the Kuroshio Current (Hsiung et al. 2022b). Yilan, Taiwan, is renowned as the largest glass-eel fishing ground in Taiwan due to its proximity to the Kuroshio. Notably, Yilan holds the distinction of being the first location in East Asia where glass eels arrive, establishing it as a significant hub for this crucial stage in the eel life cycle (Han et al. 2016a).

To date, five *Anguilla* species have been identified and recorded in Taiwan (Leander et al. 2012; Han et al. 2016b). Among these, *A. japonica*, *A. marmorata*, and *A. bicolor pacifica* are the most prevalent species (Han 2001; Hsu et al. 2019), while *A. luzonensis* and *A. celebesensis* are notably very rare and primarily observed as glass eel in Taiwan (Teng et al. 2009; Han et al. 2016b). Previous studies suggest that *A. japonica*, *A. marmorata*, and *A. bicolor pacifica* share a common spawning area near the southern West Mariana Ridge (Kuroki et al. 2009; Arai 2016b), whereas other tropical eel species (*A. celebesensis*, *A. borneensis*, *A. luzonensis*, and *A. interioris*) have been identified near southern Mindanao Island as their spawning grounds (Aoyama et al. 2003; Wouthuyzen et al. 2009; Arai 2014, 2016b). Due to the morphological challenges in distinguishing tropical eel glass eels (Minegishi et al. 2005), DNA barcoding techniques, as highlighted by Wibowo et al. (2021), provide a precise method for the identification of species. Previous research also indicates that mitochondrial cytochrome b gene fragments are suitable for the identification of freshwater eels (Han et al. 2008). This study aims to analyse glass-eel samples captured in Yilan from July 2010 to November 2023. Through DNA sequencing, the goal is to confirm the number of freshwater glass-eel species transported to Taiwan during this period.

Materials and methods

Sample collection

Glass eels were collected twice a month at night using a fyke net positioned in the estuary of the Yilan River (24.7162°N, 121.8352°E) from July 2010 to November 2023. Following the capture, all the samples were immersed in a 95% ethanol solution for measurement and preservation. All freshwater glass-eel specimens were deposited in the Institute of Fisheries, National Taiwan University (**NTUIFS**). Recent research adhered to ethical regulations set forth by the Institutional Animal Care and Use Committee (IACUC) under approval number NTU-110-EL-00152.

Morphological measurement

The method for morphological identification of anguillid glass eels was adapted from Han et al. (2012), and the description of the pigmentation stage followed Fukuda et al. (2013). Four morphological parameters were measured using digital callipers with an accuracy of 0.1 mm: total length (TL), head length (HL), pre-dorsal length (PDL), and pre-anal length (PAL). The fin-difference ratio was then calculated using the formula shown below. Glass eels with fin differences exceeding 13% in Yilan were consistently identified as *A. marmorata* (Han et al. 2012). Therefore, specimens displaying black pigment on the tail and fin differences <13% were chosen for mitochondrial cytochrome b gene sequencing.

$$\text{Fin Difference Ratio}\,(\%) = \frac{PAL(\text{mm}) - PDL(\text{mm})}{TL(\text{mm})} \times 100$$

Mitochondrial cytochrome b gene sequencing

Freshwater glass-eel specimens with a fin-difference ratio <13% were DNA sequenced for precise identification; these amounted to 281 samples. Genomic DNA was extracted from the dorsal-fin tissue of the glass eels using the FavorPrep Tissue Genomic DNA Extraction Mini Kit (Favorgen, Taiwan). Polymerase chain reaction (PCR) was carried out to amplify a segment of mitochondrial cytochrome b using forward primer: cytb-F (5'-GAT GCC CTA GTG GAT CTA CC-3') and reverse primer: cytb-R (5'-TAT GGG TGT TCT ACT GGT AT-3'), which was adapted from Han et al. (2008). The resulting PCR product (approximately

1000 bp) was sequenced using the primers cytb-F or cytb-R (by Genomic Biotech Inc., Taiwan), following protocols from Han et al. (2008). Sequencing results were submitted to the National Center for Biotechnology Information (**NCBI**) GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to confirm species.

Results

Diversity of freshwater glass eel

A total of 29,442 freshwater glass eels were collected between July 2010 and November 2023. The composition of freshwater glass-eel species is shown in Table 1. *Anguilla japonica* and *A. marmorata* were the most prevalent species, comprising 95.4% of our captures (Table 1). Although *A. bicolor pacifica* and *A. luzonensis* were infrequently captured, they still represented 3.9% and 0.7% of all specimens, respectively, and two *A. celebesensis* were also recorded (Table 1). Additionally, two species were found in Taiwan for the first time: *A. interioris* and *A. borneensis* (Table 1).

New *Anguilla* records from Taiwan

The sequencing results of the two new records, total two specimens (NTUIFS IL13’0812-76 and NTUIFS IL21’0715-207), and the best matched BLAST results are shown in Table 2.

Table 1. Number of species (*n*) and percentage contributions of freshwater glass eels collected in Yilan.

Species	*n*	Percentage contributions
A. japonica	14217	48.3
A. marmorata	13864	47.1
A. bicolor pacifica	1152	3.9
A. luzonensis	205	0.7
A. celebesensis	2	<0.01
A. interioris	1	<0.01
A. borneensis	1	<0.01

Table 2. Sequencing BLAST results of three new records freshwater glass eel.

Specimen	Species	Percent identity (%)	NCBI accession
NTUIFS IL13’0812-76	*Anguilla interioris*	99.4	HG965574.1
NTUIFS IL21’0715-207	*Anguilla borneensis*	99.4	NC_006536.1*

*NC_006536.1 was identified as *A. malgumora*, which is a junior synonym of *A. borneensis* according to Minegishi et al. (2005).

Family Anguillidae

Anguilla interioris Whitley, 1938
Figs 1, 2, Table 3

Material examined. NTUIFS IL13’0812-76, 46 mm TL, off the estuary of the Yilan River, Yilan, northeastern Taiwan (24.7162°N, 121.8352°E), 12 August 2013, fyke net, collected by Yu-San Han.

Short description. PDL 29.3% in TL; PAL 39.1% in TL; fin-difference ratio 9.78%. Body elongate, head length 13.1% TL. The specimen was in fresh condition, with black pigment distributed on the caudal fin and slightly on the caudal peduncle; pigmentation stages V_{B2} (Fig. 2).

Distribution. New Guinea (Aoyama et al. 2000); Philippines (glass eel only, Wibowo et al. 2021); Indonesia (leptocephalus only, Kuroki et al. 2006; all stages, Zan et al. 2022); Taiwan (glass eel only, present study).

Remarks. The distribution of *A. interioris* has been primarily known from only New Guinea (Aoyama et al. 2000). However, a study by Kuroki et al. (2006) documented the leptocephalus of *A. interioris* in the Indonesian Archipelago, marking the first expansion of the species beyond its then-known range. Additionally, records of *A. interioris* have been identified using DNA sequencing from Indonesia and southern Mindanao, Philippines (Wibowo et al. 2021; Zan et al. 2022). Herein, we present the first record of *A. interioris* glass eel from Taiwan.

Figure 1. *Anguilla interioris* (NTUIFS IL13’0812-76), 46 mm TL. Preserved in 95% alcohol. Scale bar: 10 mm.

Figure 2. Pigmentation on the tail tip of *Anguilla interioris* (NTUIFS IL13’0812-76).

Table 3. The morphological parameters of seven freshwater glass eel collected in Yilan.

Species	TL (mm)	PDL (mm)	PAL (mm)	Fin-difference ratio (%)
A. japonica	61.1±2.5	15.1±0.9	20.1±0.7	9.2±1.3
A. marmorata	51.4±2.7	11.8±0.8	19.4±1.1	15.5±0.8
A. bicolor pacifica	49.2±2.3	18.3±1.6	18.5±1.6	0.5±0.5
A. luzonensis	52.9±2.7	13.7±0.7	19.4±1.0	11.4±1.1
A. celebesensis	45.3	12.8	17.5	10.4
A. interioris	46.0	13.5	18.0	10.1
A. borneensis	49.5	13.0	18.0	9.8

Anguilla borneensis **Popta, 1924**

Figs 3, 4, Table 3

Material examined. NTUIFS IL21’0715-207, 49.5 mm TL, off the estuary of the Yilan River, Yilan, northeastern Taiwan (24.7162°N, 121.8352°E), 15 July 2021, fyke net, collected by Yen-Ting Lin.

Short description. PDL 26.3% in TL; PAL 36.4% in TL; fin-difference ratio 10.1%. Body extremely elongate, head length 10.1% TL. The specimen was in fresh condition, with black pigment distributed on the caudal peduncle and caudal fin; pigmentation stages V_A (Fig. 4).

Distribution. Indonesia (Watanabe et al. 2014); Taiwan (glass eel only, present study).

Remarks. The best-matched GenBank accession number for NTUIFS IL21’0715-207 was found to be NC_006536.1, which corresponds to *A. malgumora* submitted by Minegishi et al. (2005). However, it is noteworthy that *A. malgumora* was identified as a junior synonym of *A. borneensis* by Minegishi et al. (2005). Based on the comprehensive examination by Minegishi et al. (2005) and the detailed de-

Figure 3. *Anguilla borneensis* (NTUIFS IL21’0715-207), 49.5mm TL. Preserved in 95% alcohol. Scale bar: 10 mm.

Figure 4. Pigmentation on the tail tip of *Anguilla borneensis* (NTUIFS IL21’0715-207).

scription provided in NC_006536.1, we can confidently affirm that our specimen NTUIFS IL21’0715-207 is *A. borneensis*. Herein, we report the first record of *A. borneensis* outside of the Indonesia (Watanabe et al. 2014).

Discussion and conclusion

Leptocephali and glass eels primarily rely on ocean currents for transport (Kuroki et al. 2016). In Taiwan, the main current responsible for transporting glass eels is the North Equatorial Current (NEC), followed by the Kuroshio, which is known to carry the most abundant anguillid species (*A. japonica* and *A. marmorata*) to the region (Hsiung et al. 2022a). Additionally, other tropical eels (*A. bicolor pacifica*, *A. luzonensis*, and *A. celebesensis*) may reach Taiwan via the bifurcation region of the NEC near the Philippine coast, which could potentially transport glass eels from southern Mindanao Island to the Kuroshio (Aoyama et al. 2015; Rudnick et al. 2015). The two species identified in our study align with previous research on the diversity of tropical glass eels (*A. celebesensis*, *A. interioris*, and *A. borneensis*) in southern Mindanao (Shirotori et al. 2016).

Previous research based on differences in Sr:Ca ratios in the leptocephalus otoliths has shown the presence of two populations of *A. interioris*, with one population in the Indian Ocean and another in the Pacific Ocean (Kuroki et al. 2006). Furthermore, leptocephali of the Pacific Ocean population of *A. interioris* potentially are transported to Taiwan via the Mindanao Current which ultimately forms a connection with the Kuroshio and the Mindanao Eddy (Kuroki et al. 2006).

The distribution of leptocephali and glass eels of the Indonesian *A. borneensis*, which is considered the most basal *Anguilla* species, remains unclear (Aoyama et al. 2001). The spawning area of *A. borneensis* may overlap with other basal tropical eels (*A. celebesensis*, *A. interioris*, *A. marmorata*, and *A. bicolor bicolor*) in Indonesia in the western Pacific Ocean (Arai and Abdul Kadir 2017); this suggests the possibility that a similar pathway to Taiwan is followed, as by *A. interioris* and *A. celebesensis* (Han et al. 2016b).

Alternatively, it is possible that if *A. borneensis* and *A. interioris* establish a new population in the western Pacific Ocean, their larvae could be carried to Taiwan via the North Equatorial Current (NEC) and the Kuroshio. Additionally, some alien freshwater eel species have escaped from aquaculture ponds and have been reported to have similar migration behaviour of native eel in East Asia (Okamura et al. 2002). Examples include *A. rostrata*, which has been discovered in Taiwanese waters (Han et al. 2002), and the European eel, *A. anguilla*, which was captured in the East China Sea and Japanese waters (Aoyama 2000; Okamura et al. 2002). Therefore, the possibility of alien eel species establishing new populations in the West Pacific Ocean cannot be discounted, whether caused by human activities (*A. rostrata* and *A. anguilla*) or by natural phenomenon (*A. interioris* and *A. borneensis*) (Aoyama 2000; Han et al. 2002).

Although there are seven species of freshwater glass eel recorded in Taiwan, only elvers of *A. japonica*, *A. marmorata*, *A. luzonensis*, and *A. bicolor pacifica* had been found in streams (Tzeng and Tabeta 1983; Watanabe et al. 2013; Hsu et al. 2019). The existence of the elvers and adults of *A. celebesensis*, *A. interioris*, and *A. borneensis* still need confirmation in the field.

In conclusion, the present study increases the number of freshwater glass-eel species in Taiwan from five to seven (Leander et al. 2012; Han et al. 2016b), with the addition two new species records in this paper.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

The experiment and sample collecting were performed by Yu-San Han and Yen-Ting Lin. Yen-Ting Lin write the manuscript. Yu-San Han designed and supervised the experiments. All authors participated in manuscript writing and interpretation of results. All authors read and approved the final manuscript.

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

NTUIFS IL13'0812-76 sequencing data

Authors: Yen-Ting Lin, Yu-San Han

Data type: txt

Explanation note: The sequencing results of NTUIFS IL13'0812-76.

Link: https://doi.org/10.3897/zookeys.1220.125590.suppl1

Supplementary material 2

NTUIFS IL21'0715-207 sequencing data

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Data type: txt

Explanation note: The sequencing results of NTUIFS IL21'0715-207.

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Research Article

Description of a new uniformly brown estuarine moray eel (Anguilliformes, Muraenidae) from the Central Indo-Pacific Ocean

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Abstract

A new estuarine moray eel, *Uropterygius hades* **sp. nov.**, is described based on 14 specimens from Japan, Taiwan, the Philippines, southern Indonesia, and Fiji. It is a small-bodied, slender, uniformly dark-brown moray separated from congeners within the *U. concolor* species complex. The new species can be distinguished from congeners by the anteriorly positioned small eyes (5.0–7.2% of head length), absence of branchial pores, and extended inner rows of teeth which reach the posterior end of the jaws. *Uropterygius hades* **sp. nov.** represents a rare species of moray eel that inhabits turbid estuarine environments, preferring soft, muddy substrates, and burrowing and hiding among rocks or in fallen mangrove leaves. Additionally, *Uropterygius mactanensis* Huang, Balisco, Evacitas & Liao, another species recently separated from the *U. concolor* species complex, is reported for the first time from Iriomote Island in the Ryukyu Archipelago based on two specimens; this new record expands the geographic range of *U. mactanensis* from the central Philippines to southern Japan.

Key words: DNA barcoding, mangroves, unicolor snake moray, Uropterygiinae, *Uropterygius mactanensis*

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Introduction

Uropterygius Rüppell, 1838 is the most speciose genus of the subfamily Uropterygiinae (family Muraenidae), comprising 23 of the 38 valid species in the subfamily (Smith 2012; Huang et al. 2023a, 2023b; Fricke et al. 2024). The type species of the genus is *Uropterygius concolor* Rüppell, 1838, a small-bodied, uniformly brown moray eel described from Eritrea in the Red Sea. Three nominal species described outside the Red Sea have been synonymized with *U. concolor*, including *Anarchias insuetus* Whitley, 1932, *Anarchias vermiformis* Smith, 1962, and *Gymnomuraena fusca* Peters, 1866 (Böhlke and Smith 2002) (Fig. 1). Consequently, *U. concolor* was considered a widespread species in the Indo-Pacific region, distributed from South Africa to the Marquesas Islands, north to southern Japan, and south to New Caledonia (McCosker et al. 1984; Fricke et al. 2011, 2018; Delrieu-Trottin et al. 2015).

However, recent molecular studies based on cytochrome c oxidase subunit I (*COI*) sequences have revealed that, in addition to the true *U. concolor*, there are at least five deeply divergent genetic lineages identified as "*U. concolor*" (Smith et al. 2019; Huang et al. 2023a). These studies suggested that the true *U. concolor* is currently known only from the Red Sea, while other genetic lineages outside the Red Sea likely represent a species complex. Among these lineages, one was recently described as *Uropterygius mactanensis* Huang, Balisco, Evacitas & Liao, 2023 from Cebu, the Philippines, while the remaining lineages were only identified as *U.* cf. *concolor* 1 (New Caledonia and the Society Islands), *U.* cf. *concolor* 2 (South Africa), *U.* cf. *concolor* 3 (Western Australia), and *U.* cf. *concolor* 4 (Okinawa) (Smith et al. 2019; Huang et al. 2023a) (Fig. 1). Additionally, the synonymization of *Anarchias insuetus*, *A. vermiformis*, and *Gymnomuraena fusca* with *U. concolor* remain uncertain (Huang et al. 2023a).

Sakai and Sato (1982) provided the first brief description of *U.* cf. *concolor* 4 based on two specimens collected from estuaries of the Amami and Okinawa islands in southern Japan. However, they identified it as *U. concolor*, and this misidentification was perpetuated in all subsequent Japanese reports. Although McCosker et al. (1984) questioned the identification of Japanese specimens by noting the absence of a branchial pore compared to those from the Red Sea, they attributed this variation to different environmental conditions, as they did not find any other morphological differences. According to literature, photos, and specimen records worldwide, *U.* cf. *concolor* 4 is mainly found in estuarine mangrove swamps in the Ryukyu Archipelago, such as Amami, Okinawa, Ishigaki, and Iriomote islands (Hatooka and Yoshino 1982; Sakai and Sato 1982; McCosker et al. 1984; Maeda and Tachihara 2006; Kanda et al. 2009; Hibino 2018; Miyake et al. 2019). It has been listed as a Critically Endangered (CR) species in the Red Data Book by the Okinawa Prefectural Government due to its rarity and habitat destruction (Tachihara 2017). However, the molecular characteristics of *U.* cf. *concolor* 4 were not available until

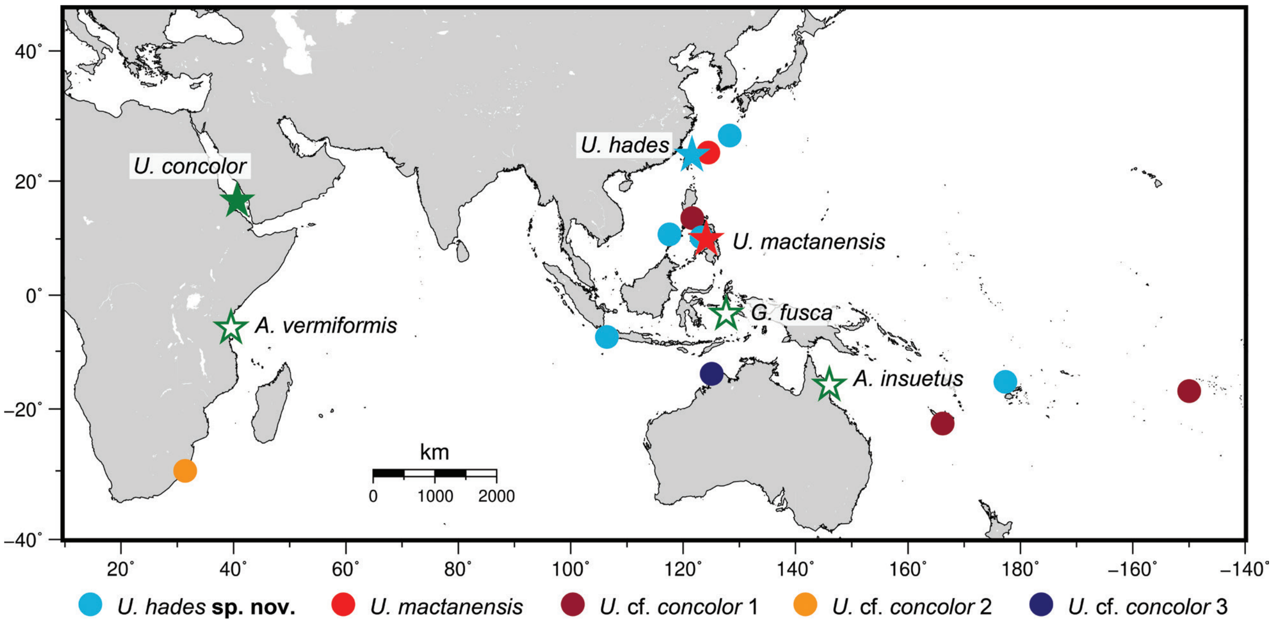

Figure 1. The distribution of nominal species and genetic lineages of the *Uropterygius concolor* species complex in the Indo-Pacific region. Each color represents a species or genetic lineage. Solid stars indicate the type localities of valid species; empty green stars indicate type localities of the three junior synonyms of *U. concolor*. Figure modified from Huang et al. (2023a).

Miyake et al. (2019) sequenced the mitochondrial genome of two specimens from Okinawa Island. Subsequently, Huang et al. (2023a) used these sequences for comparison and identified diagnostic morphological characteristics for *U.* cf. *concolor* 4, suggesting that it is possibly an undescribed species. Furthermore, they examined two specimens from Fiji and southern Java that seem similar to *U.* cf. *concolor* 4 and proposed that it may be widely distributed in the central and western Pacific Ocean, in addition to its occurrence in the Ryukyu Archipelago.

In the present study, we conducted detailed examinations of the specimens initially identified as *U.* cf. *concolor* 4 and describe it as a new species based on 14 specimens from Japan, Taiwan, the Philippines, southern Indonesia, and Fiji. This new species represents a rare case of a widespread moray eel specifically inhabiting estuarine environments. Additionally, during the examination, we found two specimens from Iriomote Island that can be recognized as *U. mactanensis*. This finding represents the first record of *U. mactanensis* in this area and signifies a northward range expansion from the central Philippines to the Ryukyu Archipelago.

Material and methods

Sixteen specimens (14 *Uropterygius* cf. *concolor* 4 and two *U. mactanensis*) were examined, mostly from museum collections, with a few newly obtained samples. Fresh specimens were photographed, and a piece of muscle tissue was obtained from a small incision in the abdomen near the anus. Tissue samples were preserved in 95% ethanol in a −20 °C freezer prior to DNA extraction, while the voucher specimens were fixed in 10% formalin before gradually transferred to 70% ethanol for long-term preservation. Morphological data were collected from the specimens deposited in different institutions, including National Museum of Marine Biology and Aquarium, Pingtung (**NMMB-P**), Kagoshima University Museum, Kagoshima (**KAUM–I**), Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka (**KMNH VR**), Kyushu University Museum, Fukuoka (**KYUM-PI**), Okinawa Churashima Foundation, Motobu, Okinawa (**OCF**; the two **URM-P** specimens have been donated to OCF), National Museum of the Philippines, Manila (**PNM**), Australian Museum, Sydney (**AMS I**), and Zoological Reference Collection, Lee Kong Chian Natural History Museum, Singapore (**ZRC**). Specimens from the Ryukyu Archipelago identified as "*U. concolor*" were deposited in various Japanese institutions. In addition to the previously mentioned museums, specimens from Graduate School & Faculty of Bioresources, Mie University, Tsu, Mie (**FRLM**), National Museum of Nature and Science, Tsukuba, Ibaraki (**NSMT-P**), and the University Museum, the University of Tokyo, Tokyo (**ZUMT**), were also examined and confirmed by the second author. However, due to their condition, only 11 specimens (nine *U.* cf. *concolor* 4 and two *U. mactanensis*) were selected for detailed examination.

Morphometrics were measured following Böhlke et al. (1989), and these characters are presented as percentages of total length (**TL**) or head length (**HL**). Meristic counts include vertebrae, teeth, and cephalic sensory pores. Vertebral numbers were counted from radiographs, and the vertebral formula is presented as pre-anus, pre-dorsal fin, pre-anal fin, and total vertebrae, following the definitions of Böhlke (1982) with slight modifications. Dentition and head pores were examined under a stereomicroscope, with terminologies following Böhlke and Smith (2002) and Smith et al. (2019), respectively.

DNA was extracted from muscle tissues of the holotype (NMMB-P039570) and a paratype (PNM 15806) of the new species. A fragment of partial *COI* gene (680 bp) was amplified by polymerase chain reaction (PCR) using the 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). Details for PCR thermal cycling conditions, PCR product purification, and DNA sequencing can be found in Huang et al. (2021a). Obtained sequences were manually edited and assembled in MEGA version 11 (Tamura et al. 2021), and the newly generated *COI* sequences were submitted to GenBank (refer to Fig. 2 for their accession numbers).

All available *COI* sequences of *U. concolor* and *U.* cf. *concolor*, as well as three sequences of *U. mactanensis*, from the online databases (GenBank and BOLD Systems) were downloaded for molecular comparisons. After aligning and trimming, a length of 652 bp was retained for analyses. A genetic tree of *COI* sequences was reconstructed based on the maximum-likelihood (ML) method conducted in MEGA v. 11. The HKY + *Γ* + *I* substitution model (Hasegawa et al. 1985) was applied, and a bootstrap analysis with 1,000 replicates was conducted (Felsenstein 1985) for tree building. Sequences of *Gymnothorax kidako* (Temminck & Schlegel, 1846) and *Gymnothorax mucifer* Snyder, 1904, from the subfamily Muraeninae, were used as outgroups. Genetic distances of *COI* sequences between the new species and *U. concolor*, *U.* cf. *concolor*, and *U. mactanensis* were also calculated using the Kimura 2-Parameter (K2P) model (Kimura 1980).

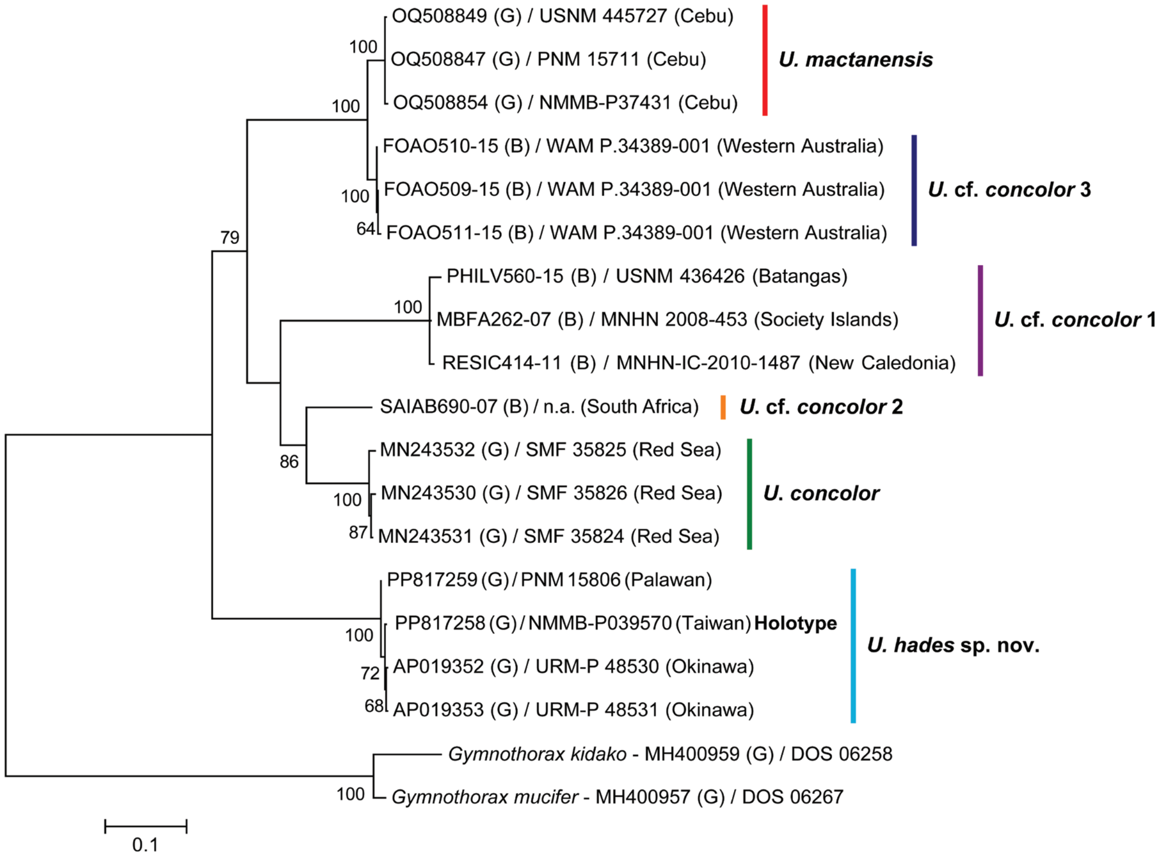

Figure 2. Maximum-likelihood tree of the *Uropterygius concolor* species complex based on *COI* sequences (652 bp). *Gymnothorax kidako* and *G. mucifer* (subfamily Muraeninae) are outgroups. Numerals beside the internal branches are bootstrap values, and values below 60 are not shown. (B) = sequence from BOLD Systems; (G) = sequence from GenBank.

Results

Taxonomy

***Uropterygius hades* sp. nov.**
https://zoobank.org/371622EE-A086-4645-8C85-2FC37461497C
Figs 3–7, Table 1
Common name: Hades' snake moray

Uropterygius concolor (not of Rüppell): Sakai and Sato 1982: 79, fig. 1, pl. I-A (Amami and Okinawa islands, Japan); Hatooka and Yoshino 1982: 95, fig. 6, pl. IV (Okinawa and Ishigaki islands, Japan); McCosker et al. 1984: 262 (Amami, Okinawa, and Ishigaki islands, Japan); Maeda and Tachihara 2006: 19, table 1 (Okinawa Island, Japan); Kanda et al. 2009: fig. 3A, table 1 (Ishigaki island, Japan); Hibino 2018 in Motomura et al. 2018: 25, unnumbered fig. (Kakeroma Island, Japan); Miyake et al. 2019: fig. S1c, table 2 (Okinawa Island, Japan).
Uropterygius cf. *concolor* 4: Huang et al. 2023a: 595, figs 1, 3, tables 2, 3 (Ryukyu Archipelago, Japan; possibly Fiji and southern Java, Indonesia).

Type material. *Holotype*. • NMMB-P039570 (349 mm TL, male); estuary of the Zhuan River (24°50'24.7"N, 121°49'18.1"E), Yilan County, northeastern Taiwan; dip net at 1.5 m, 11 January 2024, coll. W.C. Jhuang; GenBank *COI* accession number PP817258.

***Paratypes*.** 10 specimens (163–313 mm TL). **Japan:** • KAUM–I. 128986 (205 mm, sex unknown), Sumiyo Bay, Amami Island, Amami group, Kagoshima Prefecture, 20 March 2019, coll. R. Furuhashi • KAUM–I. 132509 (171 mm, mature female), tidal flat of Sumiyo Bay, Amami Island, Amami group, Kagoshima Prefecture, 31 August 2019, coll. R. Furuhashi • KAUM–I. 153507 (264 mm, mature female), mouth of Yakukachi River, Sumiyo, Amami Island, Amami group, Kagoshima Prefecture, 27 April 2002, coll. T. Yonezawa • KAUM–I. 177723 (215 mm, sex unknown) • KAUM–I. 177724 (190 mm, sex unknown), Setouchi, Kakeroma Island, Amami group, Kagoshima Prefecture, 23 November 2022, coll. S. Hashimoto • KMNH VR 100621 (231 mm, mature female), Oura River, Okinawa Island, Okinawa Prefecture, 20 May 2023, coll. K. Takatsuki • KYUM-PI 4637 (246 mm, sex unknown), Oura River, Okinawa Island, Okinawa Prefecture, 6 October 2014, coll. K. Maeda • URM-P 48530 (163 mm, sex unknown) • URM-P 48531 (204 mm, sex unknown), coll. with KYUM-PI 4637, GenBank accession numbers AP019352 and AP019353. **Philippines:** • PNM 15806 (313 mm, mature female), inside the cave, about 50 m from the entrance of the Puerto Princesa Subterranean River (10°11'55.6"N, 118°55'33.7"E), Palawan, tube trap at the bottom of the river, about 9.6 m depth, 03 May 2023, coll. W.C. Huang, R.A. Balisco, and W.C. Jhuang, GenBank *COI* accession number PP817259.

Non-type material. Three specimens (148–158 mm TL). **Fiji:** • AMS I.43866-001 (158 mm, sex unknown), mid Suetabu River, Vanua Levu, February 2006. **Indonesia:** • ZRC 44083 (148 mm, sex unknown), Ujung Genteng, southern Java, obtained through aquarium trade, 02 October 1999. **Philippines:** • ZRC 63518 (155 mm, sex unknown), Matutinao River, Badian, Cebu, 25 November 2001.

Diagnosis. A small, slender moray eel, possible maximum TL <350 mm, female mature at 171 mm TL. Anus at mid-length of body. Eyes small and anteriorly placed. Snout pointed. Upper jaw slightly longer than lower jaw. Teeth

Figure 3. Fresh colorations of *Uropterygius hades* sp. nov. **A** NMMB-P039570, holotype, 349 mm TL, male **B** PNM 15806, paratype, 313 mm TL, female. Arrows indicate the position of the anus.

sharply pointed with smooth edges and recurved tips; intermaxillary teeth in 5 rows; maxillary and dentary teeth biserial, inner rows extending to about posterior end of jaws; vomerine teeth in single row. No branchial pore. Body uniformly dark brown; head pores, oral cavity, and inner skin of posterior nostril and gill opening whitish; iris reddish-brown. Total vertebrae 117–122.

Description. Values shown below from all the 14 specimens, including holotype, paratypes, and non-types. Proportions in percentage of TL: tail length 47.6–51.4 ($\bar{x}$ = 49.6); preanal length 48.6–52.4 ($\bar{x}$ = 50.4); trunk length 35.8–41.3 ($\bar{x}$ = 38.6); head length 10.5–12.8 ($\bar{x}$ = 11.8); body depth at gill opening 2.9–4.4 ($\bar{x}$ = 3.7); body depth at anus 3.3–5.0 ($\bar{x}$ = 3.8). Proportions in percentage

Figure 4. Live photos of *Uropterygius hades* sp. nov. **A** NMMB-P039570, holotype, 349 mm TL, male **B** PNM 15806, paratype, 313 mm TL, female.

of HL: length of upper jaw 26.3–35.1 ($\bar{x}$ = 29.9); length of lower jaw 25.5–33.6 ($\bar{x}$ = 28.9); interorbital width 5.9–9.6 ($\bar{x}$ = 7.9); snout length 9.3–12.0 ($\bar{x}$ = 10.5); eye diameter 5.0–7.2 ($\bar{x}$ = 5.8). Vertebral counts: pre-anus vertebrae 55–58 ($\bar{x}$ = 57); pre-dorsal fin vertebrae 102–109 ($\bar{x}$ = 105); pre-anal fin vertebrae 103–110 ($\bar{x}$ = 106); total vertebrae 117–122 ($\bar{x}$ = 119) (Table 1).

A small, slender moray eel, anus at mid-length of body, tail laterally compressed, body depth roughly consistent throughout whole fish except for narrower, pointed head and tail tip (Figs 3, 4). Fins inconspicuous and restricted to posterior portion of tail, caudal fin short. Gill opening small and oval, below lateral midline of body. Eyes small and anteriorly placed, closer to snout tip than to mouth corner, snout/upper jaw length 0.30–0.40 ($\bar{x}$ = 0.36). Snout short and somewhat pointed, space between eyes narrow, anterior portion of head triangular in dorsal view. Jaws moderately long, upper jaw slightly longer than lower jaw, teeth not visible when mouth closed. Anterior nostril short and tubular, close to tip of snout, shorter than eye dimeter in length. Posterior nostril a large oval hole with a raised rim, above and posterior to anterior margin of eye, opening upward (Fig. 5).

Three supraorbital pores, first and second pores on tip of snout; first pore below base of anterior nostril; second pore next to upper base of anterior nostril at horizontal level of lower eye margin; third pore on upper margin of snout,

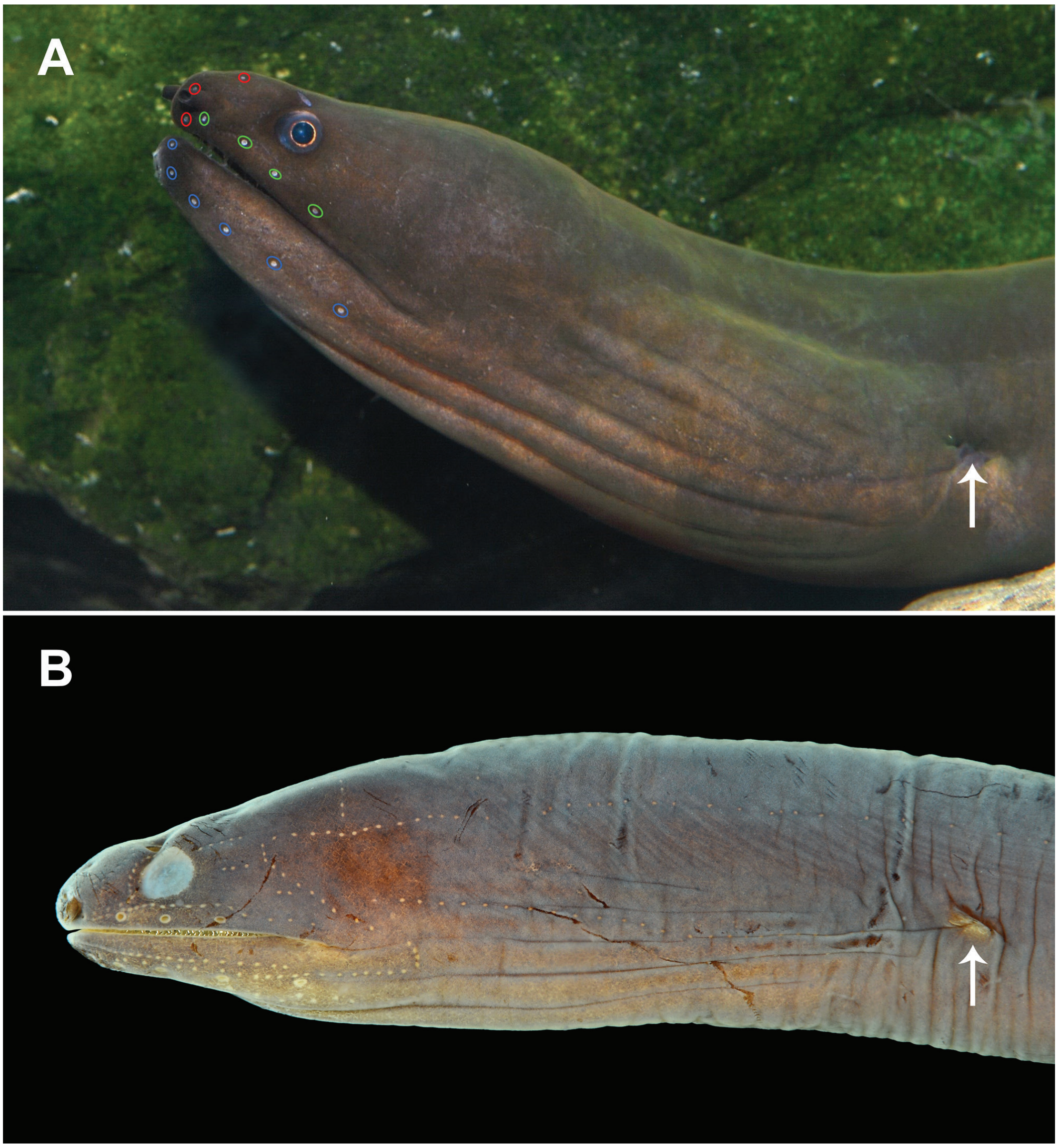

Figure 5. Lateral views of the head of *Uropterygius hades* sp. nov. showing the positions of cephalic sensory pore series and whitish superficial neuromasts **A** NMMB-P039570, holotype, 349 mm TL; red circles for supraorbital pores; green circles for infraorbital pores; blue circles for preoperculo-mandibular pores **B** ZRC 44083, non-type specimen, 148 mm TL. Arrows indicate the gill opening.

above and posterior to first infraorbital pore. Four infraorbital pores, arranged along upper jaw with equal intervals, first pore posteriorly next to base of anterior nostril; second pore below and anterior to eye; third pore below midpoint of eye; fourth pore below and posterior to eye. Six preoperculo-mandibular pores lining along lower jaw anterior to mouth corner (Fig. 5A). No branchial pore observed except in one specimen (ZRC 63518) having one pore on left side of posterior-dorsal head, representing a rare variation.

Teeth sharply pointed with smooth edges and recurved tips. Intermaxillary tooth plate with 5 rows of teeth; peripheral rows with 8–13 (mode 9) tightly arranged small teeth on each side; teeth on intermediate and median rows significantly larger than those on peripheral rows, about twice as tall and depressible, intermediate rows with 3–6 (3) teeth on each side, median row with 2–5 (3) teeth. Maxillary teeth biserial; outer row with 18–36 (26 and 28) teeth,

Table 1. Morphometric measurements, teeth, and vertebral counts of *Uropterygius hades* sp. nov. and *U. mactanensis*. Mean values are indicated in parentheses and mode values are indicated in brackets. Abbreviations: HL, head length; TL, total length.

Source	***U. hades* sp. nov.**		***U. mactanensis***	
	Holotype	**Paratypes & non-types**	**This study (Iriomote Island)**	**Huang et al. 2023a**
	NMMB-P039570	***n* = 13**	***n* = 2**	***n* = 21**
TL (mm)	349	148–313	316–370	231–342
% TL				
Tail length	47.6	47.9–51.4 (49.8)	51.4–52.5	48.5–52.7 (51.0)
Preanal length	52.4	48.6–52.1 (50.2)	47.5–48.6	47.3–51.5 (49.0)
Trunk length	41.3	35.8–40.3 (38.4)	35.4–35.8	34.5–39.2 (36.6)
Head length	11.2	10.5–12.8 (11.8)	11.7–13.2	11.0–13.5 (12.4)
Body depth at gill opening	4.4	2.9–4.4 (3.6)	5.2–5.6	5.1–6.5 (6.0)
Body depth at anus	3.9	3.3–5.0 (3.8)	4.4–4.9	4.2–6.1 (5.1)
% HL				
Length of upper jaw	35.0	26.3–35.1 (29.5)[a]	33.3–34.9	33.7–40.9 (38.7)
Length of lower jaw	33.6	25.5–33.1 (28.5)[a]	32.7–34.3	33.2–40.8 (38.1)
Snout length	11.7	9.3–12.0 (10.4)	13.8–14.3	12.6–15.7 (14.3)
Interorbital width	9.6	5.9–9.1 (7.8)[a]	9.8–13.0	9.1–12.6 (10.9)
Eye diameter	5.2	5.0–7.2 (5.9)	7.8–9.2	7.8–10.4 (8.8)
Teeth				
Intermaxillary-peripheral	11	8–13 [9][a]	10–12	9–14
Intermaxillary-intermediate	3–4	3–6 [3][a]	2	2–5
Intermaxillary-median	3	2–5 [3][a]	3	2–3
Maxillary-outer	24–28	18–36 [26][a]	17–22	16–25
Maxillary-inner	14–16	7–19 [11 & 13][a]	5–6	5–8
Vomerine	3	2–9 [5][a]	6–8	2–11
Dentary-outer	35–36	26–43 [36][a]	31–36	27–40
Dentary-inner	18	8–22 [13][a]	5–7	6–8
Vertebrae				
Pre-anus	58	55–58 (57)[b]	48–50	47–51 (49)
Pre-dorsal fin	105	102–109 (105)[b]	99	95–101 (98)
Pre-anal fin	106	103–110 (106)[b]	102	100–104 (102)
Total	119	117–122 (119)[c]	110–111	107–112 (110)

[a]Data not including AMS I.43866-001. [b]Data not including AMS I.43866-001 and URM-P 48530. [c]Data not including URM-P 48530.

continuous with peripheral intermaxillary teeth of similar size and shape, teeth slightly smaller at posterior end; inner row with 7–19 (11 and 13) straight, widely spaced teeth, continuous with intermediate intermaxillary teeth of approximately the same size and shape, extending to, exceeding, or near posterior end of outer row, with teeth becoming smaller at posterior end. Vomerine with 2–9 (5) small, conical teeth in single row. Dentary teeth biserial; outer row with 26–43 (36) teeth, small and equal-sized, closely arranged; inner row with 8–22 (13) slender and straight teeth, twice taller than teeth on outer row, widely spaced, anterior and posterior teeth smaller than middle ones, extending to or near posterior end of outer row (Fig. 6).

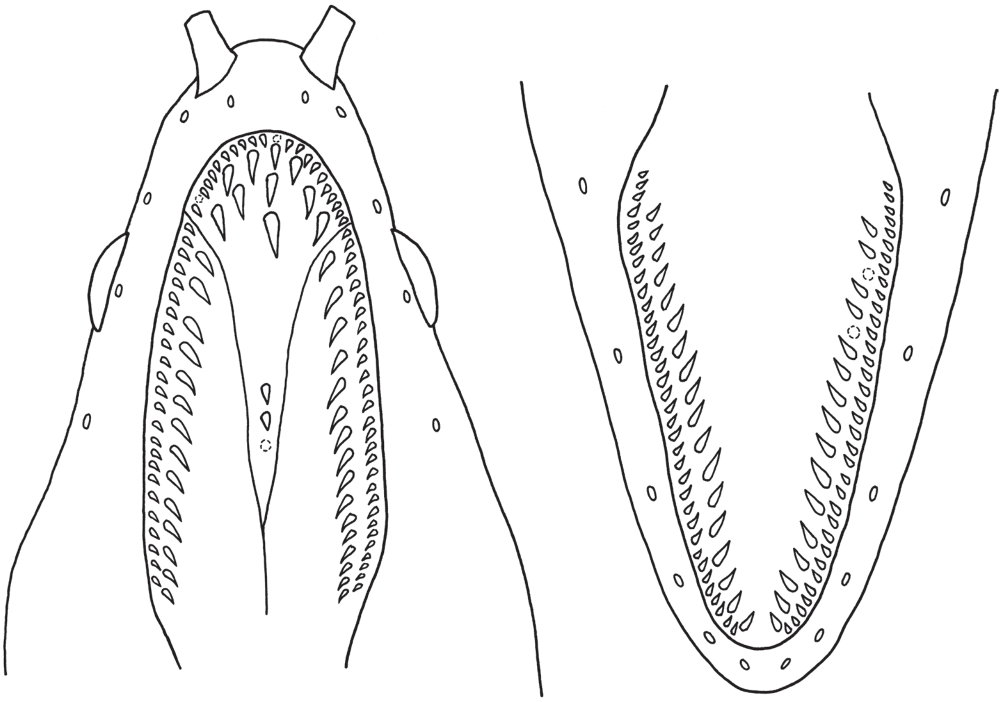

Figure 6. Dentition of *Uropterygius hades* sp. nov., NMMB-P039570, holotype. Upper jaw (left) and lower jaw (right). Dotted circles represent the sockets of missing teeth.

Body uniformly dark brown, color slightly lighter ventrally, covered with greenish mucus when alive. Head pores, oral cavity, and inner skin of posterior nostril and gill opening whitish. Iris reddish-brown. Whitish superficial neuromasts arranged in several lines on head region and in a row along lateral body (Fig. 5B). Preserved color mostly same as in fresh, but slightly faded.

Distribution. This species is widely distributed in estuaries of the Central Indo-Pacific Ocean, ranging from southern Java to Fiji, and extending north to the Ryukyu Archipelago of Japan.

Etymology. The new moray eel is named after Hades, the ancient Greek god of the underworld, in reference to its habitation in turbid estuarine waters, high sensitivity to light, and its uniformly dark coloration, reminiscent of the underworld god. A noun in apposition.

Comparisons. In molecular analyses, the topology of the *COI* tree (Fig. 2) reveals that *U. hades* sp. nov., *U. concolor*, *U.* cf. *concolor* 1, *U.* cf. *concolor* 2, *U.* cf. *concolor* 3, and *U. mactanensis* are monophyletic, which concord with the findings of Huang et al. (2023a). Two *COI* sequences from GenBank, originally identified as "*U. concolor*" (AP019352 and AP019353), clustered with the two *U. hades* sp. nov. sequences generated in this study. The two voucher specimens, URM-P 48530 and URM-P 48531, have been examined and designated as paratypes of *U. hades* sp. nov. Additionally, a sequence from BOLD Systems identified as "*Gymnothorax australicola*" (PHILV560-15) was found to cluster with *U.* cf. *concolor* 1 (Fig. 2). This extends the possible distribution range of *U.* cf. *concolor* 1 northward to the Philippines, where it overlaps with *U. hades* sp. nov. and *U. mactanensis* (Fig. 1). Lastly, large K2P genetic distances were observed between *U. hades* sp. nov. and *U. concolor* (18.1%), *U.* cf. *concolor* 1 (18.5%), *U.* cf. *concolor* 2 (17.1%), *U.* cf. *concolor* 3 (20.0%), and *U. mactanensis* (19.7%), further supporting the validity of the new species.

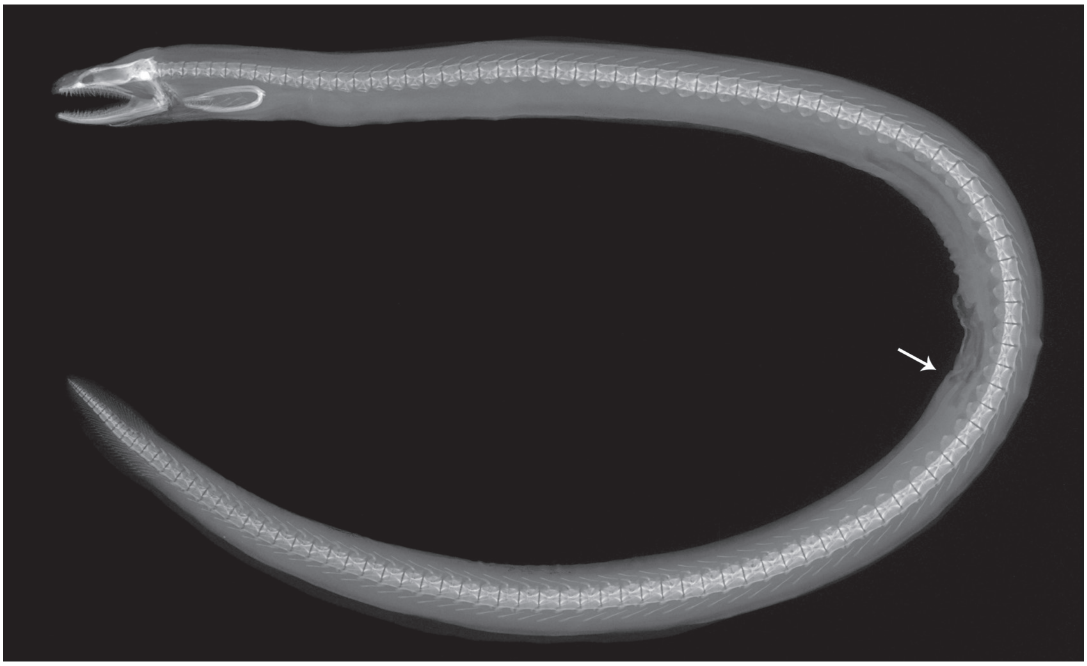

Figure 7. Radiograph showing the skeletal structure of *Uropterygius hades* sp. nov., PNM 15806, paratype, 313 mm TL. Arrow indicates the position of anus.

In morphological comparisons, *U. hades* sp. nov. can be easily distinguished from *U. concolor* (including its three synonyms) and *U. mactanensis* by its exclusively small eyes (5.0–7.2% vs 7.7–11.0% and 7.8–10.4% of HL), absence of branchial pore (vs one in both species) and extended inner rows of teeth reaching the posterior end of jaws (Table 2). *Uropterygius hades* sp. nov. has a similar vertebral formula to *U. concolor* (Fig. 7), but the former has a shorter tail compared to the latter (47.6–51.4% vs 52.4–60.0% of TL). Additionally, despite overlapping in tail length proportions, *U. hades* sp. nov. differs from *U. mactanensis* by having a narrower body depth at gill opening (2.9–4.4% vs 5.1–6.5% of TL), a shorter snout (9.3–12.0% vs 12.6–15.7% of HL), shorter jaws (25.5–35.1% vs 32.7–40.9% of HL), a narrower interorbital width (5.9–9.6% vs 9.1–13.0% of HL), and more vertebrae (117–122 vs 107–112) (Table 1). Morphological data for the remaining members of the *U. concolor* species complex (i.e., *U*. cf. *concolor* 1, *U*. cf. *concolor* 2, and *U*. cf. *concolor* 3) are quite limited and cannot be compared with the new species, except for one *COI* sequence-bearing specimen of *U*. cf. *concolor* 3 (WAM P.34389-001, 301 mm TL) with 112 total vertebrae (Huang et al. 2023a). Nevertheless, the tree topology and genetic distances between each clade strongly support their classification as different species (Fig. 2).

Uropterygius hades sp. nov. may also be confused with six uniformly brown moray eels in the genus, namely *Uropterygius cyamommatus* Huang, Liao & Tan, 2023, *Uropterygius genie* Randall & Golani, 1995, *Uropterygius golanii* McCosker & Smith, 1997, *Uropterygius inornatus* Gosline, 1958, *Uropterygius versutus* Bussing, 1991, and *Uropterygius xenodontus* McCosker & Smith, 1997. The absence of a branchial pore in *U. hades* sp. nov. can serve as the primary diagnostic characteristic to distinguish it from congeners. *Uropterygius cyamommatus*, *U. genie*, *U. golanii*, *U. inornatus*, and *U. xenodontus* each possess a single branchial pore, while *U. versutus* has two branchial pores. *Uropterygius hades* sp. nov. also has fewer

Table 2. Comparison of selected characteristics of *Uropterygius hades* sp. nov., *U. concolor*, *U. mactanensis*, and the three synonyms of *U. concolor*: *Anarchias insuetus*, *A. vermiformis*, and *Gymnomuraena fusca*.

	Eye diameter (% HL)	Tail length (% TL)	Total vertebrae	*N* of branchial pore	Teeth row extends to the posterior end of jaw?		Source
					Inner maxillary	Inner dentary	
Uropterygius hades sp. nov.	5.0–7.2	47.6–51.4	117–122	0	Yes	Yes	This study
Uropterygius concolor	7.7–11.0	52.4–60.0	117–124	1	Yes	No	1, 2
Anarchias insuetus	7.9	55.0	113	1	No	No	1, 3
Anarchias vermiformis	7.7	56.5	117	1	n/a	n/a	1
Gymnomuraena fusca	10	58.3	114+	1	No	No	1
Uropterygius mactanensis	7.8–10.4	48.5–52.7	107–112	1	No	No	3, this study

1. Böhlke and Smith 2002; 2. Smith et al. 2019; 3. Huang et al. 2023a.

vertebrae (117–122 total vertebrae) compared to *U. cyamommatus* (141–149), *U. golanii* (145–148), *U. versutus* (131–138), and *U. xenodontus* (152–157), but overlaps with *U. genie* (121–122) and *U. inornatus* (116–133). However, *U. hades* sp. nov. differs from *U. genie* and *U. inornatus* by having smaller eyes (5.0–7.2% vs 10.4–11.4% and 7.7–10.0% of HL), a shorter tail (47.6–51.4% vs 53.5–54.5% and 52.4–54.5% of TL), and different dentition (biserial maxillary teeth vs about 4 rows and uniserial). Refer to table 2 in Huang et al. (2023b) and the references cited therein for more detailed comparisons.

Note on additional records of *U. mactanensis*. During our survey at several Japanese museums, two specimens having one branchial pore on both sides of head, formerly identified as *U. concolor*, were found from the Kyushu University Museum (catalog numbers KYUM-PI 2591 and 2612) (Fig. 8). Although we were unable to assess the genetic features of these specimens, they can be identified as *U. mactanensis* based on diagnostic characteristics (Table 1). They were collected from the shallow bottoms around two adjacent small reef crests, one located off Funaura and the other off the mouth of the Kura River on Iriomote Island. The collection sites feature coarse sandy areas with large patch reefs, while the shallower regions contain scattered small patches of seagrass. Several marine muraenid species were collected by the same series of tube traps, such as *Echidna nebulosa* (Ahl, 1789), *Gymnothorax flavimarginatus* (Rüppell, 1830), *Gymnothorax javanicus* (Bleeker, 1859), *Gymnothorax thyrsoideus* (Richardson, 1845), *Gymnothorax zonipectis* Seale, 1906, and *Scuticaria tigrina* (Lesson, 1828).

The second author has examined most museum collections of "*U. concolor*" from Japanese waters, identifying the majority as *U. hades* sp. nov., with only two specimens identified as *U. mactanensis*. This implies the rarity of *U. mactanensis* in the Ryukyu Archipelago. As a rare case of confusion between the two species, the general information previously provided for Japanese "*U. concolor*" (e.g., Tachihara 2017) possibly refers solely to *U. hades* sp. nov. Many photos of "*U. concolor*" collected from the estuary of Iriomote Island can further support the identification of *U. hades* sp. nov. based on general appearance and the absence of branchial pores. These photos can be found on FishPix (https://fishpix.kahaku.go.jp/fishimage-e/) (KPM-NR 275, 3350, 20306, 42937, 42948, 42949, 42950), photographed by H. Senou and T. Suzuki.

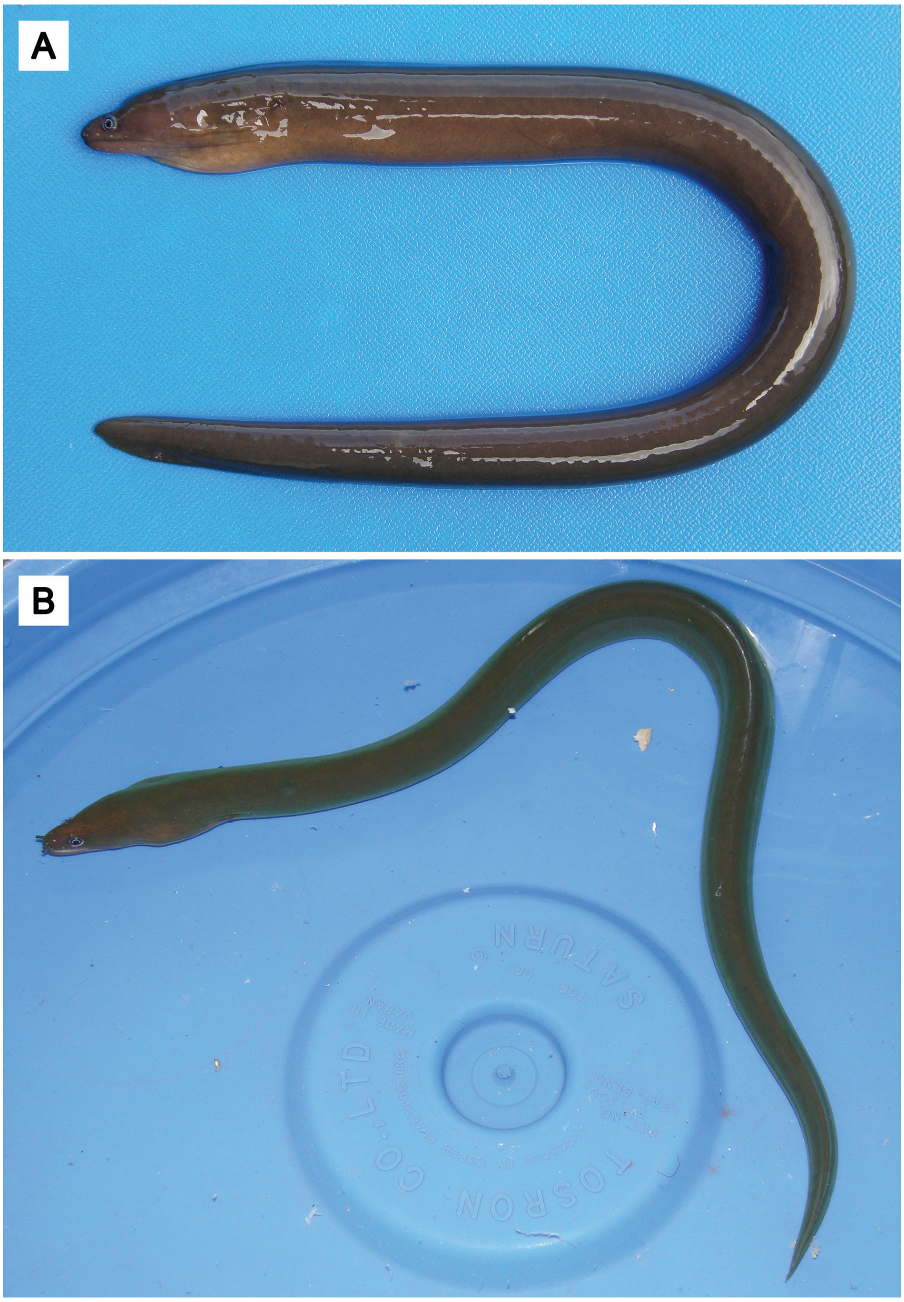

Figure 8. *Uropterygius mactanensis* collected from Iriomote Island, KYUM-PI 2591, 316 mm TL **A** fresh coloration **B** live photo. Photographed by Atsushi Tawa.

Material examined. • KYUM-PI 2591 (316 mm TL), off mouth of Kura River, Iriomote Island, Yaeyama Group, Ryukyu Islands, 1 November 2009, coll. A. Tawa • KYUM-PI 2612 (370 mm TL), off Funaura, Iriomote Island, Yaeyama Group, Ryukyu Islands, 5 November 2009, coll. A. Tawa.

Discussion

The absence of branchial pores is an important characteristic of *Uropterygius hades* sp. nov. Although one examined specimen has a branchial pore on the left side of the head, no other morphological differences were found. Intraspecific variations in head pore number are common in moray eels. For example, in the genus *Strophidon* McClelland, 1844, a fourth infraorbital pore is a diagnostic characteristic of *Strophidon tetraporus* Huang & Liao in Huang et al. 2020, distinguishing it from congeners with only three pores. Despite this, a few specimens of *Strophidon dorsalis* (Seale, 1917), *Strophidon sathete* (Hamilton, 1822), and *Strophidon ui* Tanaka, 1918 were observed with a fourth infraorbital pore on only one side of the head (Huang et al. 2020). Similarly, the additional branchial pore in *U. hades* sp. nov. should be considered a rare intraspecific variation and does not affect the general diagnostics of the taxon.

The salinity at the type locality in the Zhuan River was promptly measured using a refractometer, a day after its collection during a spring tide. Measurements showed a salinity of 5‰ during low tide and 19‰ during high tide. Similarly, surface water salinity at the sampling site in Puerto Princesa Subterranean River (PPSR) was measured at 9‰ during the high tide. These findings support that *U. hades* sp. nov. is one of the rare cases of moray eels inhabiting brackish-water environments. Another estuarine moray, *Echidna rhodochilus* Bleeker, 1863, was observed co-occurring with *U. hades* sp. nov. in Japan, Taiwan, and the Philippines (Masuda and Kobayashi 1994; Huang et al. 2021b; Wada and Hibino 2024; W.C. Huang pers. obs.).

Uropterygius hades sp. nov. seems to be closely associated with mangroves, as most of its known habitats in the Ryukyu Archipelago are mangrove swamps. The habitat on Okinawa Island is an estuary with many fallen leaves from mangrove trees (Fig. 9A). However, *U. hades* sp. nov. has never been discovered inside the mangrove forest. Instead, it rests in gaps among mangrove aerial roots and leaves (Fig. 9B). When there are fewer fallen leaves, it uses scattered stones as an alternative for concealment. On Amami Island, one collection site is far outside the river mouth and lacks mangrove trees. It consists of a muddy bottom with many gravels and stones, with a tiny freshwater seepage from the land side, similar to the environment of Kakeroma Island. For Philippine specimens, although *U. hades* sp. nov. was collected inside the PPSR, the entrance of the cave also harbors a few mangrove trees (Fig. 9C), analogous to the estuarine environment of the Matutinao River in Cebu. The Zhuan River, where the holotype was discovered, emerges as another known habitat of *U. hades* sp. nov. without mangrove trees (Fig. 9D). These observations imply that while mangroves may be important for the survival of *U. hades* sp. nov., brackish water is a more essential factor.

One possible interpretation for the preference of *U. hades* sp. nov. to mangroves as habitat is that mangroves can facilitate the accumulation of fine sediment, thereby creating a soft-mud substrate that may be suitable for *U. hades* sp. nov. (Perry and Berkeley 2009; Tachihara 2017). We observed that *U. hades* sp. nov. exhibits tail-first burrowing behavior when kept in an aquatic tank, similar to snake eels (family Ophichthidae) which typically inhabit muddy or sandy substrates. Additionally, the reduction in the number of head pores is hypothesized to help avoid clogging by the substrate, as this phenomenon is observed in certain eel species that inhabit sand and mud burrows (McCosker 1977; McCosker and Randall 2007). Although there are no mangroves directly adjacent to the sampling sites at the Zhuan River and the PPSR, both locations feature muddy, silty bottoms with rocks, similar to the substrates found in mangrove swamps.

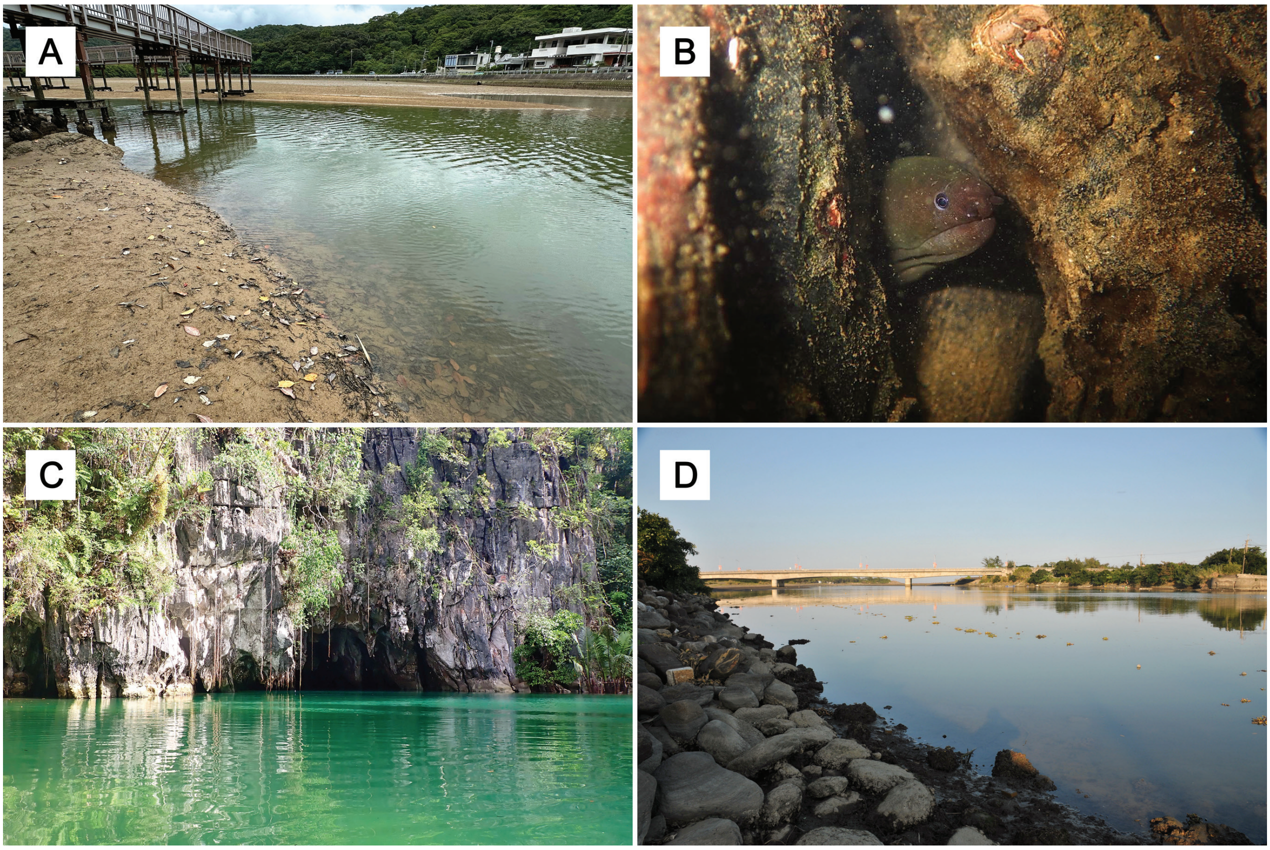

Figure 9. Different habitats of *Uropterygius hades* sp. nov. **A** Oura River, Okinawa Island, photographed by Koki Takatsuki **B** Live photo of a *U. hades* sp. nov. hiding in gaps among mangrove aerial roots, taken at night at the edge of a mangrove forest zone along the Oura River, Okinawa Island, photographed by Hirozumi Kobayashi **C** Puerto Princesa Subterranean River, Palawan, photographed by Wei-Cheng Jhuang **D** Zhuan River, northeastern Taiwan, photographed by Shan-Yu Yang.

Furthermore, we observed that *U. hades* sp. nov. is highly sensitive to light and consistently attempts to hide when exposed to it. This suggests that it may typically inhabit turbid waters such as estuaries, resulting in its lack of acclimation to light exposure. The small eye proportion of *U. hades* sp. nov. may also indicate its adaptation to low-light conditions, wherein they primarily use their chemoreception rather than vision to detect prey or avoid predators. A reduction in eye size is also observed in some congeners, such as *U. cyamommatus* (eye diameter 3.0–4.6% of HL) and *Uropterygius oligospondylus* Chen, Randall & Loh in Loh et al. 2008 (eye diameter 3.9–7.1% of HL). The former is found in anchialine caves, whereas the latter inhabits intertidal zones consisting of boulders frequently hit by strong waves. Both environments pose challenges to visual perception, making reliance on other senses more important (Loh et al. 2008; Hibino et al. 2020; Koreeda et al. 2020; Huang et al. 2023b).

Combining information from habitat type, body structure, and behavior, we propose that *U. hades* sp. nov. is an estuarine moray eel that inhabits turbid waters with muddy and soft substrates, using its tail to burrow and hide in sediments, among rocks, or in fallen mangrove leaves. While this study addresses a portion of the *U. concolor* species complex conundrum, the diversity of these small, uniformly brown moray eels may still be underestimated. For instance, morphological and genetic data reveal the presence of at least three sympatric species found in the Philippines (i.e., *U. hades* sp. nov., *U. mactanensis*, and *U.* cf. *concolor* 1), while both *U. hades* sp. nov. and *U. mactanensis* can be found at Iriomote Island. This high diversity could be triggered by niche segregation and adaptation to different environments among species; for example, *U. concolor* inhabits shallow fringing reefs, *U. mactanensis* prefers reef-seagrass interfaces, and *U. hades* sp. nov. thrives in muddy estuaries (Smith et al. 2019; Huang et al. 2023a). Additionally, a phylogenetic analysis reveals the non-monophyly of the *U. concolor* species complex, indicating that these morphologically similar moray eels have multiple evolutionary origins (Smith et al. 2019). Further studies are needed to clarify their taxonomic status, as three synonyms of *U. concolor* and at least three unresolved genetic lineages persist within the species complex.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

A gratuitous permit (GP no. 2023-06) and wildlife export certificate (WEC no. 2023-013) were granted from the Palawan Council for Sustainable Development Staff (PCSDS) before sampling in the PPSR.

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Author contributions

W.C.H. and T.Y.L. designed the study. W.C.H., Y.H., and R.A.B. collected the specimens. W.C.H. and Y.H. identified and photographed the specimens. T.Y.L. and R.A.B. provided logistical support in the field and in the lab. W.C.H., Y.H., and R.A.B. generated and analyzed data. All authors prepared and revised the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

A new species of *Phyllophichthus* Gosline, 1951 (Actinopterygii, Ophichthidae) from Taiwan

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Abstract

A unique species of the flappy-snake eel genus, *Phyllophichthus diandrus* **sp. nov.**, is described based on a single specimen (270 mm in total length) collected from Dong-gang, southwestern Taiwan. The new species possesses several characters that are distinct from the only other species in the genus, *Phyllophichthus xenodontus*. *Phyllophichthus diandrus* **sp. nov.** can be easily distinguished from *P. xenodontus* by having two papillae inside of nasal tube (vs three in *P. xenodontus*), 25 branchiostegal rays (vs 29), the dorsal-fin origin positioned behind the tip of the pectoral fin (vs not behind, usually above mid-pectoral fin), and the absence of the maxillary teeth (vs present). The relationship between *Phyllophichthus* and *Leiuranus* is discussed based on generic and morphological features.

Key words: Biodiversity, fish fauna, ichthyology, marine species, nasal tube, snake eel, taxonomy

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Introduction

The family Ophichthidae (snake eels or worm eels) is the most abundant group of the order Anguilliformes, comprising 365 species in 62 genera. While many species are recognized, most of them are belonging to several major genera, i.e. *Apterichtus* Duméril, 1805 (20 spp.), *Bascanichthys* Jordan & Davis, 1891 (19 spp.), *Ophichthus* Ahl, 1789 (97 spp.), and *Scolecenchelys* Ogilby, 1897 (20 spp.) (Y. Hibino pers. data). In contrast, several specialized monotypic genera have been discovered, such as *Glenoglossa* McCosker, 1982, which has an elongate tongue with a shrimp-like tip, and *Chauligenion* McCosker & Okamoto, 2016, which has a protruding lower jaw.

The genus *Phyllophichthus* Gosline, 1951 is one of the unique monotypic genera, established for *Phyllophichthus xenodontus* Gosline, 1951. Gosline's (1951) work, which included an osteological study, was based on various groups of Ophichthidae. He found specialization of the shape of the anterior nasal tube that has a leaf- or flower-like shaped, posterior extension in

Phyllophichthus (Gosline 1951; Hibino and Kimura 2016; Hibino 2020). In addition, *Phyllophichthus* has an acute, straight snout, as well as relatively simple sensory canals on the head.

During a survey in recent decades by our team of the snake-eel fauna of Taiwan, one particular specimen was collected that was initially identified as *Phyllophichthus* sp. by Hibino (2019), who suggested the possibility of it being an undescribed species but also noted a potential abnormality in the lower jaw. After careful re-examination, we have determined it to be the second species within the genus.

Materials and methods

All methods for morphological measurements follow Hibino et al. (2019). Measurements for total and tail lengths are taken by 300 or 600 mm rulers and others by a digital caliper to the nearest 0.1 mm. Osteological observation including counts of vertebrae and branchiostegal rays are based on the radiographs taken by a digital x-ray machine (Dexela CMOS X-ray detector, Model 2315, Dexeal Co. Ltd, UK) in the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan. Total length (**TL**) and head length (**HL**) are used throughout for expressing the body proportions.

DNA extraction, polymerase chain reaction (PCR), and sequencing methods followed Weigt et al. (2012). The total DNA was extracted from muscle tissue of samples and amplified partial regions of mitochondrial genes of 16S ribosome RNA (16S) and cytochrome c oxidase subunit I (COI). The primers for PCR and sequence were primer A (5'-GGTCCWRCCTGCCCAGTGA-3'), B (5'-CCGGTCTGRACYAGATCACGT-3') for 16S (Kurogi 2008) and FISH-BCL (5'-TCAACYAATCAYAAAGATATYGGCAC-3'), FISH-BCH (5'-ACTTCYGGGTGRCCRAARAATCA-3') for COI (Baldwin et al. 2009). Amplification of the target region was confirmed by gel electrophoresis, DNA was purified by ExoSAP-IT (Applied Biosystems) and sequenced using 3730×l DNA Analyzer (Applied Biosystems). All sequences have been deposited in the DNA Data Bank of Japan (**DDBJ**) (Table 1).

Table 1. Accession numbers of sequences for the present study.

Species	Accession no.		Voucher collection no.	Locality
	16S	COI		
Brachysonophis cirrocheilos	LC815008	LC815014	FRLM 47057	Dong-gang, Taiwan
Echelus uropterus	LC815009	LC815015	FRLM 47022	Dong-gang, Taiwan
Leiuranus semicinctus	OP035206		USNM 446167	Wallis and Futuna
Leiuranus versicolor	LC506441	LC815016	KPM-NI 50816	Miyazaki, Japan
Muraenichthys hattae	LC599668	LC815025	OMNH-P 38345	Osaka, Japan
Myrichthys maculosus	LC815010	LC815017	FRLM 38878	Wakayama, Japan
Ophichthus celebicus	LC599662	LC815018	FRLM 49737	Ha Long Bay, Vietnam
Ophichthus erabo	LC599664	LC815019	KMNH VR 100283	Nha Trang, Vietnam
Ophichthus urolophus	LC815011	LC815020	FRLM 47025	Dong-gang, Taiwan
Ophichthus zophistius	LC599660	LC815021	FRLM 36624	Shima, Mie, Japan
Phyllophichthus diandrus **sp. nov.**	LC815012	LC815022	NMMB-P28224	Dong-gang, Taiwan
Phyllophichthus xenodontus	LC815013	LC815023	KMNH VR 100268	Okinawa, Japan
Scolecenchelys aoki	LC599667	LC815024	FRLM 38979	Mie, Japan

Partial sequences of 16S (537 bp) and COI (612 bp) obtained present study and retrieved GenBank (Table 1) were aligned by MAFFT v. 7 (Katoh and Standley 2013) and a maximum-likelihood (ML) tree (16S + COI) was constructed by RAxML v. 8 (Stamatakis 2014). The evolutionary model was used GTR+G+I following the best model computing by MEGA 11 (Tamura et al. 2021). The confidence of each branch was evaluated by 1000 bootstrap replications. *Scolecenchelys aoki* (Jordan & Snyder, 1901) and *Muraenichthys hattae* Jordan & Snyder, 1901 were used as outgroups.

Specimens examined in this study are deposited in the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan (**KMNH VR**), National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (**NMMB-P**), and Museum Support Center of the Smithsonian Institution, Suitland, Maryland, USA (**USNM**).

***Phyllophichthus diandrus* sp. nov.**

https://zoobank.org/7134B3C8-04EB-4E43-9761-1AC65F70A8BE
Figs 1, 2A, 3, 4
English name: Bi-stamened Flappy Snake Eel
Chinese name: 雙蕊葉吻蛇鰻

Phyllophichthus sp.: Hibino 2019: 149 (Dong-gang, Taiwan).

Type material. ***Holotype*:** NMMB-P28224, 270 mm TL, ca 22°26'N, 120°24'E, Dong-gang, Pingtung, southwestern Taiwan, northern South China Sea, mid-water trawl, 6 Jan. 2017, collected by H.-C. Ho.

Diagnosis. Inside of anterior-nostril tube with two papillae; dorsal-fin origin well behind tip of pectoral fin, distance from the tip to the origin of dorsal fin 0.6 times of the fin; no teeth on maxilla and vomer; 25 branchial aches; vertebral formula 12-69-160.

Description. Measurements in mm (% of TL in parenthesis): HL 22.4 (8.3%); preanal length 128.1 (47.5%); tail length 141.7 (52.5%); predorsal length 29.8 (11.0%); body depth at gill opening 4.7 (1.7%); body depth at mid anus 6.2 (2.3%). Measurements in mm (% of HL) in parenthesis: snout length 5.2 (23.2%); eye diameter 1.8 (8.0%); mouth gape 5.4 (24.1%); interorbital width 1.6 (7.1%); gill opening 1.9 (8.5%); isthmus 2.7 (12.1%); pectoral-fin length 3.2 (14.3%); pectoral-fin base 1.5 (6.7%). Body elongate, slender, trunk cylindrical, compressed toward tip of tail; tip of tail hard and pointed; anus anterior to mid-body, tail 1.9 in total length (Fig. 1).

Head relatively short, 5.7 in preanal length and 12.0 in TL; contour of head smooth, slightly convex in post-temporal; snout acute and relatively pointed in lateral view, narrow from dorsal side; snout long, prominently projected anteriorly; a distinct groove ventrally of snout; mouth inferior, lower jaw short and tip below middle of base of nostril tube, distance between tips of snout and lower jaw more than eye diameter; anterior nostril tubular, towards ventrally, base of both side closed: posterior rim of tube extending posteriorly, forming a broad flap; inside of tube with two papillae (Fig. 2A); posterior nostril a slit opening inside of mouth, concealed by wide dermal flap rolling into mouth completely; eye developed, large, its diameter 2.9 times in snout length; lips smooth without cirri or protrusions, upper lip extending to inner mouth, a curved fold along

Figure 1. *Phyllophichthus diandrus* sp. nov., NMMB-P28224, holotype, 270 mm TL, Dong-gang, Taiwan **A** dorsal view **B** ventral view **C** enlarged view of lateral head. Arrows indicate origin of dorsal fin (above) and anus (below).

lower margin of eye; mouth moderate, rictus slightly behind a vertical through posterior margin of eye; interorbital region slightly convex without groove; branchial basket convex; gill opening positioned just anterior to base of pectoral fin.

Teeth small, conical, pointed; no teeth on maxilla and vomer, maxillary region completely covered by an extending upper labial flap (Fig. 3); 6 intermaxillary teeth arranged in two rows but concealed by a dermal structure and not visible; dentary teeth uniserial posteriorly, 17 on left side and 15 on right side.

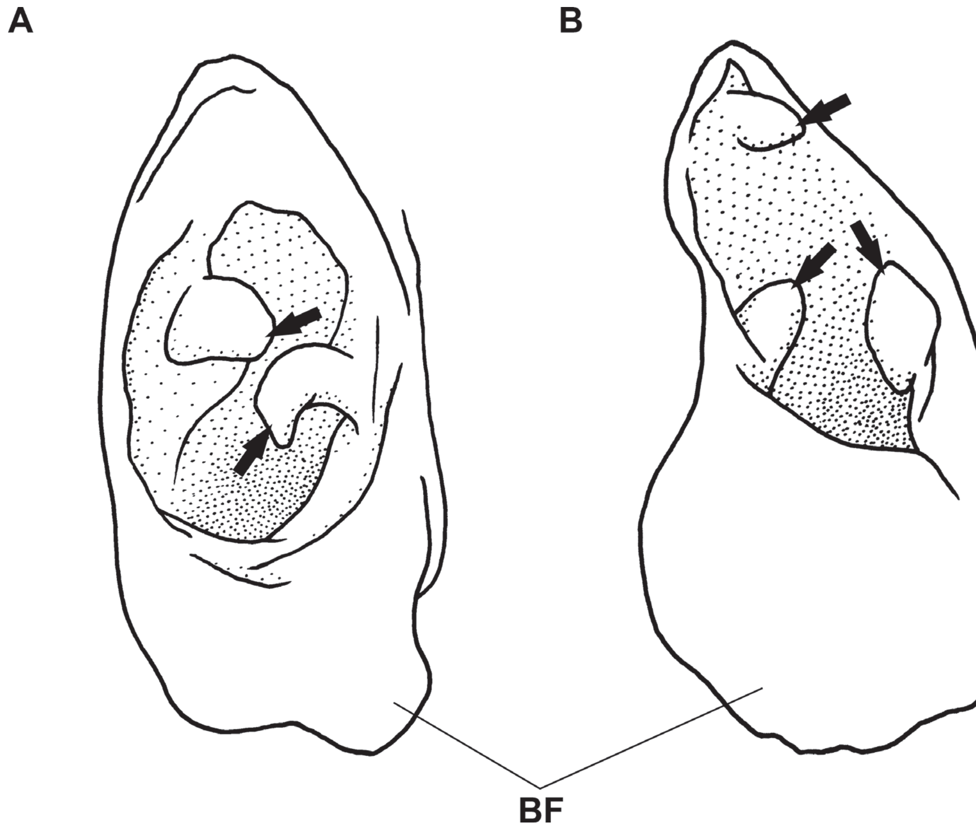

Figure 2. Closed illustration of tubular anterior nostril from ventral view **A** *Phyllophichthus diandrus* sp. nov., NMMB-P28224, holotype, 270 mm TL **B** *P. xenodontus*, NMMB-P5264 (one of two), 373 mm TL, Taiwan. **BF** broad flap. Arrows indicate papillae inside of nasal tube.

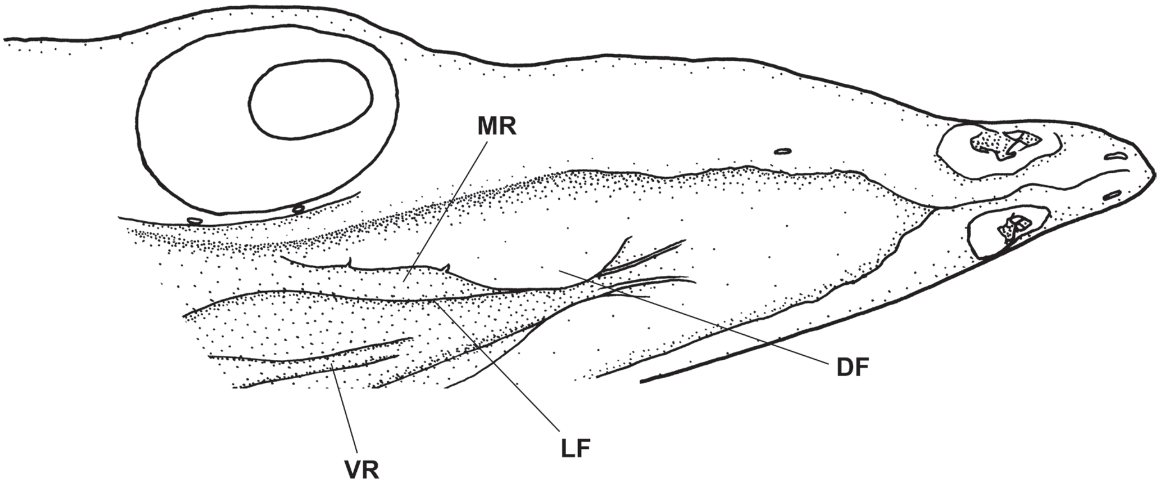

Figure 3. Ventrolateral view of palatal area of *Phyllophichthus diandrus* sp. nov., NMMB-P28224, holotype, 270 mm TL. **DF** dermal flap on posterior nostril **LF** edge of upper labial flap **MR** maxillary region **VR** vomerine region.

Sensory pores on head obvious (Fig. 4); supraorbital pores 1 + 3, 1 ethmoid and 3 pores slightly before a level of center of eye; infraorbital pores 3 + 3, first between anterior and posterior nostrils and second anteroventro-corner of eye, third behind center of eye, and remaining on postorbital; preoperculo-mandibular pores 4 + 2; 3 on supratemporal; 1 interorbital pore present; lateral-line pore slightly obscure, nearly completed except tip of tail equal to one third of HL.

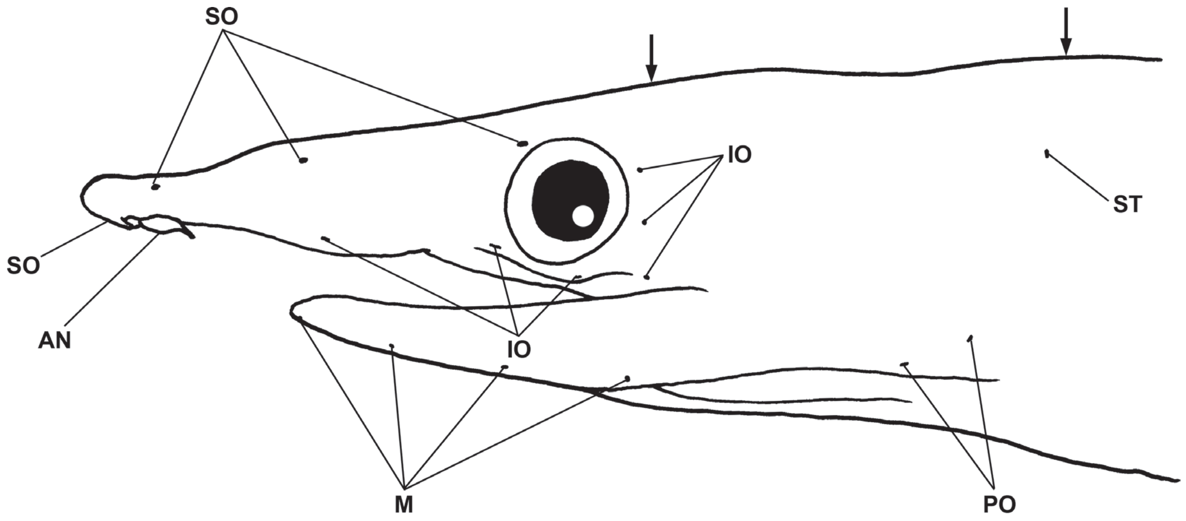

Figure 4. Lateral view of anterior head of *Phyllophichthus diandrus* sp. nov., NMMB-P28224, holotype, 270 mm TL. **AN** anterior-nostril tube **IO** infraorbital pores **M** mandibular pores **PO** preopercular pores **SO** supraorbital pores **ST** supratemporal pore. Arrows indicate interorbital (left) and mid-temporal pores (right).

Neurocranium narrow dorsally; dentary stout and recurved; branchiostegal rays developed and deeply overlapped ventrally, 25 in total. Predorsal vertebrae 12, preanal 69, and total 160.

Pectoral fin moderate, shape round, its length 1.6 in snout and 7.0 in HL; medial fins low in height, origin of dorsal fin behind tip of pectoral fin, distance from pectoral fin-tip to dorsal-fin origin 0.6 times of the fin, distance from gill opening to dorsal-fin origin 3.0 in HL; caudal fin absent.

Color in preservation light yellowish brown; abdomen slightly paler but not bicolored distinctly; all fins pale white.

Distribution. Known only by a single specimen from Dong-gang, southwestern Taiwan. Depth range estimated as more than 100 m.

Etymology. The specific name *diandrus* is the Latin compound adjective "bi-stamened", referring to the flower-like shaped tubular nostril with two papillae inside.

Discussion

Based on careful examination of the radiograph images of the holotype, we found no osteological damage on its lower jaw, despite the suspicion of an abnormal condition raised by Hibino (2019). As stated above, *Phyllophichthus* was known previously only from a single species, *P. xenodontus* which is widespread in the tropical and subtropical regions in the Indo-Pacific Ocean.

Our species represents the second species in the genus. *Phyllophichthus diandrus* sp. nov. can be easily distinguished from *P. xenodontus* by having two papillae inside of nasal tube (vs three in *P. xenodontus*), 25 branchiostegal rays (vs 29), the dorsal-fin origin behind the tip of the pectoral fin (vs usually above mid-pectoral fin), and an absence of the maxillary teeth (vs present) (McCosker 1977; Smith et al. 2014; this study). Another nominal species, *Phyllophichthus macrurus* McKay, 1970, described from Western Australia, has been regarded as a junior synonym of *P. xenodontus* by several authors (McCosker et al. 2006; Smith et al. 2014; McCosker 2022). The dorsal-fin origin of *P. macrurus* is positioned above posterior two-thirds of the pectoral fin, not behind the fin tip (McKay 1970; this study) and is clearly within the range of *P. xenodontus*. Thus, we retain this name in the synonymy of *P. xenodontus*.

Smith et al. (2014) noted that because of the wide range in the vertebral counts there might be several populations present in *P. xenodontus*. However, due to the small number of specimens, they did not separate them into different taxa. Smith et al. (2014) examined 11 specimens collected from Hawaii (type locality of *P. xenodontus*), Seychelles, the Red Sea, Taiwan, Solomon Islands, Vanuatu, and the Marquesas Islands. In their description, they clearly stated that *P. xenodontus* has three papillae inside the nasal tube, the same as the illustration of the holotype provided by Gosline (1951). Five of 11 specimens examined by Smith et al. (2014) were also checked and this character was confirmed by YH. Furthermore, our additional specimens of *P. xenodontus* from Taiwan (*n* = 3) and Japan (*n* = 2) also have characters identical to the holotype.

The genetic distance between *P. diandrus* sp. nov. and *P. xenodontus* is high, more than 5% based on a combination of mitochondrial COI and 16S sequences (Fig. 5). Furthermore, *P. diandrus* sp. nov. exhibits a distinctive characteristic of lacking teeth on the maxilla, a trait that may warrant consideration for the establishment of a new genus in Ophichthidae. However, further investigation with additional specimens and more comprehensive studies are necessary to explore this hypothesis.

The genus *Phyllophichthus* was established by Gosline (1951). While mentioning that its dentition is similar to *Leiuranus* Bleeker, 1852 (i.e. both genera lack vomerine teeth), he also noted that the condition of the mandibular teeth in *Phyllophichthus* is unique. McCosker (1977) confirmed *Phyllophichthus* as a valid genus and suggested that *Phyllophichthus* is closely related to *Leiuranus* and *Elapsopis* Kaup, 1856 in the tribe Ophichthini. McCosker et al. (1989) treated *Elapsopis versicolor* Richardson, 1848, the only species of *Elapsopis*, as a member of *Leiuranus* without further explanation. *Leiuranus versicolor* has vomerine teeth, free branchial rays, secondary ossification of the fifth ceratobranchial, and the presence of actinosts (McCosker 1977), but other osteological features, including fusion of the upper pharyngeal dermal tooth plates, are consistent with those of *Leiuranus semicinctus* (Lay & Bennett, 1839).

Based on COI and 16S sequences, *Phyllophichthus* forms a sister group with *Leiuranus*, supported by a high bootstrap value. This result supports the hypothesis proposed by McCosker (1977), which was primarily based on osteological analysis. While the shape of the neurocranium (subtruncate) of *Phyllophichthus* is similar to that of *Leiuranus*, the expanded appendage of the nasal tube, modified suspensorium, jaws, dentition, and neurocranium (McCosker 1977; this study) are distinct from the former. Consequently, we recognize both *Phyllophichthus* and *Leiuranus* as valid genera, each comprising two species.

Fricke et al. (2015) established a new genus and species, *Suculentophichthus nasus* Fricke, Golani & Appelbaum-Golani, 2015 from a single specimen collected at Eilat, Gulf of Aqaba in the Red Sea. Because of its large tubular nostril they considered the genus to be closely related to *Phyllophichthus*, distinguishing the two genera by a number of differences, including the shape of the tubular nostril, caudal vertebral counts, the position of the dorsal fin origin, and the presence of supraorbital canal/pores. However, the first three characters are within species-level variation, and there is no difference in the fourth character. It is notable that *Phyl-*

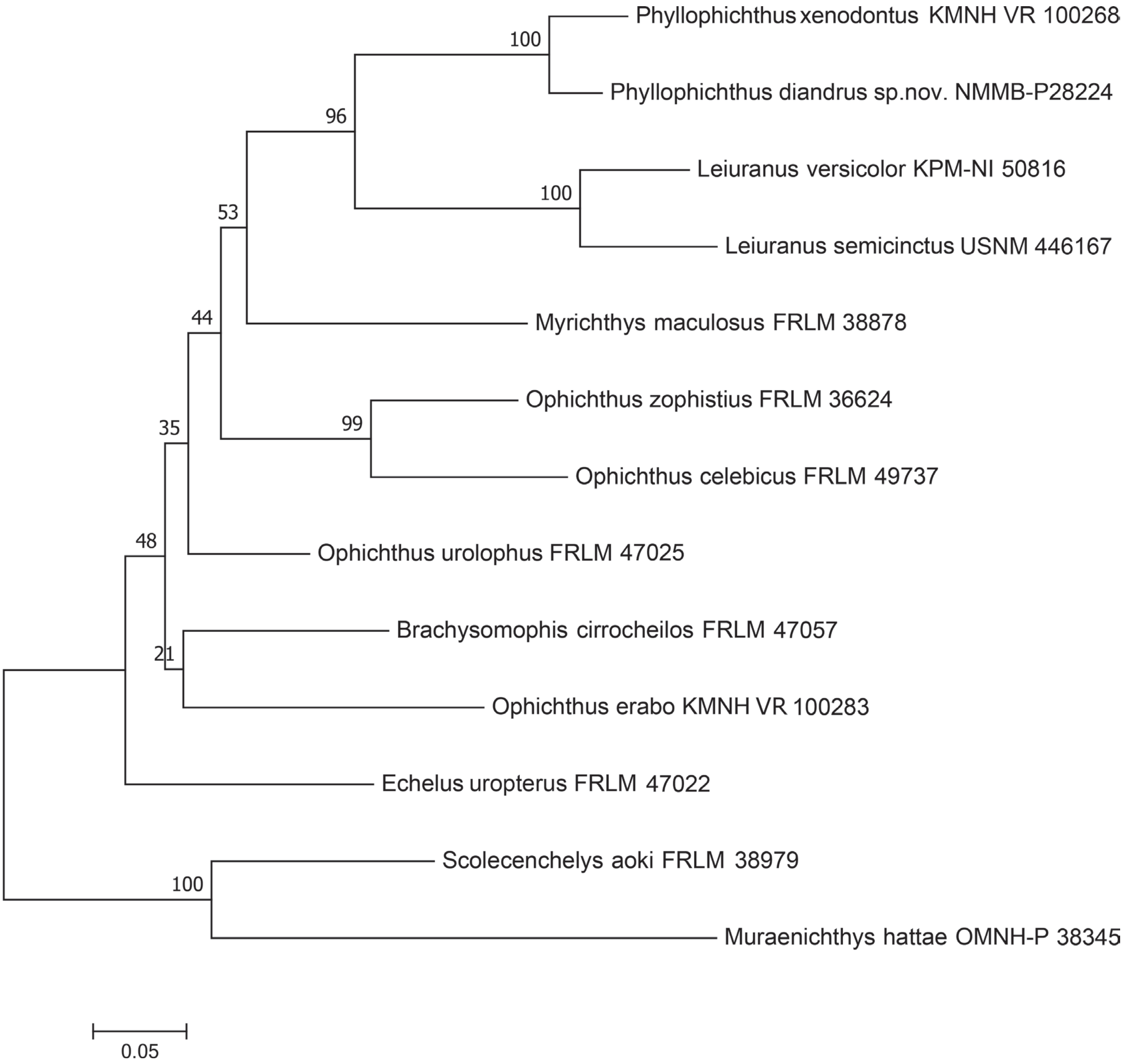

Figure 5. Maximum likelihood tree of selected genera in subfamily Ophichthinae based on partial COI and 16S sequences, including two *Phyllophichthus* species.

lophichthus has no protrusions along the upper lip, whereas *S. nasus* has at least one protrusion (one in the text, but two shown in the illustration). Further work is needed to determine whether *Phyllophichthus* and *Suculentophichthus* Fricke, Golani & Appelbaum-Golani, 2015 should be regarded as separatable genera or not.

Phyllophichthus diandrus sp. nov. is unique in having no teeth on the maxilla, which is completely covered by an extending upper labial flap. It is speculated that this species specializes in feeding on soft organisms due to the presence of dentary and intermaxillary teeth.

Comparative materials

Phyllophichthus xenodontus: USNM 162709, holotype, 238 mm TL, Oahu Island, Hawaii Islands; WAM P.4015-001, holotype of *P. macrurus*, 465 mm TL, near Albany, Western Australia (photo examination only); KMNH VR 100268, 249 mm TL, USNM 132819, 269 mm TL, Okinawa Island, Ryukyu Islands, Japan; NMMB-P2753, 283 mm TL, NMMB-P5264, two specimens, 373–422 mm TL, Hsiao-liu-chiu Island, southwestern Taiwan; USNM 121374, 349 mm TL, Batan Island, Philippines; USNM 224232, 319 mm TL, Caroline Islands, Micronesia; USNM 314690, 204 mm TL, Aldabra Atoll, Seychelles; USNM 363698, 345 mm TL, Bank Islands, Vanuatu.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: YH. Data curation: YH. Formal analysis: YH, SE. Funding acquisition: SE, YH. Investigation: SE, HCH. Methodology: YH. Project administration: HCH. Resources: HCH. Writing - original draft: YH. Writing - review and editing: SE, YH, HCH.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Species of the snake eel genus *Yirrkala* Whitley, 1940 from Taiwan, with descriptions of a new species and two new records (Anguilliformes, Ophichthidae)

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Abstract

The slender snake eel genus *Yirrkala* from Taiwan is reviewed, and a total of four species are recognized, including a new species described here. *Yirrkala nkust* **sp. nov.** is described based on four specimens collected from western Taiwan. It can be distinguished from congeners by the dorsal-fin origin situated above the gill opening, the tip of lower jaw not reaching the base of the anterior-nostril tube, 1 + 3 supraorbital pores, 7–8 predorsal vertebrae, and 147–152 total vertebrae. Two rare species, *Yirrkala kaupii* Bleeker, 1858 and *Yirrkala omanensis* Norman, 1939, are redescribed based on specimens newly collected from Taiwan. A key to all *Yirrkala* species found in Taiwan is provided.

Key words: Biodiversity, catadromous, freshwater, ichthyology, slender eel, taxonomy

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Introduction

The ophichthid genus *Yirrkala* Whitley, 1940 is a rare genus characterized by the combination of the following features: body elongate, cylindrical; tail length generally equal or less than half of total length; dorsal-fin origin generally above or behind gill openings; no pectoral fins; snout subconical; anterior nostrils tubular; teeth conical, mostly uniserial; gill openings ventral; and two preopercular pores (McCosker et al. 2007; McCosker 2022).

The name *Yirrkala* is derived from the local name of northern Caledon Bay, the type locality of its type species, *Yirrkala chaselingi* Whitely, 1940. Members of the genus mostly inhabit shallow-water habitats less than 100 m deep, such as those found in estuaries, beaches, and coral reefs; some habitats are unknown but possibly shallow (McCosker 2006, 2011, 2022; Fricke et al. 2024). Two species, *Yirrkala gjellerupi* (Weber & de Beaufort, 1916) and *Yirrkala kaupii* (Bleeker, 1858), also live in freshwater in rivers, and these species are rarely observed in the field. This genus comprises 18 nominal species, but it requires further revision due to the complicated taxonomy and a lack of samples. For example, 12 valid species are known solely from their type localities as documented in the original descriptions (Fricke et al. 2024). In contrast, *Yirrkala lumbricoides* (Bleeker, 1864) and *Yirrkala misolensis* (Günther, 1872) are known from broader areas, although only *Y. misolensis* has been mentioned frequently (McCosker et al. 2006; Ho et al. 2015; Motomura et al. 2017; Chiu et al. 2022).

In Taiwanese waters, only *Y. misolensis* was previously known (Ho et al. 2015; Chiu et al. 2022). Recent surveys in the Penghu Islands (Pescadores Islands) have revealed many rare snake eels, such as *Apterichtus hatookai* Hibino, Shibata & Kimura, 2015, *Callechelys kuro* Kuroda, 1947, and several unknown *Yirrkala* specimens. Others were collected from river mouths off Hualien by the aboriginal people using traps or fyke nets. In addition, at fish-landing port of southwestern Taiwan YH also found a fresh individual of *Yirrkala* which was identified as a species described by Norman (1939). Here, we describe a new species and redescribe two rare species; all three are newly recorded from Taiwan.

Materials and methods

Methods for taking measurements and counts and terminology generally follow McCosker (2011). Measurements for total and tail lengths were taken by 300 or 600 mm rulers and others by digital calipers to the nearest 0.1 mm. Vertebral counts were made from x-ray photographs. Mean vertebral formula (**MVF**) is expressed as the average of predorsal, preanal, and total vertebrae. Total length is abbreviated as **TL**. All materials here we used are deposited in the Natural History Museum, London, UK (**BMNH**), the California Academy of Science, San Francisco, USA (**CAS**), the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan (**KMNH VR**), and the fish collection of the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (**NMMB-P**).

Results

Family Ophichthidae

Genus *Yirrkala* Whitley, 1940

Yirrkala Whitley, 1940: 410 (type species: *Yirrkala chaselingi* Whitley, 1940, by original designation).

Distinguishing features. Body elongate, cylindrical; tail length generally equal or less than half of total length; all fins low but visible, dorsal-fin origin generally above or behind gill openings; no pectoral fins; snout subconical; anterior nostrils tubular and extremely short; teeth conical, mostly uniserial; gill openings ventral; and two preopercular pores (McCosker et al. 2007; McCosker 2022; this study).

Key to species of *Yirrkala* in Taiwan

1 Head with speckles **2**
– Head without speckles..**3**

2 Dorsal-fin origin behind gill opening by less than one head length; speckles present from head to anterior portions of trunk.. .... ***Y. misolensis*** **(Günther, 1872)**

– Dorsal-fin origin far behind gill opening and slightly behind anus; speckles restricted in head.. ***Y. omanensis*** **(Norman, 1939)**

3 Dorsal-fin origin behind gill opening; lateral-line pores margined by pale spots blank at least anterior to anus in preserved condition .... ***Y. kaupii*** **(Bleeker, 1858)**

– Dorsal-fin origin above gill opening; lateral-line pores without margin in preserved condition.. ***Y. nkust*** **sp. nov.**

Yirrkala nkust **sp. nov.**
https://zoobank.org/8EAF8FC7-BEC3-41B8-9F98-3EBEADD0DBF1
Figs 1, 2, 3A, Table 1
English name: White-mask Snake Eel
Chinese name: 高科細鋤蛇鰻

Materials examined. ***Holotype*** • NMMB-P38652, 496 mm TL, ca 23°40'N, 119°36.6'E, Chi-kan, Bai-sha, northern Penghu, western Taiwan, Taiwan Strait, ca 30–50 m depth, 12 July 2021. ***Paratypes*** • NMMB-P38645, 315 mm TL, 12 July 2021; NMMB-P39317, 462 mm TL, 16 August 2022; KMNH VR 100650, 297 mm TL, 23 July 2024; all collected from near the type locality.

Diagnosis. An elongate species of *Yirrkala* with the following combination of characters: body reddish brown without speckles, snout paler; supraorbital pores (SO) 1 + 3; dorsal-fin origin just above gill opening; lateral-line pores before anus 72–78; predorsal vertebrae 7–8, preanal 72–75, and total 147–152; MVF 8-73-150.

Description. Body elongate, subcylindrical, tip of tail laterally compressed and extremely pointed (Figs 1A, 2A). Head moderate in size, 15.7–17.0 in TL (17.0 in holotype); preanal length mostly equal to tail, 0.9–1.1 in tail length and 1.9–2.1 in TL (0.9 and 1.9 in holotype).

Snout relatively longer, 3.4–3.7 times eye diameter (3.7 in holotype), its tip pointed; distinct median groove ventrally on snout, its anterior tip reaching to midpoint of anterior-nostril-tube base; slope of dorsal surface of snout smooth, without notch or distinct hump. Anterior nostril tubular, short, tube length about equal to pupil diameter; posterior nostril oval in shape with an inner valve, located on anteroventral margin of eye, opening ventrally, covered by a flap extending slightly below edge of mouth gape. Eye small, covered by a transparent skin; center of eye anterior to mid-jaw (Figs 1B, 2B). Interorbital region wide, weakly convex (Figs 1C, 2C). Mouth inferior, distance from tip of snout to anterior tip of lower jaw 3.0–3.3 times eye diameter (3.3 in holotype); lower jaw short, its tip relatively pointed, not reaching anterior-nostril tube (Figs 1B, 2B, D); rictus short, posterior end of gape slightly behind a vertical through posterior margin of eye; lips smooth with a fold along upper lip, extending from second infraorbital pore to postorbital pore or rictus. Gill openings positioned ventrolaterally of breast, relatively close each side; shape of opening slightly curved, diameter more than twice eye diameter.

Table 1. Counts and measurements of three *Yirrkala* species newly collected from Taiwan, with type information.

	***Y. nkust* sp. nov.**		***Y. kaupii***		***Y. omanensis***	
	Holotype	**Paratypes**	**Present materials**	**Holotype**	**Present material**	**Holotype**
Total length (mm)	496	297–462 (*n* = 3)	238–331 (*n* = 3)	342	216	230[b]
As % of TL						
Head length	5.9	6.2–6.4	7.3–8.4	6.5[a]	8.1	7.7[b]
Preanal length	51.9	47.4–52.6	47.1–47.3	N/A	57.9	58.3[c]
Tail length	48.1	47.4–52.6	52.7–52.9	N/A	42.1	41.7[c]
Predorsal length	5.1	5.5–6.1	12.5–13.5	N/A	59.8	ca 59[d]
Body depth at gill opening	1.7	1.6–1.8	2.1–2.4	(1.7)[a]	2.3	(1.8)[c]
Body width at gill opening	1.5	1.5–1.6	1.4–1.7	N/A	2.1	N/A
Body depth at midanus	1.7	1.3–1.5	2.4–2.5	N/A	2.1	N/A
Body width at midanus	1.6	1.4–1.6	1.5–2.1	N/A	2.0	N/A
As % of head length						
Snout length	15.1	14.7–16.5	13.9–14.5	ca 16[a]	11.4	ca 11[b]
Eye diameter	4.5	3.6–4.5	6.1–6.5	ca 8[a]	5.7	N/A
Upper-jaw length	28.0	28.0–30.9	22.4–23.4	ca 25[a]	28.6	N/A
Gill-opening length	12.7	11.4–15.7	8.2–13.4	N/A	9.7	N/A
Interorbital width	7.9	6.6–9.8	6.5–8.2	N/A	5.1	N/A
Isthmus width	5.1	3.9–5.5	8.5–15.6	N/A	6.9	N/A
Counts						
Predorsal vertebrae	8	7–8	17–18	17	78	76
Preanal vertebrae	72	72–75	64–66	65	76	76
Total vertebrae	147	150–152	151–155	156	141	140

Body depths in parentheses are possibly the maximum depth. [a]from Bleeker (1858); [b]from Norman (1939); [c]from McCosker (2022); and [d]estimated from Norman (1939).

Sensory pores on head developed, arrangement of those pores as follows (Fig. 3A): 1 (ethmoid) + 3 on supraorbital, 3 + 3 on infraorbital, 4 on lower jaw, 2 on preopercle, and 5 on supratemporal, one of those on mid-temporal; a single median interorbital pore.

Lateral-line pores small but obvious. Lateral line almost complete except for near tip of tail, nine anterior to a vertical through gill opening, seven or eight (eight in holotype) anterior to dorsal-fin origin, 72–78 (77) anterior to mid anus, and total 149–152 (151).

Teeth pointed, slightly recurved posteriorly; 12–15 teeth on maxilla and 12–13 dentary uniserial; 10–12 vomerine teeth biserial anteriorly and uniserial posteriorly; intermaxillary with four teeth arranged in two rows.

Median fins low but obvious; origin of dorsal fin slightly behind a vertical through anterior edge of gill opening but not behind posterior edge, ending anterior to tip of tail about 1 eye diameter; origin of anal fin slightly behind anus, ending same as dorsal fin; caudal and pectoral fins absent.

Coloration. Just after captured (Fig. 1), body greenish brown anteriorly, reddish brown posteriorly; lateral-line pore not margined; head generally greenish brown, postorbital region pinkish; snout with extremely pale brown transverse band dorsally in holotype, paratype also paler but tip of snout not darker; fins similar color of body. After preservation, body color faded, changed to brown to pale brown, trunk weakly bicolored, melanophores remaining dorsally.

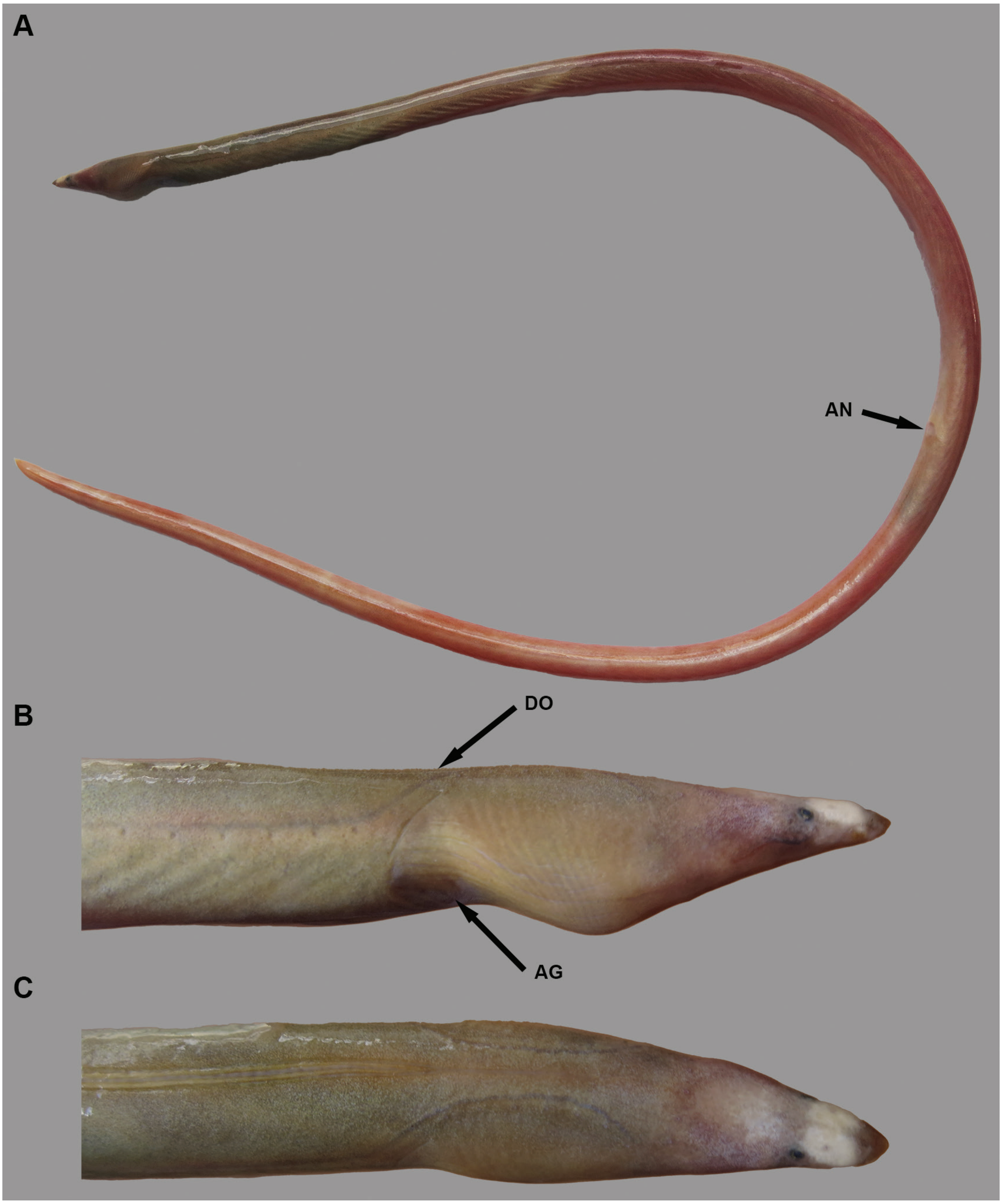

Figure 1. Fresh condition of *Yirrkala nkust* sp. nov., holotype, NMMB-P38652, 496 mm TL **A** whole body **B** lateral view of head **C** dorsal view of head. **AG** anterior edge of gill opening **AN** anus **DO** dorsal-fin origin.

Etymology. The scientific name *nkust* is the acronym of the National Kaohsiung University of Science and Technology, Kaohsiung, Taiwan, which supports our research work. Used as a noun.

Distribution. Known from the northern regions of Penghu Islands, an archipelago in the Taiwan Strait off western Taiwan. The type series was collect-

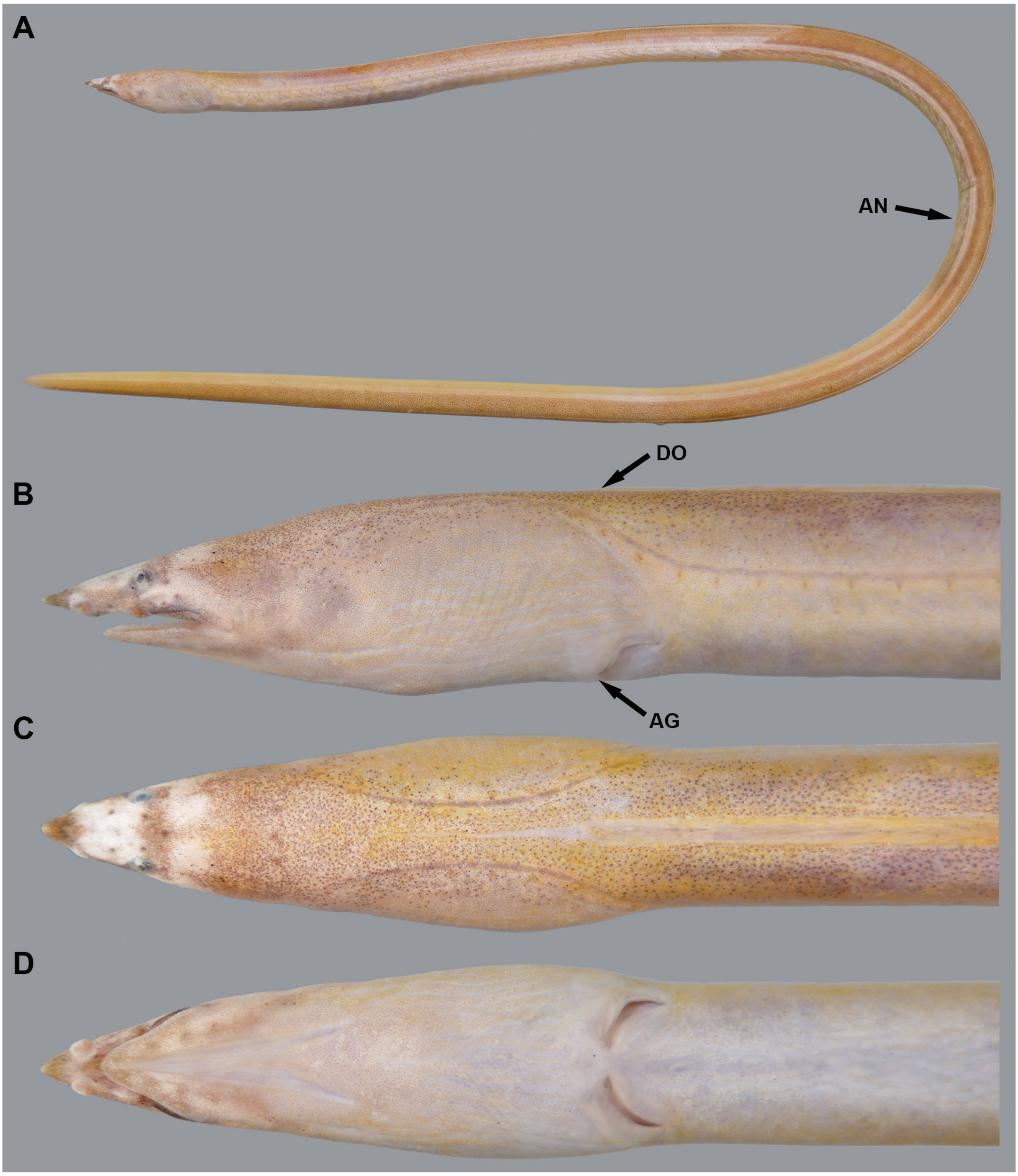

Figure 2. Fresh condition (after freezing) of *Yirrkala nkust* sp. nov., paratype, KMNH VR 100650, 297 mm TL, photographed by Y.-C. Hsu **A** whole body **B** lateral view of head **C** dorsal view of head **D** ventral view of head. **AG** anterior edge of gill opening **AN** anus **DO** dorsal-fin origin.

ed from bycatches of the Silver-stripe round herring (*Spratelloides gracilis*) at depths about 30–50 m.

Remarks. The position of the dorsal-fin origin compared to that of gill opening is an important character for diagnosing *Yirrkala* species. Based on the morphological information of several species (i.e. *Yirrkala ori* McCosker, 2011 and *Y. misolensis*), the origin of dorsal fin quite consistent, showing less intraspecific variation.

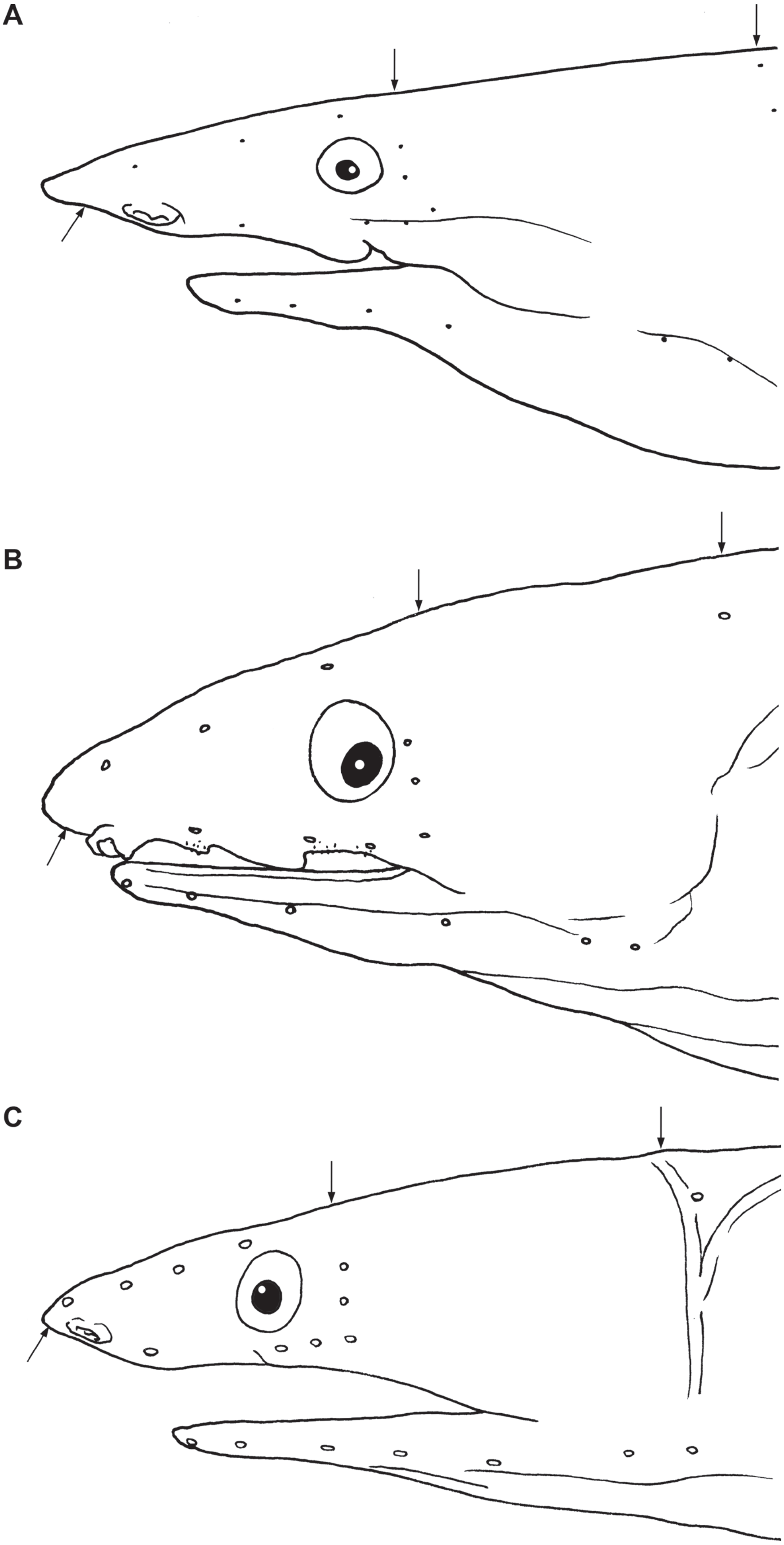

Figure 3. Line drawing of lateral head **A** *Yirrkala nkust* sp. nov., holotype, NMMB-P38652, 496 mm TL **B** *Yirrkala kaupii*, NMMB-P38424, 328 mm TL **C** *Yirrkala omanensis*, KMNH VR 100616, 216 mm TL. Arrows indicate ethmoid = 1st supra-orbital (lefts), interorbital (middles) and mid-temporal (rights) pores.

The new species has the dorsal-fin origin situated above gill opening (verticals between anterior and posterior edges of the opening). The character is shared by *Y. ori* only, as other 13 species, including *Y. chaselingi*, *Y. lumbricoides*, *Yirrkala moorei* McCosker, 2006, *Yirrkala tenuis* (Günther, 1870) before; *Yirrkala calyptra* McCosker, 2011, *Y. gjellerupi*, *Yirrkala insolitus* McCosker, 1999, *Y. kaupii*, *Yirrkala macrodon* (Bleeker, 1863), *Yirrkala maculata* (Klausewitz, 1964), *Y. misolensis*, *Yirrkala omanensis* (Norman, 1939), *Yirrkala philippinensis* (Herre, 1936), have their fin origins clearly behind the gill opening (Bleeker 1863; Whitley 1940; McCosker 1999, 2006; McCosker et al. 2007; McCosker 2011; Chiu et al. 2022; this study).

Yirrkala nkust sp. nov. differs from *Y. ori* in having 1 + 3 supraorbital pores (vs 1 + 4), and the position of the lower-jaw tip (not reaching base of the anterior-nostril tube vs beyond posterior edge of the base). The new species has similar vertebral counts of *Y. lumbricoides* but not overlapped in the count of the predorsal vertebrae (7 or 8 vs 5 in *Y. lumbricoides*), and the total vertebrae (147–152 vs 150–159) is available (McCosker 2022; this study).

In addition, although *Muraena fusca* Zuiwe, 1793 was regarded as a valid species of *Yirrkala* by Fricke et al. (2018), this name should be treated as a *nomen dubium*. Its original description is insufficient which lacks direct evidence to identify it to any ophichthid and whereabouts of its holotype is unknown. *Sphagebranchus brevirostris* Peters, 1855, which has been regarded as conspecific with *M. fusca* (Fricke et al. 2018), should be treated in a future work.

***Yirrkala kaupii* (Bleeker, 1858)**

Figs 3B, 4, Table 1
English name: Kaup’s River Snake Eel
Chinese name:考氏細鋤蛇鰻

Sphagebranchus kaupii Bleeker, 1858: 3 (type locality: Manado, Sulawesi, Indonesia); Bleeker 1864: 70 (Manado).

Ophichthys kaupi: Günther 1870: 86 (Celebes).

Sphagebranchus kaupi: Weber and de Beaufort 1916: 325 (Celebes).

?*Yirrkala kaupi*: McCosker 1977: 16 (listed; specimen collected from Philippines); McCosker 2014: 339 (listed).

Yirrkala kaupii: Kottelat et al. 1993:13 (listed, Indonesia); Smith and McCosker 1999: 1669 (listed); Miesen et al. 2016: 81 (listed, Indonesia); Jamandre 2023: 160 (listed, Indonesia).

Materials examined. • NMMB-P36108, 239 mm TL, ca 23°56.2'N, 121°36.5'E, jointed mouth of Mu-Gua River and Hualien River, Hualien, eastern Taiwan, ca 1 m, trap net (fyke net), 10 May 2021 • NMMB-P38424, 328 mm TL, NMMB-P38425, 331 mm TL, ca 23°27.9'N, 121°29.7'E, Jin-pu village, Fengbin township, Taitung, 26 May, 2023, collected after preserving in wine for several years.

Diagnosis. An elongate species of *Yirrkala* with the following combination of characters: body bicolored, dark brown dorsally and pale ventrally, lateral line pores margined as pale blank; SO 1 + 3; dorsal-fin origin behind gill opening; lateral-line pores before anus 63–65; predorsal vertebrae 17–18, preanal 64–66, and total 151–156; MVF 17-65-154.

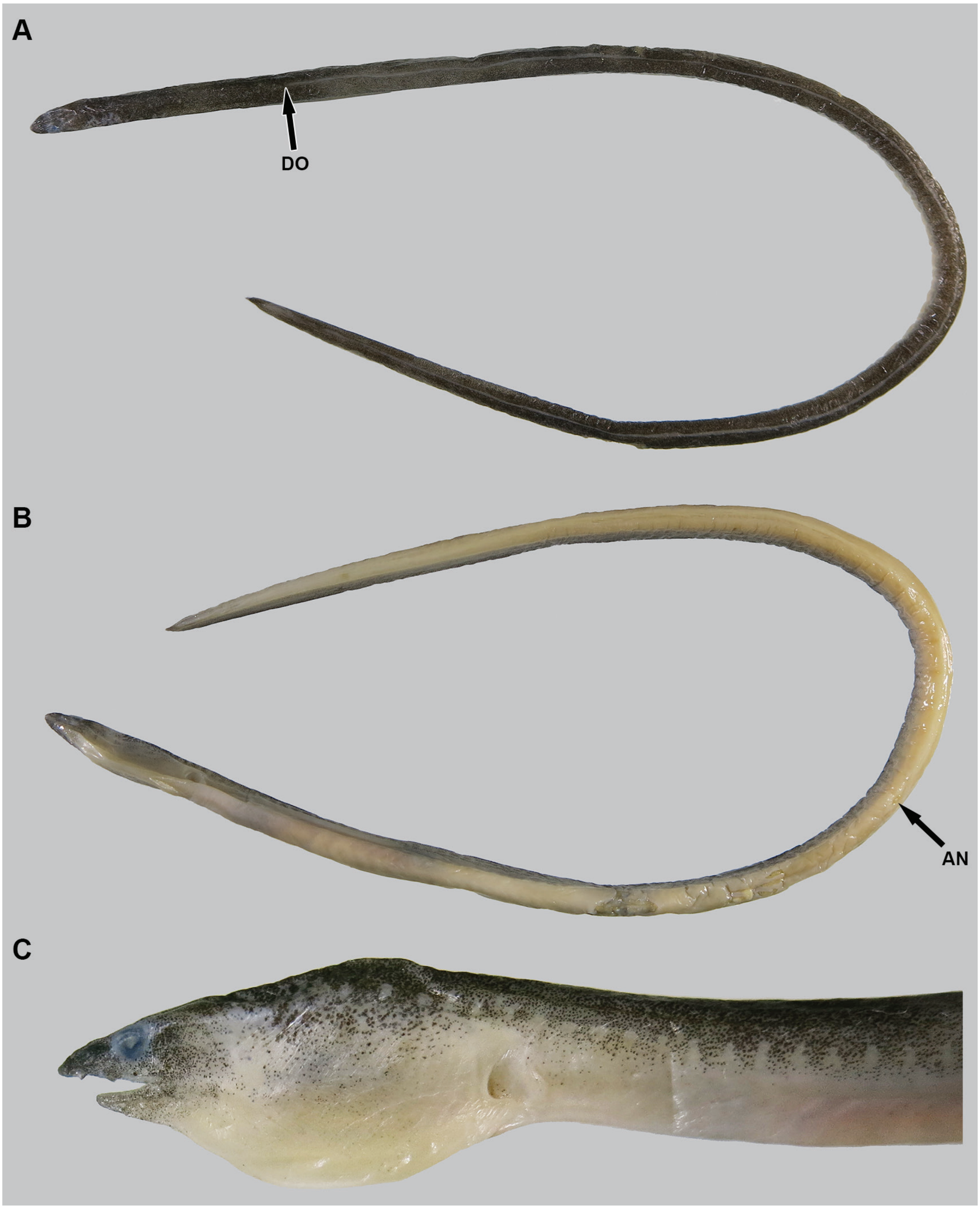

Figure 4. Preserved specimen of *Yirrkala kaupii*, NMMB-P36108, 239 mm TL **A** whole body (dorsal view) **B** whole body (ventral view) **C** enlarged view of head (lateral). **AN** anus **DO** dorsal-fin origin.

Description of Taiwanese specimens. New record. Body elongate, subcylindrical, tip of tail laterally compressed and extremely pointed (Fig. 4A, B). Head moderate in size, 11.8–13.7 in TL; preanal length shorter than tail, 1.1 in tail length and 2.1 in TL.

Snout relatively longer, more than twice eye diameter, its tip pointed; distinct median groove ventrally on snout but the groove mostly not teared, its anterior tip beyond ethmoid pore; slope of dorsal surface of snout smooth, without notch or hump. Anterior nostril tubular, moderate in length, tube length about equal to pupil diameter; posterior nostril oval in shape with an inner valve, located on anteroventral margin of eye, opening ventrally, covered by a flap extending slightly below edge of mouth gape. Eye moderate in size, covered by a transparent skin; center of eye anterior to mid-jaw (Fig. 4C). Mouth inferior, distance from tip of snout to anterior tip of lower jaw slightly longer than eye diameter; lower jaw short, its tip relatively pointed, slightly beyond or reaching posterior base of anterior-nostril tube (Fig. 4C); rictus short, posterior end of gape slightly behind a vertical through posterior margin of eye; lips smooth with folds, the fold along upper lip extending from second infraorbital pore to posterior rictus, but absent in one specimen (NMMB-P38425); the fold along lower lip extending from position between first and second mandibular pores to anterior of first preopercular pore. Gill openings positioned ventrolaterally of breast, not close each side; shape of opening curved, diameter more than twice eye diameter.

Sensory pores on head developed, arrangement of those pores as follows (Fig. 3B): 1 (ethmoid) + 3 on supraorbital, 3 + 3 on infraorbital, 4 or 5 on lower jaw, 2 on preopercle, and 3 on supratemporal, one of those on mid-temporal; a single median interorbital pore.

Lateral-line pores small but obvious. Lateral line almost complete except for near tip of tail, eight or nine anterior to a vertical through gill opening, 16–18 anterior to dorsal-fin origin, 63–65 anterior to mid anus, and total 116–138.

Teeth pointed, slightly recurved posteriorly; teeth on maxilla, vomer and dentary uniserial; maxilla comprising 19 (right)/25 (left) teeth and mandible comprising 21/23 teeth in NMMB-P36108; intermaxillary with four or five teeth arranged in two rows or a chevron shape.

Median fins low but obvious; origin of dorsal fin behind gill opening, ending anterior to tip of tail about 1 eye diameter; origin of anal fin slightly behind anus, ending same as dorsal fin; caudal and pectoral fins absent.

Coloration. No information of fresh coloration. After the preservation by alcohol (ca 60%) directly, body clearly bicolored, generally darkish brown dorsally and pale yellowish brown ventrally; numerous melanophores present dorsally, the border going down toward tip of tail; lateral-line pores margined by pale spots blank at least anterior to anus, but in tail the pattern gradually faded; head darker dorsally, lower jaw also dusky; dorsal fin dusky but margin pale yellowish white; eye with whitish margin by skin covering eye; anal fin pale yellowish white except dusky tip of tail ca 1/2 HL.

Distribution. Manado, Sulawesi, Indonesia (holotype) and eastern Taiwan. In both places, this species was collected from rivers, but there is no detailed information for the holotype.

Ecological note. One specimen was collected from a river mouth together with many *Lamnostoma* spp., a genus which is commonly found in the freshwater environments. However, the species might be rare because only one individual was found among approximately 200 individuals of *Lamnostoma*.

Remarks. *Sphagebranchus kaupii* is one of the oldest names in the genus *Yirrkala*, and it lacks detailed morphological information except for the original description (Bleeker 1858). Based on YH's investigation, the only known Bleeker

Figure 5. Holotype of *Sphagebranchus kaupii*, BMNH 1867.11.28.304, 342 mm TL **A** whole body **B** lateral view of head **C** dorsal view of head. All photos provided by Natural History Museum.

specimen, deposited in the Natural History Museum (BMNH 1867.11.28.304), should be regarded as the holotype because its similar length agrees with the original description (e.g. 342 mm TL vs 362 mm TL in the original description) (Fig. 5).

Our specimens closely match the holotype in body proportions and vertebral counts in the original description. Bleeker (1858) noted that it has drop-shaped markings on the lateral line, which are also found in our specimens. Although Günther (1870) mentioned that it has uniform body coloration, it is assumed that holotype specimen was once dried and bleached beforehand because its very poor present condition had been caused by the drying process. There are several differences in the proportions of the head, snout, eye, and upper-jaw lengths between the original description of *S. kaupii* and Taiwanese specimens (Table 1). The Taiwanese population is possibly an undescribed species, but the morphological differences could also be due to intraspecific variation or differences in the method of preservation, or the time in preservative. As we were unable to directly observe the holotype and the number of specimens observed was limited, we refrain from considering it a separate species.

Most of congeners of *Yirrkala* have a dorsal fin that originates around, and usually slightly behind, the gill opening (see above). Only four species, *Y. gjellerupi*, *Y. kaupii*, *Y. insolitus*, and *Y. omanensis*, have the origin of the fin located more than half a head length behind the gill opening. Moreover, the latter two species are unique because their dorsal-fin origins are situated far behind, near the anus. *Yirrkala kaupii* is most similar to *Y. gjellerupi* in the vertebral counts and body proportions, including head length, tail length, and snout length. Both species inhabit rivers far from the river mouth (McCosker et al. 2007). However, *Y. kaupii* can be distinguished from *Y. gjellerupi* by the position of the rictus (behind a vertical through posterior margin of eye, vs before), and the presence of a small protrusion along around margin of posterior nostril (vs absent).

Yirrkala misolensis **(Günther, 1872)**

English name: Misol Snake Eel
Chinese name:米蘇爾細鋤蛇鰻

Ophichthys misolensis Günther, 1872:426 (type locality: Misool [Misol] Island, Irian Jaya, Indonesia).

Dalophis misolensis: Jordan and Seale 1906: 194 (Misol).

Yirrkala misolensis: McCosker 1977: 69 (listed); Smith and McCosker 1999: 1669 (listed); McCosker et al. 2006: 277 (listed, Queensland, Australia); Menes et al. 2010: 98 (Bago River, Negros and Panay, Philippines); McCosker 2014: 339 (listed, Philippines); Ho et al. 2015: 177 (Taiwan, listed as a new record); Motomura et al. 2017: 35 (Panay, Philippines); Hibino 2019: 154 (Dong-gang, Taiwan); Hibino et al. 2021: 21 (Okinawa, Japan); Chiu et al. 2022: 117 (Taiwan, redescription); McCosker 2022: 136 (Maldives, but photographed specimen collected from Taiwan).

Diagnosis. An elongate species of *Yirrkala* with the following combination of characters: body pale to dark brown with mottled patterns from snout to anterior trunk; SO 1 + 3; dorsal-fin origin behind gill opening; lateral-line pores before anus 76–85; total vertebrae 165–180, MVF 10-77-173 (Hibino et al. 2021; Chiu et al. 2022).

Distribution. Indo-Pacific from India to Fiji, including Indonesia (holotype), north to Ryukyu Islands, Japan; specimens collected from Dong-gang, Ke-tzu-liao, southwestern part of Taiwan (Chiu et al. 2022).

Remarks. Ho et al. (2015) first listed this species from Taiwan with voucher specimens. Chiu et al. (2022) provided a detailed redescription and the results of DNA barcoding. It is notable that McCosker (2022) provided the MVF 12-75-168 and total vertebrae 166–169 which is slightly different from our observation. It is likely that the *Y. misolensis* from Taiwan may include different populations. Without an explanation, McCosker (2022) regarded *Caecula maculata* Klausewitz, 1964 (type locality: Nicobar Islands) as a junior synonym of *Y. misolensis*. However, we cannot make any judgment about this synonymy without examining specimens from the type locality of *C. maculata*. The correct catalog number of the holotype of *Ophichthys misolensis* is BMNH 1870.8.31.112 (https://data.nhm.ac.uk/dataset/56e711e6-c847-4f99-915a-6894bb5c5dea/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/3103514), although Hibino et al. (2021) and Chiu et al. (2022) erred and gave the wrong catalogue number (Fig. 6).

Yirrkala omanensis (Norman, 1939)

Figs 3C, 7, Table 1
English name: Oman Snake Eel
Chinese name: 阿曼細鋤蛇鰻

Sphagebranchus omanensis Norman, 1939 (type locality: Gulf of Oman).

Ichthyapus omanensis: Randall 1995: 61 (Gulf of Oman); Manilo and Bogorodsky 2003: S95 (list, coast of Oman).

Yirrkala omanensis: McCosker 2022: 136 (Gulf of Oman).

Material examined. • KMNH VR 100616, 216 mm TL, Ke-tzu-liao, Kaohsiung, southwestern Taiwan, 6 March 2024, collected H. Kobayashi and Y. Hibino.

Diagnosis. A relatively elongate species of *Yirrkala* with the following combination of characters: body reddish brown mostly except yellow tail end, with speckled patterns on head; SO 1 + 4; dorsal-fin origin well behind gill opening,

Figure 6. Holotype of *Ophichthys misolensis*, BMNH 1870.8.31.112, 280 mm TL **A** whole body **B** head and breast.

slightly behind anus; lateral-line pores before anus 77; total vertebrae 140–141, MVF 77-76-141.

Description based on KMNH VR 100616. New record. Counts and measurements are shown in Table 1. Body elongate, cylindrical, tip of tail laterally compressed and extremely pointed (Fig. 7A). Head moderate in size, 12.3 in TL; preanal length much longer than tail, 0.7 in tail length and 1.7 in TL.

Snout moderate in length, twice eye diameter, its tip weakly pointed; distinct median groove ventrally on snout but the groove opened completely, its anterior tip beyond anteriormost margin of first infraorbital pore; slope of dorsal surface of snout smooth, without notch or hump. Anterior nostril tubular but extremely short, tube length about half of pupil diameter; posterior nostril oval in shape with an inner valve, located on anteroventral margin of eye, opening ventrally. Eye moderate in size, covered by a transparent skin; center of eye anterior to mid-jaw (Fig. 7B). Interorbital region relatively narrow, weakly convex with an extremely shallow dim-

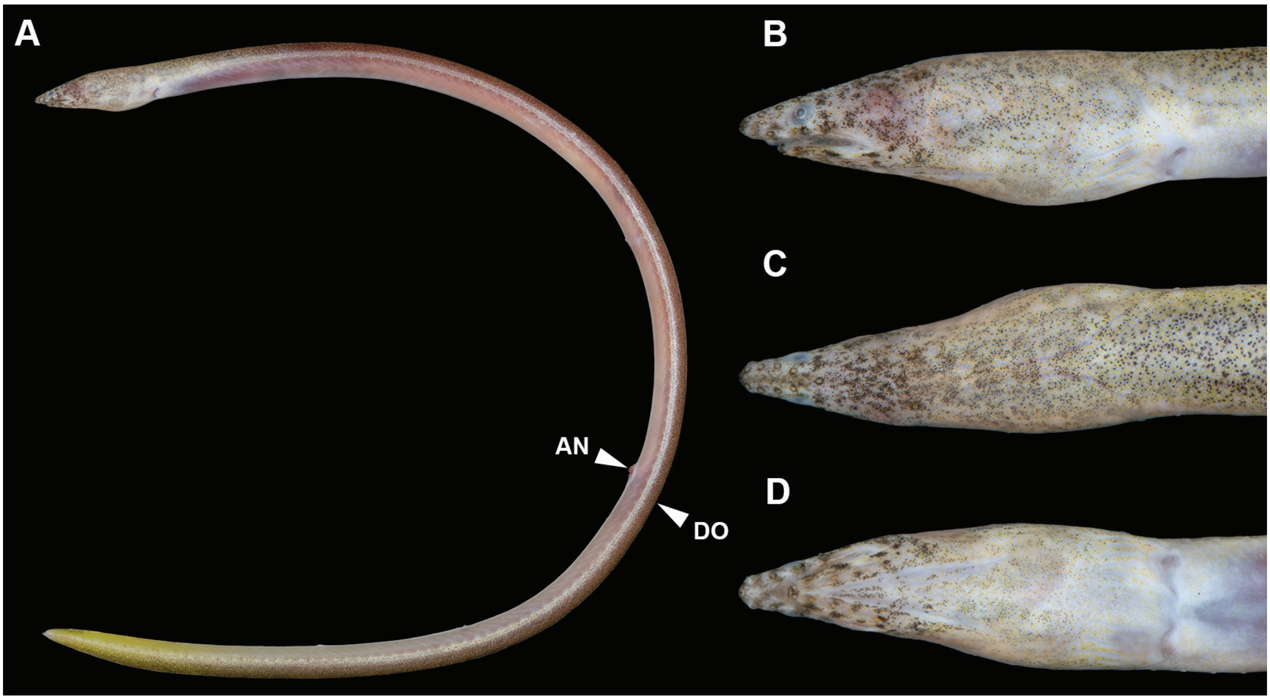

Figure 7. Fresh condition of *Yirrkala omanensis*, KMNH VR 100616, 216 mm TL, photographed by H. Kobayashi **A** whole body **B** lateral view of head **C** dorsal view of head **D** ventral view of head. **AN** anus **DO** dorsal-fin origin.

ple (Fig. 7C). Mouth inferior, distance from tip of snout to anterior tip of lower jaw slightly shorter than twice eye diameter; lower jaw short, its tip relatively pointed and located anterior to a vertical through anterior margin of eye (Fig. 7B, D); rictus short, posterior end of gape well behind a vertical through posterior margin of eye; lips smooth with folds, the fold along upper lip weak, extending from a vertical through second infraorbital pore to posterior rictus; the fold along lower jaw short but obvious, extending from fourth mandibular pore to just before of first preopercular pore. Gill openings positioned ventrolaterally of breast close but not connected each side; shape of opening curved, diameter less than twice eye diameter.

Sensory pores on head developed, arrangement of those pores as follows (Fig. 3C): 1 (ethmoid) + 4 on supraorbital, 3 + 3 on infraorbital, 5 on lower jaw, 2 on preopercle, and 3 on supratemporal, one of those on mid-temporal; a single median interorbital pore. Lateral-line pores small but obvious. Lateral line almost complete except for near tip of tail, 8 anterior to a vertical through gill opening, 77 anterior to mid anus, 79 anterior to dorsal-fin origin, and total 136.

Teeth pointed, slightly recurved posteriorly; teeth on maxilla and dentary uniserial; teeth on vomer biserial irregularly anterior one-third and remaining uniserial; intermaxillary teeth slightly larger and more slender than maxillary teeth, three teeth arranged in a chevron shape along with edge of pre-ethmoid; intermaxillary teeth visible when mouth is closed.

Median fins very tiny and rudimental; origin of dorsal fin slightly behind that of anal fin, ending anterior to tip of tail about one snout length; origin of anal fin slightly behind anus, ending same as dorsal fin; caudal and pectoral fins absent.

***Coloration*.** Just after captured (Fig. 7), body generally reddish brown, gradually changing to yellowish brown to brilliant yellow in posterior tail; numerous tiny melanophores covering dorsolateral body, ventral side without melanophores except tip of tail; numerous xanthophores also present including ventral side. Base color of head pale brown, coloring weaker than body; head with both melanophores and xanthophores, the former gathering and making speckles, arranged as a row along lips and postorbital region; pores on snout prominently margined, but others not margined necessarily, some connected with speckle. Dorsal and anal fins semitransparent white without darker margin. After preservation, brilliant yellow and red completely faded but all speckled remaining; transparent skin on eye becoming whitish.

Distribution. Gulf of Oman (holotype) and southwestern Taiwan (this study). The Taiwanese specimen was estimated to be collected from a depth of around 10–50 m, based on the bycatches collected in the same haul.

Remarks. Our specimen agrees well with the holotype in counts and body proportions (Table 1), as well as in the diagnostic feature of the speckles on head (Figs 7, 8). The present specimen represents the second known specimen of *Y. omanensis* and the first record from the Pacific Ocean. This may suggest that *Y. omanensis* has a wide distribution in the Indo-West Pacific Ocean. However, additional specimens are needed to fully understand the complete distribution range of the species.

Yirrkala omanensis, originally *Sphagebranchus omanensis*, was described by Norman (1939) with a simple line drawing. McCosker (1977) suggested it is an *incertae sedis*, but subsequently, McCosker (2011) included it in *Yirrkala* without further explanation. Notably, this species is very unique in having the dorsal-fin origin situated far posterior, behind the anus, compared to a more anterior origin near the gill opening, such as in all other species of the genus except *Y. insolitus*. However, we agree with the McCosker's (2011) taxonomic placement of this species in *Yirrkala* because all other characters of *Y. omanensis* are consistent with this genus.

Comparative materials. *Yirrkala kaupii*: BMNH 1867.11.28.304 (holotype), 342 mm TL, Manado, Sulawesi, Indonesia. *Yirrkala lumbricoides*: BMNH

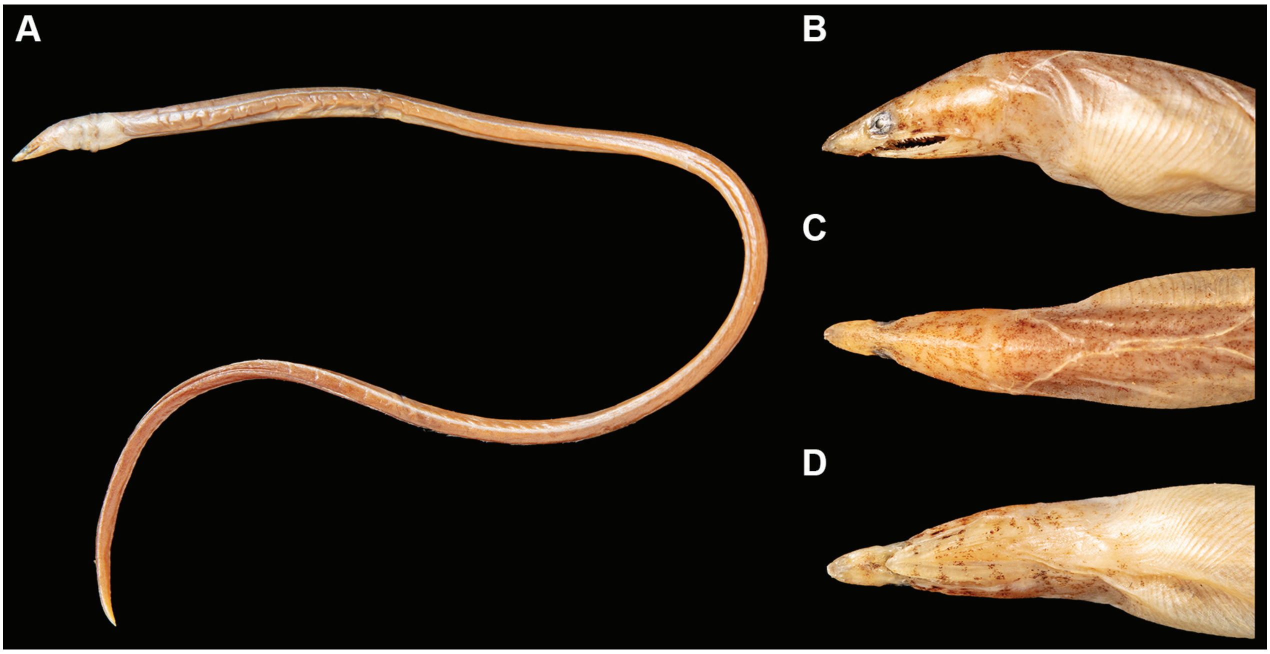

Figure 8. Holotype of *Sphagebranchus omanensis*, BMNH 1939.5.24.650, 230 mm TL **A** whole body **B** lateral view of head **C** dorsal view of head **D** ventral view of head. All photos provided by Natural History Museum.

1867.11.28.322 (holotype), 229 mm TL, Timor, southern Malay Archipelago. *Yirrkala misolensis*: BMNH 1870.8.31.112 (holotype), 280 mm TL, Misol Island, Irian Jaya, Indonesia. *Yirrkala omanensis*: BMNH 1939.5.24.650 (holotype), 230 mm TL, Gulf of Oman. *Yirrkala philippinensis*: SU (CAS) 30977 (holotype), 365 mm TL, Dumaguete, Oriental Negros, Philippines. *Yirrkala tenuis*: BMNH 1965.1.2.1 (lectotype), no locality.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: HCH, YH. Data curation: YH. Funding acquisition: YH, HCH. Investigation: YH. Methodology: YH. Writing - original draft: YH. Writing - review and editing: HCH.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Descriptions of two new dark-body snake eels of the genus *Ophichthus* (Anguilliformes, Ophichthidae) from Taiwan

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Abstract

Two new species of dark-body snake eels are described based on specimens collected from Taiwan. *Ophichthus kbalanensis* **sp. nov.** has a long tail; dorsal-fin origin above posterior third of pectoral fin; tip of lower jaw anterior to anterior-nostril tube; two simple, pointed protrusions along upper lip; preoperculomandibular pores 6 or 7 + 3; teeth on jaws and vomer mostly uniserial, except for biserial on posterior portion of maxilla and anterior portion of symphysis of dentary; vertebral formula 12-55-153 and median fins with narrow dark margins, except the pale fin origins. *Ophichthus multidentis* **sp. nov.** has a dorsal-fin origin well behind gill opening; mainly 4 rows of teeth on jaws; no protrusions along upper lip; a smaller head; mean vertebral formula 24-64-163 and pale median fins. Based on some recent papers and our result, a revised key to species is herein provided.

Key words: Biodiversity, Elopomorpha, ichthyology, taxonomy, Teleostei

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Introduction

The genus *Ophichthus* is the most speciose taxon in the snake eel family Ophichthidae, comprising more than 100 species worldwide, including undescribed ones (Hibino pers. data). The genus is also a major component of snake eels in Taiwan (more than one-third of all species; Ho et al. 2015, 2018, 2022). In the last decade, more than 20 new *Ophichthus* species have been described (e.g., McCosker et al. 2012; McCosker and Ho 2015; Hibino et al. 2019a, 2019b). All these species were collected from the Indo-western Pacific Ocean. More species are waiting to be investigated and named (Hibino and Ho pers. obs.).

McCosker and Ho (2015) recognized 18 *Ophichthus* species from Taiwan, which included two new species. In recent years, several authors continued to explore the eel diversity around Taiwan, which brought the total number of species in the genus to 22 (Hibino et al. 2019a, 2019b; Hibino 2019; Hibino and McCosker 2020; Ho et al. 2022).

During our survey, many different *Ophichthus* eels were collected from the fish landing ports, and two of them have been described recently (Hibino et al. 2019a; Ho et al. 2022). Three species in Taiwan, *Ophichthus aphotistos* McCosker & Chen, 2000, *Ophichthus macrochir* (Bleeker, 1852), and *Ophichthus obtusus* McCosker, Ide & Endo, 2012 have distinctly uniformly dark body. A fourth species with dark body, *Ophichthus kusanagi* Hibino, McCosker & Tashiro, 2019, was described from Japan and subsequently reported from the Dongsha Islands (Ho et al. 2022).

In this study, several unidentified dark body specimens were found in the collections collected from around Taiwan in recent years. These specimens do not match any other nominal species, but they are two distinct new species. Herein, we provide descriptions of these two new species that possess distinct characters.

Materials and methods

All methods for counts and measurements follow McCosker (2010). Measurements for total and tail lengths are taken by 300 or 600 mm rulers and others by digital calipers to the nearest 0.1 mm. Vertebral counts were made from radiograph films or digital radiograph photographs. Mean vertebral formula (**MVF)** is expressed as the average of predorsal, preanal, and total vertebrae, and vertebral formula (**VF**) is the solo number of each (Böhlke 1982). Terminology of head structures around lips (cf. protrusions) and head pore system follow Hibino et al. (2019b), and are abbreviated as **IO** (infraorbital pores), **SO** (supraorbital pores), **POM** (preoperculomandibular pores), and **ST** (supratemporal pores). Total and head lengths are abbreviated as **TL** and **HL**, respectively.

Specimens of types including new species were deposited at Pisces Collection of National Museum of Marine Biology & Aquarium, Pingtung, Taiwan (**NMMB-P**) and the National Taiwan Ocean University, Laboratory of Aquatic Ecology, Department of Aquaculture, Keelung, Taiwan (**TOU-AE**). Other materials were those deposited at the above and the National Zoological Museum of China, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (**ASIZB**), Fisheries Research Laboratory, Mie University, Tsu, Mie, Japan (**FRLM**), Kagoshima University Museum, Kagoshima, Japan (**KAUM**), and National Museum of Nature & Science, Tsukuba, Ibaraki, Japan (**NSMT**). The data provided in key to species include our materials and those used by Hibino et al. (2019b), as well as comparative data provided in McCosker and Ho (2015), Hibino et al. (2019a), and Vo et al. (2019).

The information for the key and materials examined is from specimens mostly larger than 300 mm TL. We estimate some characters, such as tooth arrangement and shape of protrusions, which may have ontogenetical changes; however, the meristic and pore counts can be used for all sizes. The key to species and Table 2 are based on Hibino (2019), Hibino et al. (2019a, 2019b), Hibino and McCosker (2020), Ho et al. (2022), Lee and Asano (1997), McCosker and Ho (2015), comparative materials, and a future publication prepared by Quang Van Vo.

Results

Family Ophichthidae
Genus *Ophichthus* Ahl, 1789

Ophichthus kbalanensis Hibino & Ho, sp. nov.
https://zoobank.org/3A13F9F3-BD1E-4AF5-B1A3-4BBD7D604634
Figs 1, 2; Tables 1, 2
English name: Kbalan's Snake Eel
Chinese name: 噶瑪蘭蛇鰻

Material examined. ***Holotype*:** NMMB-P26381, 414 mm TL, ca 24°54.0'N, 121°56.0'E, Da-xi, Yilan, northeastern Taiwan, northwestern Pacific Ocean, 1 Jul. 2017.

Diagnosis. A relatively short *Ophichthus* with the following combination of characters: head 10.3% TL; tail 62.7% TL; dorsal-fin origin above about middle of pectoral fin; tip of lower jaw anterior to anterior-nostril base; two simple, distally pointed protrusions along upper lip; SO 1 + 4; POM 6 or 7 + 3; teeth on jaws and vomer mostly uniserial but posterior ends of maxilla and anterior end of symphysis biserial; body dark; median fins with narrow dark margins, except the pale fin origins; 14 predorsal and 53 preanal lateral-line pores; VF 12-55-153.

Description. Counts and measurements are mostly shown in Tables 1, 2.

Body elongate, but relatively short, subcylindrical, its depth at gill opening 11.9 in head and trunk, 31.8 in TL (Fig. 1); tail more compressed, tapering slowly towards tip of tail, its length 1.6 in TL. Skin of body wrinkled; relatively strong wrinkles on snout, with numerous fine longitudinal wrinkles on remaining head and body.

Head moderate, 3.6 in head and trunk and 9.7 in TL; dorsal contour of head weakly curved above eye, occipital weakly convex; branchial basket slightly swollen, its maximum depth 2.9 in head. Snout tip relatively blunt and robust, moderate in length, 6.1 in HL and 0.4 in eye. Anterior nostril a simple tube opening anteroventrally; posterior nostril a hole at inner margin of upper lip, completely covered by a wide dermal flap. Eye relatively small, 2.4 in snout length. Mouth subterminal, tip of lower jaw anterior to anterior base of anterior nostril tube. Rictus well behind posterior margin of eye. Lips smooth without small papillae; two low, small, simple, thorn-shaped protrusions, their tips pointed. Interorbital region smooth, transverse contour rounded, convex. Gill openings located ventrolaterally, upper ends slightly above middle of pectoral fin.

Sensory pores on head (Fig. 2A) developed but very small, not obvious; SO 1 + 4, first one (ethmoid) on ventral surface of snout; IO 3 + 3, the first behind anterior nostril base, 2 below eye, and 3 arranged in a vertical row behind eye; POM 6 (left) or 7 (right) + 3, the 6 (or seventh on right side) below rictus; ST 3, single pore on mid-temporal; and single interorbital pore. Lateral-line nearly complete, end anterior to about 1/2 HL before tail tip; canal on branchial basket slightly arched, 10 on branchial basket before gill opening, 14 anterior to origin of dorsal fin, 53 anterior to anus, and total 138.

Teeth moderate, conical, pointed (Fig. 2B); teeth on maxilla mostly uniserial, ending with an additional row consisting of 5 teeth on inner side; dentary mostly uniserial but an additional row of small teeth in outer region of symphysis

Figure 1. *Ophichthus kbalanensis* sp. nov., NMMB-P26381, holotype, 414 mm TL, Da-xi, Taiwan **A** fresh condition **B** preserved condition. Arrows indicate positions of dorsal-fin origin (lefts) and anus (rights).

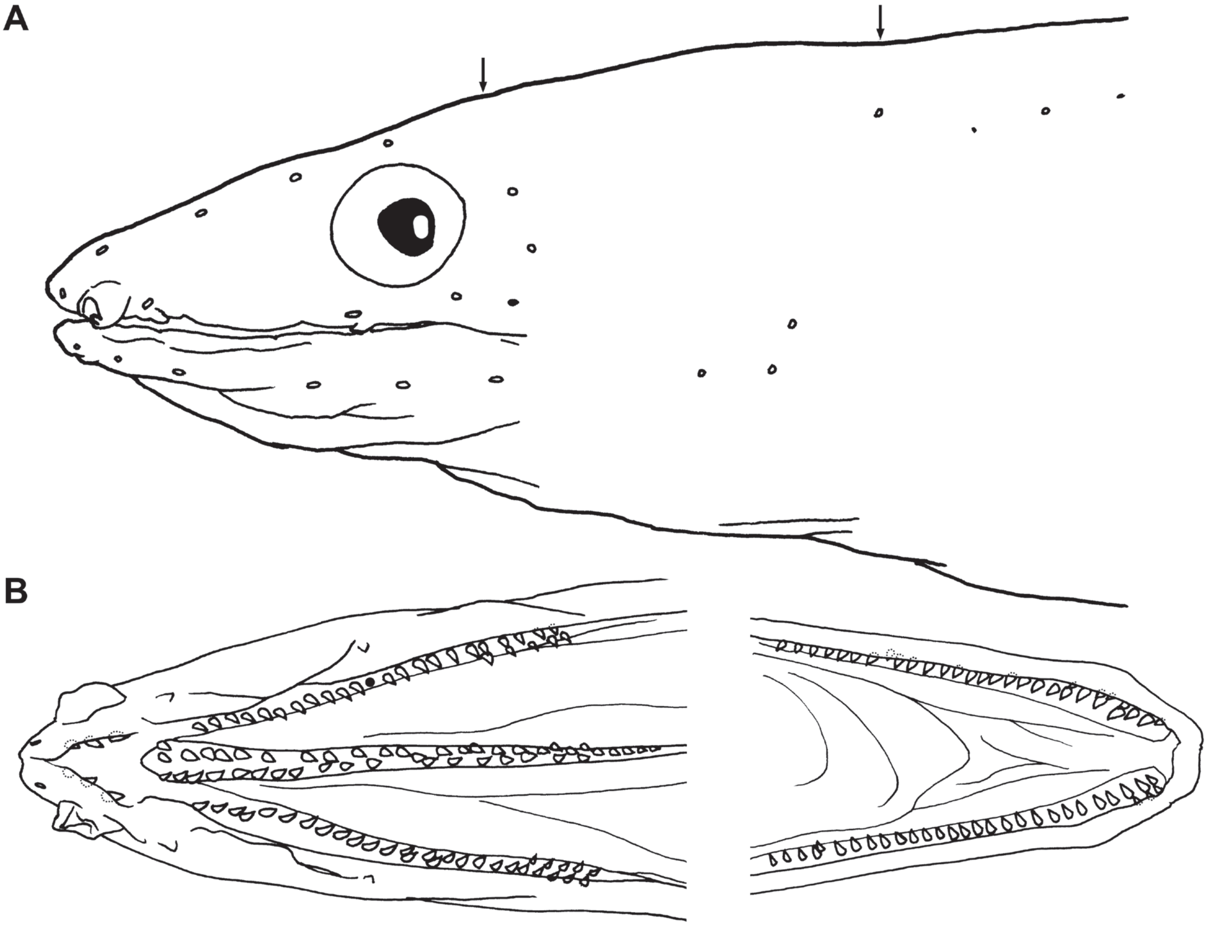

Figure 2. Line drawings of *O. kbalanensis* sp. nov., NMMB-P26381, holotype, 414 mm TL **A** sensory pores on head **B** teeth on upper (left) and lower jaws (right). Arrows indicate interorbital (left) and mid-temporal pores (right); black solid circle indicates holes of lost tooth; and broken lines indicate concealed teeth by fleshy lips.

anteriorly; vomerine biserial anteriorly and medially, uniserial at posterior end; 6 large teeth on intermaxillary, arranged as chevron-shape.

Dorsal and anal fins low, anal fin slightly higher than dorsal fin; both ending slightly anterior to tail tip. Dorsal-fin origin over about posterior third of pectoral fin. Pectoral fin tip weakly pointed, not lanceolate (somewhat damaged by trawl operation). Caudal fin absent, rear end of tail tip pointed.

Coloration. Freshly caught specimen has a somewhat purplish body, darker dorsally and paler ventrally; pectoral fin dark brown and anal fin with dark brown to black margin; tail tip relatively pale (Fig. 1A). Preserved condition in 50% isopropanol ethanol (Fig. 1B): head and body dark brown, abdomen slightly paler, densely covered with melanophores; branchial basket darker and blueish. Anterior nostril tube similar to body color; sensory pores not prominently margined. Mouth cavity dusky brown. Membrane of gill opening paler than body. Anterior portion of dorsal fin creamy white, gradually becoming dark brown similar in color to dorsal surface; narrow black margin along entire dorsal fin. Anterior portion of anal fin creamy white, gradually becoming dark brown on anterior one-third of its length, with black margin becoming broader posteriorly. Pectoral fin yellowish brown, gradually darkening posteriorly.

Table 1. Counts and measurements of two new *Ophichthus* from Taiwan.

	***O. kbalanensis* sp. nov.**	***O. multidentis* sp. nov.**				
	Holotype	**Holotype**	**Paratypes**			
	NMMB-P26381	**NMMB-P36205**	**TOU-AE 7802**	**TOU-AE 8998**	**TOU-AE 8999**	**TOU-AE 9294**
Total length (mm)	414	433	519	554	597	696
As % of TL						
Head length (HL)	10.3	8.1	8.0	8.2	8.8	8.5
Preanal length	37.3	41.2	41.5	43.2	43.2	42.9
Tail length	62.7	58.8	58.5	56.8	56.8	57.1
Predorsal length	12.6	16.5	15.1	16.1	17.4	18.0
Body depth at gill opening	3.1	2.2	2.7	2.4	2.7	3.3
Body width at gill opening	2.0	1.6	2.3	1.7	1.9	2.7
Body depth at mid-anus	2.5	2.1	2.9	2.3	3.0	2.9
Body width at mid-anus	2.4	2.1	2.8	2.4	2.6	3.0
As % of HL						
Snout length	16.4	20.6	20.1	21.2	18.8	20.9
Eye diameter	6.8	8.6	9.2	8.3	8.4	9.1
Upper-jaw length	27.9	28.6	28.1	29.5	29.8	28.3
Gill-opening length	9.2	11.1	8.2	9.4	9.7	11.3
Interorbital width	9.9	10.0	10.2	12.7	12.9	16.5
Isthmus width	15.0	16.0	22.8	13.8	16.9	28.2
Pectoral-fin length	27.9	26.0	24.2	29.8	29.5	24.6
Pectoral-fin base	12.0	11.7	9.7	9.6	10.8	10.1
Counts						
Predorsal vertebrae	13	24	23	23	25	26
Preanal vertebrae	55	62	64	66	65	65
Total vertebrae	153	163	162	163	164	162

Etymology. The specific name is derived from the type locality "Kbalan", an old name of Yilan region (Kat-má-lán in Taiwanese or Cabaran in Spanish) dated back to 1300–800 years ago. Kbalan means "people who live in the plain" in the Taiwanese aboriginal race Kebalan. The earliest record of Kbalan occurred in the occupation of the Spanish (~1632) which was replaced by the Dutch East India Company in 1642.

Comparison. The first distinctive character found in *Ophichthus kbalanensis* sp. nov. is the unique tooth arrangement. In most species of *Ophichthus* we examined, the tooth rows on jaws maintained the same number or reduced to fewer row(s) posteriorly. However, in the new species, there is a short additional row of teeth on posterior portion of upper jaw.

Secondly, the tip of lower jaw extends beyond anterior margin of base of anterior nostril tube is also quite distinct among *Ophichthus* species (Hibino pers. obs.). *Ophichthus ishiyamorum* McCosker, 2010 shares this character with *O. kbalanensis*, as well as the dorsal-fin origin above middle of the pectoral fin, and similar body

Table 2. Selected characters of *Ophichthus* species reported from Taiwan, except patterned species.

	SO	POM	Protrusion number	PALL	PDV	PAV	TV	TYPE V	Protrusion shape
O. aphotistos	1+4	6+2	0	59–61	16–19	57–61	157–162	18/59/161	Absent
O. apicalis	1+4	5 or 6+3	2	NO DATA	12–14	50–53	138–141	NO TYPE	Small, thorn-shape
O. asakusae	1+4	7-10+3	0 or 1	51–58	10–12	49–57	123–132	11/54/128	Robust hump shape, weak in smaller specimens
O. bicolor	1+4	6+2	0	63–67	15–23	61–66	155–163	19/65/160	Absent
O. kbalanensis sp. nov.	1+4	6 or 7+3	2	53	12	55	153	12/55/153	Simple thorn-shape
O. kusanagi	1+4	6+2	0	61–65	17–22	59–62	158–163	18/61/161	Absent
O. machidai	1+4	5 or 6+2 or 3	2	51–59	11–16	52–59	150–161	16/58/158	Simple thorn-shape
O. macrochir	1+4	4-6+2	2	68–73	11–12	67–71	207–221	11/70/221	Simple thorn-shape
O. megalops	1+4	6+3	0	59–64	28–35	59–63	157–168	29/60/160	Absent
O. multidentis sp. nov.	1+3	5+2	0	63	24	62	163	24/62/163	Absent
O. obtusus	1+4	4 or 5+3	2	57	11–19	52–57	148–159	12/57/151	Stout, with wrinkles in larger specimens
O. pratasensis	1+4	6+2	0	59–60	20	59	177	20/59/177	Absent
O. rotundus	1+3	5+2	2	65–66	14?	64?	178–184	14/64/182	Short, simple thorn-shape
O. sangjuensis	1+4	5 or 6+3	2	53	13–14	48–52	143–153	13/50/153	Simple thorn-shape
O. semilunatus	1+3	7+2	0	65	29	64	176	29/64/176	Absent
O. shaoi	1+4	6 or 7+3	1	69–72	10–13	68–72	155–168	12/68/155	Small, thorn-shape
O. urolophus	1+3 or 4	5-8+3	1	51–58	13–18	51–56	134–140	16/54/136	Robust hump shape, weak in smaller specimens
O. zophistius	1+4	5 or 6+3	2	59–64	11–13	61–63	177–184	12/62/181	Simple thorn-shape

coloration. However, *O. kbalaneisis* sp. nov. differs from *O. ishiyamorum* in having a smaller head (10.3% TL vs 14–15% TL), more vertebrae (153 vs 130–132), maxillary teeth mostly uniserial but ending in biserial (vs mostly uniserial and biserial anteriorly), and median fins with dark margined (vs pale) (McCosker 2010).

The tip of lower jaw is also before the anterior nostril tube in *Ophichthus alleni* McCosker, 2010, several specimens of *Ophichthus asakusae* Jordan & Snyder, 1901 and *Ophichthus urolophus* (Temminck & Schlegel, 1846); however, they have only one or no protrusions on upper lip, much fewer total vertebrae (131–133 in *O. alleni*, 126–132 in *O. asakusae* and 134–139 in *O. urolophus*), and a bicolored body with a mostly pale ventral surface (McCosker 2010; Hibino et al. 2019b; this study).

In Taiwan, *O. kbalanensis* sp. nov. is also similar to *O. obtusus* in the uniformly black body and vertebral count, but it can be distinguished by the different tooth arrangement on the jaws, more mandibular pores (6 or 7 vs 4 or 5), position of the end of the rictus (behind posterior margin of eye vs not behind), and two small, simple, thorn-like labial protrusions on the upper lip (vs at least anterior one fat, cauliflower-shaped protrusion with weak wrinkles) (McCosker et al. 2012; Chiu et al. 2013; this study).

Ophichthus multidentis **Hibino, Ho & Huang, sp. nov.**

https://zoobank.org/56CD9529-C140-4DCE-8691-59492233FB42
Figs 3, 4; Tables 1, 2
English name: Many-teeth Snake Eel
Chinese name: 多齒蛇鰻

Material examined. ***Holotype*****:** NMMB-P36205, 433 mm TL, ca 22°42.5'N, 120°10.8'E, off Ke-tzu-liao, Kaohsiung, southwestern Taiwan, northern South China Sea, 4 Sep. 2019, collected by H.-C, Ho. ***Paratypes*****:** Four specimens, all collected from Daxi fish landing port, 24°56.5'N, 121°54.0'E, northeastern Taiwan, southern East China Sea, collected by J.-F. Huang: TOU-AE 7802, 519 mm TL, 25 July 2020; TOU-AE 8998, 554 mm TL, TOU-AE 8999, 597 mm TL, 28 Nov. 2022; TOU-AE 9294, 696 mm TL, 9 Jan. 2023.

Diagnosis. An elongate *Ophichthus* with the following combination of characters: head 8.0–8.8% TL; tail 56.8–58.8% TL; dorsal-fin origin behind pectoral-fin tip by 3.0 times the pectoral fin length; no protrusions along upper lip; SO 1 + 3 ; POM 5 or 6 + 2; teeth on maxilla in 4 irregular rows or 5 rows anteriorly and 4 rows posteriorly, teeth on vomer in up to 4 rows, teeth on dentary in 4 rows anteriorly, 3 rows posteriorly; body uniformly dark with creamy white median fins; 22–26 predorsal and 63–65 preanal lateral-line pores; total vertebrae 162–164, MVF 24-64-163.

Description. Counts and measurements are mostly shown in Tables 1, 2.

Body elongate, slender (Fig. 3), cylindrical, its depth at gill opening 13.1–18.4 (18.4 in holotype) in head and trunk, 30.5–44.7 (44.7 in holotype) in TL; tail weakly compressed, tapering slowly toward tip, its length 1.7–1.8 (1.7 in holotype) in TL; skin of body nearly smooth, with numerous extremely small longitudinal wrinkles ventrolaterally.

Head small, 4.9–5.2 (5.1 in holotype) in head and trunk and 11.3–12.6 (12.4 in holotype) in TL; dorsal contour of head relatively linear above eye, occipital weakly convex; branchial basket moderately swollen, maximum depth 3.2 in head. Snout relatively acute but bulbous, relatively long, 4.7–5.3 (4.9 in holotype) in HL; a dermal groove ventrally on snout. Anterior nostril tubular, towards anteriorly; opening with moderately expanded flap anteriorly; posterior nostril a hole at inner margin of upper lip, completely covered by a wide but low dermal flap. Eye moderate in size, 1.7–2.6 (2.4 in holotype) times in snout length. Mouth inferior, tip of lower jaw below middle of anterior nostril tube base; rictus slightly behind posterior margin of eye. Lips without any sensory papillae and protrusions; inside along base on anterior nostril tube with several small low hump arranged as a row. Interorbital region smooth, gently convex. Gill openings located ventrolaterally, upper ends slightly below insertion of pectoral fin.

Sensory pores on head (Fig. 4A) developed but very small and not obvious; SO 1 + 3, first (ethmoid pore) on underside of snout tip and 3 along dorsal surface of snout, the last above upper margin of eye; IO 3 + 3, 1 pore behind base of anterior nostril, 2 below eye, and 3 arranged in a vertical row behind eye; POM 5 or 6 + 2 (6 in holotype), last pore behind rictus; ST 3, 1 on mid-temporal; single interorbital pore. Lateral line nearly complete, ending by about 1 HL before tail tip; canal on branchial basket weakly arched, 8 on branchial basket before gill opening, 22–26 anterior to origin of dorsal fin, 63–65 anterior to anus, and total 145–148 (8, 24, 63 and 145 in holotype).

Figure 3. *Ophichthus multidentis* sp. nov., NMMB-P36205, holotype, 433 mm TL, Ke-tzu-liao, Kaohsiung, Taiwan **A** fresh condition **B** preserved condition. Arrows indicate positions of dorsal-fin origin (lefts) and anus (rights).

Teeth numerous, conical, pointed but shape and size variable (Fig. 4B); multiserial teeth on maxilla and dentary, outermost rows slightly larger and more robust than others, innermost teeth slender and more recurved posteriorly. Those on maxilla in 4 irregular rows in holotype, but in larger specimens (TOU-AE 8999 and 9294) 5 rows anteriorly and 4 rows posteriorly; on dentary arranged in 4 rows anteriorly

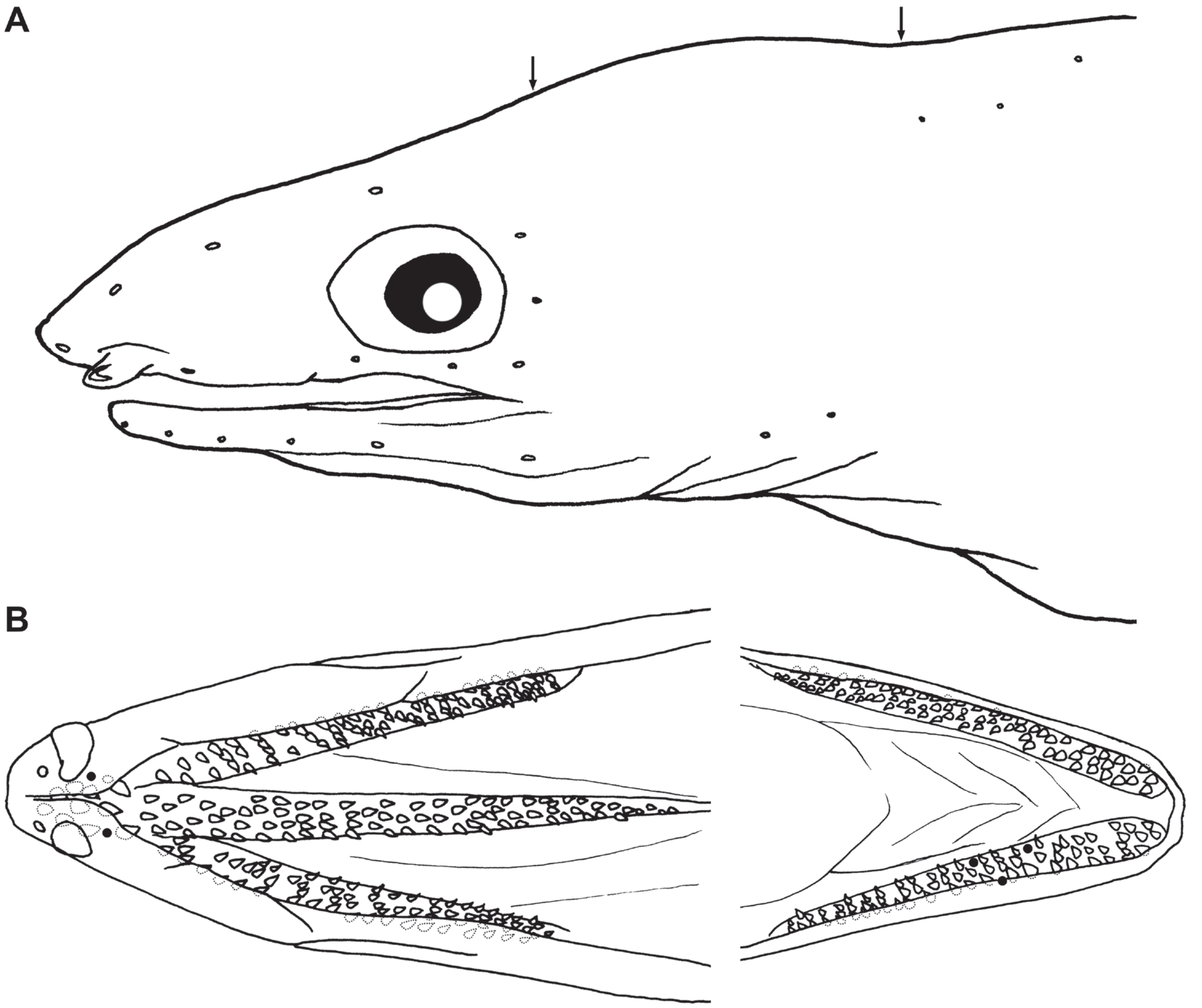

Figure 4. Line drawings of *O. multidentis* sp. nov., NMMB-P36205, holotype, 433 mm TL **A** sensory pores on head **B** teeth on upper (left) and lower jaws (right). Arrows indicate interorbital (left) and mid-temporal pores (right); black solid circles indicate holes of lost tooth; and broken lines indicate concealed teeth by fleshy lips.

and 3 rows posteriorly; on vomer moderate in size, becoming smaller posteriorly, 4 rows maximum and decreasing to single row posteriorly; 6 or 7 (6 in holotype) large and robust, close-set teeth on intermaxillary, mostly concealed by lips.

Dorsal and anal fins low; ending slightly before tail tip; dorsal-fin origin well behind pectoral-fin tip by 2.3–3.5 (2.8 in holotype) times the pectoral-fin length; pectoral-fin tip pointed but not lanceolate; caudal fin absent.

Coloration. Freshly caught specimen has a uniformly purplish to blackish brown body, pectoral fin dark gray, and dorsal and anal fins pale; tail tip pale (Fig. 4A). Preserved condition in 50% isopropanol ethanol (Fig. 3B): head and body dark brown except pale anus and tail tip; lips relatively darker than other skin; branchial basket and chest darker; anterior nostril tube same as body color; sensory pores not prominently margined; mouth cavity various, completely creamy white or dusky anteriorly, completely dusky on inside of lower jaw in three specimens; membrane of gill opening paler than body; head partly faded with some pale patches possibly imprinted by fishing net; dorsal and anal fins creamy white without melanophores; pectoral fin dark brown.

Etymology. The specific name is derived from the Latin *multi* (many) and *dentes* (teeth), referring to the diagnostic character of four tooth rows on jaws.

Comparison. The tooth pattern of *Ophichthus multidentis* sp. nov. is unique among the congeners. It is the only member of *Ophichthus* that possesses up to 5 rows of small teeth on jaws and vomer in the northwestern Pacific region.

Ophichthus multidentis sp. nov. is similar to a number of species that have the dorsal-fin origin situated behind the head by more than twice the pectoral-fin length (or predorsal length more than 1.5 times head length) and no blackened anal-fin base in advance of tail tip (Vo and Ho 2021: table 1; Ho et al. 2022). *Ophichthus multidentis* sp. nov. is most similar to *Ophichthus longicorpus* Vo & Ho, 2021 in having a uniformly dark body, dorsal-fin origin 3 times the pectoral-fin length behind the pectoral fin tip (cf. 3.4–5.7 times in *O. longicorpus*), but differs in having more tooth rows on jaws and vomer (at least 4 irregular rows on maxilla and vomer vs mainly 2 rows on jaws and 2 or 3 rows anteriorly and uniserial posteriorly on vomer), a longer tail (56.8–58.8% TL vs 50.0–52.9% TL), and different vertebral formula (MVF 24-64-163 vs 27-68-159).

Ophichthus multidentis sp. nov. is also similar to *O. aphotistos* and *O. kusanagi* in having a uniformly colored body, similar vertebral counts and proportions of head length, tail length, and body depth. It differs from these species in having more predorsal vertebrae (23–26 vs 16–20 in *O. aphotistos* and 17–22 in *O. kusanagi*), more numerous and smaller teeth on maxilla arranged irregularly in up to 5 rows (vs relatively few and large teeth, arranged in biserial or mostly biserial anteriorly) and fewer mandibular pores (5 or 6 vs 6) (Hibino et al. 2016; Hibino et al. 2019b; this study). We do not have the sufficient information of the molecular evidence of the new species with other congeners, while the partial sequence of *O. multidens* sp. nov. differs from *O. aphotistos* (S. Endo pers. comm.).

Key to species of *Ophichthus* from Taiwan, including the Dongsha Islands

1 Body coloration markedly spotted or with distinct blotches or saddles......**2**
– Body coloration uniform or darker dorsally, without distinct spots, blotches or saddles (rarely obscure distorted bars present dorsally)..................**6**
2 A dark brown or black saddle on posterior half of head; body brown, without spots or prominent saddles but with or without irregular markings present **3**
– Head without a broad dark dorsal saddle; distinct spots, blotches, or saddles on body...**4**
3 Body with irregular markings dorsally; median fins without broad white margin .... ***O. lithinus*** **(Jordan & Richardson, 1908)**
– Body pale, without markings; median fins dark brown with broad white margin .... ***O. cephalozona*** **Bleeker, 1864**
4 Body with 18–27 distinct black saddles, head with golden to brownish (in life) dark-margined marbling and spots; total vertebrae 156–164 ....***O. bonaparti*** **(Kaup, 1856)**
– Head and body without bars, with spots only; total vertebrae 141–155 ......**5**

5 Head and body overlain with numerous ocellated spots, those on body in 3 regular alternating rows, the spots separated by pale interspaces; total vertebrae141–148 .... ***O. polyophthalmus* Bleeker, 1864**

– Head and body overlain with numerous brown spots, those on body in 2–4 irregular rows, the spots about equal in size to their interspaces; total vertebrae 151–155 .... ***O. erabo* (Jordan & Snyder, 1901)**

6 Body extremely slender, depth at gill openings 1.6–2.3% TL **7**

– Body stout, moderate or relatively slender, depth at gill openings 2.4–4.2% TL **8**

7 Body black to dark brown; teeth on maxilla uniserial at least in anterior part; total vertebrae 207–221 .... ***O. macrochir* Bleeker, 1852**

– Body pale brown; teeth on maxilla completely biserial; total vertebrae 178–184 .... ***O. rotundus* Lee & Asano, 1997**

8 Dorsal-fin origin (DFO) equal or more than two pectoral-fin lengths behind gill openings **9**

– DFO in advance of, above, or behind gill openings by less than two (generally less than 1.5) pectoral-fin lengths **15**

9 Eyes large, more than 70% of snout length **10**

– Eyes small to moderately large, less than 70% of snout length **12**

10 Anal fin pale uniformly, without darkened base in advance of tail tip .... ***O. pratasensis* Ho, Ng & Lin, 2022**

– Anal fin pale but with darkened base in advance of tail tip **11**

11 SO 1+4, 3 preopercle pores; anterior tube mostly white; total vertebrae 157–168 .... ***O. megalops* Asano, 1987**

– SO 1+3, 2 preopercle pores; anterior tube brownish; total vertebrae 176 .... ***O. semilunatus* Hibino & Chiu, 2019**

12 Body pale brown, bicolored; tail 53–57% TL .... ***O. bicolor* McCosker & Ho, 2015**

– Body darker, uniformly dark brown or weakly pale on abdomen but with melanophores; tail 58–62% TL **13**

13 Teeth numerous, vomer maximum 4 rows, maxilla to 4 or 5 rows; 5 or 6 mandibular pores; median fins white .... ***O. multidentis* sp. nov.**

– Teeth moderate, vomer and maxilla maximum 2 rows; 6 mandibular pores; median fins dusky to dark brown **14**

14 DFO behind gill opening by less than two pectoral-fin lengths; HL 8.9–11% TL .... ***O. aphotistos* McCosker & Chen, 2000**

– DFO behind gill opening by more than three pectoral-fin lengths; HL 7.3–9.1% TL .... ***O. kusanagi* Hibino, McCosker & Tashiro, 2019**

15 DFO above or slightly behind level of gill openings; body with obscure distorted bars (both in life and preservation) but sometime faded; sensory pit black, conspicuous .... ***O. zophistius* (Jordan & Snyder, 1901)**

– DFO clearly behind level of gill openings; body without bars; sensory pit same as body color, not conspicuous **16**

16 Body pale to moderate, abdomen with or without scattered melanophores **17**

– Body uniformly dark or abdomen paler but completely covered by melanophores **22**

17 One low labial protrusion (or rarely absent); posterior nostril opening outside mouth **18**

– One or two thorn-shaped labial protrusions; posterior nostril opening inside mouth **19**

18 DFO before pectoral-fin tips; tip of tail stout, skin strongly wrinkled; head and body pale yellowish brown when fresh .... ***O. asakusae* Jordan & Snyder, 1901**

– DFO usually behind pectoral-fin tips; tip of tail rather slender, skin smooth; head and body yellowish or reddish brown when fresh .... ***O. urolophus* (Temminck & Schlegel, 1846)**

19 One labial protrusion; lateral-line pores before anus 69–72; tail 50–52% TL; 1 teeth row on vomer .... ***O. shaoi* McCosker & Ho, 2015**

– Two labial protrusions; lateral-line pores before anus 51–59; tail 53–67% TL; 2 or more teeth rows on vomer **20**

20 Preopercle pores with dark margin; dorsal fin with dark narrow margin; total vertebrae 138–141 .... ***O. apicalis* (Anonymous, 1830)**

– Preopercle pores not margined; dorsal fin without dark margin, except for the darker rear portion **21**

21 Tail 53–61% TL; preanal vertebrae 52–59; snout rather sharp .... ***O. machidai* McCosker, Ide & Endo, 2012**

– Tail 61–67% TL; preanal vertebrae 48–52; snout rather swollen .... ***O. sangjuensis* (Ji & Kim, 2011)**

22 Lower-jaw tip anterior to base of anterior nostril tube; 6 or 7 mandibular pores; tooth rows on maxilla with a short additional row posteriorly .... ***O. kbalanensis* sp. nov.**

– Lower-jaw tip below about middle of base of anterior-nostril tube; 4 or 5 mandibular pores; tooth rows on maxilla without a short additional row posteriorly .... ***O. obtusus* McCosker, Ide & Endo, 2012**

Discussion

Diversity of the genus *Ophichthus* in Taiwan

There is confusion surrounding some records of *Ophichthus* species in Taiwan, probably due to the close similarity and presence of many unknown species. A total of 23 species were included in the key to species of Taiwan above, although we expect more species come out in the near future. The species composition largely overlaps with that of Japanese waters, except some rare species in each country.

Some changes were made among the previously recorded species. For example, *Ophichthus fasciatus* Ju, Wu & Jin, 1981 has been synonymized under *Ophichthus zophistius* (Jordan & Snyder, 1901) by Hibino and McCosker (2020). The records of the narrowly distributed species *Ophichthus altipennis* (Kaup, 1856) from Taiwan (Ho et al. 2015; McCosker and Ho 2015) are reidentified as *O. zophistius* by Y.H. *Ophichthys stenopterus* Cope, 1871 was synonymized under *Ophichthus pallens* (Richardson, 1848) by Hibino et al. (2019b). *Ophichthus pallens* was originally described based on a specimen collected by John

Reeves from China, but no precise locality was provided. No confirmed voucher of *O. pallens* can be found from Taiwan (incl. John E. McCosker pers. com.), and it is excluded here from the Taiwanese fauna.

Ophichthus retrodorsalis Liu, Tang & Zhang, 2010 was described from the Taiwan Strait. Although it was originally placed in *Ophichthus*, we exclude it from this work and tentatively include it in *Pisodonophis*, based on H.C.H.'s examination of the holotype and an additional specimen collected from Ke-tzu-liao (NMMB-P28996, 622 mm TL). Both specimens have all jaw and vomer teeth blunt, molariform or granular and are closely similar to *Pisodonophis boro*. Future studies may prove that both species are synonymous.

We keep *Ophichthus apicalis* (Anonymous, 1830) in the *Ophichthus* fauna of Taiwan. However, no voucher specimen has been recognized from Taiwanese waters (Hibino pers. obs.). The species was originally described from Sumatra, Indonesia, and recorded as widespread in the Indo-West Pacific. However, the true *O. apicalis* has not been well defined, and its taxonomic status is still uncertain (Hibino pers. data). We tentatively keep *O. apicalis* in the key, with the data taken from specimens collected from Vietnam and Thailand, South China Sea (see comparative materials).

Hibino (2019) reported newly collected specimens of *Ophichthus rotundus* Lee & Asano, 1997 and *Ophichthus sangjuensis* (Ji & Kim, 2011) from Taiwanese waters. The former is based on an old specimen collected from southwestern Taiwan in 1965. Many specimens of *O. sangjuensis* were also found in the collection, and some of them were previously misidentified as *Ophichthus machidai* McCosker, Ide & Endo, 2012. The vomerine tooth arrangement for *Ophichthus machidai* was formerly defined as biserial centrally and uniserial anteriorly and posteriorly (McCosker et al. 2012); however, we found that there is some variability in this character, some individuals have biserial or triserial tooth bands on vomer.

Among the Taiwanese species, *O. urolophus* is the most common and abundant and was collected from continental shelf and upper continental slope to depths of about 400 m. Despite few species being common inhabitants in coral reef areas, *O. asakusae*, *Ophichthus erabo* (Jordan & Snyder, 1901), *O. machidai*, and *O. sangjuensis* are also commonly seen in the bycatches of bottom trawlers, especially in the shallow waters of the west coast of Taiwan. Conversely, *O. lithinus* (Jordan & Richardson, 1908) is quite common in the catches of small set nets or fyke nets set up in mouths of rivers of southwestern Taiwan. Other species are either uncommon, rare, or rarely seen in the bycatches of fish landing grounds.

Comparative materials

Ophichthus apicalis: FRLM 49738, 412 mm TL, FRLM 51386, 425 mm TL, FRLM 51388, 434 mm TL, FRLM 51390, 502 mm TL, FRLM 51391, 477 mm TL, Ha Long Bay, Vietnam; NSMT-P 104757, 361–380 mm TL (2), fish market at Songkhla, Thailand. *Ophichthus machidai*: KAUM–I. 113140, 363 mm TL, NMMB-P23329, 435 mm TL, NMMB-P23330, 414 mm TL, NMMB-P23333, 443 mm TL, NMMB-P23334, 407 mm TL, NMMB-P27925, 456 mm TL, NMMB-P28997, 504 mm TL, Ke-tzu-liao, Kaohsiung, Taiwan. *Ophichthus obtusus*: NMMB-P16467, 438 mm TL, NMMB-P21764, 387 mm TL, Dong-gang, Taiwan. *Ophichthus rotundus*: NMMB-P05312, 475 mm TL, Shao-liu-qiu, Taiwan. *Ophichthus sangjuensis*: NMMB-P23331, 468 mm TL, NMMB-P23332, 473 mm TL, NMMB-P28998, 316 mm TL, Ke-tzu-liao, Kaohsiung, Taiwan. *Pisodonophis retrodorsalis*: ASIZB [now NZMC] 50929, 517 mm TL, Taiwan Strait, Fujian, China; NMMB-P28996, 622 mm TL, Ke-tzu-liao, Kaohsiung, Taiwan.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Data curation: YH. Funding acquisition: HCH, YH. Investigation: JFH. Project administration: HCH. Resources: HCH. Writing – original draft: YH. Writing – review and editing: YH, HCH, JFH.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Verification of two barracudina species *Lestrolepis japonica* (Tanaka, 1908) and *L. philippina* (Fowler, 1934) (Aulopiformes, Paralepididae)

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Abstract

Examination of the type series of *Lestidium japonica* Tanaka reveals that the generally accepted concept of this species does not accord with the type series. A historical review of the literature showed that the characterization of *L. japonica* changed over time, and what has been recognized as "*L. japonica*" for more than 70 years actually represents a distinct and different species. Among the junior synonyms of "*L. japonica*", *Paralepis philippinus* Fowler, 1934 is resurrected as a valid species herein in a new combination, *Lestrolepis philippina*. *Lestrolepis nigroventralis* Ho, Tsai & Li is recognized as a junior synonym of *L. japonica* herein. Revised diagnostic characteristics for both *L. japonica* and *L. philippina* are provided, along with comments on related names to verify their nomenclatural status.

Key words: Biodiversity, ichthyology, ICZN, nomenclature, taxonomy

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Introduction

Naked barracudinas, often classified as the Lestidiini, Lestidiinae, or sometimes Lestidiidae, are a group of small, slender fishes found worldwide from the surface to the deep sea. This group comprises seven genera with approximately 60 species, although some remain problematic (Ho et al. 2019a, 2019b; Ho pers. data). Among the genera, *Lestrolepis* can be distinguished from all others by having a small light organ (black dot) in front of the orbital margin and a ventral light organ divided into two branches, which are located inside the belly but visible through the translucent muscle. The genus *Lestrolepis* had few nominal species until recently when Ho and Golani (2019) and Ho et al. (2019a) reviewed and described several new species.

The taxonomic history of *Lestrolepis* is complex and somewhat confusing, even more so as the author, Robert Rees Harry (Harry 1953a, 1953b), later published under the name Robert R. Rofen (Rofen 1960, 1966). Three species have been commonly recognized in the previous literature, namely

Lestrolepis japonica (Tanaka, 1908), *Lestrolepis intermedia* (Poey, 1868), and *Lestrolepis luetkeni* (Ege, 1933). However, Ho and Golani (2019) suggested that *L. luetkeni* belongs to *Lestidiops* and resurrected *Lestrolepis pofi* (Harry, 1953a), a name previously considered a junior synonym, as a valid name for the fish formerly referred to as *L. luetkeni*. Furthermore, Ho et al. (2019a) proposed that *L. intermedia* is restricted to the Atlantic Ocean and designated the western Pacific population as a new species, *Lestrolepis nigroventralis* Ho, Tsai & Li, 2019.

Recently, the second author (TK) examined specimens deposited in the fish collection of Hokkaido University and identified inconsistencies between the original description and the specimens currently recognized as *L. japonica*. Examination of the holotype (Fig. 1) and paratype of *L. japonica* showed them to be indistinguishable from *L. nigroventralis*, suggesting that the latter should be regarded as a synonym of *L. japonica* and that the species previously generally referred to as "*L. japonica*" requires a new name. The first author (HH) examined the type series of *Paralepis philippinus* (Fig. 2), previously regarded as a junior synonym of *L. japonica*, and found them to be identical to what was commonly recognized as *L. japonica* in the western Pacific Ocean. Additionally, several other names were implicated in the synonymy or misidentifications under these names (Table 1).

To clarify the identification of these species, we conducted a study on the type series of *Lestrolepis japonica* and *L. philippinna* and provide here revised diagnoses or comments for the species related to these names. In the present study we confirm the validity of *L. japonica*, synonymize *L. nigroventralis* with *L. japonica*, resurrect *L. philippina*, and clarify the taxonomic history of these species.

Materials and methods

Methods for taking morphometrics and meristics followed Ho et al. (2019a). Most morphometric and meristic data are adopted from Ho et al. (2019a), with those of additional specimens examined.

Abbreviations

SL, standard length; **HL**, head length; **TL**, total length; **VFO, DFO, AFL**, the origins of pelvic fin, dorsal fin and anal fin, respectively; **V–D**, space between VFO and DFO; **V–A**, space between VFO and AFO. Other abbreviations followed Ho and Lin (2023).

Results

Genus *Lestrolepis* Harry, 1953

On the taxonomic issues

Lestidium japonicum was described based on two types collected from Sagami Bay (ZMUT 2013 and 2014). In the synonymy of this species, Harry (1953a) included *Paralepis bellottii* Ege, 1933 as a queried synonym and *Paralepis philippinus* Fowler, 1934 as a junior synonym of *L. japonicum*. Subsequently, Harry (1953b) re-assigned *japonicum* to *Lestrolepis*, and this placement in *Lestrolepis* has been widely accepted by subsequent authors.

Post (1972) suggested that *L. japonica* "possibly is a synonym of *Lestrolepis intermedia* Poey, 1868". Examination of the holotype of *L. japonica* revealed that it is indeed similar to *L. intermedia* but that it differs in several characters. Consequently, specimens recognized as "*Lestrolepis japonica*" in much of the literature belong to another species that requires a name, and the following two names listed as synonyms of "*japonicum*" by Harry (1953a) should be considered as candidates for this species.

The original description of *Paralepis bellottii* was based on a single specimen (60 mm SL, 64 mm TL). This species was synonymized with *Lestidium nudum* Gilbert, 1905 and *Paraelpis luetkeni* Ege, 1933 by Ege (1953:52). Rofen (1960: 206) synonymized the name with "*Lestidium leutkeni*" and Rofen (1966) later placed it in the genus *Lestrolepis*. The first author examined the holotype of *bellottii* and found it to be very similar to the holotype of *luetkeni*. Type specimens of both are also different from *Lestidium nudum*, rejecting the synonymy proposed by Ege (1953). In fact, *luetkeni* is placed in the genus *Lestidiops* by Ho and Golani (2019), and the status of *bellottii* will be discussed in another work prepared by HH.

The original description of *Paralepis philippinus* was based on eight type specimens collected from the Philippines. Examination of the type series revealed that it is different from that of *L. japonica* and is what has been commonly recognized as "*L. japonica*" in the western Pacific Ocean.

Consequently, neither *philippinus* nor *leutkeni* or *bellottii*, can be regarded as synonyms of *japonica*, but can be considered here to represent what has been called "*L. japonica*" in the western Pacific (Table 1). The oldest name, *philippina* is herein resurrected as valid in a new combination *Lestrolepis philippina* (Fowler, 1934) for this species.

Ho et al. (2019a) described *Lestrolepis nigroventralis* to accommodate the population of what has been called "*Lestrolepis intermedia*" in the western Pacific Ocean, i.e. Japan, Korea, and Taiwan, etc. As the type series is the same as that of *L. japonica* (Table 1), this name is now recognized as a junior synonym of *L. japonica*. In addition, the specimens recognized as *L. japonica* by Ho et al. (2019a) are now re-identified as *L. philippina*.

Records of *Lestrolepis japonica* and *L. intermedia* in the western Pacific

As mentioned above, Harry (1953a) mistakenly considered *Lestrolepis philippina* as a junior synonym of *L. japonica* without examining the vertebral counts of the type series of *L. japonica*. This oversight led to a change in the definition of *L. japonica* based on the type series of *L. philippina*, resulting in subsequent effects. For instance, Rofen (1966: 381) differentiated *L. intermedia* from *L. japonica* based on different vertebral numbers (91–98, vs 84–89), indicating that his *L. japonica* was actually *L. philippina*. Subsequent literature records of *L. japonica* following Harry's definition recognized those with fewer vertebrae as *L. japonica* (see synonymy below).

The earliest records of *Lestrolepis intermedia* in the Western Pacific Ocean are found in Ege (1953), who documented juveniles of *L. intermedia* collected from various locations worldwide, including Japan, Taiwan, and the Philippines (also see Rofen 1966). However, subsequent publications in the western Pacific Ocean (e.g., Matsubara 1955) did not evidently document this name.

Table 1. Verification of some name records of *Lestrolepis* and their current status.

Publication	Name used	Correct names
Poey 1868	*Paralepis intermedius*	Valid as *Lestrolepis intermedia*
Tanaka 1908	*Lestidium japonicum*	Valid as *Lestrolepis japonica*
Ege 1933	*Paralepis luetkeni*	Valid as *Lestidiops luetkeni*
Ege 1933	*Paralepis bellottii*	Synonym of *Lestidiops luetkeni*
Fowler 1934	*Paralepis philippinus*	Valid as *L. philippina*
Fowler 1944	*Sudis vanderbilti*	Synonym of *L. intermedia*
Harry 1953a	*Lestidium japonicum*	*L. philippina*
Ege 1953	*Lestidium intermedium* (in part)	*L. japonica*
Kamohara 1955	*Lestidium japonicum*	*L. japonica*
Rofen 1966	*Lestrolepis japonica*	*L. philippina*
Fujii 1984	*Lestrolepis japonica*	*L. philippina*
Fujii 1984	*Lestrolepis intermedia*	*L. japonica*
Nakabo 2000, 2002	*Lestrolepis japonica*	*L. philippina*
Kim et al. 2007, 2020	*Lestrolepis japonica*	*L. philippina*
Ho et al. 2019a	*Lestrolepis nigroventralis*	Synonym of *L. japonica*
Ho et al. 2019a	*Lestrolepis japonica*	*L. philippina*

Fujii in Masuda et al. (1984:77) provided a brief description of *Lestrolepis intermedia* and mentioned that "*L. intermedia* and *L. japonica* are often collected by shrimp-trawl net in Suruga Bay". Fujii also provided total vertebrae counts of 95–97 and total lateral-line scales of 74–81 for his *L. intermedia*, and 84–87 and 62–69, respectively, for his *L. japonica*. These definitions for both species evidently were followed by all subsequent publications in Japan and nearby areas (e.g., Nakabo 1993, 2000, 2002; Shen et al. 1993, Kim et al. 2007), while Ho et al. (2019a) went further and mistakenly recognized the western Pacific population of *L. intermedia* as a new species, *L. nigroventralis*.

Lestrolepis japonica **(Tanaka, 1908)**

Figs 1, 3, Table 2

Lestidium japonicum Tanaka, 1908:27 (type locality: Sagami Sea, Japan); Jordan et al. 1913: 50 (Sagami Sea, Japan; list); Okada and Matsubara 1938: 61 (Sagami Sea, Japan; key); Matsubara 1941: 8 (in part: Japan); Matsubara 1955: 262 (in part: Sagami Sea, Wakayama and Mie, Suruga Bay, Japan; key); Matsubara 1963: 262 (in part: Sagami Sea, Wakayama and Mie, Suruga Bay, Japan; key).

Lestrolepis intermedia (non Poey, 1868): Fujii in Masuda et al. 1984:77 (Japan; short description); Chen and Yu 1986:324 (Taiwan; synopsis); Nakabo 1993:319 (Japan, picture key); Shinohara et al. 1996:164 (Honshu; list); Nakabo 2000:371 (Japan, picture key); Nakabo 2002:371 (Japan, picture key); Shinohara et al. 2005:409 (Ryukus Is.; list); Kim et al. 2007:63 (Korea; new record); Ikeda and Nakabo 2015: 312 (Japan; short description).

Lestrolepis nigroventralis Ho, Tsai & Li, 2019:123 (type locality: off Dong-gang, Pingtung, southwestern Taiwan).

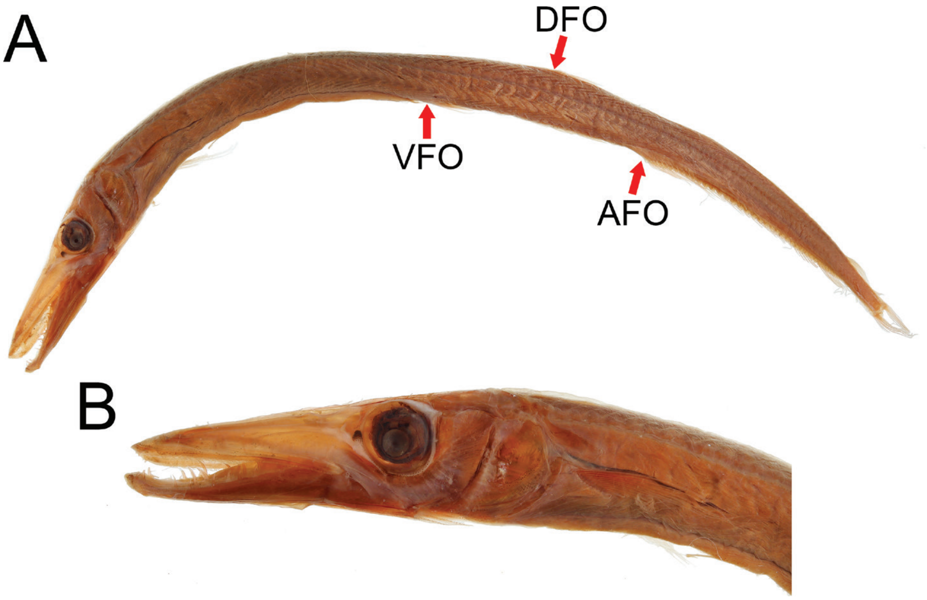

Figure 1. Holotype of *Lestidiun japonicum* Tanaka, 1908 **A** lateral view; arrows point to origins of dorsal fin (DFO), pelvic fin (VFO), and anal fin (AFO) **B** lateral view of head.

Status of the holotype. Tanaka (1908) indicated that the holotype of his *Lestidium japonicum* was registered as 2013 (now ZMUT 2013) with a length of 174 mm SL, and the paratype (in the Table, without a catalog number) was 190 mm SL. Regardless, Harry (1953a) gave the holotype as ZMUT 2014, and the paratype as ZMUT 2013. Notwithstanding, Post (1972) documented the types and recognized ZMUT 2013 as the holotype and ZMUT 2014 as the paratype. We examined both types and re-measured the holotype (ZMUT 2013) as 159.5 mm SL and the paratype (ZMUT 2014) as approximately 180 mm SL, the latter being in poor condition.

Synonym name. *Lestrolepis nigroventralis* was described to accommodate the Pacific population of *L. intermedia*. However, because of its nearly identical morphology (Table 2), it is now recognized here as a junior synonym of *L. japonica*. The following data are mainly derived from types and non-types of *L. nigroventralis*, combined with the type series examined by us.

Distinguishing features. A species of *Lestrolepis* with DFO situated at about midline of V–A, V–D 46.8–55.0% of V–A; anal-fin rays 41–43 (mainly 41–42); lateral-line scales: PVLL 33–36 (34–35), PDLL 43–46 (44–46), PALL 53–57 (55–56), TLL 75–81 (77–80); vertebral counts: PHV 32–35 (mainly 32–34), PVV 33–35 (34–35), PDV 43–46 (44–45), PAV 53–57 (54–55), CV 60–66 (61–64), TV 94–98 (94–97); vertebrae between DFO and VFO 9–11. Body slender, body depth at pectoral-fin base 15–19 times in SL; band of melanophores along abdominal margin. Attains 249 mm SL.

Distribution. Known from the northwestern Pacific Ocean off Japan, Taiwan, and Korea. Records from other localities require verification.

Remarks. The taxonomic concept of what has long been called *Lestrolepis japonica* is now revised based on the type series and additional specimens. A review of the literature with documentation of *L. japonica* is listed in the synonymy above, although there might be more records that are not included therein. Detailed comparisons with congeners are provided in Ho et al. (2019a, as *L. nigroventralis*).

Table 2. Selected morphological and meristic data of *L. japonica* and *L. philippina*. * Data of "*L. nigroventralis*" and ** of "*L. japonica*" taken from Ho et al. (2019a). HT = holotype; PT = paratype(s).

	L. japonica				***L. philippina***		
	Types		**Types of *L. nigroventralis***		**Types**		**Non-types****
	HT	**PT**	**HT**	**Types***	**HT**	**PT**	
SL (mm)	159.5	ca 180	230	180–249 (*n* = 11)	118.2	109.6–128.0 (*n* = 4)	88.0–222 (*n* = 29)
Proportion (%)				Mean (Range)			Mean (Range)
HL/SL	20.9	21.1	20.0	19.6 (18.9–20.7)	20.8	21.3–22.0	20.5 (18.0–21.8)
BD/SL	5.7	5.2	5.3	5.2 (4.9–5.6)	8.5	7.1–7.9	6.9 (5.9–8.6)
PreD/SL	63.7	–	62.8	62.7 (61.7–63.3)	58.8	59.4–60.9	61.8 (60.2–63.5)
PreV/SL	52.7	–	52.1	51.6 (50.6–52.6)	51.2	51.6–53.4	53.0 (52.3–55.2)
PreA/SL	73.3	–	73.5	73.3 (71.9–74.8)	72.8	73.0–75.2	74.9 (75.8–76.6)
ED/HL	20.1	17.9	15.5	16.1 (14.8–17.3)	19.1	18.1–19.1	18.4 (15.9–22.6)
SN/HL	54.7	53.8	52.4	54.4 (52.4–57.0)	52.8	49.8–52.8	50.8 (47.7–53.4)
HD/HL	27.1	24.8	26.3	26.4 (25.4–27.4)	30.9	27.8–30.8	28.5 (28.6–28.5)
UJ/HL	51.4	49.6	49.1	49.0 (47.2–50.4)	47.6	47.7–49.5	46.8 (44.0–50.0)
V–D/V–A	53.1	51.0	50.0	51.0 (47.6–55.0)	35.3	34.0–36.1	39.1 (32.5–43.1)
Meristics							
Anal-fin rays	42	ca 40	42	41–43	ca 38	37–38	36–40
Vertebrae							
PHV	34	33	33	32–35	29	30–31	29–32
PVV	33	34	34	33–35	30	30–32	30–33
PDV	43	44	44	43–46	38	38–39	36–40
PAV	53	55	55	53–57	48	49–51	48–51
CV	60	61	62	60–66	55	56–59	52–58
TV	94	95	95	94–98	85	86–89	84–88
V–D	9	10	10	9–11	8	7–8	5–9
Lateral-line scales							
PVLL	34	–	34	33–36	30	30–32	31–32
PDLL	44	–	44	43–46	38	39–40	38–40
PALL	54	–	54	53–57	49	49–51	49–50
TLL	ca 81	–	78	75–81	71	68–70	65–72

There are some minor differences found in the types compared to the non-types (Table 2). The head length is slightly larger (20.9–21.1%, vs 18.9–20.7% SL); the predorsal length is slightly larger in the holotype (63.7%, vs 61.7–63.3% SL; not available for the paratype); the eye diameter is slightly larger (17.9–20.1%, vs 14.8–17.3% HL); the upper jaw of the holotype is slightly longer (51.4%, vs 47.2–50.4% HL). These proportional measurements may be attributed either to population variation or due to long-term preservation of the types. The meristic values of types fall entirely within the range of non-types (Table 2).

Lestrolepis philippina **Fowler, 1934**

Figs 2, 4, Table 2

Paralepis philippinus Fowler, 1934: 281, fig. 42 (type locality: Varadero Harbor, Philippines).

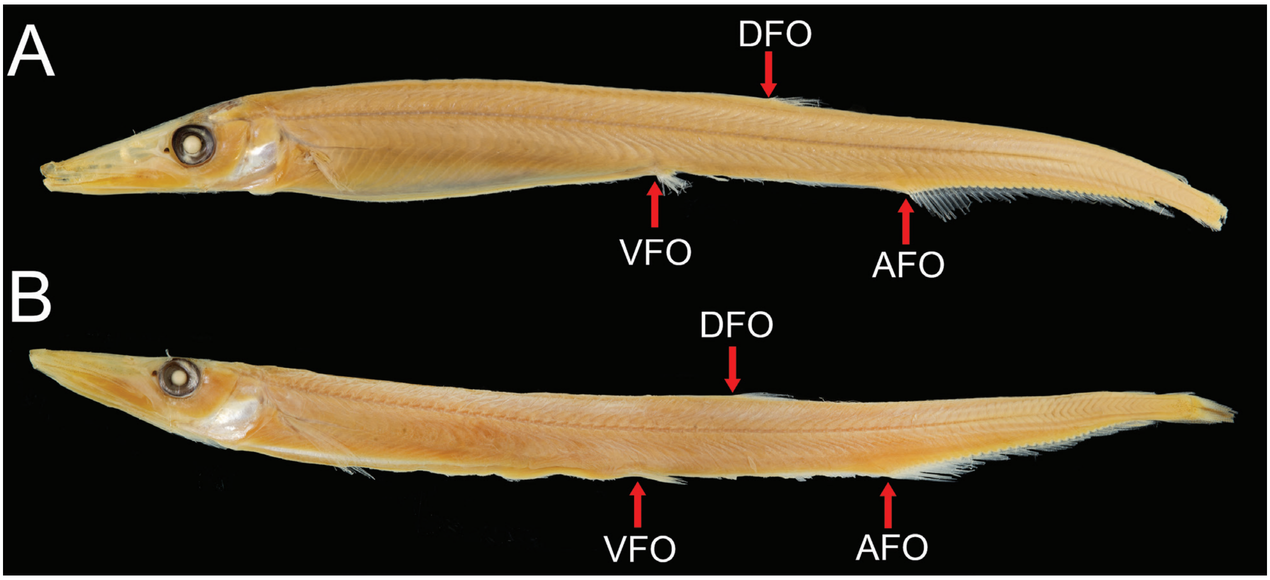

Figure 2. Types of *Paralepis philippinus* (= *Lestrolepis philippina*) **A** holotype, USNM 92323, ca 118 mm SL **B** paratype, USNM 93414, 126 mm SL; arrows point to origins of dorsal fin (DFO), pelvic fin (VFO), and anal fin (AFO).

Lestidium japonicum (not of Tanaka): Matsubara 1941: 8 (in part: Japan); Matsubara 1955: 262 (in part: Sagami Sea, Wakayama and Mie, Suruga Bay, Japan; key); Matsubara 1963: 262 (in part: Sagami Sea, Wakayama and Mie, Suruga Bay, Japan; key).

Lestrolepis japonica (not of Tanaka): Fujii in Masuda et al. 1984:77 (Japan; short description); Nakabo 2000:371 (Japan; picture key); Paxton in Randall and Lim 2000:592; Nakabo 2002:371 (Japan; key); Shinohara et al. 2005:409 (Honshu; list); Kim et al. 2007:64 (Korea; new record); Ikeda and Nakabo 2015: 312 (Japan; short description); Motomura et al. 2017:51; Ho and Golani 2019:578 (mentioned); Ho et al. 2019a:127 (Taiwan and Japan; description); Kim et al. 2020:67; Misawa et al. 2020:273.

Taxonomy. Fowler (1934) originally described *Lestrolepis philippina* from the Philippines. Subsequently, Harry (1953a) synonymized *L. philippina* with *L. japonica*, providing a description based on the type series of *L. japonica*, *L. philippina*, and additional specimens. Although the name *L. philippina* was not mentioned in subsequent literature, it is likely that many records recognized as *L. japonica* are, in fact, misidentifications of *L. philippina*. In a more recent study, Ho et al. (2019a) presented a detailed description of what was previously identified as *L. japonica*, now re-identified as *L. philippina*.

Distinguished features. A species of *Lestrolepis* with DFO situated well before midline of V–A, V–D 32.5–43.1% of V–A; anal-fin rays 36–40 (mainly 37–39); lateral-line scales: PVLL 30–32 (31), PDLL 38–40 (38–39), PALL 49–51, TLL 65–72 (65–68); vertebral counts: PHV 29–32, PVV 30–33 (30–32), PDV 36–40 (37–40), PAV 48–51, CV 52–58 (54–57), TV 82–88 (84–88); vertebrae between DFO and VFO 5–9 (7–8). Body moderately slender, body depth at pectoral-fin base 13–16 times in SL; narrow band of melanophores along abdominal margin. Attains 222 mm SL.

Distribution. Widespread in the western Pacific Ocean, with confirmed records from Japan, Taiwan, the Philippines, northwestern Australia, and the South China Sea.

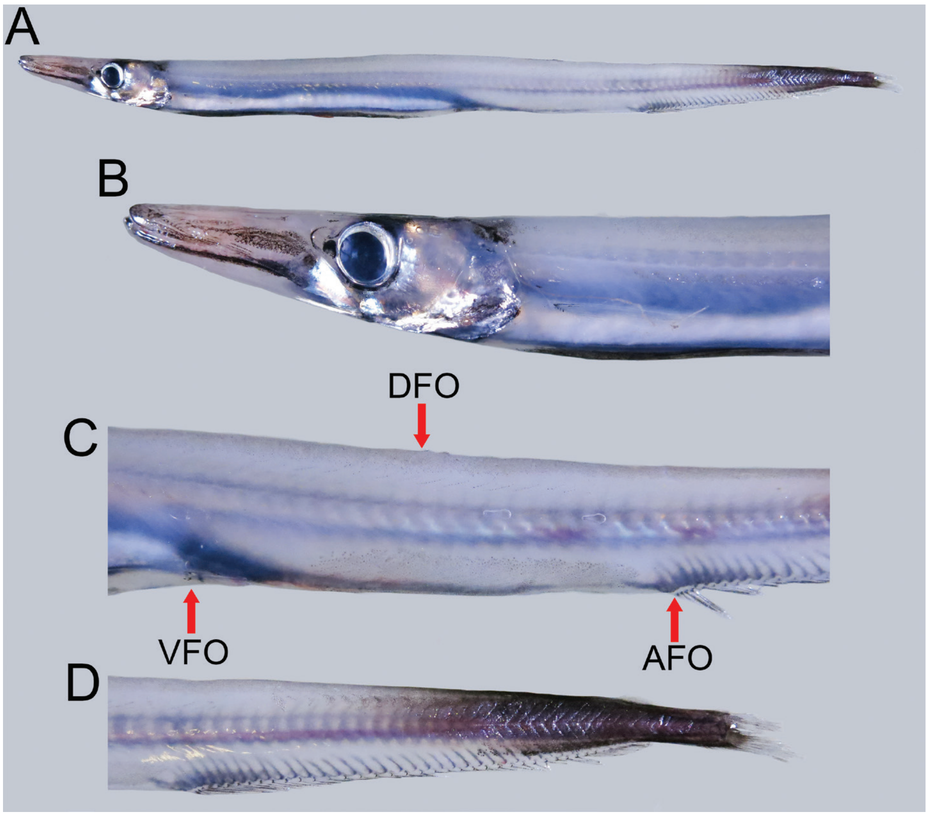

Figure 3. Fresh condition of *Lestrolepis japonica* (Tanaka, 1908), NMMB-P027930, 244 mm SL **A** lateral view **B** lateral view of head **C** lateral view of body showing origin of dorsal fin (DFO), pelvic fin (VFO), and anal fin (AFO) **D** lateral view of caudal region.

Remarks. Some minor differences are observed between the holotype and non-types (Table 2). The predorsal length (58.8%, vs 60.2–63.5% SL), preventral length (51.2%, vs 52.3–55.2% SL), and preanal length (72.8%, vs 75.8–76.6% SL) are slightly smaller in the holotype compared to paratypes and non-types. The head depth is slightly larger (30.9% SL) compared to that of paratypes and non-types (27.8–30.8% SL). These differences may be attributed to individual variation or long-term preservation effects. The meristic values of the type series fall well within those of the non-types (Table 2).

Discussion

Several ambiguities in earlier studies have led to subsequent problems, including the inadvertent naming of a new species. Tanaka (1908) described *Lestidium japonicum* with 42 anal-fin rays in the holotype and 49 in the paratype. Harry (1953a) counted 42 and 41, respectively, for the same individual (note that Harry switched the holotype and paratype). Jordan et al. (1913) and Okada and Matsubara (1938) included *Lestidium japonicum* in their species list as known from Sagami Sea. On the other hand, Hubbs (1916) cited Tanaka (1908) and gave 42–49 anal rays. Parr (1928) noted that *Lestidium japponicum* [sic] is only known from the coast of Japan.

Matsubara (1941) reported two specimens (178.8 mm SL and 102.2 mm SL) of this species collected from Suruga Bay, Japan, the former specimen having

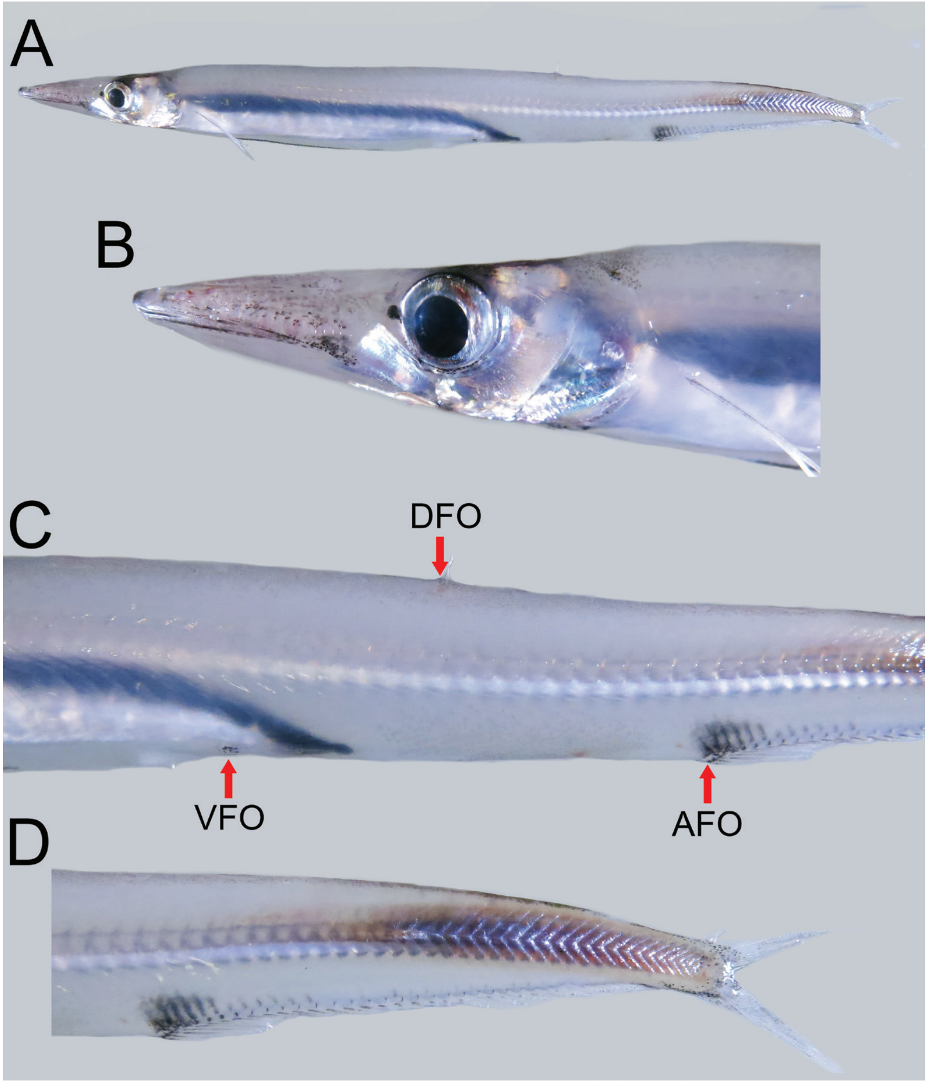

Figure 4. Fresh condition of *Lestrolepis philippina* (Fowler, 1934), NMMB-P027934 (1 of 17), ca 175 mm SL **A** lateral view **B** lateral view of head **C** lateral view of body showing origin of dorsal fin (DFO), pelvic fin (VFO), and anal fin (AFO) **D** lateral view of caudal region.

43 anal-fin rays, and the latter 35. Harry (1953a: 187) suggested the first one is *Lestidium japonicum*, whereas the latter was unknown. We concur that the former is *Lestrolepis japonica*, and the latter is *L. philippina* based on their counts of anal-fin rays (cf. 40–43 in *L. japonicus* and 36–40 in *L. philippina*; Table 2). Matsubara (1941) also mentioned that *japonicum* closely resembles *L. philippinus*. This could have been the beginning of confusion of the species (see also Matsubara 1955, 1963).

Harry (1953a) reported examining the types and additional specimens of *L. japonica* and identified *L. philippina* as a junior synonym. However, given clear differences, such as the position of DFO, the relatively slender body, snout, and jaws, as well as different vertebral and lateral-line counts, it remains uncertain why Harry considered them senior synonyms of *L. philippina*, perhaps being influenced by Matsubara (1941). It seems likely that Harry never examined radiographs of the types of *L. japonica*; otherwise, he might have noticed the distinctly high vertebral counts in these two specimens.

Ege (1953) documented juveniles of *Lestrolepis intermedia* (as *Lestidium intermedium*) from the western Pacific, i.e. Japan, Taiwan, and the Philippines, etc. Assuming he identified these specimens correctly, for example, regarding the position of DFO, his specimens should be *L. japonica* in this work. However, he never considered the names "*japonicum*" or "*philippinus*" in his publication. Based on the museum collection (Ho pers. obs.), *L. philippina* is far more abundant compared to *L. japonica*, and it remains unknown why Ege did not recognize such a distinct form. It is notable that Ege (1953) recognized from this region *Lestidium nudum*, which has similar fin position. It is likely Ege misidentified *L. philippina* as *Lestidium nudum*, because the latter is more or less restricted to the Hawaiian Islands and the central Pacific (Ho pers. data).

Fujii in Masuda et al. (1984) appears to have followed Harry's (1953b) definition and recognized the population with few vertebrae as *L. japonica*, which is now confirmed to be a misidentification of *L. philippina*. He also identified *L. intermedia* from Japan and provided a short description. His provided counts of 95–97 total vertebrae and 74–81 lateral-line scales indicate that his description was, in fact, that of *L. japonica*.

Regarding other paralepidid species, some taxonomic problems have been reviewed, such as the resurrection of *Lestrolepis pofi* and the placement of *L. leutkeni* in *Lestidiops* (Ho and Golani 2019). Matching adults to these species with only juveniles known, or redescriptions of species have been undertaken (Ho and Huang 2022a, 2022b; Ho and Lin 2023; Ho and Tsai 2023). However, there are several species with unknown status that still require further investigation (Ho pers. data).

This work provides an opportunity to underscore the importance of not relying solely on previously published works but also examining type material in museum collections, even for well-known species.

Material examined

Lestrolepis japonica: **Holotype.** ZMUT 2013 (159.5), Sagami Bay, Japan. Paratype. ZMUT 2014 (ca. 180), same as holotype. **Non-types.** HUMZ 71212 (1, 183), Fukushima, Japan, trawl net, 200–300 m, 8 Nov. 1977. HUMZ 71248 (1, 243), Hayakawa Port, Odawara, Kanagawa, Japan, 7 Nov. 1977. HUMZ 71844 (1, 193), HUMZ 71845 (1, 296), HUMZ 71846 (1, 184), HUMZ 71847 (1, 213), HUMZ 71848 (1, 186), Hayakawa Port, Odawara, Kanagawa, Japan, 5 Nov. 1977. HUMZ 134997 (1), 38°35'30.0"N 141°59'48.0"E, off Minamisanriku, Miyagi, Japan, bottom trawl, 331 m, 17 Oct. 1994. HUMZ 163755 (1, 120), 38°24'32.4"N, 142°04'13.2"E Miyagi, 461 m, 12 Oct. 1999. HUMZ 163832 (1, 123), HUMZ 163833 (1, 125), Miyagi, 38°23'09.6"N, 142°07'27.0"E, 552 m, 26 Oct. 1999. HUMZ 206777 (1, 162), 38°24'57"N, 142°02'50.4"E, Miyagi, Japan, 425–430 m, 30 Oct. 2009. HUMZ 206833 (1, 140), 38°22'13.2"N, 142°03'13.8"E, Miyagi, bottom trawl, 412 m, 9 Oct. 2009. HUMZ 209243 (1, 92), 39°35'24.6"N, 142°31'E, 890-897 m, 7 Oct. 2010. HUMZ 214579 (1, 134), 39°05'15.6"N, 142°09'34.8"E, off Tohoku, 398–412 m, 19 Oct. 2011. HUMZ 222513 (1, 183), Miyagi, 38°52'01.2"N, 142°04'24.6"E, 357 m, bottom trawl, 23 Oct. 2013. HUMZ 226859 (1, 155), 39°01'59.4"N, 142°12'55.8"E, off Kesennuma, Miyagi, Japan, bottom trawl, 575 m, 23 Oct. 2015. HUMZ 226876 (1, 146), HUMZ 226877 (3), 37°36'56.4"N, 141°50'31.8"E, off Souma, Fukushima, Japan, 380 m, 5 Nov.

2015. HUMZ 226942 (2), 37°43'N, 141°53'51"E, off Souma, Fukushima, Japan, bottom trawl, 411 m, 29 Oct. 2015. NSMT-P13816 (2, 147–154), Suruga Bay, Shizuoka, Japan, 17 Nov. 1968. NSMT-P48916 (1, 168), south of Sagami Bay, Japan, 4 Nov. 1995. NSMT-P48931 (1, 154), off Tohoku, northern Japan, trawl, 5 Nov. 1995. NSMT-P58786 (3, 75–130), 39°00'36"N, 143°32'06"E, off Pacific coast between Miyagi Pref. and Iwate, 550–578 m, Japan, mesopelagic trawl, 29 Jul. 1996. NSMT-P 58787 (1, 100), 39°00'36"N, 143°32'06"E, between Miyagi Pref. and Iwate, 650–677 m, mesopelagic trawl, 29 Nov. 1996. NSMT-P58788 (1, 115), NSMT-P58789 (1, 93), 39°02'24"N, 143°30'07.2"E, between Miyagi Pref. and Iwate, northern Japan, 650–677 m, mesopelagic trawl, 30 Jul. 1996. NSMT-P65464 (1, 176), 37°45'54"N, 142°09'32"E, off Fukushima, northern Japan, 647–676 m, otter trawl, 19 Oct. 2002. NSMT-P65466 (1, 136), 36°53'45.6"N, 141°33'43.2"E, off Ibaraki, Japan, 495–530 m, otter trawl, 20 Oct. 2002. NSMT-P67563 (1, 158), 31°20'39.1"N, 128°10'53"E, southern Japan, 392 m, otter Trawl, 8 Nov. 2003. NSMT-P67589 (1, 237), 28°59'47"N, 127°09'21.2"E, Ryukyus, 350 m, otter Trawl, 5 Nov. 2003. NSMT-P91547 (1, 170), 38°21'32.4"N, 141°56'24.0"E, off Miyagi, Japan, 280 m, trawl, 3 Oct. 2007. NSMT-P102802 (1, 169), 36°58'26.4"N, 141°25'43.3"E, off Fukushima, Japan, 251-252 m, otter trawl, 26 Oct. 2006. Also listed as *Lestrolepis nigroventralis* in Ho et al. (2019a), including the type series.

Lestrolepis philippina: **Holotype.** USNM 92323 (118.2), Varadero Bay, southern Luzon, Mindoro, Philippine, 22 Jul. 1908. Paratypes. USNM 93414 (2, 109.6–125), Noble Point, Tulayan Island, Sulu, Philippine, 283 m, 15 Sep. 1909. CAS-SU 14970 (1), USNM 135257 (2, 121–128), Anchorage, Dupon Bay, Leyte, Philippine, 17 Mar. 1909. **Non-types.** HUMZ 146645 (1, 228), 25°37'16.8"N, 126°05'21"E, Miyoko, Okinawa, 388–394 m, 2 Aug. 1994. HUMZ 222365 (1, 153), HUMZ 222366 (1, 165), HUMZ 222367 (1, 180), HUMZ 222368 (1, 185), HUMZ 222462 (1, 144), Dong-gang, Taiwan, 7 Nov. 2013. NSMT-P59709 (2, 87–96), 35°50'38.4"N, 152°59'49.2"E, 0–20 m, trawl, 24 May 1995. NSMT-P67590 (2, 185-232), 28°59'47"N, 127°09'21.2"E, East China Sea, 350 m, otter Trawl, 5 Nov. 2003. NSMT-P94628 (8, 123–160), Sagami Bay, southern Japan, set net, Tokyo Sea Life Park, 15 Nov. 1988. NSMT-P115090 (1, 138.2), NSMT-P115091 (1, 154.5), Dong-gang fishing port, Taiwan, 17 Oct. 2013, G. Shinohara et al. NSMT-P115637 (1, 142), Dong-gang fishing port, Taiwan, 19 Oct. 2013. NSMT-P128174 (1, 268.8), off Amami-Oshima Is., Ryukyus, Japan, Yamakawa, 26 Jun. 1972. NSMT-P128175 (1, 226.1), off Amami-Oshima Is., Ryukyus, Japan, 26 Jun. 1972. Also listed as *L. japonica* in Ho et al. (2019a)

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Only museum collection specimens were used in present study.

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Author contributions

H.-C. Ho and T. Kawai took data, photos, and composed and reviewed the manuscript. All authors approved the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Redescription of *Malacosarcus macrostoma* (Günther, 1878) from the abyssal zone off Taiwan, northwestern Pacific Ocean (Beryciformes, Stephanoberycoidei, Stephanoberycidae)

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Abstract

The large-mouth pricklefish, *Malacosarcus macrostoma* (Günther, 1878), previously known from five specimens collected from the central Pacific Ocean, is redescribed based on three specimens collected from the abyssal zone (4,412–4,813 m) off the southeastern coast of Taiwan. These specimens contribute to a more comprehensive description of *M. macrostoma* and represent this species' westernmost and deepest record. This study provides a detailed description, fresh photographs, and notes on their morphological characteristics of the specimens. Lastly, the distributional records of *M. macrostoma* are discussed.

Key words: Biodiversity, biogeography, deep sea, ichthyology, taxonomy

Introduction

The pricklefish family Stephanoberycidae comprises benthopelagic or abyssal-benthic fishes, which can be found worldwide reaching depths down to 5,300 m (Kotlyar 1996; Moore 2003, 2016). They are characterized by having a single dorsal fin positioned posteriorly, symmetrical with the anal fin, 0–3 weak spines and 9–14 soft rays on dorsal and anal fin, 0 spines and 5–6 soft rays on the pelvic fin, 9–12 procurrent caudal-fin rays, no teeth on the vomer and palatine, minute spines on bony ridges of the head, and a single supramaxilla (Moore 2003, 2016).

Presently, four species, each belonging to distinct monotypic genera, are recognized as valid: *Abyssoberyx levisquamosus* Merrett & Moore, 2005, *Acanthochaenus luetkenii* Gill, 1884, *Malacosarcus macrostoma* (Günther, 1878), and *Stephanoberyx monae* Gill, 1883 (Fricke et al. 2024). Among these, *M. macrostoma* was originally described from the tropical mid-Pacific region based on a specimen (Günther 1878). However, specimens of this species appear to be extremely rare in collections worldwide, which were known from five specimens collected from sparse localities in the central Pacific Ocean (Günther 1878; Boehlert and Mundy 1992; Nonaka et al. 2021). Moreover, adult specimens are either disintegrated or in poor condition, including the fragmented holotype (Merrett and Moore 2005; J. Maclain pers. comm. 11 Apr. 2024). Currently, the available specimens of *M. macrostoma* are predominantly in the larval stage (Nonaka et al. 2021). Therefore, information regarding the biology, ecology, and detailed morphology remains incomplete.

During a revision of stephanoberycoid fishes in Taiwan, three specimens collected by R/V *Ocean Researcher I* from the abyssal zone (4,412–4,813 m) off southeastern Taiwan were discovered in the collection of the Biodiversity Research Center, Academia Sinica, Taiwan (ASIZP). Upon detailed examination, these specimens were confirmed to be *Malacosarcus macrostoma* based on diagnostic characteristics. Consequently, these specimens represent both the westernmost record and the first record from Taiwan and the northwestern Pacific Ocean.

Given the importance of establishing a clear taxonomic status for *M. macrostoma*, a species reported based on limited specimens, this study aims to provide a precise, specimen-based description, fresh photographs, morphological characters, and distribution records of *M. macrostoma*.

Materials and methods

The specimens were fixed in 95% EtOH and permanently preserved in 70% EtOH. They are deposited at Biodiversity Research Center, Academia Sinica, Taipei, Taiwan (**ASIZP**). The distribution map was generated using Ocean Data View (Schlitzer 2024).

Terminology and methodology follow Kotlyar (1996) and Su et al. (2023a). Gill rakers were counted on the outer faces of all four arches and abbreviated as GRI–IV. Body depth was measured at the greatest depth. Counts of paired-fin characters were presented as left/right whenever available.

Measurements were made using 150 mm digital calipers under a stereomicroscope (Olympus SZ51) and rounded to the nearest 0.1 mm. Morphometric data were expressed as percentages or ratios of standard length (**SL**) and/or head length (**HL**), except otherwise indicated.

Results

Family Stephanoberycidae Gill, 1884

Malacosarcus macrostoma (Günther, 1878)

Figs 1–3, Tables 1, 2
English name: Large-mouth pricklefish
Chinese name: 大口軟冠鯛

Scopelus macrostoma Günther, 1878: 186 (type locality: Mid Pacific, 0°33'S, 154°34'W, depth 2,425 fathoms (4,435 m). Holotype: BMNH 1887.12.7.11).

Malacosarcus macrostoma: Günther 1887: 30 (new genus and new combination). Goode and Bean 1896: 182 (in part). Grey 1956: 191 (listed). Ebeling and Weed 1973: 416 (in part). Kotlyar 1996: 261 (in part). Kotlyar 2004: 2 (listed). Merrett and Moore 2005: 1708 (in part, compared to the new genus and species described). Mundy 2005: 301 (listed, Hawaiian Islands). Nonaka et al. 2021: 153, fig. 9B (in part, larval record from the Hawaiian Islands).

Stephanoberycidae sp.: Boehlert and Mundy 1992: 83, fig. 4 (larval record from Hancock Seamount, Hawaiian Islands).

Specimens examined. Taiwan • ASIZP 73637, 65.5 mm SL, off southeastern Taiwan, Philippine Sea, 22°3'38.16"N, 121°10'6.95"E, R/V Ocean Researcher I, sta. CP 413, beam trawl, depth 4,412–4,458 m, 12 Jun. 2008; ASIZP 73644, 55.7 mm SL, off southeastern Taiwan, Philippine Sea, 22°7'32.15"N, 122°5'35.87"E, R/V Ocean Researcher I, sta. CP 415, beam trawl, depth 4,806–4,813 m, 14 Jun. 2008; ASIZP 73646, 61.2 mm SL, off southeastern Taiwan, Philippine Sea, 22°12'28.07"N, 122°6'56.16"E, R/V Ocean Researcher I, sta. CP 415, beam trawl, depth 4,801–4,813 m, 15 Jun. 2008. All collected by M.-Y. Lee.

Diagnosis. A species of Stephanoberycidae characterized by the absence of dorsal-and anal fin-spines (vs fin spines present in other genera, sometimes absent in *Acanthochaenus*); 11–12 anal-fin rays (vs 9–10 in *Acanthochaenus*); GRI 7–8 + 1 + 15–19 = 23–27 (vs 5–7 + 1 + 13–14 = 19–21 in *Abyssoberyx* and

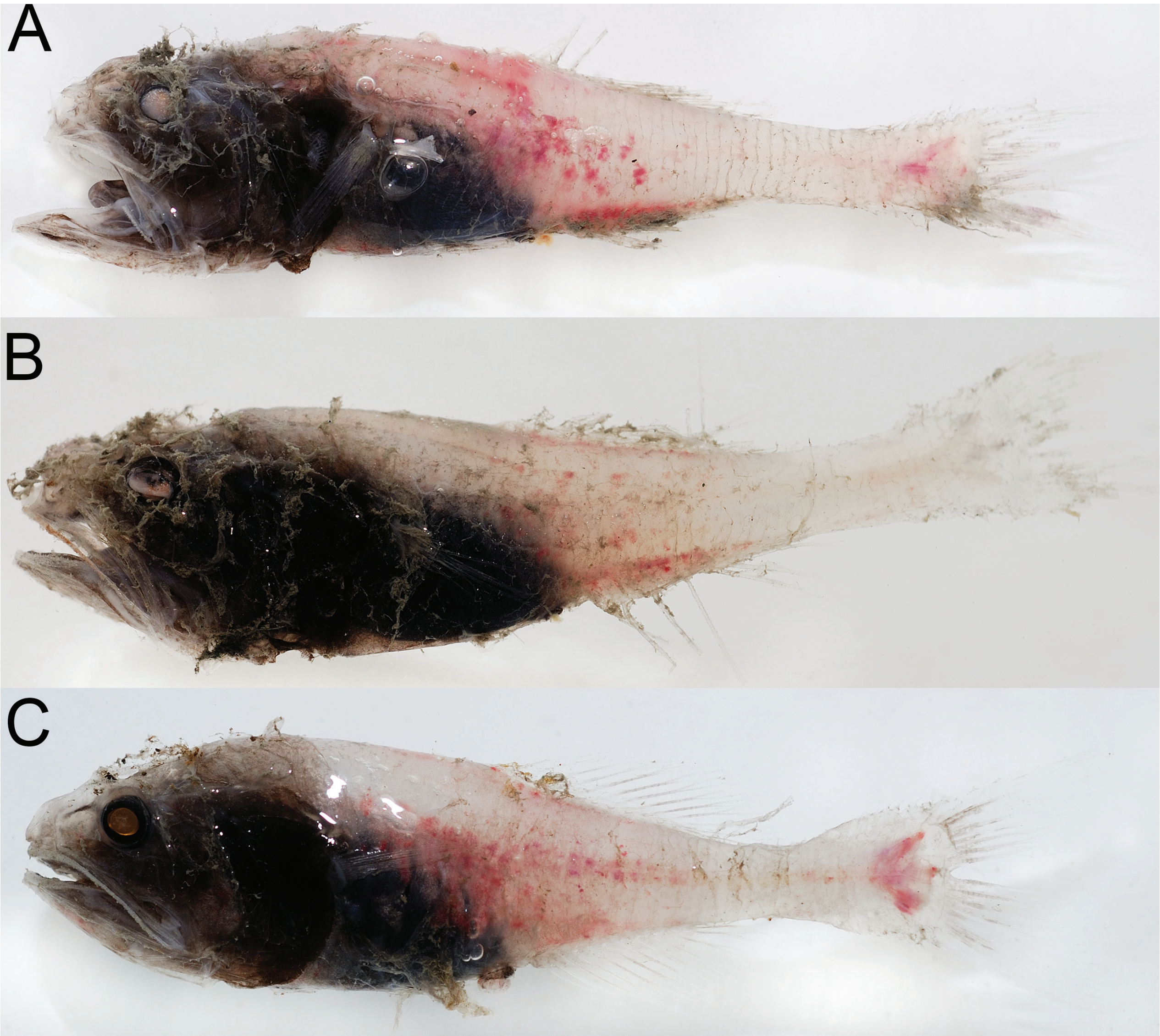

Figure 1. Fresh specimens of *Malacosarcus macrostoma* (Günther, 1878) **A** ASIZP 73637, 65.5 mm SL, left-right reversed **B** ASIZP 73644, 55.7 mm SL, left-right reversed **C** ASIZP 73646, 61.2 mm SL.

Figure 2. Preserved specimens of *Malacosarcus macrostoma* (Günther, 1878) **A** ASIZP 73637, 65.5 mm SL **B** ASIZP 73644, 55.7 mm SL **C** ASIZP 73646, 61.2 mm SL. Photos by Y.-C. Hsu.

12–15 + 1 + 24–27 = 37–40 in *Stephanoberyx*); lateral line forms flaps in approximately 42–46 vertical rows (vs lateral line without distinct vertical flaps in *Acanthochaenus* and *Stephanoberyx*); vertebrae 10 + 20–21 = 30–31 (vs 10–11 + 21–23 = 32–34 in *Abyssoberyx*); body scales cycloid and deciduous (vs body scales ctenoid and adherent in *Acanthochaenus* and *Stephanoberyx*); and origin of pelvic fin situated nearer to pectoral fin than to anal fin (vs pelvic fin situated nearer to anal fin than to pectoral fin in *Acanthochaenus*).

Description of Taiwanese specimens. Meristic and morphometric data are provided in Tables 1 and 2.

Dorsal-fin rays 13–14. Pectoral-fin rays 12–13/12–13. Pelvic-fin rays 4–6/4–5. Anal-fin rays 11–12. Principal caudal-fin rays 10 + 9, uppermost and lowermost rays unbranched; procurrent caudal-fin rays 9 and 10–11 on upper and lower lobes, respectively. GRI 7–8 + 1 + 15–18 = 23–27 (total); GRII 6–7 + 1 + 15–17 = 22–25; GRIII 3 + 1 + 14 = 18; GRIV 1–2 + 0–1 + 10–12 = 12–14. Pseudobranchial filaments 5–6 (*n* = 2). Lateral-line flaps in approximately 42–46 vertical rows. Vertebrae 10 + 20–21 = 30–31; branchiostegal rays 8.

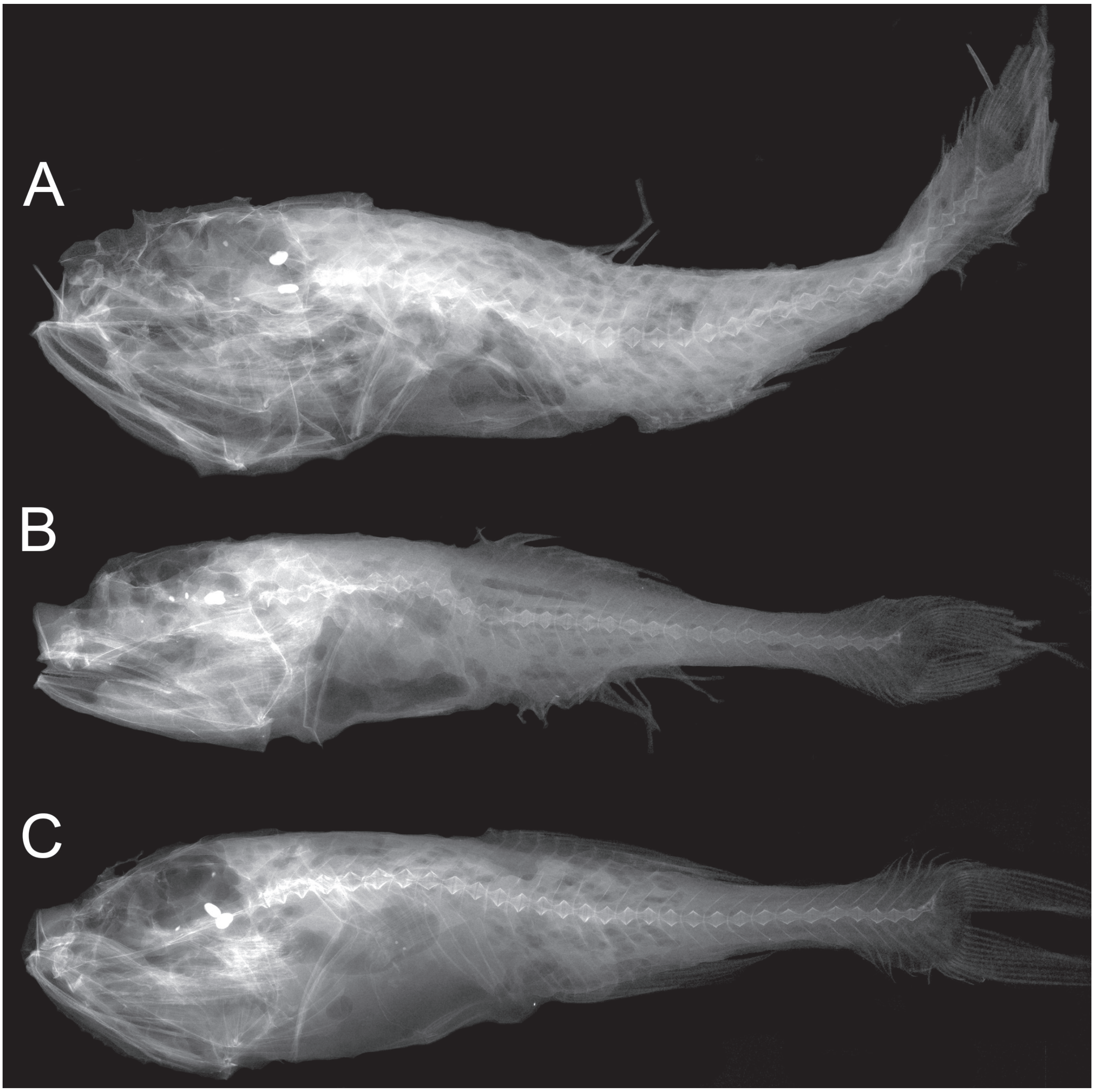

Figure 3. X-radiographs of *Malacosarcus macrostoma* (Günther, 1878) **A** ASIZP 73637, 65.5 mm SL **B** ASIZP 73644, 55.7 mm SL **C** ASIZP 73646, 61.2 mm SL.

Body slender, greatest depth 4.1–4.3 in SL; body laterally compressed. Head oval, length 2.7–2.8 in SL; its height 1.3–1.6 in HL; upper profile of head slightly rounded, with nearly straight profile to dorsal-fin origin; forehead slightly convex, its height 6.1–7.3 in HL; eye diameter 4.6–4.9 in HL; tip of snout rounded, extending slightly before premaxilla, its length 3.9–4.6 in HL; interorbital width 2.9–3.1 in HL.

Mouth oblique, upper-jaw length 1.4–1.6 in HL; posterior end of maxilla rounded, exceeding beyond vertical through posterior margin of eye; lower jaw slightly larger than upper jaw, length 1.4 in HL; its anterior tip protruding before upper jaw when closed. Two nostrils situated in front of eye; both at same horizontal through center of eye; both nostrils rounded and nearly same in size. No trace of nasal organs in all specimens (possibly shrunk during preservation). Symphysis of premaxillae notched and naked. Symphysis of dentaries forming single and blunt knob. Supramaxilla single, with needle-like process anteriorly and rectangular, slightly oval process posteriorly; its posterior tip in advance of tip of maxilla.

Head skeletons and their ridges delicate. Opercle with one central ridge but not forming spine. Small spines on posteroventral margins of both inner and outer ridges of preopercle. Posttemporal ridge rounded, with small spines on its outer margin. Both premaxilla and dentary with villiform teeth on outer and medial surfaces. Palatine and vomer edentate.

Gill rakers on outer face of all four arches rod-shaped and laterally compressed, their inner surfaces covered with small teeth; rakers on outer row of first arch longer than remainder, longest gill raker in 4.0–4.6 in HL; rakers on inner surfaces of outer three arches absent or forming minute bumps; no tooth patches present between rakers on all four arches. Fourth gill arch largely attached to the wall leaving slit between arch and gill chamber. No tooth on fifth ceratobranchial. Oval, conical tooth patch on second epibranchial arch. Large, moon-shaped conical tooth patch on fourth pharyngobranchial. Gill filaments present on all four rakers. Gill filaments on first arch very short, 8.4–14.9 in length of longest opposite rakers. Pseudobranch present, short and poorly developed.

Body scales cycloid and deciduous, embedded under skin; those covered by pectoral fin smaller than rest. Lateral-line scales and abdominal scutes absent. No scales on gular region and isthmus. Cycloid scales present on cheek.

Dorsal fin situated posteriorly, its origin about same vertical of anus. Pectoral-fin length 2.3–2.5 in HL; its origin at horizontal through ventral margin of eye; its tip reaching vertical through anus. Pelvic-fin length 5.0 in HL; its origin behind pectoral-fin base and tip reaching anus when adpressed. Anal-fin origin at vertical through fifth dorsal-fin ray; its posterior end at same vertical through that of dorsal fin. Caudal fin moderately small, forked. All fin rays delicate, with smooth surfaces.

Skins on surface of lateral line forming many vertical rows of flaps. Its main branch forming canal, originating behind and below posttemporal bone; its anterior portion gently curved down, becoming nearly straight on posterior portion. Anus situated immediately anterior to anal-fin origin. Caudal peduncle slender, with postdorsal and postanal length 1.4–1.5 and 1.3 in HL, respectively; its height 5.1–5.7 in HL. Light organs absent.

Table 1. Meristic characters of *Malacosarcus macrostoma* (Günther, 1878). Paired-fin characters are presented as left/right whenever available. Abbreviations: GRI–IV = gill rakers on first to fourth arches.

	ASIZP 73637	**ASIZP 73644**	**ASIZP 73646**
Dorsal-fin rays	13	13	14
Pectoral-fin rays	13/12	12/13	12/13
Pelvic-fin rays	6/5	5/5	4/4
Anal-fin rays	11	12	11
Caudal-fin rays	N/A	9+10+9+10	9+10+9+11
GRI	8+1+16=25	7+1+15=23	8+1+18=27
GRII	6+1+17=24	6+1+15=22	7+1+17=25
GRIII	3+1+14=18	3+1+14=18	3+1+14=18
GRIV	1+1+10=12	2+0+11=13	1+1+12=14
Pseudobranchial filaments	N/A	5	6
Lateral-line flaps	ca 46	N/A	ca 42
Vertebrae	10+20=30	10+20=30	10+21=31

Coloration. When fresh (Fig. 1), body pale and somewhat translucent; head and abdominal region uniformly black; all fins pale; lateral-line flaps forming vertical dark bands on lateral side of body. When preserved (Fig. 2), body and fins uniformly pale; oral cavity, including underside of tongue, inner face of operculum, and gill arches brown; gill rakers pale.

Table 2. Morphometric characters of *Malacosarcus macrostoma* (Günther, 1878). Abbreviations: A = anal-fin; C = caudal-fin; D = dorsal-fin; HL = head length; N/A = not available; P = pectoral-fin; SL = standard length; V = pelvic-fin.

	ASIZP 73637	**ASIZP 73644**	**ASIZP 73646**
SL (mm)	65.5	55.7	61.2
% SL			
HL	35.8	36.0	37.5
Head depth	24.2	23.1	28.9
Predorsal length	51.1	49.4	50.2
Prepectoral length	38.2	39.7	40.5
Prepelvic length	45.8	40.3	44.5
Preanal length	59.7	51.3	58.1
Snout length	7.8	9.1	9.0
Eye diameter	7.6	7.3	8.2
Interorbital width	12.5	N/A	12.2
Forehead height	5.9	N/A	5.1
Postorbital length	19.0	21.5	22.0
Upper-jaw length	N/A	24.9	24.0
Lower-jaw length	25.6	26.3	27.0
D–P length	18.0	14.0	16.2
D–V length	19.8	18.9	24.9
Greatest body depth	23.5	23.4	24.4
P length	14.2	N/A	16.3
V length	7.1	N/A	N/A
P–V length	9.2	9.3	9.5
D–A length	19.8	18.3	22.5
V–A length	15.4	12.4	16.1
D length	23.4	24.3	24.8
A length	17.9	18.2	19.6
Postanal length	28.0	26.9	28.1
Postdorsal length	25.8	24.5	27.4
C length	N/A	N/A	23.8
Caudal-peduncle height	7.0	6.3	6.8
Longest gill raker	8.1	7.8	9.5
Gill filament at angle	1.0	0.5	0.8
%HL			
Head depth	67.6	64.1	77.1
Snout length	21.9	25.4	24.0
Eye diameter	21.3	20.4	21.8
Interorbital width	35.0	N/A	32.5
Forehead height	16.4	N/A	13.7
Postorbital length	53.1	59.7	58.8
Upper-jaw length	N/A	69.2	64.0
Lower-jaw length	71.5	73.2	72.0

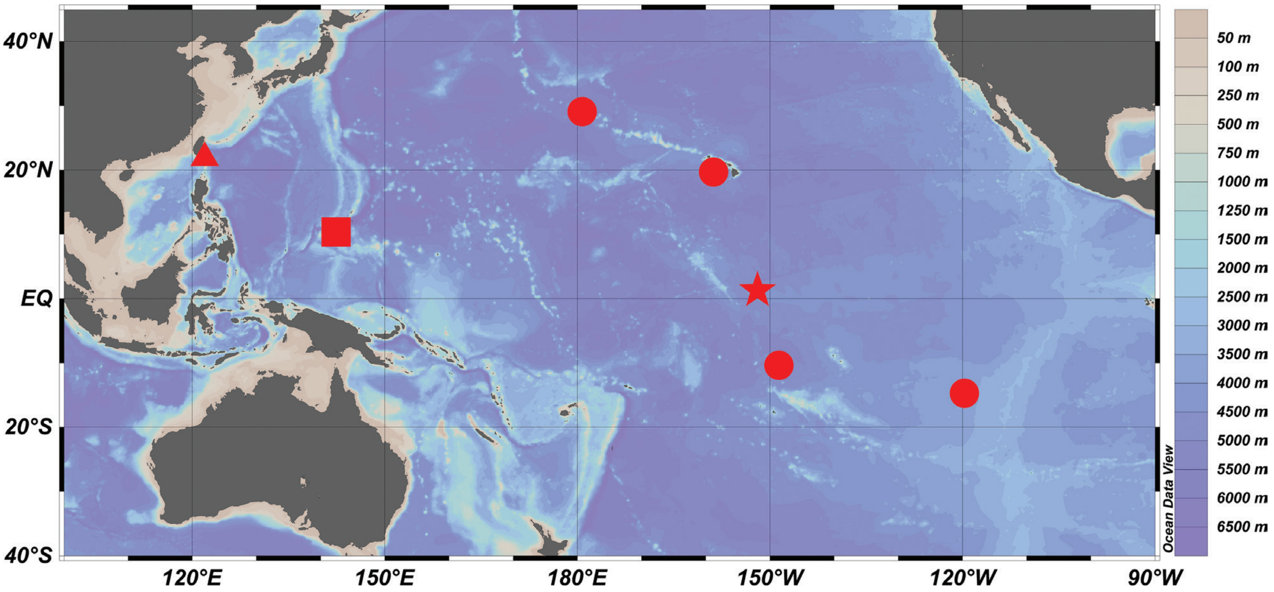

Figure 4. Distribution map of *Malacosarcus macrostoma* (Günther, 1878). Data source: triangle = this study; star = type locality; circle = other records (Günther 1887; Ebeling and Weed 1973; Boehlert and Mundy 1992; Nonaka et al. 2021); square = possible records (Jamieson et al. 2021).

Osteology (Fig. 3). Three supraneurals. First dorsal-fin pterygiophore inserts between eighth and ninth or seventh and eighth vertebra. Pleural ribs present on sixth to tenth vertebra; epineurals present. Anal-fin origin below twelfth vertebra.

Size. A rather small species, reported up to 8.9 cm (Günther 1878).

Distribution. Known from specimens collected from the tropical central Pacific Ocean at depths 2,777–4,434.8 m (Günther 1878; Ebeling and Weed 1973; Mundy 2005). Our specimens were collected from the northwestern Pacific at depths 4,412–4,813 m (Fig. 4).

Discussion

Comments on morphological characters

Our specimens were identified as *Malacosarcus macrostoma* based on several distinguishing features, including the absence of dorsal-fin spines, 7–8 + 1 + 15–18 = 23–27 rakers on the first gill arch, 9–11 procurrent caudal-fin rays, and deciduous and cycloid scales on the body (Kotlyar 1996; Merrett and Moore 2005). Among the four stephanoberycids, *M. macrostoma* is most similar to *Abyssoberyx levisquamosus*, sharing similar head and body shapes, deciduous and cycloid body scales, and dark vertical bars on the body (Kotlyar 1996; Merrett and Moore 2005). However, *M. macrostoma* can be differentiated from *A. levisquamosus* by the absence of dorsal- and anal-fin spines (vs one dorsal-fin spine and one or two anal-fin spines in *A. levisquamosus*; Merrett and Moore 2005), 7–8 + 1 + 15–18 = 23–27 gill rakers (vs 5–7 + 1 + 13–14), 10 + 20–21 = 30–31 vertebrae (vs 10–11 + 21–23 = 32–34), and pectoral-fin origin at horizontal ventral margin of eye (vs distinctly below).

All of our specimens exhibit dark vertical flaps along the lateral side of the body, similar to those of *A. levisquamosus* (Merrett and Moore 2005). While Merrett and Moore (2005) identified these structures as scale pockets, we propose that they are fused vertical papillae formed by the lateral-line system, akin to those observed in *Rondeletia* (Paxton 1999) and *Gibberichthys* (de Sylva and Eschmeyer 1977; Ho et al. 2023), based on our observation that the body scales are much smaller than the width of these vertical flaps.

In this study, we did not find either nasal organs or Tominaga's organ (sensu Paxton et al. 2001) in the nasal chamber of all specimens. However, nasal organs are present in other stephanoberycoid taxa, such as *Rondeletia loricata* Abe & Hotta, 1963, *Gibberichthys pumilus* Parr, 1933, *Hispidoberyx ambagiosus* Kotlyar, 1981, and cetomimids (Paxton 1989; Paxton et al. 2001; Su et al. 2023b). Therefore, there is a possibility that they deteriorated during the preservation process.

Possible records of *M. macrostoma*

In their description of *Abyssoberyx levisquamosus*, Merrett and Moore (2005) noted the Hawaiian record of *M. macrostoma* (Boehlert and Mundy 1992) may represent their new species. Additionally, they mentioned that the specimen has dorsal- and anal-fin rays and vertebrae differing by one or two counts from the Atlantic specimens of *A. levisquamosus*. Since the diagnostic characters (i.e., numbers of dorsal- and anal-fin spines, gill rakers, and vertebrae) used to distinguish *M. macrostoma* from *A. levisquamosus* are difficult to observe and determine in subadult or larval specimens, and the total counts of fin rays and vertebrae of our specimens are one or two elements lesser than those of *A. levisquamosus*, the Hawaiian record may represent *M. macrostoma*.

Previous records of *M. macrostoma* from the northeastern Atlantic (Merrett and Marshall 1981; Merrett 1992) were re-identified as a possible specimen of *A. levisquamosus* by Merrett and Moore (2005). Therefore, the occurrence of *M. macrostoma* in Atlantic Ocean is pending till other materials become available.

Another photograph taken at the Mariana Trench (northwestern Pacific Ocean) at a depth of 5,961 m by Jamieson et al. (2021: fig. 3k), was identified as "aff. *Abyssoberyx*". Nevertheless, judging by the distribution of all stephanoberycids, we lean toward the individual being *M. macrostoma*.

Ontogenetic migration

Ontogenetic migration to deeper depths has been observed in other stephanoberycids. For example, larvae of *Acanthochaenus luetkenii* were collected at a depth of 30 m (Kotlyar and Evseenko 1989), while larger or adult specimens were collected at depths of 1,183–5,400 m (Moore et al. 2003; Mincarone et al. 2014). To date, adult specimens of *M. macrostoma* have been collected at depths of 2,777–4,813 m (Ebeling and Weed 1973; this study), and a juvenile specimen was observed and collected via blackwater diving (Nonaka et al. 2021). Based on this information, we suggest that an ontogenetic migration to deeper depths occurs in *M. macrostoma*.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: YS. Formal analysis: YS. Funding acquisition: HCH. Investigation: MYL. Supervision: HCH. Writing - original draft: YS. Writing - review and editing: HCH, MYL.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

Polymixia melanostoma, a new beardfish from the western Pacific (Teleostei, Polymixiiformes, Polymixiidae)

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Abstract

A new species of beardfish, genus *Polymixia*, is described based on three specimens collected in Taiwanese waters and off the Chesterfield Islands of New Caledonia. It can be distinguished from its congeners by the following characters: dorsal-fin rays IV–V, 35–37; gill rakers on outer face of first gill arch 3+1+6=10; scales row between dorsal-fin origin and lateral line vertically 6–8 (S1) and posteriorly 12–14 (S2); pyloric caeca 40; snout rounded, with its surface rough and gelatinous, its tip evidently protrude anterior margin of premaxilla; ctenii on body scales arranged in a wedge-shape, forming three rows; 4th anal-fin spine long, 1.0%–1.2% eye diameter; longer dorsal-fin, 49.6–53.0% SL; blackish oral-branchial cavity. Our maximum-likelihood tree based on mitochondrial *COI* sequences revealed that the new species is distinct from six congeneric species. Our findings indicate the presence of at least six *Polymixia* species in Taiwan, highlighting Taiwan and adjacent areas as a region with the highest diversity of this genus.

Key words: *COI*, K2P distance, new species, Taiwan, taxonomy

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Introduction

The beardfish genus *Polymixia* Lowe, 1838 comprises the sole surviving clade within the family Polymixiidae (Nelson et al. 2016). Species of *Polymixia* are distinguished by a pair of hyoid barbels attached to the lower jaw, two supramaxillae, villiform teeth on both jaws, vomer, palatine, endopterygoid, and tongue, and the absence of luminous organs (Paxton 1999). They are deep-sea demersal fishes, inhabiting depths of 18–800 m; they are commonly found along the edges of continental shelves, continental slopes, oceanic islands, and near submarine mountains in the Indian, Pacific, and Atlantic oceans (about 45°N to 45°S) (Kotlyar 1986, 1996; Paxton 1999; Hayashi 2013; Nelson et al. 2016; Priede 2017; Anderson 2022).

Currently, 12 species of *Polymixia* are recognized as valid (Caixeta et al. 2024). In the Atlantic Ocean, four species have been documented: *Polymixia nobilis* Lowe, 1836, *P. lowei* Günther, 1859, *P. hollisterae* Grande & Wilson, 2021, and *P. carmenae* Caixeta, Oliveira & Melo, 2024. There is one species, *P. fusca* Kotthaus, 1970, in the northwestern Indian Ocean, and two species, *P. berndti* Gilbert, 1905 and *P. busakhini* Kotlyar, 1993, in the Indo-Pacific. Five species occur in the Pacific Ocean, including three species, *P. japonica* Günther, 1877, *P. longispina* Deng, Xiong & Zhang, 1983, and *P. sazonovi* Kotlyar, 1992, in the western Pacific Ocean and two species, *P. yuri* Kotlyar, 1982 and *P. salagomeziensis* Kotlyar, 1991, in the southeastern Pacific Ocean. The Pacific Ocean is the most specious region.

Species of *Polymixia* are similar in general appearances, and some of the diagnostic characters previously used (e.g. Kotlyar 1993, 1996) show high inconsistency. Therefore, genetic characteristics can be useful. However, works on this group including the genetics are limited. Borden et al. (2019), using two mitochondrial and five nuclear loci, revealed nine species-level clades, including five nominal species and four potential new species. Subsequently, only *Polymixia* sp. from Bermuda (*sensu* Borden et al. 2019) has been described as *P. hollisterae* by Grande and Wilson (2021).

Caixeta et al. (2024) used three mitochondrial loci (*COI*, 12S, and 16S) to reconstruct the phylogenetic relationship within *Polymixia* and described a new species, which was previously misidentified as *P. lowei*, from the southwestern Atlantic Ocean. Nonetheless, both the morphological examinations conducted by Borden et al. (2019) and Caixeta et al. (2024) were restricted to a small number of specimens, particularly from the Pacific Ocean (*P. japonica*, *P. berndti*, *P. longispina*, and *P. sazonovi*). Koeda (2019) reported and identified a specimen from southern Taiwan as *P.* cf. *salagomeziensis*, which suggests the possibility of additional undescribed *Polymixia* species and highlights the lack of information on Pacific species.

In this study, three specimens of an undescribed *Polymixia* species were collected from southwestern and eastern Taiwan, and the Chesterfield Islands of New Caledonia. This species can be distinguished from its congeners by having more dorsal-fin soft rays, a blackish oral coloration, a long fourth anal-fin spine, and a longer dorsal-fin. Additionally, DNA barcoding provides compelling evidence in support of these specimens as a new species. A detailed species description and comparison with congeners are provided.

Materials and methods

All the specimens examined are deposited in the following institutions: Hokkaido University, Laboratory of Marine Zoology, Faculty of Fisheries, The Hokkaido University Museum, Hakodate, Hokkaido, Japan (**HUMZ**), Muséum national d'Histoire naturelle, Paris, France (**MNHN**), and Pisces collection of the National Museum of Marine Biology and Aquarium, Taiwan (**NMMB-P**).

Specimens were fixed in 4% formaldehyde and then transferred to 70% ethanol or 50% isopropanol for permanent preservation. Sagittal otoliths were isolated using "lateral extraction" (Wakefield et al. 2016) and deposited at the Marine Paleontology Lab, Biodiversity Research Center, Academia Sinica, Taipei, Taiwan with catalog numbers CHLOL25609 and CHLOL25610.

Morphological analyses

The methodology and terminology employed in this study are based on Kotlyar (1996) with some modifications, including forehead height was determined from the upper margin of the orbit to the center of the interorbital space, and the length of the longest dorsal-fin spine was measured additionally. Moreover, the numbers of pseudobranchial filaments were recorded.

All counts of paired elements were conducted on the left side unless damaged, in which case the right side was used and noted. The number of gill rakers represents developed rakers on the outer side of the first arch (upper limb + angle + lower limb). Scale rows were defined and counted as follows: scale rows between dorsal-fin origin and lateral line counted vertically (S1) and counted posteriorly (S2); scale rows between lateral line and anal-fin origin (S3). Vertebral counts were obtained using x-radiographs taken by a digital radiograph machine located at the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan.

Measurements were taken using 150 mm digital calipers rounding to the nearest 0.1 mm, except for lengths longer than 150 mm, which were taken using a regular ruler rounding to the nearest 1 mm. Data of measurements are expressed as ratios or percentages to standard length (SL) or head length (HL), except where noted. The description of otoliths follows Lin and Chang (2012).

Phylogenetic analyses

Before fixation in the formaldehyde, tissue samples were taken from the base of the anal fin or dorsal fin of each specimen, fixed in 95% ethanol, and stored at room temperature. DNA extraction method followed the protocol of the Tissue & Cell Genomic DNA Purification Kit (Biokit, Taiwan). A fragment of mitochondrial cytochrome c oxidase I gene (*COI*) was amplified and sequenced using the published primer pair FishF1 (5'-TCA ACC AAC CAC AAA GAC ATT GGC AC-3') and FishR1 (5'-TAG ACT TCT GGG TGG CCA AAG AAT CA-3') from Ward et al. (2005).

Sequences generated in this study were submitted to GenBank (Benson et al. 2012) with accession numbers PP556533 to PP556549 (Table 1). Other sequences of *Polymixia* were retrieved from GenBank and BOLD systems (Ratnasingham and Hebert 2007) (Table 1). Additionally, sequences of *Gadus morhua* (MT893167.1 and MT455539.1) were selected as the outgroup. Sequences were aligned by the ClustalW model (Thompson et al. 1994) using the default settings in Geneious v. 8.1.9 (Kearse et al 2012).

A hypothesized phylogenetic tree was reconstructed using the maximum-likelihood method, employing the Hasegawa-Kishino-Yano (HKY) model (Hasegawa et al. 1985), and 1,000 bootstrap pseudoreplicates were performed by the software MEGAX (Kumar et al. 2018). Genetic distances were calculated also using the K2P model (Kimura 1980).

Results

Genus *Polymixia* Lowe, 1836

Type species. *Polymixia nobilis* Lowe, 1836.

Polymixia melanostoma **sp. nov.**

https://zoobank.org/783ECB16-7601-4FE9-AAC6-907EE440BB65
Figs 1–3, 4A, 5B, 6, 7; Tables 1–4
New English name. Black-mouth beardfish
New Chinese name. 黑口鬚銀眼鯛

Polymixia japonica (non Günther): Li 2010: 12–13 (in part, specimens were mixed with *P. japonica*).

Type specimens. *Holotype*: Taiwan • NMMB-P39587 (110.2 mm SL); northern South China Sea, Pingtung, off Dong-gang fishing port; ca 22°22'22"N, 120°27'34"E; 27 January 2023; Y. Su leg.; in bottom trawl; *COI*: PP556538.

Paratypes (*n*=2; SL 122.5–153.0 mm): Taiwan • 1 specimen; NMMB-P39588 (SL 122.5 mm); Taitung, off Chenggong fishing port; ca 23°05'52.93"N, 121°22'43.05"E; 11 September 2009; purchased by C.-W. Chang; hook and line; *COI*: PP556540. – New Caledonia • 1 specimen; MNHN 2014-2291 (153 mm SL); Coral Sea, Chesterfield Islands; 21°10'2.40"S, 158°37'24.01"E; 765–778 m deep; 11 October 2005; EBISCO, at st. CP2545.

Etymology. The specific name *melanostoma* is a combination of Greek *melano* and *stoma*, meaning "black mouth", in reference to its unique black oral cavity.

Diagnosis. *Polymixia melanostoma* sp. nov. differs from its congeners in having the following combination of characters: dorsal-fin rays IV–V, 35–37; gill rakers on the outer face of first gill arch 3+1+6=10; S1 6–8; S2 12–14; pyloric caeca 40; snout rounded, with surface rough and gelatinous, its tip evidently protrude anterior margin of premaxilla; ctenii on body scales arranged in wedge shape, forming three rows; 4th anal-fin spine long, 1.0–1.2 in eye diameter; dorsal-fin long, 49.6–53.0% SL; oral-branchial cavity, not including the underside of tongue, black.

Description. Meristic and morphometric data are provided in Tables 1, 2. Data below are for the holotype, followed by a range of paratypes in parentheses, except where indicated.

Dorsal-fin rays V, 35 (IV–V, 36–37); pectoral-fin rays 17 (15–16); pelvic-fin rays i+6 (i+6); anal-fin rays IV, 14 (IV, 14–16); principal caudal-fin rays 9+9=18 (9+9=18), uppermost and lowermost rays unbranched; procurrent caudal-fin rays 5 (6) dorsally and 5 (5) ventrally; lateral-line scales 35 (35–39); S1 6 (7–8); S2 12 (14); S3 15 (16, n=1); gill rakers on the outer face of first gill arch 3+1+6=10 (3+1+6=10); pseudobranchial filaments 27 (33); pyloric caeca 40; branchiostegal rays 7 and only posterior 4 visible. Vertebrae 12+17=29 (12+17=29); supraneural and pterygiophore insertion formula: 0/0//0/1+1/1+1/1+1/1+1/1+1/1+1/1+1/1+1/1+1/1+1/1+1+1/1+1/1+1/1+1/1+1/1+1/1+1+1/1+1+1/2 (0/0//0/1+1/1+1/1+1/1+1/1/1+1/1+1/1+1+1/1+1+/1+1+1/1+1/1+1/1+1+1/1+1/1+1+1/1+1/1+1+1/1+2, n=1).

Body rather slender, longer than deep, depth at dorsal-fin origin 2.8 (2.5–3.0) in SL. Head large, its length 2.9 (2.8–2.9) in SL; from snout to forehead rising gently; upper profile in front of dorsal fin slightly concave; forehead narrow, its width 6.1 (7.5–7.6) in HL; eyes large, 2.8 (2.6–3.0) in HL; snout rounded, its surface rough and gelatinous with several small bumps, tip protruding anteriorly from premaxilla, its length 6.1 (5.8–6.1) in HL; space between eyes convex and rather narrow, interorbital width 3.0 (3.1–3.4) in HL.

Table 1. *COI* sequences of *Polymixia* used for genetic analyses in this study. Sequences marked with an asterisk (*) were generated for this study and others were retrieved from GenBank (Benson et al. 2012) or BOLD system (Ratnasingham and Hebert 2007).

Species	Accession numbers
Polymixia melanostoma **sp. nov.**	PP556538*, PP556540*
P. japonica	PP556536*, PP556546*, PP556547*, PP556548*, ZOSKT1538-16, GBMTG154-16, ON398672.1
P. fusca	KU375762.1
P. lowei	SCAFB121-07, SCAFB144-07, SCFAC471-06, GBGCA12516-15, BCOLL237-06, BCOLL238-06, BCOLL239-06, BCOLL240-06, BCOLL241-06, ANGBF40917-19, ANGBF40918-19, UKFBI1117-08, GBMTG226-16, MLIII513-08
P. carmenae	OR660087.1, OR660087.1
P. longispina	PP556537*, PP556539*, PP556541*, PP556543*, PP556545*, PP556549*, FOAM828-11, FOAM829-11, FOAO209-14, FOAO212-14, FOAO213-14, FOAO214-14, FOAO2368-20, ZOSKT314-16, GBMIN94135-17
P. berndti	PP556533*, PP556534*, PP556535*, PP556542*, PP556544*, FOAF463-07, FOAF464-07, FOAF772-07, FOAN778-11, TZMSC367-05, TZMSC405-05, TZMC409-05, DSFSF399-09, DSFSF720-09
Gadus morhua	MN893167.1, MT455539.1

Table 2. Meristic and morphological characters of *Polymixia melanostoma* sp. nov. and three similar sympatric congeners. Abbreviation: NT, non-types.

	***P. melanostoma* sp. nov.**		***P. japonica***	***P. berndti***	***P. longispina***
	Holotype	**Paratype (*n*=2)**	**NT (*n*=20)**	**NT (*n*=39)**	**NT (*n*=29)**
Dorsal-fin rays	V, 35	IV–V, 36–37	IV–VI, 31–34	IV–VI, 28–31	V, 28–32
Pectoral-fin rays	17	15–16	15–17	13–17	15–17
Pelvic-fin rays	i+6	i+6	i+6	i+6	i+6
Anal-fin rays	IV, 14	IV, 14–16	IV–V, 14–16	III–IV, 13–17	IV, 13–16
Gill rakers	3+1+6=10	3+1+6=10	3–4+1+7–9=11–14	3–4+1+7–8=11–13	4+1+6–9=11–14
Pseudobranchial filaments	27	33	26–35	21–32	20–25
Pyloric caeca	40	—	37–56 (*n* = 2)	41–55 (*n* = 7)	26–30 (*n* = 3)
Vertebrae	12+17=29	12+17=29	12+16–17=28–29	12–13+17=29–30	12+17=29
Lateral line scales	35	35–39	30–34	27–36	29–36
S1	6	7–8	6–8	5–7	4–7
S2	12	14	11–16	8–11	8–11
S3	15	16	13–17	11–16	10–16
Snout tip	Protruded		Not protruded	Protruded	Not or slightly protruded
Oral cavity	Black		White or partly black	White	White
Branchial cavity	Black		Black	White	White
Scales ctenii distribution	Wedge		Wedge	Vertical	Vertical

Mouth large, posterior end of maxilla extending distinctly beyond vertical through posterior margin of eye. Nostrils close together but separated by narrow membranes, both immediately in front of anterior margin of eye and below horizontal through of eye; posterior nostril much larger than anterior one. No knob at symphysis of dentaries. Two supramaxillae, with anterior one triangular and posterior one rectangular, rounded posteriorly, not covering posterior portion of maxilla; postventral corner of maxilla exposed. Posterior-ventral margin of preopercle serrated with tip slightly pointed. Lower-jaw barbels, length 1.2 (1.0–1.1) in HL, its end exceeds pelvic-fin origin.

Most portions of lateral and medial surfaces of premaxilla and dentary covered with villiform teeth. Palatine and ectopterygoid with narrow band of villiform teeth; vomer with an oblong patch of villiform teeth. Endopterygoid with a large

Table 3. Morphometric data for *Polymixia melanostoma* sp. nov. and three similar sympatric congeners. Abbreviations: A, anal-fin; D, dorsal-fin; NT, non-types; P, pectoral-fin; V, pelvic-fin.

	***P. melanostoma* sp. nov.**			***P. japonica***		***P. berndti***		***P. longispina***	
	Holotype	**All types (*n* = 3)**		**NT (*n* = 20)**		**NT (*n* = 39)**		**NT (*n* = 30)**	
SL (mm	110.2	128.5 (110.2–152)		98.2 (88.7–107.1)		106.3 (62.0–173)		104.8 (62.4–135.5)	
% SL		Mean(range)	S.D.	Mean(range)	S.D.	Mean(range)	S.D.	Mean(range)	S.D.
Head length	34.3	34.6 (34.2–35.4)	0.7	32.6 (30.1–34.9)	1.4	34.8 (32.8–37.7)	1.8	34.3 (30.2–36.5)	1.5
Body depth	35.6	36.2 (33.3–39.6)	3.2	35.4 (30.3–41.4)	2.9	35.9 (32.7–40.6)	1.8	38.9 (33.9–42.2)	1.9
Eye diameter	12.1	12.4 (12.0–13.2)	0.7	11.2 (8.8–12.5)	0.9	11.2 (9.7–12.9)	0.8	11.1 (8.9–12.9)	0.8
Interorbital	11.6	11.0 (10.5–11.6)	0.5	10.3 (8.8–12.3)	0.9	10.6 (8.7–12.4)	1.0	11.1 (9.4–12.7)	0.7
Upper-jaw length	17.8	18.6 (17.8–19.1)	0.7	17.4 (16.1–19.2)	0.9	18.9 (17.2–20.3)	0.6	17.9 (15.3–19.4)	0.9
Lower-jaw length	15.3	16.3 (15.3–17.0)	0.9	15.8 (14.4–19.5)	1.3	17.4 (16.0–19.8)	0.9	16.6 (12.9–21.7)	1.3
Snout length	5.6	5.8 (5.6–6.1)	0.3	6.0 (5.1–7.0)	0.5	5.9 (4.3–7.0)	0.7	7.1 (3.7–8.8)	1.3
Postorbital length	17.0	17.5 (17.0–18.3)	0.7	17.1 (15.3–18.8)	1.1	19.1 (16.9–20.8)	1.0	18.4 (17.3–19.5)	0.6
Forehead height	5.6	4.9 (4.6–5.6)	0.6	5.6 (4.2–7.6)	0.9	5.8 (3.9–10.7)	1.2	7.4 (3.8–10.7)	1.4
Predorsal length	46.3	46.6 (46.3–47.1)	0.4	48.4 (45.4–51.6)	1.8	51.2 (48.5–54.7)	1.7	55.1 (49.1–58.5)	2.7
Prepectoral length	33.8	34.1 (33.8–34.5)	0.4	32.5 (29.5–34.6)	1.1	34.5 (32.3–37.4)	1.2	35.1 (31.3–37.3)	1.6
Prepelvic length	38.4	40.5 (38.4–43.0)	2.3	39.2 (36.4–42.0)	1.3	41.4 (35.8–43.7)	1.7	41.4 (35.3–44.4)	2.0
Preanal length	66.0	68.5 (66.0–71.5)	2.8	68.3 (65.1–71.3)	1.6	72.9 (67.3–77.7)	2.0	70.0 (63.3–75.7)	2.6
D length	49.6	51.1 (49.6–53.0)	1.7	45.3 (42.5–48.3)	1.5	42.8 (40.7–47.1)	1.2	43.2 (40.7–46.4)	1.5
D height	13.7	14.7 (13.7–16.6)	1.7	14.7 (12.1–17.0)	1.2	17.1 (13.1–20.1)	1.6	15.1 (12.7–19.3)	1.8
Longest D spine	10.5	10.7 (10.1–11.5)	0.8	13.1 (11.3–15.0)	1.1	10.6 (5.7–15.0)	2.0	12.8 (9.5–19.7)	2.4
A length	18.9	17.6 (16.8–18.9)	1.1	19.3 (17.9–21.2)	0.9	17.5 (15.0–21.6)	1.5	18.5 (16.5–20.7)	1.1
A height	13.5	14.1 (13.5–15.0)	0.8	12.8 (11.5–15.8)	1.2	12.2 (7.2–15.2)	1.5	13.9 (12.2–19.0)	1.6
Longest A spine	14.9	14.0 (12.0–15.2)	1.7	12.9 (10.3–15.2)	1.2	10.1 (7.7–13.5)	1.5	15.1 (12.6–22.9)	2.6
D–P length	27.6	28.0 (23.6–33.0)	4.7	29.2 (25.8–32.7)	2.0	29.0 (17.8–31.5)	2.2	31.1 (26.9–34.6)	1.6
D–V length	35.5	36.2 (33.3–39.8)	3.3	36.4 (32.9–41.4)	2.7	36.3 (33.3–39.3)	1.6	39.0 (35.9–42.6)	1.7
D–A length	44.7	45.8 (44.3–48.3)	2.2	43.9 (40.9–47.6)	2.0	42.5 (37.9–47.4)	1.7	45.9 (42.4–50.6)	1.7
P–A length	28.2	28.4 (26.1–30.8)	2.3	31.2 (28.7–33.8)	1.2	33.4 (29.4–38.8)	2.1	30.3 (26.6–33.7)	1.8
P–V length	12.1	12.8 (12.1–13.6)	0.7	11.8 (10.1–13.8)	1.1	11.4 (7.1–15.5)	1.7	12.9 (11.6–14.9)	0.6
P length	22.1	21.9 (19.5–24.1)	2.3	18.3 (14.8–21.4)	1.6	20.5 (18.2–22.2)	1.0	20.4 (17.8–23.2)	1.5
V length	14.1	14.1 (12.9–15.1)	1.1	12.5 (10.7–14.6)	1.1	13.9 (12.3–15.7)	0.9	13.0 (11.3–14.6)	0.8
Caudal-peduncle length	11.0	12.4 (11.0–13.4)	1.2	13.5 (11.7–16.4)	1.3	12.7 (10.2–16.2)	1.8	12.9 (10.4–15.5)	1.1
Caudal-peduncle height	11.0	10.7 (10.6–11.0)	0.2	10.9 (10.0–11.9)	0.6	10.1 (9.0–12.3)	0.7	10.7 (9.7–13.4)	0.8
Caudal-fin length	27.4	28.6 (27.4–29.7)	1.7	28.8 (24.9–33.8)	2.4	27.6 (24.6–30.3)	1.7	28.4 (24.6–38.1)	2.4
Barbel length	29.4	31.8 (29.4–34.5)	2.6	29.3 (26.1–35.6)	2.6	28.8 (23.6–32.8)	2.2	33.9 (22.6–40.0)	5.5

Table 4. Interspecific genetic distance of *COI* sequences of *Polymixia* species calculated with Kimura-2-parameter model (Kimura 1980). The number in the first row correspond to the species names in the first column. Values are presented as percentage (%).

		1	**2**	**3**	**4**	**5**	**6**	**7**
1	*P. melanostoma* **sp. nov.**	–	–	–	–	–	–	–
2	*P. japonica*	4.4	–	–	–	–	–	–
3	*P. fusca*	5.3	5.1	–	–	–	–	–
4	*P. longispina*	8.8	8.3	9.8	–	–	–	–
5	*P. carmenae*	9.7	9.4	9.1	8.9	–	–	–
6	*P. lowei*	10.0	9.7	8.9	8.8	2.7	–	–
7	*P. berndti*	14.5	16.0	13.2	15.3	14.5	14.1	–

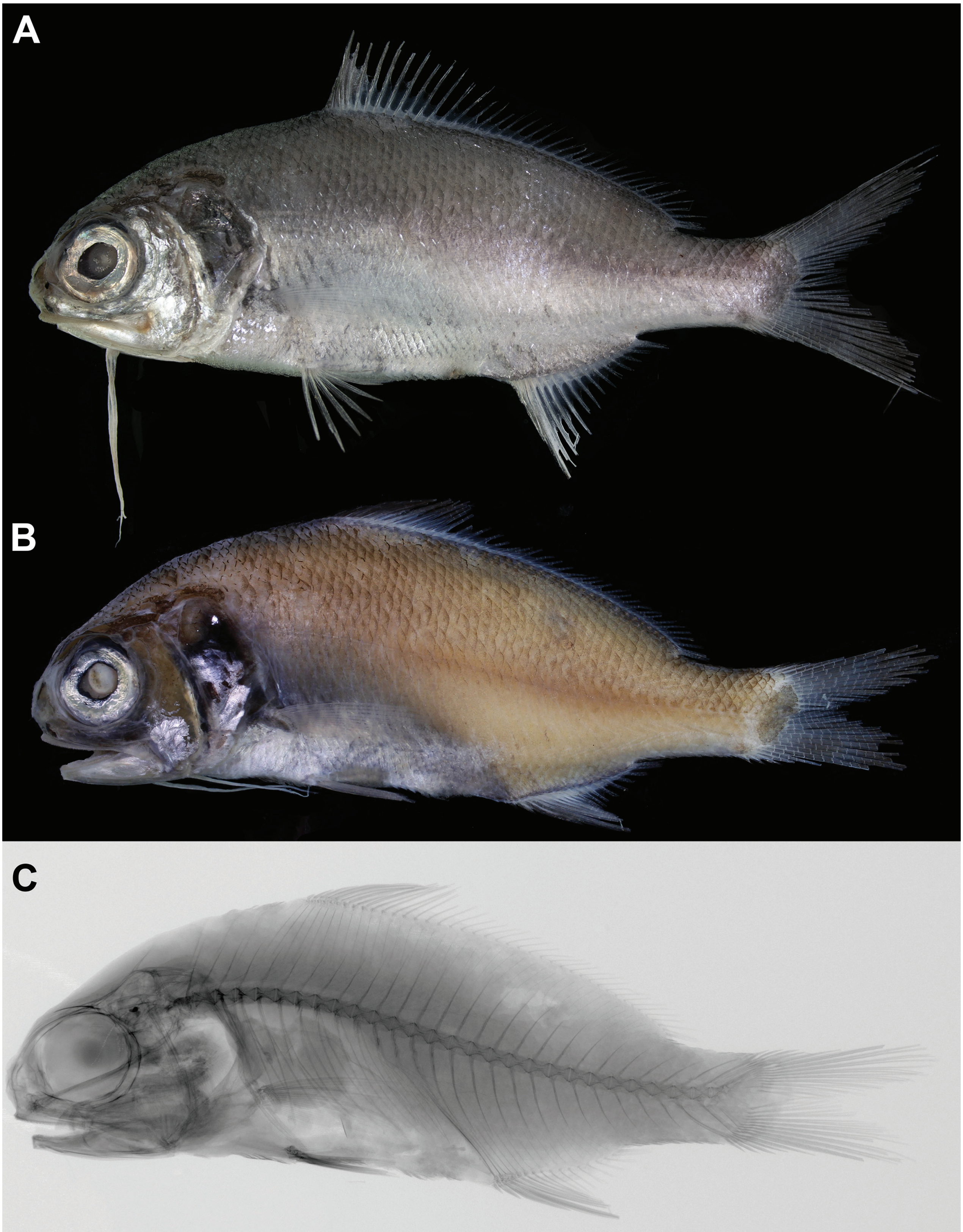

Figure 1. *Polymixia melanostoma* sp. nov., holotype, NMMB-P39587, 110.2 mm SL **A** fresh **B** preserved **C** x-radiograph.

patch of villiform teeth. Gill rakers rod-shaped, somewhat laterally compressed, with villiform teeth on inner surfaces; those in outer row of the first arch longest; rakers on inner row of the first arch and both inner and outer rows of the second

Figure 2. Preserved paratypes of *Polymixia melanostoma* sp. nov. **A** MNHN 2014-2291, 153 mm SL **B** NMMB-P39588, 122.5 mm SL.

to third arches short, forming bumps; those on the fourth arch forming bumps; small tooth patches forming bumps, present on midline of all four outer arches. Villiform, teardrop-like tooth patches present on the fifth ceratobranchial. Small villiform teeth patch on the second pharygobranchial forming oval patches. Large, teardrop-like tooth patches on the third pharyngobranchial.

Body covered with firmly attached ctenoid scales; ctenii on body scales arranged in a wedge shape, forming three rows (Fig. 3A). Isthmus with ctenoid scales; gular region naked, without scales.

Dorsal fin long, 2.0 (1.9–2.0) in SL. Dorsal-fin spines progressively longer posteriorly, length of the longest spine 0.9 (0.8–0.9) in eye diameter; outer margin of soft rays slightly concave; the first soft ray longest, and gradually shorter posteriorly. Anal-fin spines progressively longer posteriorly, length of the longest spine rather long, 1.2 (1.0–1.2) in eye diameter; outer margin of soft rays slightly concave; first soft ray longest. Pectoral fin short, 1.6 (1.5–1.8) in HL, its tip not reaching lateral line when adpressed to body. Pelvic fin without spine, its end slightly exceeds through pectoral-fin end vertical. Caudal-fin concave and pointed. Pyloric caeca pale, unbranched.

Size. Moderately small species. The biggest specimen examined was 153.0 mm SL.

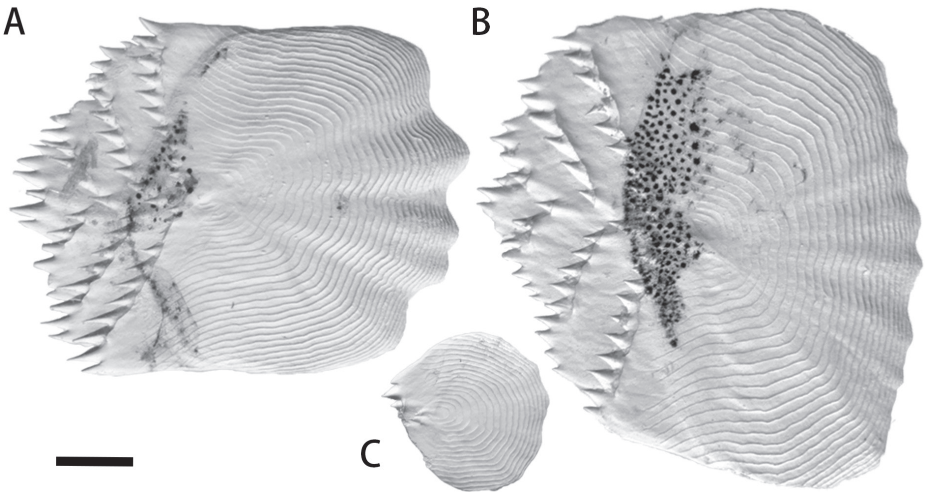

Figure 3. Right-side scales of *Polymixia melanostoma* sp. nov., holotype, NMMB-P39587, 110.2 mm SL **A** scale on caudal peduncle **B** scale on anterior dorsal-fin base **C** scale on isthmus. Scale bar: 1 mm.

Coloration. When fresh, body silvery, with dorsum slightly dusky (Fig. 1A). Tip of anteriormost nine dorsal-fin soft rays black, forming distinct spot (paratype). Anal-fin rays pale, second to fourth spines and anteriormost five soft rays with few black pigmentations. Caudal fin grayish. Pelvic fin pale, with black pigmentations on first, fifth, and seventh rays.

Body color, when preserved, similar to when fresh, slightly yellowish (Figs 1B, 2). Snout semitransparent. Oral cavity, including dorsal surface of tongue black (Fig. 4A). Underside of tongue pale. Inner side of opercle and peritoneum black (Fig. 5A). Tip of lower jaw without black spots.

Otolith. The sagittal otolith was taken from NMMB-P39588 (122.5 mm SL) and measured 6.8 mm in length (Fig. 6). Otolith rhomboidal (length/height ratio 1.36), moderately thick (Fig. 6A). Dorsal margin gently raised, lobed, highest at central; ventral margin slightly crenulated, regularly curved, deepest slightly anterior to central; posterior margin blunt, crenulated, not extending posteriorly; anterior margin triangular with incised notch; rostrum short and broad; antirostrum pointed; inner face convex; outer face slightly concave; sulcus centrally positioned, well divided into ostium and cauda; ostium wider than cauda, short, oblong, nearly filled with colliculum; cauda elongated, strongly curved at posterior with tip directing ventrally; cristae well developed; dorsal depression shallow, just above crista superior.

Distribution. This species is known from specimens collected from southwestern and eastern Taiwan and the Chesterfield Islands of New Caledonia, suggesting a broad distribution in the western Pacific Ocean. Inhabits at depth down to 778 m (based on MNHN 2014-2291).

Genetic analysis. The phylogenetic tree of *Polymixia* was reconstructed by the maximum-likelihood method with HKY+G+I (Hasegawa et al. 1985) nucleotide substitution models. The monophyly of *P. melanostoma* sp. nov. specimens is strongly supported by a bootstrap value of 99% (Fig. 7).

The pairwise genetic distance analysis with the K2P model reveals an average interspecific distance of 4.4–14.5% between *P. melanostoma* sp. nov. and the other six congeneric species (Table 4). The shortest genetic distance is with *P. japonica*, while the farthest is with *P. berndti*.

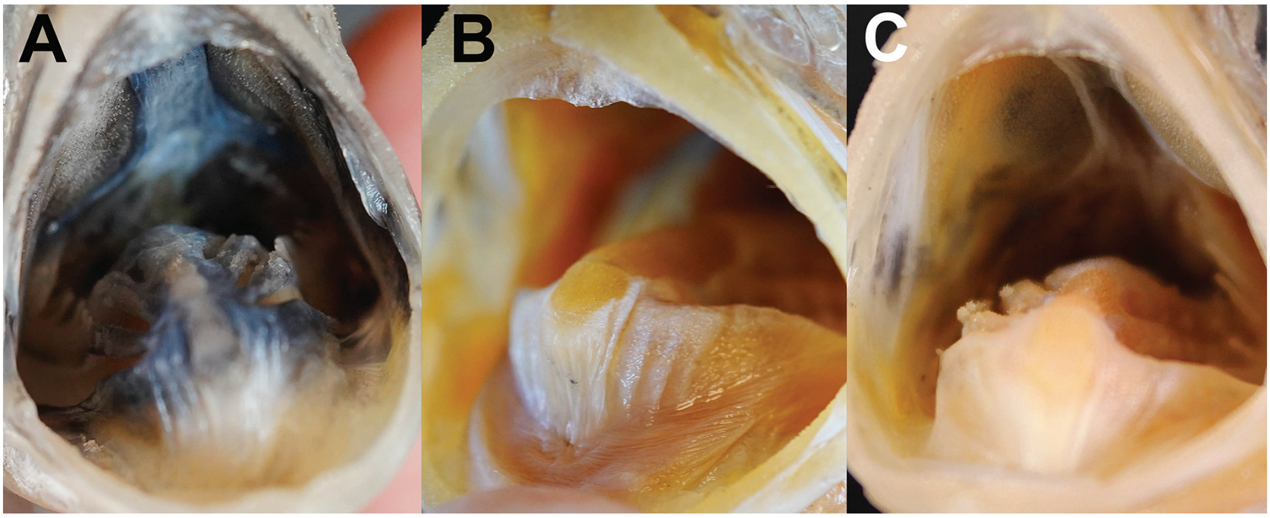

Figure 4. Close-up image of oral-cavity coloration of preserved **A** *Polymixia melanostoma* sp. nov., holotype, NMMB-P39587, 110.2 mm SL **B** *P. longispina*, NMMB-P39585, 128.5 mm SL **C** *P. japonica*, NMMB-P39573, 104.9 mm SL. Figure not to scale.

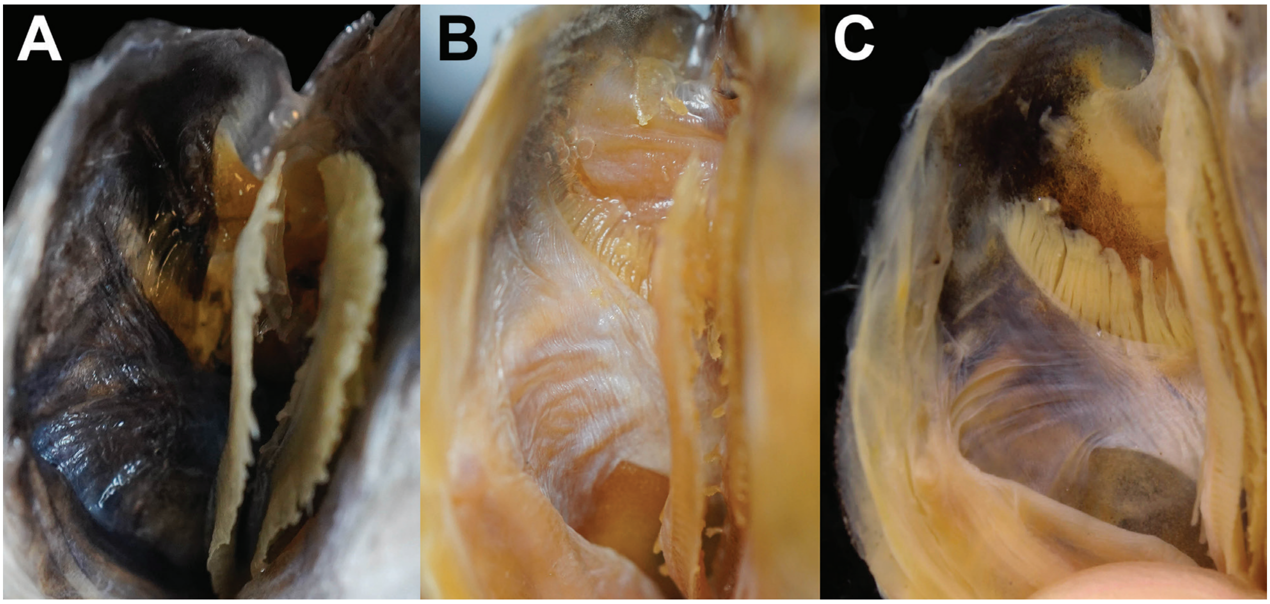

Figure 5. Close-up image of branchial-cavity coloration of preserved **A** *Polymixia melanostoma* sp. nov., holotype, NMMB-P39587, 110.2 mm SL **B** *P. longispina*, NMMB-P39585, 128.5 mm SL **C** *P. japonica*, NMMB-P39573, 104.9 mm SL. Figure not to scale.

Comparison. *Polymixia melanostoma* sp. nov. can be distinguished from 10 of the 12 congeneric species in having fewer gill rakers (3+1+6=10 vs 3–13+1+6–13=11–24 in *P. lowei*, *P. japonica*, *P. berndti*, *P. fusca*, *P. yuri*, *P. longispina*, *P. salagomeziensis*, *P. busakhini*, *P. sazonovi*, and *P. carmenae*; Table 2; Kotlyar 1996; Caixeta et al. 2024). Among these congers, only *P. nobilis* has a count that overlaps with *P. melanostoma* sp. nov. Borden et al. (2019) suggested that *P. nobilis* might not only occur in the Atlantic Ocean but also the Pacific. However, in comparison to the description and data provided by Kotlyar (1996), *P. melanostoma* sp. nov. differs from *P. nobilis* in having fewer pyloric caeca (40 vs 108 in *P. nobilis*), fewer S2 (12–14 vs 15–16), different

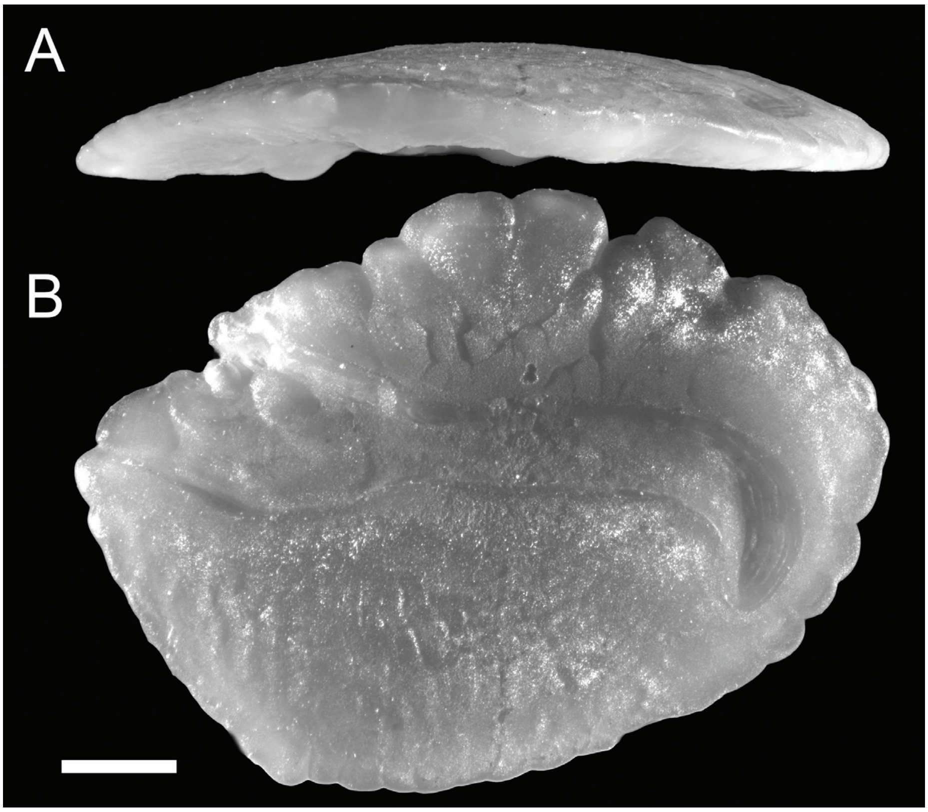

Figure 6. Right sagittal otolith of *Polymixia melanostoma* sp. nov., paratype (CHLOL25610, from NMMB-P3988, 122.5 mm SL) **A** ventral face **B** inner face. Scale bar: 1 mm.

vertebral formula (12+17=29 vs 14+15=29), a longer head (34.2–35.4% SL vs 30.8–32.3% SL), a longer dorsal fin (49.6–53.0% SL vs 41.3–44.3% SL), and a more protruding snout (vs slightly protruding).

Although the number of gill rakers for *Polymixia hollisterae* was not documented by Grande and Wilson (2021), *P. melanostoma* sp. nov. differs from *P. hollisterae* in having more dorsal-fin rays (IV, 35–37 vs V, 31–32), more pyloric caeca (40 vs 30), and higher numbers of S1 (6–8 vs 5), S2 (12–14 vs 10), and S3 (15–16 vs 12–14).

Compared with the species co-occurring in Taiwan (*Polymixia japonica*, *P. longispina*, and *P. berndti*), *P. melanostoma* sp. nov. exhibits meristic counts overlapping with *P. japonica* and shares distinctive characteristics, including a black branchial cavity (Fig. 5) and ctenii on scales distributed in a wedge shape (Fig. 3). It differs from *P. japonica* in having fewer number of gill rakers (3+1+6=10 vs 3–4+1+7–9=11–14; Table 2), more dorsal-fin rays (IV–IV, 35–37 vs IV–VI, 31–34; Table 2), a longer dorsal fin (49.6–53.0% SL vs 42.5–48.3% SL; Table 3), a fully black oral cavity (vs partly black; Fig. 4, Table 2), and a more protruding snout (vs not protruding; Table 2).

Additionally, *P. melanostoma* sp. nov. is also similar to *P. longispina* in having a long fourth anal-fin spine (12.0–15.2% SL, mean 14.0 vs 12.6–22.9% SL, mean 15.1; Table 3) but differs from it in having less gill rakers (3+1+6=10 vs 4+1+6–9=11–14; Table 2), more dorsal-fin rays (IV, 35–37 vs V, 28–32; Table 2), more pyloric caeca (40 vs 26–30; Table 2), more S2 (12–14 vs 8–11; Table 2), a shorter predorsal length (46.3–47.1% SL vs 49.1–58.5% SL; Table 3), a longer dorsal-fin (49.6–53.0% SL vs 40.7–46.4% SL; Table 3), a black oral cavity (vs white; Fig. 4; Table 2), a black branchial cavity (vs white; Fig. 5; Table 2), a more protruding snout (vs slightly protruding; Table 2), and the wedge-shaped distribution of ctenii on scales (vs vertical; Fig. 3; Table 2).

Polymixia melanostoma sp. nov. differs from *P. berndti* in having less gill rakers (3+1+6=10 vs 3–4+1+7–8=11–13; Table 2), more dorsal-fin rays (IV, 35–37 vs IV–VI, 28–31; Table 2), more S2 (12–14 vs 8–11; Table 2), a shorter predorsal length (46.3–47.1% SL vs 48.5–54.7% SL; Table 3), a longer dorsal-fin (49.6–53.0% SL vs 40.7–47.1% SL; Table 3), a black oral cavity (vs white; Fig. 4; Table 2), a black branchial cavity (vs white; Fig. 5, Table 2), and the wedge-shaped distribution of ctenii on scales (vs vertical; Fig. 3, Table 2).

Discussion

Previous studies of *Polymixia* mostly focused on morphological characters (Kotlyar 1986, 1996), while knowledge of genetic distinctions within *Polymixia* is limited. Although Borden et al. (2019) and Caixeta et al. (2024) utilized several genetic loci to reconstruct their phylogenetic relationships, they included only a few sequences of each species. Our study retrieved a total of 55 *COI* sequences, including 17 newly obtained sequences, for the reconstruction of a maximum-likelihood tree. This tree revealed seven distinct species-level clades (Fig. 7). Among these clades, the new species, *P. melanostoma* sp. nov. shows a close relation to *P. japonica* with the lowest genetic distance of 4.4% (Table 4). *P. melanostoma* sp. nov. and *P. japonica* share several morphological characteristics: higher numbers of dorsal-fin rays (≥31), higher numbers of S2 (≥11), a black branchial cavity, and ctenii on scales distributed in wedge shape.

Based on the sampling locations retrieved from the BOLD system and GenBank, the distribution of the other six *Polymixia* species are updated as follows (Fig. 7): *P. japonica* is only found in the northwestern Pacific Ocean (Taiwan and Japan), presenting a comparatively smaller geographic distribution when compared to its congeners. *Polymixia longispina* is distributed in the northwestern Pacific Ocean (Taiwan, China, and Japan) and in the eastern Indian Ocean (off Western Australia). *Polymixia lowei* is found in the Western Atlantic Ocean off the eastern United States, Mexico, and Canada. *Polymixia carmenae* is distributed in southwestern Atlantic Ocean. *P. berndti* is widely distributed in the Indian Ocean (South Africa and off Western Australia) and in the northwestern Pacific Ocean (Taiwan and Japan). However, the absence of sequences from the type locality, Hawaii, of *P. berndti* raises questions about whether this clade represents true *P. berndti*. Lastly, the sampling location for the sequence of *P. fusca* in the study remains unknown, casting uncertainty on its representation and distribution.

Taiwan exhibits a remarkable diversity of *Polymixia* species. Koeda (2019) documented four species and one undescribed species in Taiwan, namely *P. japonica*, *P. berndti*, *P. longispina*, *P. sazonovi*, and *P.* cf. *salagomeziensis*. The current study recognizes four species, *P. japonica*, *P. berndti*, *P. longispina*, *P. sazonovi*, and describes an additional new species, *P. melanostoma* sp. nov. To summarize, these findings suggest that at least six *Polymixia* species have been distributed in Taiwan, highlighting Taiwan as a region with the highest diversity of *Polymixia*.

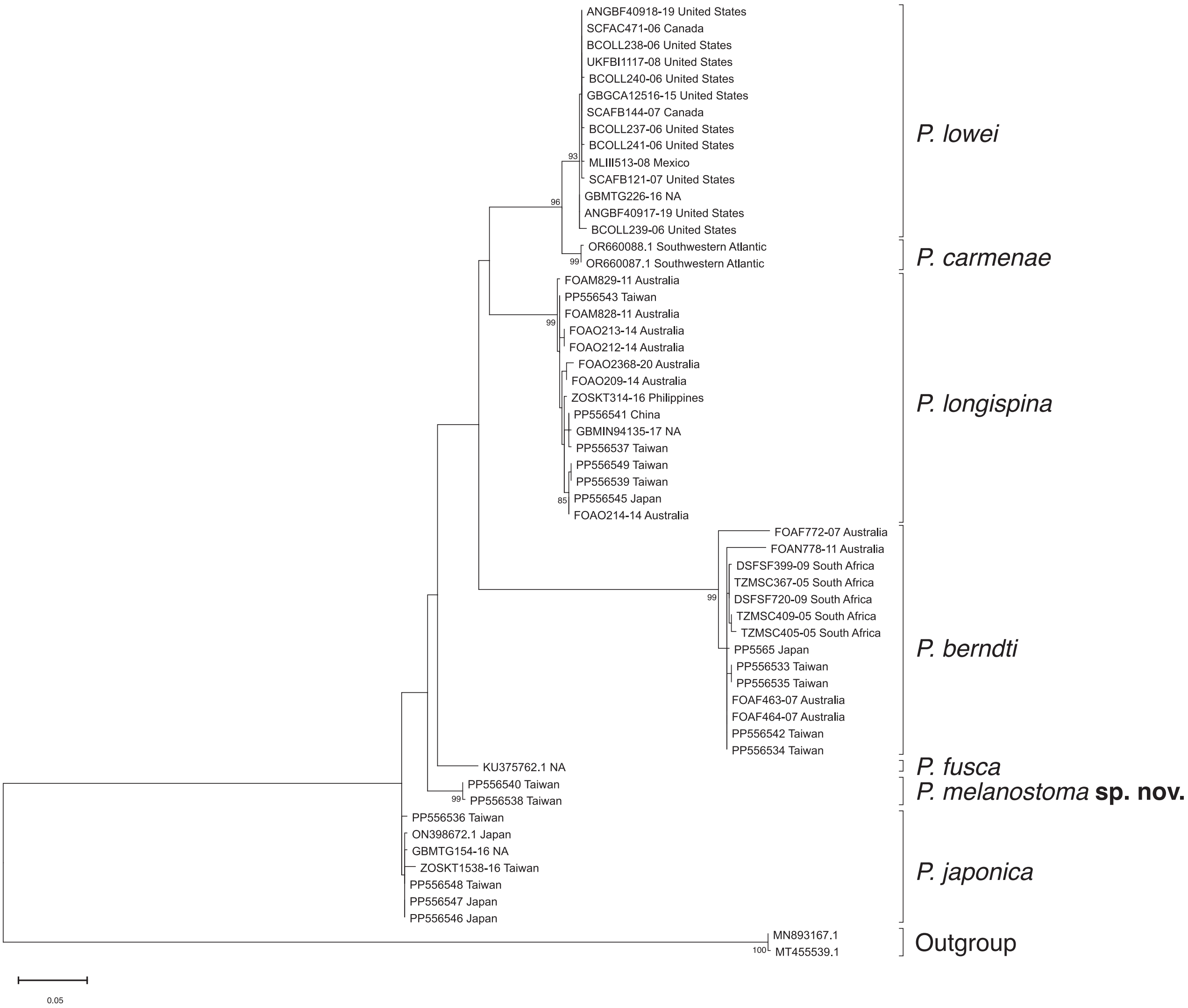

Figure 7. Maximum-likelihood tree reconstructed using *COI* sequence. The number next to each node represents bootstrap value >75%. Scale bar at bottom corner represents the number of substitutions per unit length on the tree.

Comparative materials

Polymixia japonica (20 specimens, 88.7–107.1 mm SL): HUMZ 207076, 104.2 mm SL, Isshiki Fish Market Aichi, Japan, 14 February, 2010; HUMZ 207259, 91.4 mm SL, Numazu fish market, Shizuoka, Japan, 16 February, 2010; HUMZ 226776, 2 specimens, 88.7–89.0 mm SL, 36°29.03"N, 140°57.73"E, off Hitachi, Ibaraki, Japan, 3 November, 2015; HUMZ 231889, 89.3 mm SL, Nishiura fish market, Aichi, Japan, 15 March 2021, *COI*: PP556546; HUMZ 231090, 91.9 mm SL, 36°28'55.20"N, 140°58'44.40"E, off Hitachi, Ibaraki, Japan, 12 November 2019, *COI*: PP556547; NMMB-P39573, 10 specimens, 96.7–105.5 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 6 January 2023, *COI*: PP556536, PP556548; NMMB-P3954, 99.7 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 6 January 2023; NMMB-P39575, 94.6 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 19 February 2023; NMMB-P31551, 107.1 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 31 March 2018; NMMB-P16414, 96.6 mm SL, Dong-gang, Pingtung, northeastern Taiwan, 21 February 2012.

Polymixia berndti (39 specimens, 62.0–173 mm SL): HUMZ 226763, 67.7 mm SL, 36°29'2.40"N, 140°57'43.20"E, off Hitachi, Ibaraki, Japan, 3 November 2015, *COI*: PP556544; NMMB-P39578, 8 specimens, 86.2–134.2 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 6 January 2023, *COI*: PP556533–PP556535; NMMB-P39579, 88.1 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 6 January 2023; NMMB-P39580, 3 specimens, 74.7–130.8 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 14 January 2023; NMMB-P39582, 3 specimens, 85.1–90.5 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 3 November 2022; NMMB-P39581, 15 specimens, 61.9–107.2 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 19 February 2023; NMMB-P29357, 2 specimens, 154–155 mm SL, Nan-Fang-ao, Yilan, northeastern Taiwan, 5 April 2018; NMMB-P36406, 2 specimens, 148.3–151 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 4 March 2022; NMMB-P16154, 155 mm SL, Hualien, eastern Taiwan, 27 May 2010; NMMB-P8730, 173 mm SL, Nanwan, Pingtung, southern Taiwan, 23 June 2005; NMMB-P 35954, 164 mm SL, Kinmen, western Taiwan, 17 July 2020; NMMB-P39583, 148.6 mm SL, Nan-fang-ao, Yilan, northeastern Taiwan, 5 July 2010; NMMB-P39967, 67.8 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 21 August 2023, *COI*: PP556542.

Polymixia longispina (30 specimens, 62.4–135.5 mm SL): HUMZ 229136, 36°55'44.40"N, 141°32'34.80"E, off Iwaki, Fukushima, Japan, 3 November 2017, *COI*: PP556545; NMMB-P39584, 74.2 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 6 January 2023, *COI*: PP556537; NMMB-P9908, 110.7 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009; NMMB-P9902, 135.5 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009; NMMB-P9904, 112.0 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009; NMMB-P36407, 88.9 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 12 March 2022; NMMB-P9060, 2 specimens, 64.6–68.6 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 13 June 2008; NMMB-P9909, 117.4 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009; NMMB-P9903, 131.1 mm SL, Cheng-gung, Taitung, eastern Taiwan, 11 September 2009; NMMB-P9910, 122.3 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009; NMMB-P35563, 3 specimens, 62.4–69.2 mm SL, Dongsha, Kaohsiung, Southern Taiwan, 18 April 2021; NMMB-P36409, 2 specimens, 63.5–66.0 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 9 April 2022; NMMB-P39585, 15 specimens, 99.1–129.4 mm SL, Cheng-gung, Taitung, eastern Taiwan, 4 June 2009, *COI*: PP556539; NMMB-P39586, 2 specimens, 109.4–126.1 mm SL, Cheng-gung, Taitung, eastern Taiwan, 11 September 2009; NMMB-P39969, 66.4 mm SL, Hainan, China, 18 July 2022, *COI*: PP556541; NMMB-P39970, 64.9 mm SL, Dong-gang, Pingtung, southwestern Taiwan, 3 April 2023, *COI*: PP556543.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Y.-C. Fan conducted the experiments and composed the manuscript. Y. Su and C.-W. Chang collected and processed the specimens. Y. Su, C.-H. Lin, and H.-C. Lin revised the manuscript and gave critical comments. H.-C. Lin provided facilities and funding. All authors read and approved the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Research Article

A review of the genus *Pempheris* (Teleostei, Pempheridae) found in Japan and Taiwan

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Abstract

Species of the genus *Pempheris* Cuvier, 1829 (Pempheridae) from Japan and Taiwan are taxonomically reviewed based on morphology supported by molecular phylogenetic analysis. Ten species are recognized from these countries: *Pempheris adusta* Bleeker, 1855, *Pempheris familia* Koeda & Motomura, 2017, *Pempheris japonica* Döderlein, 1883, *Pempheris nyctereutes* Jordan & Evermann, 1902, *Pempheris oualensis* Cuvier, 1831, *Pempheris sasakii* Jordan & Hubbs, 1925, *Pempheris schwenkii* Bleeker, 1877, *Pempheris ufuagari* Koeda, Yoshino & Tachihara, 2013, *Pempheris vanicolensis* Cuvier, 1831, *Pempheris xanthoptera* Tominaga, 1963. Nine of them are distributed in Japan, and five of them in Taiwan. *Pempheris sasakii* and *P. xanthoptera*, nominal species that have been regarded as invalid are revalidated, redescribed with diagnoses based on examinations of the holotypes and the specimens collected from Japan. *Pempheris sasakii* is morphologically similar to *P. nyctereutes* and has been thought to be a senior synonym of the latter, but the comparison of the holotypes and non-types of both species revealed that the former species is distinguishable from the latter species in having fewer counts of body scales, also genetically supported with a 3.1% mitochondrial DNA sequence divergence. *Pempheris xanthoptera* is similar to *P. schwenkii*, but the coloration of their caudal fins is different, and the genetic analysis supported the difference. The distributions of all species of the genus *Pempheris* in Japanese waters are also described, based on the specimen localities from literature and new material herein.

Key words: Distribution, morphology, *Pempheris sasakii*, *Pempheris xanthoptera*, sweepers, taxonomy

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Introduction

The family Pempheridae, also known as sweepers, is a group of nocturnal fish widely distributed in the Indo-Pacific and western Atlantic Ocean. This family is currently divided into two genera: *Parapriacanthus* Steindachner, 1870 and *Pempheris* Cuvier, 1829. The latter is characterized by having anal-fin soft rays numbering 30–45, the anal-fin base covered with scales and longer than 40% of the standard length, the lateral line extending onto the posterior margin of the caudal fin, and the first interhaemal angled toward the posterior end of the dorsal-fin base

(Tominaga 1963). The genus *Pempheris* was first proposed by Cuvier (1829) for *Pempheris touea* Cuvier, 1829, which is presently recognized as a junior synonym of *Pempheris compressa* (Shaw, 1790) (Tominaga 1968). In total, 84 nominal species have been described for the genus to date (Fricke et al. 2024), with almost half of them newly described from the western Indian Ocean from 2014 to 2015 (e.g., Randall and Victor 2014; Randall and Victor 2015). Because the validity of these Indian Ocean species needs to be reassessed, the taxonomy of the whole genus has long been confused due to difficulties in identifying its species.

The taxonomy of the family Pempheridae in Japanese waters was reviewed by Tominaga (1963) based on a comparison of morphology, and he recognized four species of the genus *Pempheris* from Japan. Since then, two new species have been described: *Pempheris familia* Koeda & Motomura, 2017 and *Pempheris ufuagari* Koeda, Yoshino & Tachihara, 2013, and two new-to-Japan species were reported, *Pempheris oualensis* Cuvier, 1831 and *Pempheris vanicolensis* Cuvier, 1831, from the Japanese waters (Koeda et al. 2010a, b, 2013a; Koeda and Motomura 2017a). However, the validity of *Pempheris sasakii* Jordan & Hubbs, 1925 and *Pempheris xanthoptera* Tominaga, 1963, both described from Japan, have never been evaluated. Therefore, the present study conducted a direct comparison of the morphology, including of the type specimens of *Pempheris nyctereutes* Jordan & Evermann, 1902 and *Pempheris schwenkii* Bleeker, 1877. Although many species of the genus commonly distributed in Japan are also found in Taiwan, the taxonomy of the genus in Taiwan has never been reviewed, and misidentifications are occasionally observed in the Taiwanese literature. Here, we reviewed the species of the genus *Pempheris* that occurred in Japan and Taiwan with detailed descriptions, based on the type specimens and large numbers of non-types, providing diagnoses, identification keys, and distributional ranges. Additionally, the published literature which relates to the genus *Pempheris* of Japan and Taiwan was re-examined and corrected as much as possible.

Materials and methods

Preserved materials examined in the present study including large numbers of specimens collected by KK are listed in Suppl. material 1. Comparative materials of the type specimens of species of the genus *Pempheris* are listed in Koeda et al. (2013a, 2014) and Koeda and Motomura (2017a). Counts and measurements followed Koeda et al. (2014). All measurements were made on the left side when possible, using digital calipers and rounded to the nearest 0.1 mm. Standard and head lengths are abbreviated as **SL** and **HL**, respectively. Osteological characters, including vertebral counts, were observed from radiographs. The descriptions of general morphology shared by species of the genus are not repeated here. Data of type specimens are given in parentheses. The distribution maps were made based on the specimens examined and collected by KK, quality underwater photographs, and literature records with a good illustration and/or sufficient diagnostic information to provide for positive identification. Photographs were taken by KK except when a credit line is given. Synonym lists for each species are shown only for the related references for Japan and Taiwan and the original descriptions. Institutional codes used in this study follow Fricke et al. (2024) with an addition: University of the Ryukyus, Ichthyological Laboratory (**URIL**).

The nucleotide sequences of mitochondrial 16S ribosomal RNA (*16S*) and cytochrome oxidase I (*COI*) were analyzed to infer phylogenetic relationships. DNA was extracted from ethanol-fixed specimens and the sequences of *16S* and *COI* were obtained as described by Koeda et al. (2014). We concatenated and aligned the obtained *16S* and *COI* sequences using MAFFT alignment (v. 7.490) (Katoh and Standley 2013) with default settings in Geneious Prime software (v. 2023.2.1) (Biomatters). Uncorrected pairwise distances (p-distances) among the sequences of different specimens were estimated using Geneious Prime software. Phylogenetic relationships were inferred using maximum-likelihood (ML) inference, neighbor-joining (NJ), and Bayesian inference (BI) methods. The ML tree was reconstructed using IQ-TREE 1.6.12 (Trifinopoulos et al. 2016) with a partitioned model for *16S* (sites 1–481) and *COI* (sites 482–837). The best-fit substitution model was chosen by ModelFinder with “Auto” option which automatically selects the best-fit model for each partition. We performed the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT) 1,000 times to assess the nodal support (Guindon et al. 2010). The NJ tree was reconstructed using the Tamura-Nei model, and a consensus tree was generated by resampling 10,000 replicates of bootstrap analysis. The BI tree was constructed with MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001), using the GTR substitution model and the invgamma rate variation model. Four independent Markov chain Monte Carlo (MCMC) runs were conducted for 2,100,000 generations, subsampling trees every 200 cycles, with the initial 100,000 trees discarded as burn-in. The majority rule consensus of the remaining trees was used to determine clade posterior probabilities.

Taxonomic account

Genus *Pempheris* Cuvier, 1829
Standard Japanese name: Hatampo-zoku

Pempheris Cuvier, 1829: 195 [type species: *Pempheris touea* = *Kurtus argenteus* Bloch & Schneider, 1801 = *Sparus*? *compressus* (Shaw, 1790): junior synonym of *Pempheris compressa* (Shaw, 1790)].
Priacanthopsis Fowler, 1906: 122 (type species: *Pempheris mulleri*: junior synonym of *Pempheris schomburgki* Müller & Troschel, 1848)].
Catalufa Snyder, 1911: 528 (type species: *Catalufa umbra*: junior synonym of *Pempheris japonica* Döderlein, 1883).
Liopempheris Ogilby, 1913: 61 (type species: *Pempheris multiradiatus* Klunzinger, 1879).

Description. Body shape oval, strongly compressed laterally; body deep, deepest at or near origin of dorsal fin; dorsal outline of head nearly straight or generally curved from snout to origin of dorsal fin; ventral outline of body generally curved to origin of pelvic fin; body depth rapidly decreases at posterior half of body; depth of caudal peduncle < 1/4 of maximum body depth.

Eye large; snout very short; interorbital space slightly convex or flat; two nostrils located just anterior to anterior margin of eye. Mouth large, strongly oblique; lower jaw slightly project beyond upper jaw; villiform teeth on jaws; tip of tongue free from floor of mouth. Lips thin. Gill opening large; outer margin of opercle and preopercle smooth. Gill membranes on left and right sides separate, free from isthmus. Gill rakers long, 6–13 (upper)+17–28 (lower) on first gill arch.

Body and head almost fully covered by strongly or weakly ctenoid scales except for lips and anterior to eye; ~ 1/3 of basal part of anal fin covered with small scales. Lateral line starts from uppermost position of opercle, generally follows dorsal outer margin, through middle of caudal peduncle, and extending to middle of posterior end of caudal fin. Anus slit-like, located just anterior to anal fin. Light organ present in some species (absent in species distributed in the Northern Hemisphere).

Vertebral counts 10+15 (abdominal + caudal), very rarely 10+16; predorsal interneurals 3; 4th interneural supporting 1st dorsal-fin spine, inserted between 2nd and 3rd vertebrae; last interneural with last dorsal ray inserted between neural spines of 11th and 12th vertebrae, or 12th and 13th. First interhaemal supporting 1st and 2nd anal-fin spine, inserted in front of haemal spine of 11th vertebra, and pointing to posterior end of dorsal fin.

Dorsal fin single, triangular; its base short, shorter than longest ray; 5–7 spines, last longest; 8–13 soft rays, 1st or 2nd longest, rapidly shorter posteriorly. Anal fin low, its base very long, length longer than body depth; three spines, last longest; 24–49 soft rays, 1st longest, gradually shorter posteriorly. Pectoral fin pointed posterodorsally; 15–20 rays, uppermost two rays unbranched, 3rd or 4th ray longest, shorter in lower; pectoral-fin length longer than length of longest dorsal-fin ray. Pelvic fin small, with one spine and five soft rays, 1st longest; last ray not connected to body with membrane. Caudal fin triangular, weakly forked.

Body color uniformly silver, copper, or golden without distinct patterns except for *Pempheris ornata* Mooi & Jubb, 1996 (not in the Northern Hemisphere) which has longitudinal golden stripes on body laterally.

Distribution. Indo-Pacific Ocean: north to southern Japan, east to Easter Island (not including Hawaii Islands), south to Tasmania, west to South Africa, and the Red Sea (some species migrated from the Red Sea to the eastern part of Mediterranean); western Atlantic Ocean: north to Florida; south to Brazil (Mouneimne 1979; Golani and Ben-Tuvia 1986; Golani and Diamant 1991; Koeda et al. 2014).

Remarks. This genus includes a large number of species, and the counts, measurements, and colorations are not very informative in distinguishing them from each other because of the interspecific uniformity and the intraspecific diversity of the results. This had led to significant taxonomic confusions, and the recent jumbled descriptions of abnormally high numbers of new species reported from the Indian Ocean have caused further misunderstandings in the taxonomy of the genus.

Fowler (1906), Snyder (1911), and Ogilby (1913) attempted to divide the genus *Pempheris* into two genera based on scale morphology. Tominaga (1968) described and compared the internal anatomy of many species of the genus and suggested that several species of genus *Pempheris* possess transitional characteristics to the genus *Parapriacanthus*. Therefore, he subdivided the genus *Pempheris* into seven groups. That work indicated that a systematic revision of the genus should be pursued. Although the authors of the present study are now revising the systematic taxonomy of the family Pempheridae on the basis of morphology and molecular approaches, the present classification of the genus *Pempheris* is tentatively used only for the species of Japan and Taiwan.

Molecular phylogenetic analysis using three methods (ML, NJ, and BI) showed consistent topology, except for the placement of *P. ufuagari*. In the ML and BI trees, *P. ufuagari* is positioned as a sister to a clade composed of

P. vanicolensis and *P. oualensis* with low node supporting values. In contrast, the NJ tree places *P. ufuagari* as a sister to a clade composed of *P. vanicolensis* and *P. adusta*. All species analyzed in this study displayed monophyly with high supporting values on their respective nodes.

Key to the species of genus *Pempheris* in Japan and Taiwan (with distributions in parentheses after the species name)

1 12–15 scale rows above lateral line; scales on lateral body strongly ctenoid and adherent, with distinct basal and distal portions (Koeda et al. 2013a: fig. 2b); ventral surface of abdomen rounded, cross-sectional outline U-shaped; coracoid slightly expanded posteriorly; large ventral fenestra between coracoid and cleithrum **2**

– 3½–10½ scale rows above lateral line; scales on lateral body weakly ctenoid and deciduous (Koeda et al. 2013a: fig. 2a), semicircular in shape; ventral surface of abdomen slightly or well keeled, cross-sectional outline V-shaped; coracoid enormously expanded posteriorly; very small ventral fenestra between coracoid and cleithrum **3**

2 69–82 pored lateral-line scales; 12 or 13 scale rows above lateral line; 40–44 predorsal scales; 22–24 circumpeduncular scales; blackish blotch on the pectora-fin base absent or faint .... ***P. japonica*** (southern Japan, Izu Islands, western Japan Sea, rarely in Ryukyu Archipelago; southern Korea)

– 84–88 pored lateral-line scales; 14 or 15 scale rows above lateral line; 50–55 predorsal scales; 26 circumpeduncular scales; distinct pupil-sized blackish blotch on the pectoral-fin base present .... ***P. familia*** (Ogasawara Islands)

3 67–81 pored lateral-line scales; 8½–9½ scale rows above lateral line; 19–27 scale rows below lateral line; snout pointed; scales on ventral and pored lateral-line scales strongly ctenoid; body brownish with golden reflection; lateral line distinctly whitish **4**

– 44–71 pored lateral-line scales; 3½–7½ scale rows above lateral line; 10–18 scale rows below lateral line; snout weakly pointed or rounded; scales on ventral and pored lateral-line scales weakly ctenoid; body pale brown to grey with golden, silver, or copper reflections; lateral line same as uniform color of body **5**

4 67–77 pored lateral lateral-line scales, usually fewer than 73; 19–22 scale rows below lateral line; body brown, with golden reflection in fresh specimen .... ***P. sasakii*** (southern Japan, northern Ryukyu Archipelago)

– 72–81 pored lateral lateral-line scales, usually > 79; 23–28 scale rows below lateral line; body silver to dark brown in fresh specimen...................... .... ***P. nyctereutes*** (Taiwan; Vietnam)

5 44–65 pored lateral lateral-line scales; 3½–6½ scale rows above lateral line; black blotch on pectoral-fin base absent; pectoral fin uniformly pink or bright yellow **6**

– 51–71 pored lateral lateral-line scales; 4½–7½ scale rows above lateral line; black blotch on pectoral fin-base present; pectoral fin uniformly pink or upper half dusky... **8**

6 57–65 pored lateral lateral-line scales; 5½–6½ scale rows above lateral line; 12–15 scale rows below lateral line; body with silver reflection;

pectoral fin bright yellow; outer margin of anal fin distinctly blackish......... .... ***P. vanicolensis*** (Ryukyu Archipelago, Taiwan; western Pacific)

– 44–54 pored lateral lateral-line scales; 3½–4½ (usually 3½) scale rows above lateral line; 10–12 scale rows below lateral line; body with golden or silver reflection; pectoral fin pink; outer margin of anal fin faint blackish or translucent **7**

7 Posterior nostril usually oval, rounded; caudal fin bright yellow .... ***P. xanthoptera*** (southern Japan, Izu Islands, western Japan Sea, northern Ryukyu Archipelago, Ogasawara Islands; southern Korea)

– Posterior nostril usually slit-like; caudal fin pink to brown............................... ***P. schwenkii*** (southern Kyusyu, Ryukyu Archipelago; Taiwan; western Pacific)

8 51–62 pored lateral lateral-line scales; 4½–5½ scale rows above lateral line; black blotch on pectoral-fin base faint, usually on posterior 2/3 of its base....................................***P. adusta*** (southern Japan, Izu Islands, Ryukyu Archipelago, Daito Islands, Ogasawara Islands; Taiwan; western Pacific)

– 60–71 pored lateral lateral-line scales; 6½–7½ scale rows above lateral line; distinct black blotch covering entire pectoral-fin base present..........**9**

9 Usually 7½ scale rows above lateral line; tooth band absent at outside of lips; dorsal and caudal fins bright yellow; pectoral fin uniformly pink; tip of dorsal fin black, but anterior margin not black; outer margin of anal fin distinctly blackish..............***P. ufuagari*** (Daito Islands, Ogasawara Islands)

– Usually 6½ scale rows above lateral line; tooth band present at outside of lips (in large individuals); dorsal and caudal fins brown; upper half of pectoral fin dusky; anterior margin to tip of dorsal fin black; outer margin of anal fin without black coloration..............................***P. oualensis*** (Ryukyu Archipelago, Daito Islands, Ogasawara Islands; Taiwan; Western Pacific)

Pempheris adusta **Bleeker, 1877**

Figs 1, 2, Suppl. material 2
Standard Japanese name: Ryukyu-hatampo

Pempheris adusta Bleeker, 1877: 50, pl. 383, fig. 1 (type locality: Ambon Island, Molucca Islands, Indonesia); Koeda et al. 2013a: 235; Koeda et al. 2013b: 221, fig. 1; Koeda et al. 2013c: 123, fig. 1; Koeda et al. 2014: 303, fig. 1; Motomura and Matsuura 2014: 270, unnumbered figs; Koeda and Motomura 2015: 139, fig. 1; Koeda et al. 2015: 279; Kaburagi 2016: 98, upper fig. (without scientific name; shown as “Ryukyu-hatampo” in Japanese); Koeda et al. 2016a: 519; Koeda et al. 2016b: 50, fig. 224; Koeda et al. 2016c: 8, fig. 3-G; Koeda and Motomura 2017a; Koeda 2017a: 5, fig. 1 (middle fig.); Kimura et al. 2017: 119, fig. 5; Planning and Tourism Division of Kikai Town 2017: 4, unnumbered figs; Nakae et al. 2018: 266; Koeda 2018a: 193, unnumbered figs; Koeda 2018b: 298, unnumbered fig.; Koeda 2018c: 340, unnumbered figs; Mochida and Motomura 2018: 30; Koeda 2019: 926, unnumbered figs; Murase et al. 2019: 132, fig. 283; Fujiwara and Motomura 2020: 28; Koeda 2020a: 407, unnumbered figs; Koeda 2020b: 926, unnumbered figs; Motomura and Uehara 2020: 45; Murase et al. 2021: 166, fig. 339; Koeda et al. 2022: 5; Motomura 2023: 126.

Pempheris mangula (not Cuvier, 1829): Schmidt 1913: 121; Randall and Lim 2000: 622.

Pempheris oualensis (not Cuvier, 1831): Snyder 1912: 497; Okada 1938: 179; Okada and Matsubara 1938: 179; Aoyagi 1948: 49; Matsubara 1955: 590; Tominaga 1963: 289; Honda 1972: 72; Masuda et al. 1975 (in part): 199, pl. 33-D; Yoshino et al. 1975: 75; Hayashi 1984 (in part): 160, pl. 151-E; Shen 1984: 74, pl. 74, fig. 334-1; Shao et al. 1992: 177, unnumbered fig.; Shen 1993: 390, pl. 114 (fig. 1); Shao and Chen 1991: 162, unnumbered fig.; Chen et al. 1995 (probably in part): 25; Mochizuki 1995: 389; Yoshigou et al. 2001: 141; Chen 2003 (in part): 134; Ito 2009: 80, unnumbered fig.; Shao et al. 2008: 254; Chen et al. 2010: 265, fig. D; Chang et al 2011: 46; Shen and Wu 2011: 498, unnumbered fig; Shao et al. 2013 (in part): 163, unnumbered fig. (upper left); Chiang et al. 2014: 183, unnumbered fig.

Pempheris sp.: Uchida 1933: 218 (in part); Senou et al. 2006a: 77; Senou et al. 2007: 56; Hatooka 2002 (in part): 878; Senou et al. 2002: 212; Yoshino 2008: 211, unnumbered figs (lower two); Koeda et al. 2010a: 75; Motomura et al. 2010 (in part): 131; Koeda et al. 2012a: 71; Koeda et al. 2012b: 1086; Hatooka and Yagishita 2013 (in part): 984; Motomura et al. 2013: 169, unnumbered figs.

Pempheris vanicolensis (not Cuvier, 1831): Chen et al. (2010): 266, fig. B.; Shen and Wu 2011: 498, unnumbered fig.

Diagnosis. Counts of holotype and non-types are given in Table 1 of Koeda et al. (2013b). Dorsal-fin spines 5 or 6, very rarely 5, soft rays 8–10, very rarely 8 or 10; anal-fin spines 3, soft rays 37–45, usually > 40; pectoral-fin rays 16–19, usually 17 or 18; pored lateral-line scales 51–62, usually > 54; scale rows above lateral line 4½–5½ (usually 4½); scale rows below lateral line 11–16, usually 12–14; predorsal scales 26–38; circumpeduncular scales 12–18, usually 16; gill rakers 7–10+20–23 = 28–32, usually 8–9+20–22 = 29–31; head length 26.3–31.8% SL; body depth 40.2–47.3% SL; eye diameter 36.0–47.1% HL; upper jaw length 48.1–57.1% HL; maximum 182.7 mm SL, usually < 160 mm SL; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long; body copper to brownish, whiter in nighttime; faint blackish blotch on pectoral-fin base; tip and/or anterior margin of dorsal fin blackish; blackish band on outer margin of anal fin usually absent; blackish or dusky band on posterior edge of caudal fin; narrow band of villiform teeth in jaws; abdomen cross-sectional outline V-shaped.

Distribution. Widely distributed in the western Pacific Ocean excepting small oceanic islands and atolls in central and southeastern Pacific. In Japanese waters, this species is known from Yaizu in Shizuoka Prefecture, Iburi and Otsuki in Kochi Prefecture, Nagasaki in Nagasaki Prefecture, Uchinoura Bay in Kagoshima Prefecture, Hachijo-jima islands in Izu Islands, Tanega-shima to Yonaguni-jima islands in the Ryukyu Archipelago, Minamidaito-jima Island in the Daito Islands, Miyake-jima and Hachijo-jima islands in the Izu Islands, Haha-shima and Chichi-jima islands in the Ogasawara Islands. In Taiwanese waters, this species is known from Daxi in Yilan County, Yeh Liu in New Taipei City, Sihhu in Yunlin County, Tainan County, Checheng County, Hengchung, and Kenting in Pingtung County, Fugang in Taitung County, Lyudao, Lanyu, Xiao Liuqiu, and Penghu (Fig. 2). Common in coral-reef areas of the Ryukyu Archipelago of Japan, the southern coast, and eastern islands (Lyudao and Lanyu) of Taiwan, but few in other areas. Specimens collected from 0–20 m depth.

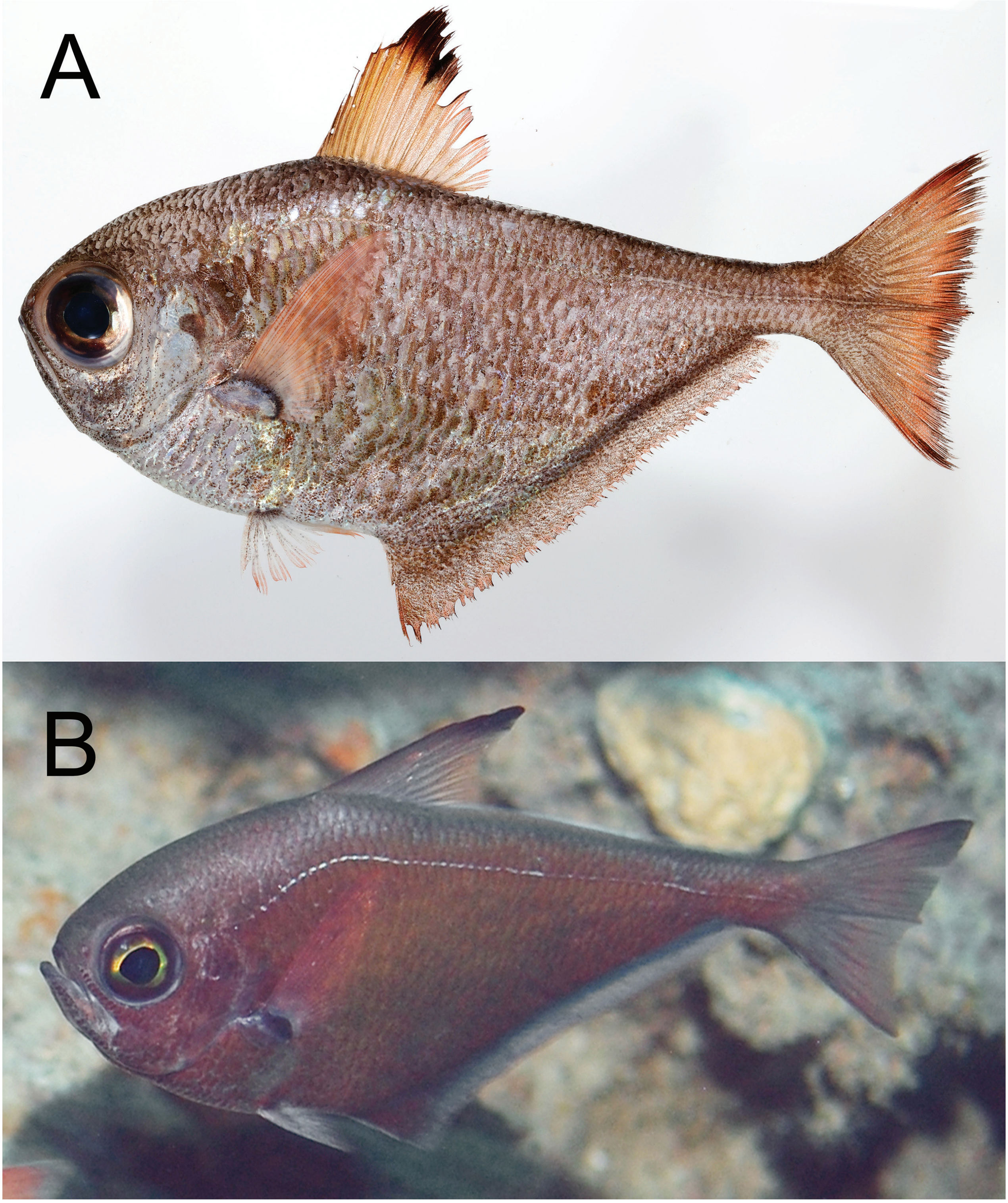

Figure 1. *Pempheris adusta* **A** fresh specimen (ZUMT 62301, Nishidomari, Otsuki, Kochi, Japan) and **B** underwater photograph (Maeda, Onna, Okinawa-jima Island, Japan).

Remarks. Although the taxonomic position of *P. adusta* was unsettled for a long time, the holotype (RMNH.PISC.6161: Ambon, Indonesia) matches well with the specimens in Koeda et al. (2013b). The original description of the species is also supported as follows: figures of six species (*P. mangula* Cuvier, 1829, *P. schwenkii*, *P. vanicolensis*, *P. adusta*, *P. otaitensis* Cuvier, 1831, and

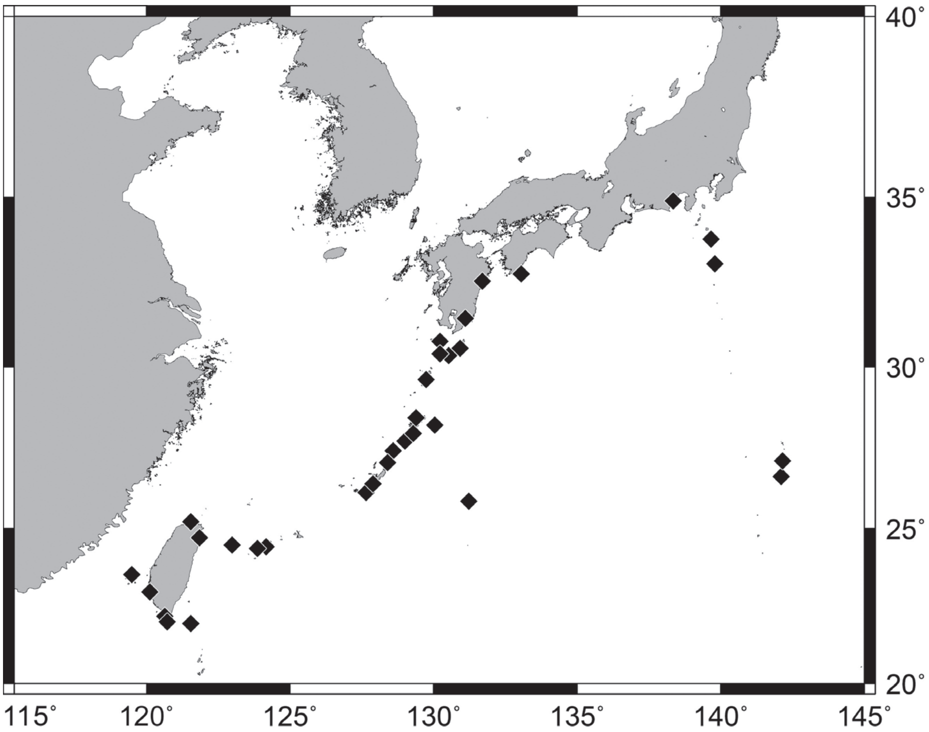

Figure 2. Distribution of *Pempheris adusta* based on the collection localities of specimens.

P. oualensis) were illustrated in the plate of Bleeker (1877); the first three species have no black blotch and the latter three species possess a black blotch on the pectoral-fin base. This was also mentioned in the text descriptions, where he specified that *P. oualensis* and *P. otaitensis* had a black blotch, but *P. adusta* has a black or brown blotch on the pectoral-fin base visible in the figure and clearly corresponding with the descriptions of the three species. Koeda et al. (2014) indicated that *Pempheris adusta* was widely distributed species from the Indian to Pacific oceans and had intraspecific variations in their morphology. The Pacific group differs from the Indian Ocean group in the following characters and individuals from Andaman Sea have characters intermediate between these two groups: pored lateral-line scales 51–62 (vs 56–63 in Indian Ocean; 53–57 in Andaman Sea); scale rows above lateral line usually 4½ (vs usually 5½ in Indian Ocean; 4½ in Andaman Sea); usually no blackish band on anal fin (vs distinct blackish band on outer margin of anal fin in Indian Ocean and Andaman Sea); blackish band on anal-fin base (no band on anal-fin base in Indian Ocean and Andaman Sea); and anterior margin of dorsal fin blackish (tip of dorsal fin blackish in Indian Ocean and Andaman Sea). Furthermore, Koeda et al. (2014) demonstrated that nucleotide sequences of specimens collected from the Red Sea, the Andaman Sea, and the Pacific Ocean showed only 0.4% difference in mitochondrial *16S* ribosomal DNA. Coupled with the observation of small morphological differences, they considered *Pempheris flavicycla* Randall, Satapoomin & Alpermann, 2014 (type locality: Mafia Island, Chole Islands, Chole Bay, Tanzania) to be a junior synonym of *P. adusta*. However, Randall et al. (2014) countered this opinion based on the 2.5% difference in *COI* sequences, stating that *P. adusta* is a species in Pacific Ocean, *P. flavicycla* is the valid species in Indian Ocean, and described the Andaman group as a subspecies *Pempheris flavicycla marisrubri* Randall, Bogorodsky & Alpermann, 2014. Based on the genetic comparison incorporating the *COI* and *16S* genes in the present study, it was shown that there is more than a 2% genetic difference between *P. adusta* and *P. flavicycla* (Fig. 3), which is not a subtle difference when compared to differences among other similar species in the genus. Although the issue of overlapped morphological differences remains in *P. adusta* and *P. flavicycla*, it is reasonable to support the opinion of Randall et al. (2014) that *P. flavicycla* is considered as a valid species distributed in Indian Ocean at the present time.

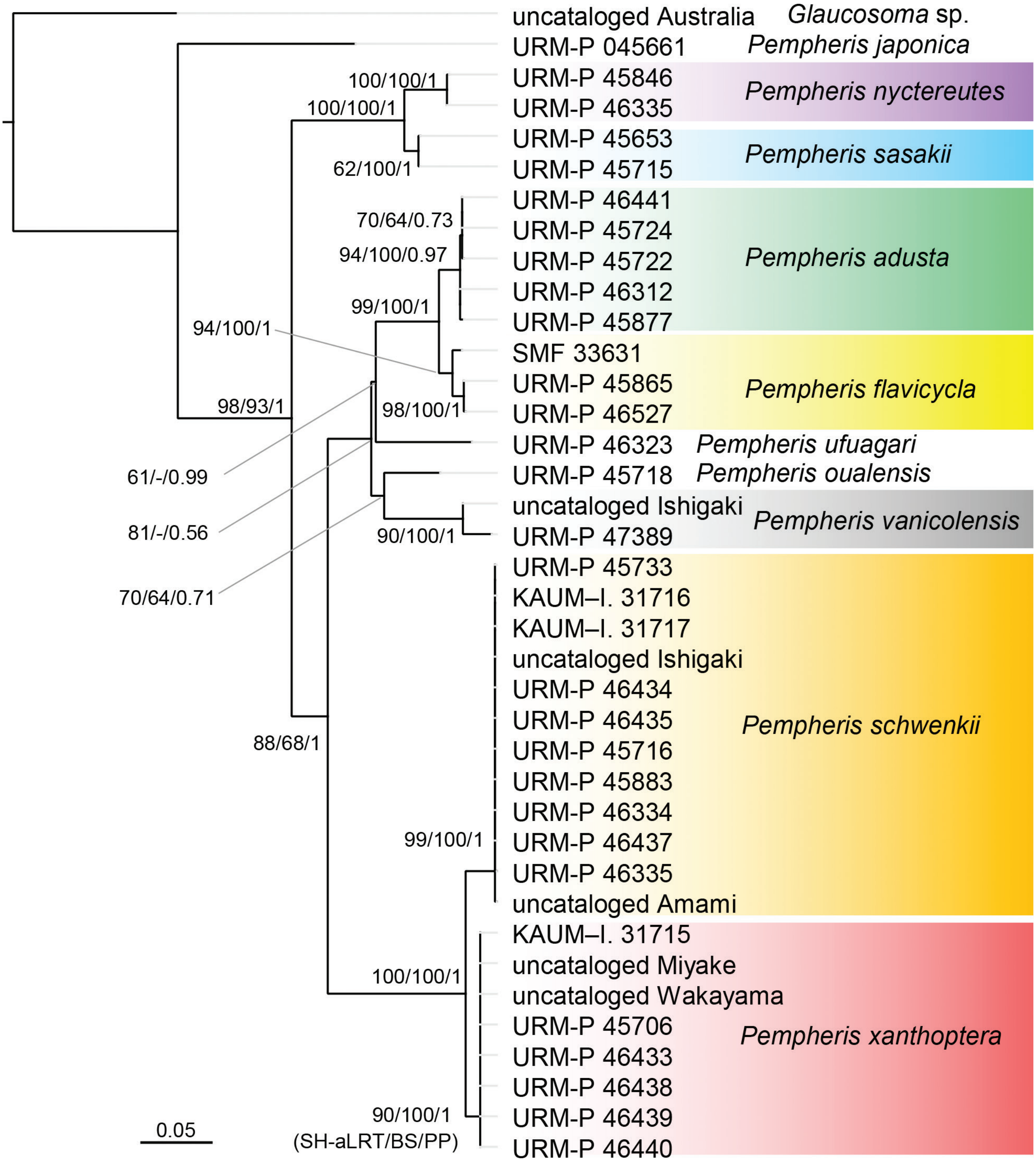

Figure 3. The Maximum-Likelihood (ML) tree of *Pempheris* species recovered from mitochondria *16S* and *COI*. Values of the Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT) for the ML tree, bootstrap values (BS) of the NJ tree, and the posterior probability (PP) for the BI tree are indicated at the nodes unless the branch lengths are < 0.01. The museum voucher number of specimens are listed next to the taxon name.

***Pempheris familia* Koeda & Motomura, 2017**

Figs 4, 5, Suppl. material 2
Standard Japanese name: Bonin-hatampo

Pempheris familia Koeda & Motomura, 2017a: figs 1–3 (type locality: off Ototo-jima Island, Ogasawara Islands, Japan); Koeda 2018b: 299, unnumbered fig.

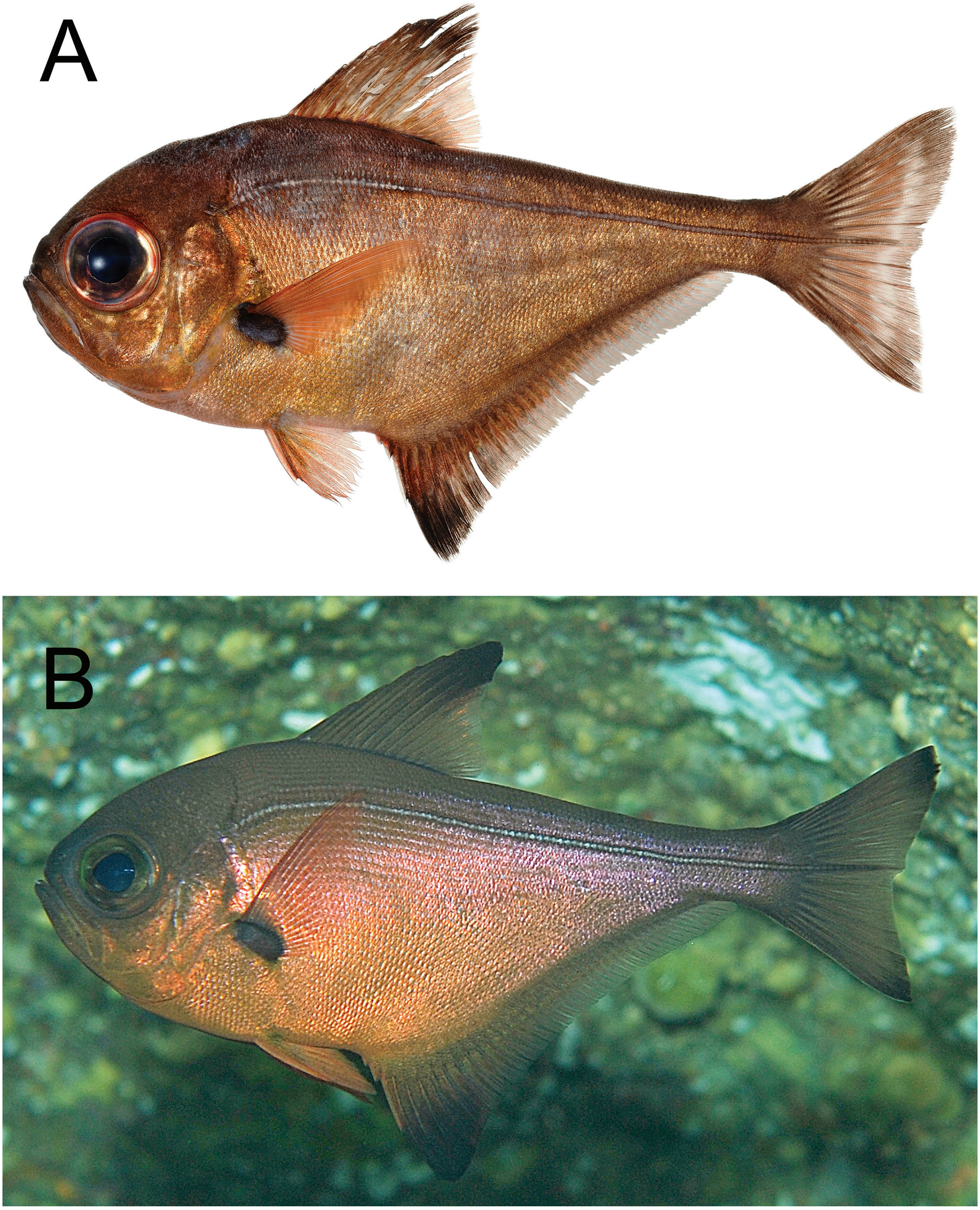

Figure 4. *Pempheris familia* **A** fresh specimen (KAUM–I. 74713, 153.1 mm SL, holotype, Ototo-jima Island, Ogasawara Islands, Japan, photo taken by K. Kuriiwa) and **B** underwater photograph (Ani-jima Island, Ogasawara Islands, Japan).

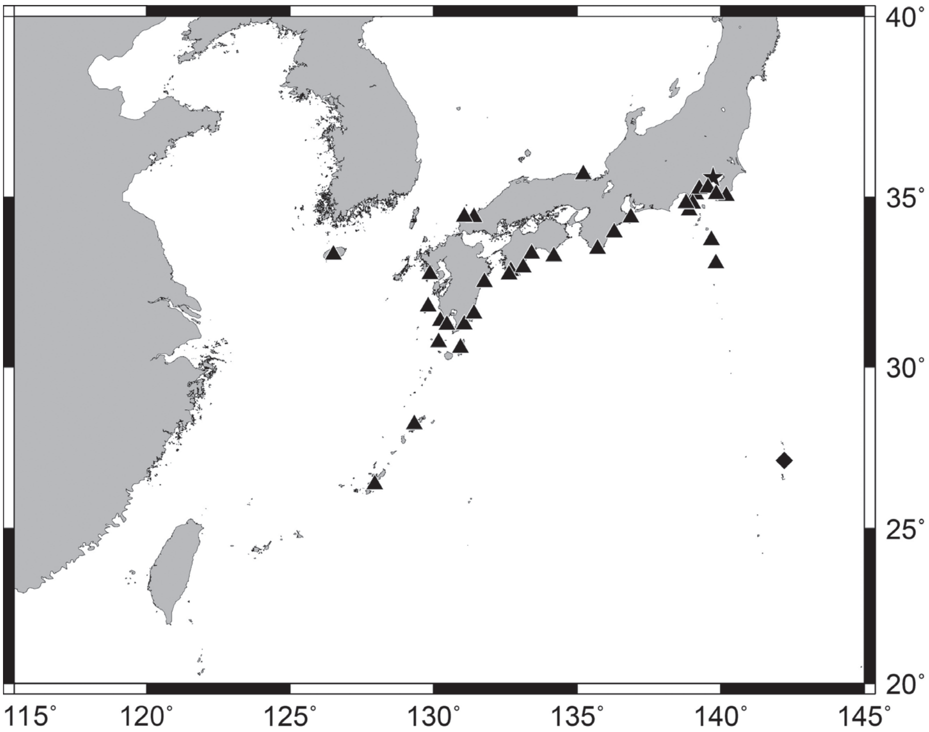

Figure 5. Distribution of *Pempheris familia* (diamond) and *Pempheris japonica* (triangles and star for type locality) based on the collection locality of the specimens.

Pempheris japonica (not Döderlein, 1883): Toyama 1937: 36; Kurata et al. 1971: 25; Zama and Fujita 1977: 102; Randall et al. 1997: 35; Hatooka and Yagishita 2013: 983 (in part); Koeda 2017a: 6, fig. 1 (lower fig.).

Diagnosis. Counts of holotype and paratype are given in Table 1 of Koeda and Motomura (2017a). Dorsal-fin rays VI, 9–10; anal-fin rays III, 35–36; pectoral-fin rays 17; pored lateral-line scales 84–88; scale rows above lateral line 14–15; scale rows below lateral line 28–30; predorsal scales 50–55; circumpeduncular scales 26; gill rakers 12–13+22–26 = 34–39; head length 28.8–30.1% SL; body depth 42.9–43.7% SL; eye diameter 46.8–47.6% HL; upper jaw length 50.0–56.3% HL; maximum 153 mm SL; scales strongly ctenoid, adherent, divided into basal and distal halves (Koeda et al. 2013a: fig. 2b); body copper; distinct blackish blotch on pectoral-fin base; tip of dorsal and anal fins broadly black, and rest brown; narrow band of villiform teeth in jaws; abdomen cross-sectional outline U-shaped.

Distribution. Endemic to the Ogasawara Islands (Fig. 5).

Remarks. *Pempheris familia* is a second species of the species group that is characterized by strongly ctenoid, adherent body scales with distinct basal and distal portions (see Koeda et al. 2013a: fig. 2b) in the Northern Hemisphere shared only with *P. japonica* (Koeda et al. 2012a, 2013a; Koeda and Motomura 2017a). The remaining six species of this group are endemic to Australia, New Zealand, or French Polynesia (Mooi and Jubb 1996; Mooi 1998, 2000). Although *P. familia* shares most morphological characteristics with *P. japonica*, the former can be clearly distinguished from the latter in scale counts and the distinct black blotch on pectoral-fin base (Koeda and Motomura 2017a).

***Pempheris japonica* Döderlein, 1883**

Figs 5, 6, Suppl. material 2
Standard Japanese name: Tsumaguro-hatampo

Pempheris japonica Döderlein, 1883: 125 (type locality: Tokyo, Japan); Jordan et al. 1913: 137; Tanaka 1931: 25; Uchida 1933: 208; Okada 1938: 179; Okada and Matsubara 1938: 179; Matsubara 1955: 590; Tominaga 1963: 278, fig. 6; Takemura and Yasuda 1965: 159; Masuda et al. 1975: 199, pl. 33-B; Hayashi 1984 (in part): 160, pl. 151-C; Kohno 1986: 135, fig. 1; Masuda and Kobayashi 1994: 180, fig. 4; Mochizuki 1995: 389, unnumbered fig.; Hatooka 1997: 380, unnumbered fig.; Hatooka 2002 (in part): 877; Senou et al. 2002: 212; Senou et al. 2006b: 463; Aramata 2007: 171, unnumbered fig.; Yoshino 2008: 211, unnumbered fig.; Koeda et al. 2010a: 74; Koeda et al. 2010b: 81; Motomura et al. 2010: 131; Takagi et al. 2010: 69, unnumbered figs; Kohno et al. 2011: 208, unnumbered fig.; Koeda et al. 2012a: 65; Hatooka and Yagishita 2013 (in part): 983; Koeda et al. 2013b: 235; Motomura et al. 2013: 168, unnumbered fig.; Kawano et al. 2014: 48; Koeda et al. 2014: 327; Koeda and Motomura 2015: 139; Koeda et al. 2015: 275; Ikeda and Nakabo 2015: 159, figs 5–7; Takeuchi et al. 2015: 8; Koeda 2017b: 190, unnumbered fig.; Koeda and Motomura 2017a; Fujiwara et al. 2018: 58, Fig. 8L; Kagoshima City Aquarium Foundation 2018: 210, unnumbered fig.; Koeda 2018b: 298, unnumbered fig.; Nakae et al. 2018: 266; Koeda 2018c: 341, unnumbered figs; Murase et al. 2019: 132, fig. 282; Koeda 2020a: 408, unnumbered figs; Sonoyama et al. 2020: 78; Murase et al. 2021: 166, fig. 338; Koeda 2022: 158, unnumbered fig.; Koeda et al. 2022: 6; Motomura 2023: 127; Sakurai et al. 2024: 77, fig. 4D.
Catalufa umbra Snyder, 1911: 528 (Misaki, Japan).
Catalufa japonica (not Döderlein, 1883): Jordan and Hubbs 1925: 227.
Pempheris umbra (not Snyder, 1911): Okada 1938: 179; Okada and Matsubara 1938: 179; Matsubara 1955: 59, pl. 54 (fig. 189); Takemura and Yasuda 1965: 159; Abekawa and Nishi 1969: 24.

Diagnosis. Counts of syntypes and non-types are given in Table 1 of Koeda and Motomura (2017a). Dorsal-fin rays VI, 10–12; anal-fin rays III, 34–40; pectoral-fin rays 16–17; pored lateral-line scales 69–82; scale rows above lateral line 12–13; scale rows below lateral line 26–30; predorsal scales 40–44; circumpeduncular scales 22–24; gill rakers 8–12+19–25 = 28–35; head length 28.3–31.4% SL; body depth 43.2–47.7% SL; eye diameter 38.1–50.0% HL; upper jaw length 50.0–56.3% HL; maximum 153 mm SL; scales strongly ctenoid, adherent, divided into basal and distal halves (see Koeda et al. 2013a: fig. 2b); body copper; no or faint blackish blotch on pectoral-fin base; tip of dorsal and anal fins broadly black, remainder brown; narrow band of villiform teeth in jaws; abdomen cross-sectional outline U-shaped.

Distribution. Endemic to the region from southern Korea to southern Japan. In Japanese waters, *P. japonica* is distributed in the Pacific coast (north to Ishinomaki in Miyagi Prefecture, south to Kagoshima Prefecture), Japan Sea coast (east to Miyazu in Kyoto Prefecture, west to Tsuno-shima Island in Yamaguchi Prefecture), Tsushima Island, East China Sea coast (north to Nagasaki, south to Kagoshima prefectures), Miyake-jima and Hachijo-jima islands in Izu Is-

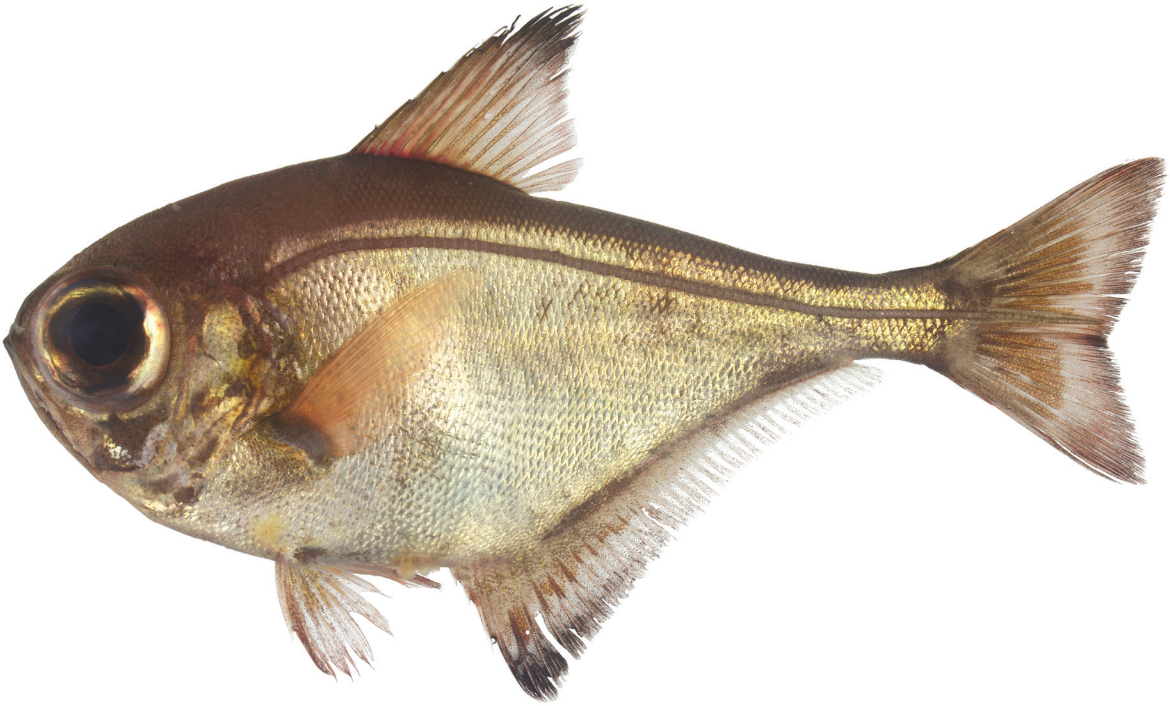

Figure 6. Fresh specimen of *Pempheris japonica*, KAUM–I. 89834, 125.0 mm SL, Nakakoshiki-jima Island, Koshiki Islands, Japan.

lands, Tanega-shima, Yaku-shima, Iou-jima, Amami-oshima, and Okinawa-jima in Ryukyu Archipelago (very rare in the latter two islands) (Fig. 5).

Remarks. Döderlein (1883) described *P. japonica* based on syntypes collected from Tokyo Bay, and Snyder (1911) described *Catalufa umbra* based on the holotype collected from Kanagawa Prefecture. The type specimens of the two nominal species were compared in the present study, and no differences were observed. Therefore, *C. umbra* is confirmed as a junior synonym of *P. japonica*, in agreement with Tominaga (1963).

Snyder (1912) and Shao et al. (2008) reported *P. japonica* in the fish checklists of Okinawa Island and southern Taiwan, respectively. However, the specimens they observed and identified as *P. japonica* (CAS-SU 22002; ASIZP 61383) are identified as *P. schwenkii* and *P. vanicolensis*, respectively (Koeda et al. 2012a). Subsequently, Randall et al. (1997) reported *P. japonica* from the Ogasawara Islands. However, that report was not based on specimens and/or underwater observations (refer to pers. comm. of R. Mooi on p. 35) and was probably the misidentification of *P. familia* which is similar to *P. japonica*. Although Hayashi (1984) and Hatooka (2000, 2002) included the Philippines, and Hatooka and Yagishita (2013) included Taiwan in the distributional range of *P. japonica*, specimens of *P. japonica* from these localities have never been discovered. Our results indicate that *P. japonica* is not distributed in these localities, and the species is endemic to Japan and southern Korea. Compared to the distribution of other species of the same genus found in the Northern Hemisphere, this species can be said to be the most temperate species adapted to the lowest water temperatures. Until the 2010s, this species was distributed only as far as the Boso Peninsula, a trend known for many tropical fish species. However, in recent years, new distribution records have been reported from Fukushima and Miyagi Prefectures, likely a result of northward range expansion due to global warming.

Pempheris nyctereutes **Jordan & Evermann, 1903**
Figs 7, 8; Table 1, Suppl. material 2
Standard Japanese name: Taiwan-hatampo

Pempheris nyctereutes Jordan & Evermann, 1903: 339, fig. 14 (type locality: Taipei City [Hokoto], Taiwan); Okada 1938: 179; Okada and Matsubara 1938: 179; Matsubara 1955:590; The Marine Ecological Researching Society of Kagoshima University 1966: 19; Shen 1993: 390, unnumbered fig.; Koeda et al. 2013a: 237; Koeda et al. 2014: 327; Tominaga 1963: 281, fig. 8; Hayashi 1984 (in part): 161; Randall and Lim 2000: 622; Hatooka 2002 (in part): 877; Hatooka and Yagishita 2013 (in part): 984; Shen and Wu 2011: 497, unnumbered fig.; Chiang et al. 2014: 183, unnumbered fig.; Koeda 2019: 927, unnumbered figs; Koeda 2020b: 927, unnumbered figs; Koeda et al. 2022: 9.

Pempheris schwenkii (not Bleeker, 1855): Lee 1996: 97, unnumbered fig.

Diagnosis. Counts of holotype and non-types are given in Table 1. Dorsal-fin rays VI, 9; anal-fin rays III, 42–44; pectoral-fin rays 18–20; pored lateral-line scales 72–81 usually > 79; scale rows above lateral line 8 1/2–9 1/2; scale rows below lateral line 23–28; circumpeduncular scales 22–24; gill rakers 8+19–20 = 27–28; head length 30.0–30.9%; body depth 44.6–46.9%; eye diameter 41.0–46.4%; upper jaw length 51.3–53.5%; maximum 161 mm SL; snout sharp; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (see Koeda et al. 2013a: fig. 2a); body silver to dark brown in fresh specimens; tip and anterior margin of dorsal fin zonally blackish; anal fin pale with faint black band on base; paired fins pink; posterior half of caudal fin dusky; body light brown in fixed specimen; black pigmentation on each fin usually persistent, but not in holotype; no blackish blotch on pectoral-fin base; narrow band of villiform teeth in jaws; abdomen cross-sectional outline is V-shaped.

Distribution. Recorded only from Taiwan, Hong Kong, and Vietnam. In Taiwanese waters, this species is known from Nang-fang-ao in Yilan County, Keelung City, Aodi, Wanli, and Gongliao in New Taipei City, Tainan County, Fugang in Taitung County, Hengchung and Maobitou in Pingtung County, Lyudao, and Penghu (Fig. 8).

Remarks. The taxonomic status of *P. nyctereutes* and *P. sasakii* that have similar morphology have been commonly confused. A comparison between these two species is discussed in the remarks for *P. sasakii*. *Pempheris nyctereutes* is sometimes collected by fisherman in southern Taiwan as bycatch with *P. schwenkii* and *P. adusta*, which are mainly distributed in coral-reef areas, suggesting that *P. nyctereutes* might be distributed in coral-reef areas. This species is also known from Ha Long Bay in Vietnam (FRLM 49700; Koeda 2018d) and Hong Kong (BMNH 1939.3.23.48). Okada (1938), Okada and Matsubara (1938), and Matsubara (1955) admitted *P. nyctereutes* and *P. sasakii* as valid species being endemic to Taiwan and Japan, respectively, and Okada (1938) gave the Japanese name “Taiwan-hatampo” and “Mie-hatampo” to them. Tominaga (1963) later proposed “Takasago-hatampo” for *P. nyctereutes* as a new Japanese name without any reasons (probably overlooking the original designation), and Koeda et al. (2022) followed that. Based on Rule 6 of the guidelines for the naming of standard Japanese names for fishes (The Ichthyological Society of Japan 2021), “Taiwan-hatampo” proposed by Okada (1938) should be adopted for *P. nyctereutes*.

Figure 7. Fresh specimen of *Pempheris nyctereutes*, NMMB-P 27469, 149.4 mm SL, Penghu, Taiwan.

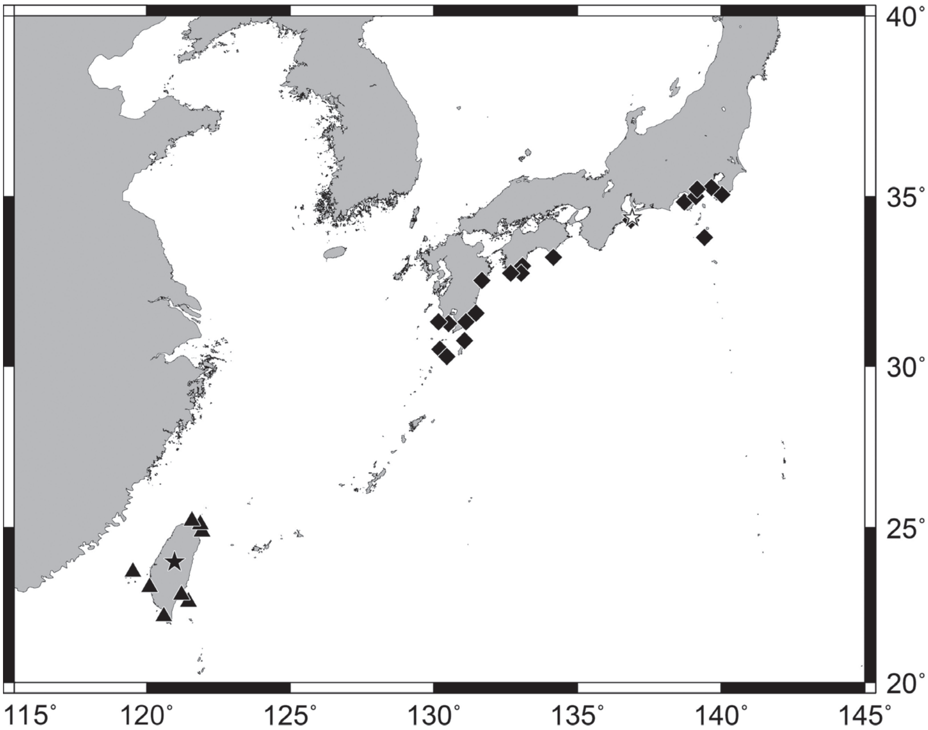

Figure 8. Distribution of *Pempheris nyctereutes* (solid triangles and solid star for holotype locality) and *Pempheris sasakii* (solid diamonds and open star for holotype locality) based on the collection localities of the specimens.

Table 1. Counts of *Pempheris nyctereutes* and *P. sasakii*.

	P. nyctereutes		***P. sasakii***	
	Holotype	**Non-types**	**Holotype**	**Non-types**
Number of individuals	1	18	1	47
Standard length (mm)	160.5	100.5–162.4	93.1	87.7–169.8
Dorsal fin rays	VI, 9	VI, 9	VI, 9	VI–VII, 9–10
Anal fin rays	III, 44	III, 42–44	III, 43	III, 40–46
Pectoral fin rays	19	18–20	19	17–20
Left pored lateral-line scales	79	72–81	72	67–78
Right pored lateral-line scales	77	74–82	73	66–78
Scale above lateral line	8 1/2	8 1/2–9 1/2	8 1/2	8 1/2–10 1/2
Scale rows below lateral line	23	23–28	22	19–22
Circumpeduncular scales	22	22–24	damaged	24
Gill rakers	8+20	8+19–20	8+19	7–9+19–22

Pempheris oualensis **Cuvier, 1831**

Figs 9, 10, Suppl. material 2
Standard Japanese name: Yume-hatampo

Pempheris oualensis Cuvier in Cuvier & Valenciennes, 1831: 299 (type locality: Kosrae, Caroline Islands); Masuda et al 1975 (in part): 199; Hayashi 1984 (in part): 161; Chen et al. 1995 (probably in part): 25; Shao et al. 2008: 254; Koeda et al. 2010a: 72, fig. 1; Koeda et al. 2010b: 81; Koeda et al. 2012a: 71; Koeda et al. 2013a: 231, fig. 1b; Koeda et al. 2013b: 126; Koeda et al. 2014: 327; Koeda and Motomura 2015: 139; Koeda et al. 2015: 276, fig. 1; Koeda et al. 2016b: 50, fig. 225; Koeda and Motomura 2017a; Koeda 2017a: 7, fig. 2 (upper fig.); Kimura et al. 2017: 119, fig. 7; Planning and Tourism Division of Kikai Town 2017: 4, unnumbered figs; Nakae et al. 2018: 266; Koeda 2018a: 194, unnumbered figs; Koeda 2018b: 298, unnumbered fig.; Mochida and Motomura 2018: 30; Koeda 2019: 928, unnumbered figs; Motomura and Uehara 2020: 45; Koeda 2020b: 928, unnumbered figs; Motomura 2023: 129.

Pempheris otaitensis (not Cuvier, 1831): Schmidt 1913: 121; Randall et al. 1997 (in part): 35, pl. 8 (fig. F).

Pempheris sp.: Hatooka 2002 (in part), 878; Motomura et al. 2010 (in part): 131, fig. 253; Hatooka and Yagishita 2013 (in part): 984.

Diagnosis. Counts of holotype and non-types are given in Table 2 of Koeda et al. (2010a). Dorsal-fin rays VI, 9–10; anal-fin rays III, 38–46; pectoral-fin rays 17–19; pored lateral-line scales 60–72; scale rows above lateral line 5 1/2–7 1/2, usually 6 1/2; scale rows below lateral line 13–17; predorsal scales 33–44; circumpeduncular scales 18–22; gill rakers 8–9+20–22 = 28–31; head length 27.7–31.5%; body depth 40.9–48.2%; eye diameter 36.4–43.9%; upper jaw length 50.0–56.0%; maximum 208 mm SL, usually < 180 mm SL; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (Koeda et al. 2013a: fig. 2a); body silver; distinct blackish blotch on pectoral-fin base; anterior margin of dorsal fin

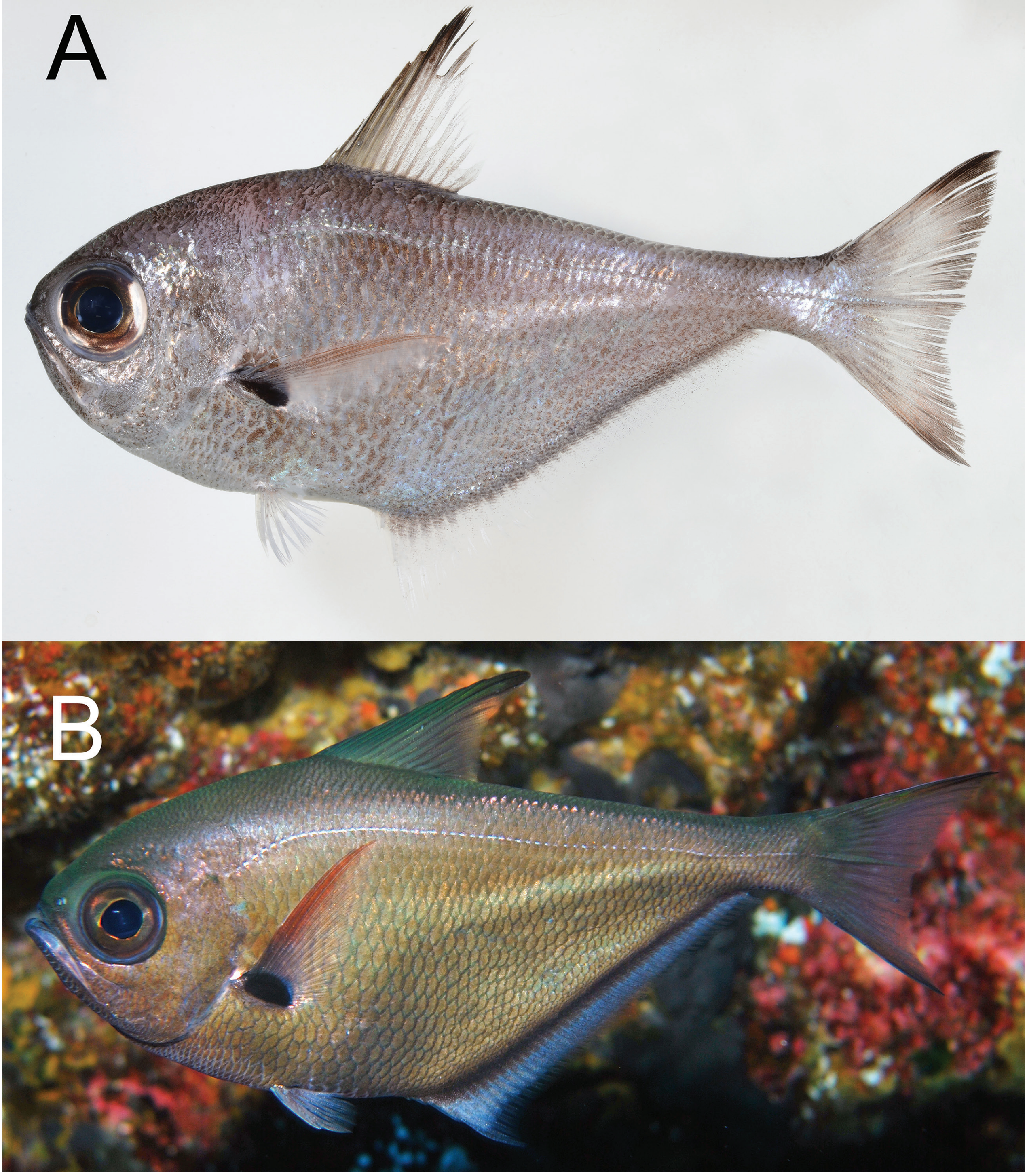

Figure 9. *Pempheris oualensis* **A** fresh specimen (NMMB-P 27821, 175.4 mm SL, Hengchung, Pingtung, Taiwan) and **B** underwater photograph (Dobuiso, Ogasawara Islands, Japan).

zonally blackish; blackish band on anal-fin base with rarely blackish band on its margin; upper margin of pectoral fin dusky; villiform tooth band extending outside lips on large specimen; abdomen cross-sectional outline V-shaped.

Distribution. Widely distributed in the western to central Pacific Ocean (not in the Hawaiian Islands), and Christmas Island and Cocos-Keeling Island in the Indian Ocean. In Japanese waters, this species is known from Tanega-shima to Yonaguni-jima islands in the Ryukyu Archipelago, Minamidaito-jima Island in

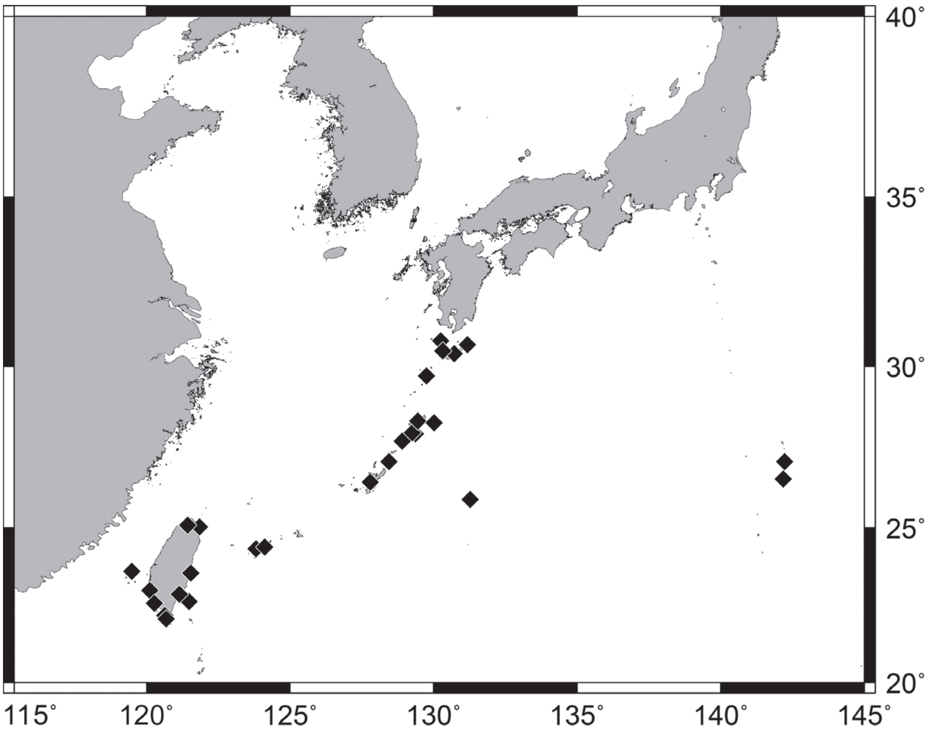

Figure 10. Distribution of *Pempheris oualensis* based on the collection locality of the specimens.

the Daito Islands, and Haha-shima and Chichi-jima islands in the Ogasawara Islands. In Taiwanese waters, this species is known from Nang-fang-ao in Yilan County, Yeh Liu in New Taipei City, Tainan County, Chung-chou in Kaohsung County, Hengchung, and Kenting in Pingtung County, Fugang in Taitung County, and Lanyu (Fig. 10).

Remarks. This species has similar characters as *Pempheris otaitensis* Cuvier, 1831 and *Pempheris ufuagari* which share a distinct black blotch on pectoral-fin base and whose large body sizes reaches > 160 mm SL. However, *P. oualensis* is unique in having a dark coloration on the upper margin of its pectoral fin and a villiform tooth band extends outside the lips on large specimens. The scale count of this species varies among populations that specimens collected from the northwestern Pacific have 61–66 pored lateral-line scales, but specimens collected from southern Pacific have 67–71. Additionally, specimens collected from Andaman Sea have 5½ scale rows above lateral line, whereas those from the Pacific Ocean have 6½ or 7½, with the frequency of specimens with 7½ scale rows above lateral line being lower in the northwestern Pacific than in southern areas. In particular, the Andaman population may be a species distinct from the Pacific populations, but more specimens and genetic evidence are necessary to discuss whether the differences are interspecific or intraspecific.

Although Okada (1938) gave the Japanese name "Ryukyu-hatampo" to *P. oualensis* which was listed in Snyder (1912), specimen (USNM 75468) used for the list was re-identified to *P. adusta* (Koeda et al. 2013b). Therefore, the standard Japanese name "Ryukyu-hatampo" was adopted for *P. adusta* and the standard Japanese name "Yume-hatampo" was provided to *P. oualensis* by Koeda et al. (2010a) who first reported this species from Japanese waters.

This species is the largest species of *Pempheris* that reaches > 200 mm SL; the largest specimen was collected from the Ogasawara Islands and measured 208.8 mm SL (KAUM–I. 74584).

Pempheris sasakii **Jordan & Hubbs, 1925**

Figs 8, 11, Suppl. material 2
Standard Japanese name: Mie-hatampo

Liopempheris sasakii Jordan & Hubbs, 1925: 228, pl. 10, fig. 1 (type locality: Toba, Mie Prefecture, Japan); Tanaka 1931: 25.

Pempheris sasakii: Uchida 1933: 217; Okada 1938: 179; Okada and Matsubara 1938: 180; Matsubara 1955: 590; Tominaga 1963: 283, fig. 10; Koeda et al. 2013a: 231; Koeda et al. 2014: 327.

Pempheris nyctereutes (not Jordan & Evermann, 1903): Hayashi 1984 (in part): 160, pl. 350-G; Hatooka 2002 (in part): 879; Senou et al. 2006b: 463; Koeda et al. 2010a: 75; Koeda et al. 2010b: 81; Hatooka and Yagishita 2013 (in part): 984; Koeda and Motomura 2015: 139; Koeda et al. 2015: 275; Ikeda and Nakabo 2015: 160, figs 4–6; Kaburagi 2016: 99, upper fig. (without scientific name; shown as “Mie-hatampo”); Kimura et al. 2017: 119, fig. 6; Kagoshima City Aquarium Foundation 2018: 210, unnumbered fig.; Koeda 2018b: 298, unnumbered fig.; Koeda 2018c: 342, unnumbered figs; Murase et al. 2019: 132, fig. 285; Koeda 2020a: 409, unnumbered figs; Murase et al. 2021: 166, fig. 341; Koeda 2022: 158, unnumbered fig.; Koeda et al. 2022: 9; Motomura 2023: 128.

Diagnosis. Counts of holotype and non-types are given in Table 1. Dorsal-fin rays VI–VII, 9–10; anal-fin rays III, 40–46; pectoral-fin rays 17–20; pored lateral-line scales 67–78, usually fewer than 73; scale rows above lateral line 8½–10½; scale rows below lateral line 19–22; circumpeduncular scales 24; gill rakers 7–9+19–22 = 28–30; head length 28.1–29.7%; body depth 40.6–44.6%; eye diameter 38.9–43.2%; upper jaw length 50.0–55.6%; maximum 170 mm SL; snout sharp; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (see Koeda et al. 2013a: fig. 2a); dorsal half of body brown, with golden reflection in fresh specimen; ventral half golden; tip and anterior margin of dorsal fin zonally blackish; faint blackish band on anal-fin base; dusky band on outer edge of anal fin; paired fins pink; posterior half of caudal fin dusky; body pale brown in fixed specimen; black pigmentation on each fins usually persistent, but not in holotype; no blackish blotch on pectoral-fin base; narrow band of villiform teeth in jaws; abdomen cross-sectional outline V-shaped.

Distribution. Endemic to southern Japan known from Tateyama at Boso Peninsular in Chiba Prefecture, Misaki and Manazuru in Kanagawa Prefecture, Nishi-izu at Izu Peninsular in Shizuoka Prefecture, Toba and Shima in Mie Prefecture, Muroto, Susaki, Tosashimizu, Iburi, and Otsuki in Kochi Prefecture, Nobeoka and Nango in Miyazaki Prefecture, Uchinoura Bay, Kagoshima Bay, Ibusuki, and Minami-satsuma in Kagoshima Prefecture, Miyake-jima Island in Izu Islands, Tanega-shima, Yaku-shima, and Kuchinoerabu-jima islands in the northern Ryukyu Archipelago (Fig. 8).

Remarks. *Pempheris sasakii* has been commonly confused with *P. nyctereutes* and has been presumed to be the junior synonym (e.g., Hayashi 1984), even

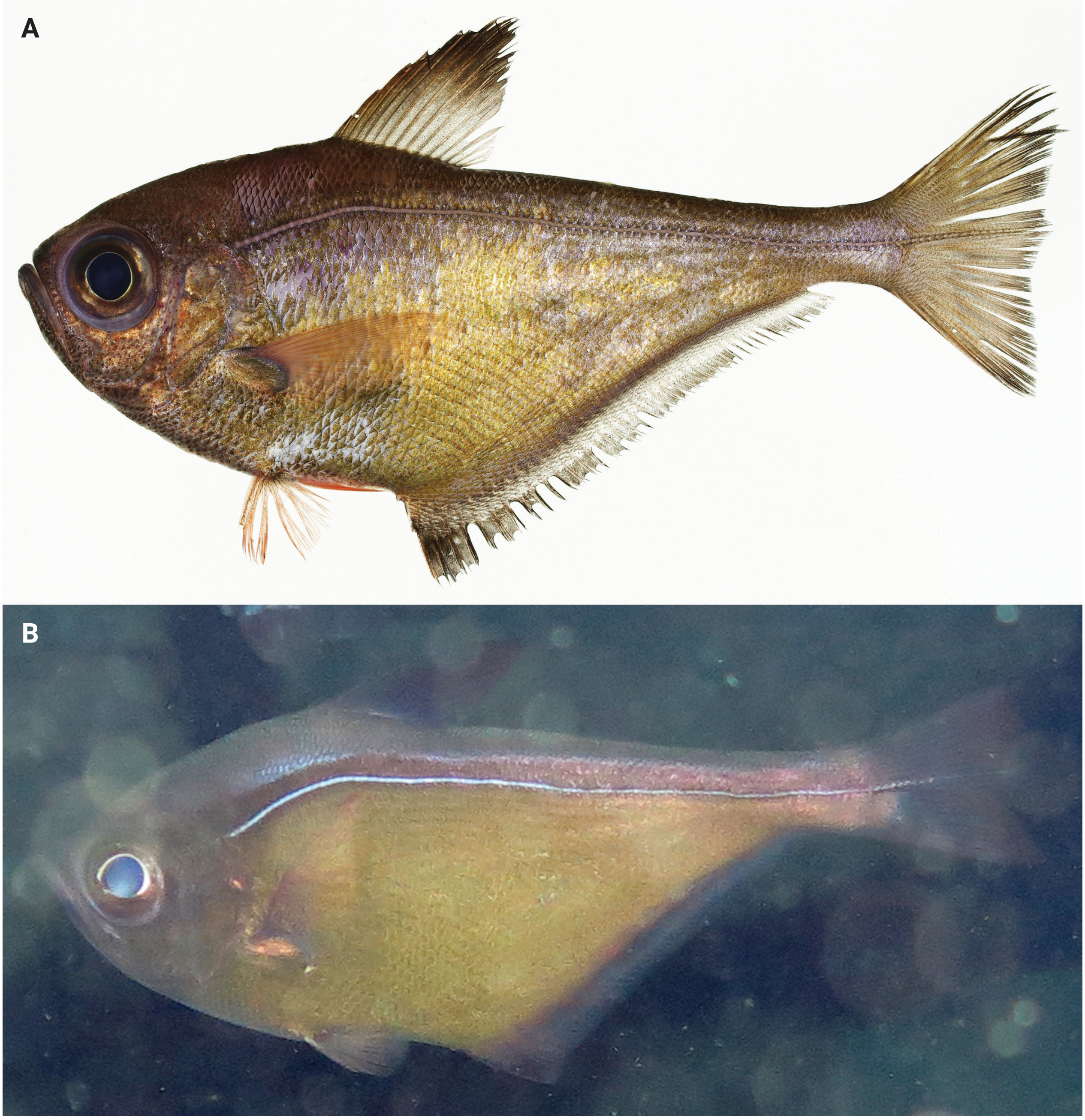

Figure 11. *Pempheris sasakii* **A** fresh specimen (KAUM–I. 94368, 126.7 mm SL, Uchinoura Bay, Kimotsuki, Kagoshima) and **B** underwater photograph (lower: Minamisatsuma, Kagoshima, Japan).

though both species were described by the same first author. Only Tominaga (1963) showed the difference in anal fin coloration (*P. sasakii*: margin of anal fin fuscous vs *P. nyctereutes*: margin of anal fin pale) between these two species and described the details of both as valid species. In our morphological observations, however, several *P. nyctereutes* specimens have dusky margins on the anal fin; thus, this character was not diagnostic for identifying those species. The present comparison based on both species indicated that these two species can be distinguished by the counts of scale rows below lateral line (19–22 in *P. sasakii* vs 25–27 in *P. nyctereutes*) with modal difference of pored lateral-line scales (72–81 usually > 79 vs 67–78 usually fewer than 73). The coloration of the species slightly differs in that the former has golden body (sometimes silverish) in fresh condition, but the latter has copper to silver coloration: compare Figs 7, 11). Although the morphological differences between the two species are very few, the molecular analyses strongly supported the intraspecific difference which revealed that sequences of *P. nyctereutes* and *P. sasakii* differed by more than 3.1% over mitochondrial *16S* ribosomal DNA and *COI*, comprising different monophyletic groups (Fig. 3).

Pempheris sasakii is widely distributed in the Pacific coast of southern Japan, and commonly collected by set nets (but not abundant compared to *P. xanthoptera*). However, no specimens of this species have ever been collected from the Japan Sea coast, East China Sea coast, and the Ryukyu Archipelago. The distributions of both *P. sasakii* and *P. nyctereutes* are clearly isolated from each other (Fig. 8).

***Pempheris schwenkii* Bleeker, 1855**

Figs 12, 13, Suppl. material 2
Standard Japanese name: Minami-hatampo

Pempheris schwenkii Bleeker, 1855: 314 (type locality: Batu Islands, Sumatera Utara Province, Indonesia); Hatooka 1997 (in part): 380, unnumbered fig. (p. 381, lower middle fig.); Randall and Lim 2000: 622; Hatooka 2002 (in part): 878; Yoshigou and Nakamura 2002: 107; Yoshigou and Nakamura 2003: 49; Yoshigou 2004: 19; Chen 2003: 134, unnumbered fig.; Senou et al. 2006a: 77; Senou et al. 2007: 56; Shao et al. 2008: 254; Yoshino 2008 (in part): 211; Ito 2009: 80, unnumbered fig.; Chen et al. 2010: 265, fig. C, E; Koeda et al. 2010a: 75; Koeda et al. 2010b: 81; Motomura et al. 2010: 131, fig. 252; Shen and Wu 2011: 498, unnumbered fig.; Koeda et al. 2012a: 71; Koeda et al. 2012b: 1086; Miura 2012: 59 (without scientific name; shown as "Minami-hatampo"); Chiang et al. 2014: 183, unnumbered fig.; Hatooka and Yagishita 2013 (in part): 984; Koeda et al. 2013a: 235; Koeda et al. 2013b: 222, fig. 1; Koeda et al. 2013c: 126; Motomura et al. 2013 (in part): 168; Shao et al. 2013 (in part): 163, unnumbered fig. (lower); Koeda et al. 2014: 314; Koeda and Motomura 2015: 139 ; Motomura and Matsuura 2014: 271, unnumbered figs; Koeda et al. 2015: 275; Koeda et al. 2016a: 519; Koeda et al. 2016c: 8, fig. 3H; Koeda and Motomura 2017a; Koeda and Motomura 2017b: 266, fig. 3D, E; Kimura et al. 2017 (in part): 120, fig. 1; Planning and Tourism Division of Kikai Town 2017: 4, unnumbered figs; Nakae et al. 2018: 266; Koeda 2018b: 298, unnumbered fig. (lower right fig.); Koeda 2018b: 194, unnumbered figs; Mochida and Motomura 2018: 30; Koeda 2019: 929, unnumbered figs; Fujiwara and Motomura 2020: 28; Koeda 2020b: 929, unnumbered figs; Motomura and Uehara 2020: 45; Koeda et al. 2022: 10; Motomura 2023: 129 (in part).
Pempheris adusta (not Bleeker, 1877): Shimose 2021: 122, fig. B.
Pempheris japonicus (not Döderlein, 1883): Snyder 1912: 497.
Pempheris oualensis (not Cuvier, 1831): Chen 2003: 134, unnumbered fig.; Shao and Chen 2003: 255, unnumbered figs; Yang et al. 2013: 167, unnumbered fig.
Liopempheris vanicolensis (not Cuvier, 1831): Jordan and Hubbs 1925: 229.
Pempheris vanicolensis (not Cuvier, 1831): Okada 1938: 179; Okada and Matsubara 1938: 179 (in part); Matsubara 1955: 590 (in part); Aoyagi 1948: 49; The Marine Ecological Researching Society of Kagoshima University 1966: 19; The Marine Ecological Researching Society of Kagoshima University

1967: 32; Takahashi 1970: 58; Chen et al. 2010: 266, fig. A; Chang et al 2011: 46.

Pempheris xanthoptera Tominaga, 1963 (in part paratypes): 287; Masuda et al 1975 (in part): 199, pl. 33-C; Yoshino et al. 1975: 75; Hayashi 1984 (in part): 160.

Pempheris sp.: Uchida 1933: 218 (in part).

Diagnosis. Counts of holotype and paratypes are given in Table 2. Dorsal-fin rays VI–VII, very rarely VII, 9–10, very rarely 10; anal-fin rays III, 35–42, usually > 37; pectoral-fin rays 16–18; pored lateral-line scales 44–53; scale rows above lateral line 3½ or 4½, very rarely 4½; scale rows below lateral line 10–13; predorsal scales 23–30; circumpeduncular scales 10–12; gill rakers 6–9+18–22 = 25–30; head length 27.9–33.0%; body depth 40.2–47.2%; eye diameter 35.5–45.5%; upper jaw length 50.0–56.7%; maximum 126 mm SL; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (see Koeda et al. 2013a: fig. 2a); body golden in day time and silverish in night time; tip of dorsal fin and/or anterior margin of dorsal fin blackish; faint blackish band on anal-fin outer margin; blackish band on anal-fin base; posterior margin of caudal fin dusky; no blackish blotch on pectoral-fin base; posterior nostril usually slit-like; narrow band of villiform teeth in jaws; abdomen cross-sectional outline V-shaped.

Distribution. Widely distributed in the western Pacific Ocean. In Japanese waters, this species is known from Tanega-shima to Yonaguni-jima islands in the Ryukyu Archipelago, Minamidaito-jima Island in Daito Islands, and very rarely collected from Minamisatsuma in Kagoshima Prefecture. In Taiwanese waters, this species is known from Daxi in Yilan County, Gungliau and Yeh Liu in New Taipei City, Chi-gu in Tainan County, Ke-tzu-liao in Kaohsiung County,

Figure 12. Fresh specimen of *Pempheris schwenkii*, NMMB-P 27013, 100.3 mm SL, Hengchung, Pingtung, Taiwan.

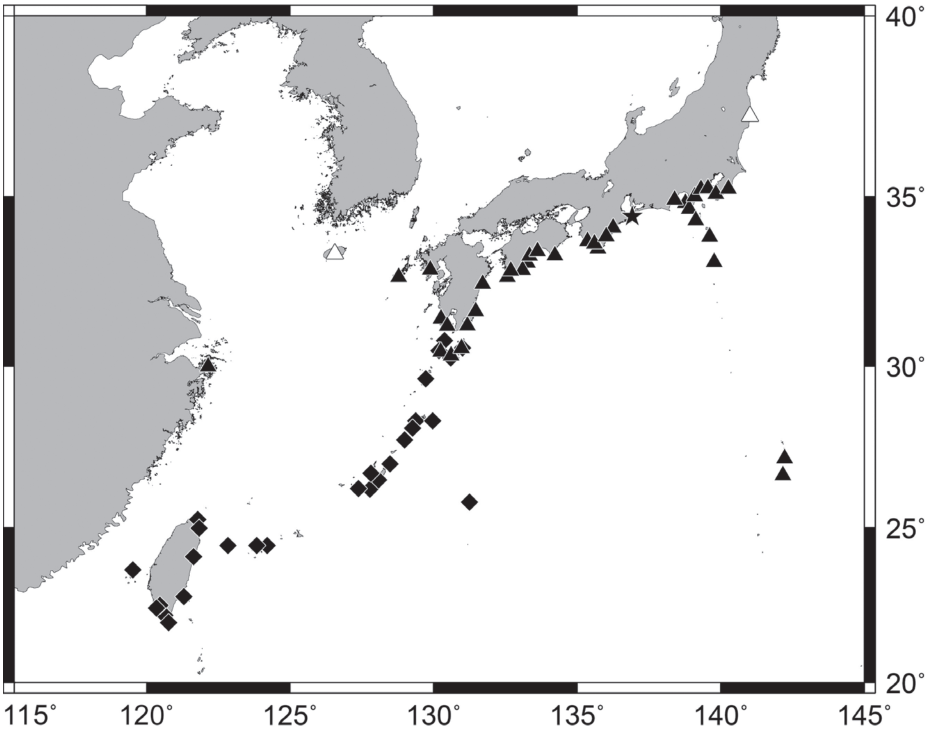

Figure 13. Distribution of *Pempheris schwenkii* (diamonds) and *P. xanthoptera* (solid triangles and star for type locality) based on the collection locality of the specimens. Open triangles for literature records of *P. xanthoptera*.

Hengchung, and Dong-gang, Kenting in Pingtung County, Fugang in Taitung County, Lanyu, and Penghu (Fig. 13). Specimens are collected from the caves or crevasses in coral reef areas of 0–25 m depth.

Remarks. *Pempheris schwenkii* has been thought to be widely distributed in the Indo-Pacific Ocean. However, our genetic study revealed the interspecific difference between specimens from the Indian and Pacific oceans, and southern Japan. Bleeker (1855) described *P. schwenkii* based on type specimens collected from Batu Island of western Indonesia, eastern Indian Ocean. Although a significant genetic difference is observed among the specimens from these three localities, the morphologies of the species are very similar. Furthermore, the morphological characters were difficult to determine from the dehydrated condition of the syntypes of *P. schwenkii* (RMNH.PISC.6160). The species composition of genus *Pempheris* around this area was closer to that of the western Pacific than that of the Indian Ocean. Therefore, *P. schwenkii* was determined as the name of the Pacific Ocean species (Koeda et al. 2014) and the Indian Ocean species described as a new species, *P. tominagai* Koeda, Yoshino & Tachihara, 2014. In the present study, a single specimen collected from the Andaman Sea was discovered, and is identified as *P. schwenkii* based on the pink caudal fin (vs yellow in *P. tominagai*). This fact supports the conclusion of Koeda et al. (2014) that *P. schwenkii* may be widely distributed from the Pacific to the Andaman Sea including the type locality (Batu Islands, Sumatera Utara Province, Indonesia) of the species.

Similarly, the Pacific species and the southern Japanese species also showed significant difference between specimens from south of the Ryukyu

Archipelago and specimens from mainland Japan (unpublished data). These two are clearly different species, because both species are distributed in the Osumi Islands (Tanega-shima, Yaku-shima, and Kuchinoerabu-jima islands; Fig. 13), but the genetic mixability did not appear in the genetic structure analysis (unpublished data); the genetic identification and the diagnostic caudal-fin colorations (pink to brown in *P. schwenkii* vs yellow in *P. xanthoptera*) were well matched (Fig. 3).

On the basis of the taxonomic confusion between *P. schwenkii* and *P. xanthoptera*, the standard Japanese name “Minami-hatampo” was used for both species, and recently, *P. schwenkii* was tentatively recognized as having “Pacific” and “southern Japan” types, the latter closely matching *P. xanthoptera* sensu Tominaga (1963) (e.g., Koeda 2017b, 2018a, b, 2020a; Kimura et al. 2017); see remarks of *P. xanthoptera*]. The Japanese name “Minami-hatampo” was first given by Okada (1938) for *P. vanicolensis* in his list. His identification may follow Jordan and Hubbs (1925) which indicated that Snyder (1912)’s *P. japonica* from Okinawa-jima Island was a misidentification of *P. vanicolensis*. However, *P. vanicolensis* is very rare in Japanese waters, and has never been collected from Okinawa-jima Island (Nakamura et al. 2022). In addition, the re-examination of the Snyder’s specimen of *P. japonica* (CAS-SU 22002) revealed that it was in fact a misidentification of *P. schwenkii*, which is the most common species around Okinawa Island. Although Okada (1938) included Kyushu in the distribution of “Minami-hatampo” which is the range of *P. xanthoptera*, the situations mentioned above suggest that his species should be *P. schwenkii*. These facts indicate that the standard Japanese name “Minami-hatampo” should be adopted for the species *P. schwenkii*.

The juveniles of *P. schwenkii* were collected from Minami-daito Island in the Daito Islands. *Pempheris ufuagari* is known as an endemic species which is found in the Daito and Ogasawara islands (see below), meaning that interaction between the species can occur at these localities. However, *P. schwenkii* and *P. xanthoptera* have never been collected from the Ogasawara and Daito islands, respectively, indicating that the *P. ufuagari* and *P. schwenkii* group (with *P. xanthoptera*) may have a different dispersal strategy.

Table 2. Counts of *Pempheris schwenkii* and *P. xanthoptera*.

	P. schwenkii		***P. xanthoptera***	
	Syntypes	**Non-types**	**Holotype**	**Non-types**
Number of individuals	2	232	1	355
Number of individuals	87.2, 89.7	20.4–125.9	116.8	28.2–136.6
Standard length				
Dorsal fin rays	VI, 9	VI–VII, 9–10	VI, 9	VI–VII, 9
Anal fin rays	III, 35–36	III, 35–42	III, 38	III, 35–42
Pectoral fin rays	17–18	16–18	18	16–19
Left pored lateral-line scales	48	44–53	48	45–54
Right pored lateral-line scales	48–49	45–53	47	46–54
Scale above lateral line	3 1/2	3 1/2–4 1/2	3 1/2	3 1/2
Scale rows below lateral line	10	10–13	10	10–13
Circumpeduncular scales	12	10–12	12	12–14
Gill rakers	7+18–19	6–9+18–22	N/A	7–9+18–21

Pempheris ufuagari **Koeda, Yoshino & Tachihara, 2013**

Figs 14, 15, Suppl. material 2
Standard Japanese name: Daito-hatampo

Pempheris ufuagari Koeda et al. 2013a: 232, fig. 1a (type locality: Minamidai-to-jima Island, Daito Islands, Japan); Koeda and Motomura 2015: 275; Koeda 2017a: 11, fig. 2 (lower fig.); Koeda and Motomura 2017a; Koeda 2018b: 299, unnumbered fig.

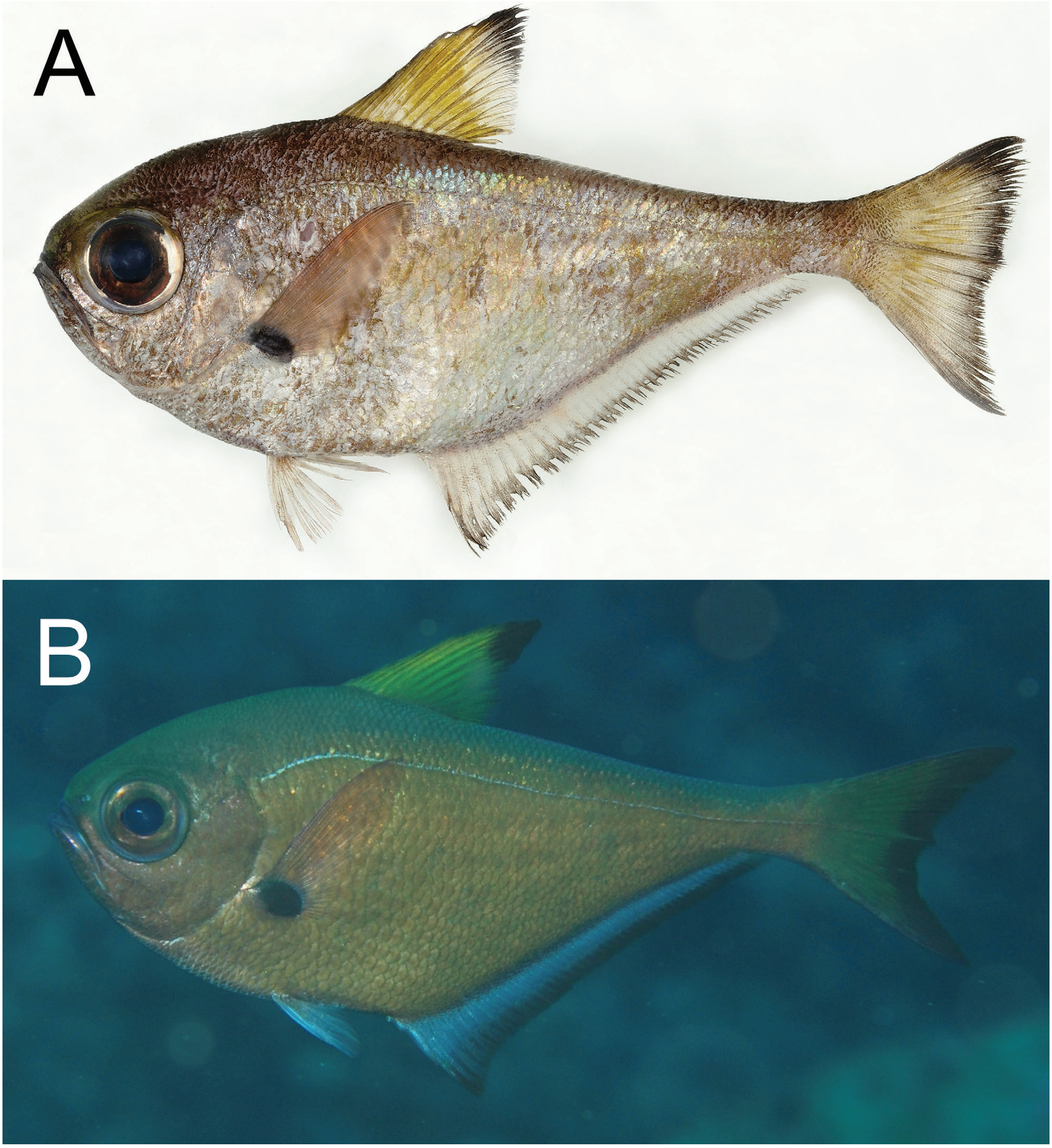

Figure 14. *Pempheris ufuagari* **A** fresh specimen (KAUM–I. 74550, Chichi-jima Island, Ogasawara Islands, 170.3 mm SL, photo taken by K. Kuriiwa) and **B** underwater photograph (Dobuiso, Ogasawara Islands, Japan).

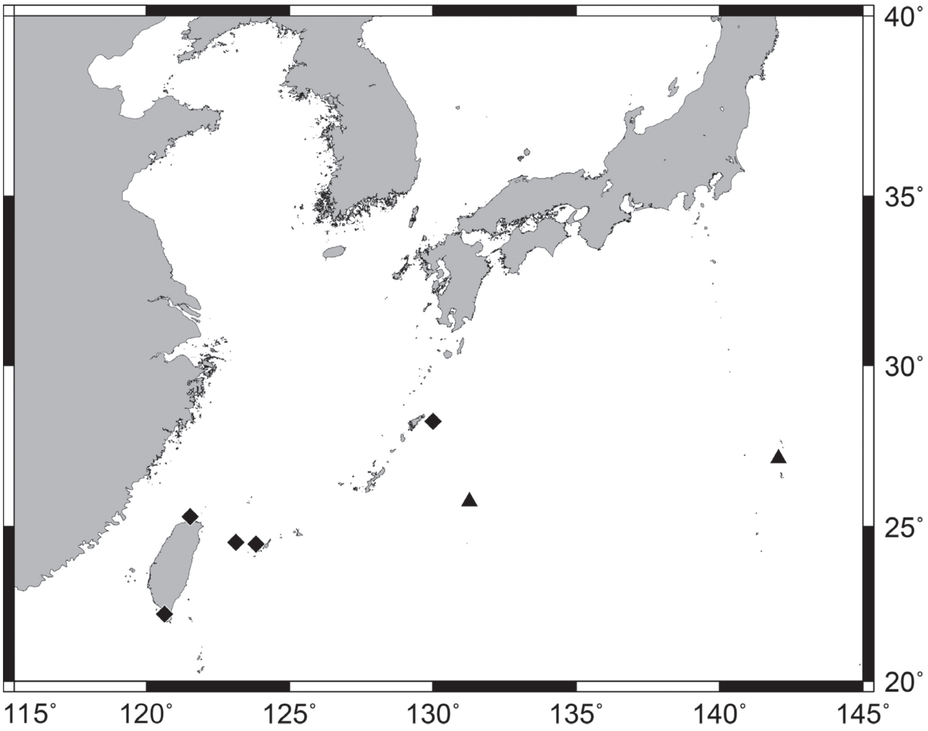

Figure 15. Distribution of *Pempheris ufuagari* (triangles) and *P. vanicolensis* (diamonds) based on the collection localities of the specimens.

Pempheris oualensis (not Cuvier, 1831): Masuda and Kobayashi 1994 (in part); 180, fig. 5; Hatooka 1997 (in part): 380, unnumbered fig. (p. 381, upper left fig.).

Pempheris otaitensis (not Cuvier, 1831): Randall et al. 1997 (in part): 35, pl. 8, fig. F.

Diagnosis. Counts of holotype and paratypes are given in Table 1 of Koeda et al. (2013a). Dorsal-fin rays VI, 9; anal-fin rays III, 39–43; pectoral-fin rays 17–18; pored lateral-line scales 62–71; scale rows above lateral line 6½–7½ (usually 7½); scale rows below lateral line 15–18; predorsal scales 37–44; circumpeduncular scales 20–22; gill rakers 8–9 + 20–21 = 28–30; head length 26.2–29.9%; body depth 39.7–44.4%; eye diameter 37.5–45.8%; upper jaw length 48.8–53.4%; maximum 197 mm SL, usually < 170 mm SL; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (Koeda et al. 2013a: see fig. 2a); body silver; distinct blackish blotch on pectoral-fin base; dorsal fin yellow with tip blackish; blackish band on anal-fin outer margin; caudal fin bright yellow with blackish posterior margin; lacking villiform tooth band extending outside lips; abdomen cross-sectional outline V-shaped.

Distribution. Endemic to the Daito and Ogasawara islands (Fig. 15). Specimens collected from the crevasses with strong current in coral reef areas of 0–20 m depth.

Remarks. *Pempheris ufuagari* is most similar to *P. otaitensis*, known only from French Polynesia and Samoa, sharing a distinct black blotch on the pectoral-fin base, yellow dorsal and caudal fins, and a blackish band on the anal-fin outer margin. However, the former can clearly be distinguished from the latter in having 62–71 pored lateral-line scales (vs 69–79 in *P. otaitensis*), 6½–7½ scale rows above lateral line (vs 8½), 37–43 predorsal scales (vs 44–48), and the tip of the dorsal fin blackish (vs anterior margin to tip blackish).

***Pempheris vanicolensis* Cuvier, 1831**

Figs 15, 16, Suppl. material 2
Standard Japanese name: Kibire-hatampo

Pempheris vanicolensis Cuvier, 1831: 305 (type locality: Vanikoro Island, Santa Cruz Islands); Shao and Chen 1991: 163, unnumbered fig.; Shao et al. 1992: 177, unnumbered fig.; Shen 1993: 391, pl. 114, fig. 2; Koeda et al. 2010b: 78, fig. 1; Koeda et al. 2012a: 71; Koeda et al. 2013a: 237; Koeda et al. 2013b: 127; Chiang et al. 2014: 183, unnumbered fig.; Koeda et al. 2014: 327; Koeda and Motomura 2015: 139; Koeda et al. 2015: 275; Koeda et al. 2016b: 50, fig. 226; Koeda 2017a: 5; Koeda 2018b: 299, unnumbered fig.; Koeda 2019: 929, unnumbered figs; Koeda et al. 2022: 11; Nakamura et al. 2022: 1, fig. 1.

Pempheris sp.: Shao et al. 2013 (in part): 161, unnumbered fig. (middle fig.); Shao et al. 2008: 254; Hatooka and Yagishita 2013 (in part): 984.

Diagnosis. Counts of holotype and non-types are given in Table 2 of Koeda et al. (2010b). Dorsal-fin rays VI, 9; anal-fin rays III, 38–43; pectoral-fin rays 17–19; pored lateral-line scales 56–65; scale rows above lateral line 5½–6½, usually 5½; scale rows below lateral line 12–15; predorsal scales 30–35; circumpeduncular scales 16–18; gill rakers 8+19–21 = 27–29; head length 29.1–31.7%; body depth 42.4–46.3%; eye diameter 37.5–42.9%; upper jaw length 48.9–55.3%; maximum 156 mm SL; snout rounded; scales weakly ctenoid, deciduous, thin, semicircular in shape, far wider than long (Koeda et al. 2013a: see fig. 2a); body silverish to copperish in fresh specimen collected in day time, but silver in night time; tip of dorsal fin distinctly blackish; usually distinct blackish band on outer edge of anal fin; pectoral fin bright yellow (disappear in fixed specimens) with lacking blackish blotch on its base; posterior margin of caudal fin blackish; narrow band of villiform teeth in jaws; abdomen cross-sectional outline V-shaped.

Distribution. Widely distributed in the western Pacific Ocean except for small islands and atolls in central Pacific. In Japanese waters, this species is known from Iriomote-jima and Yonaguni-jima islands in the southern Ryukyu Archipelago. In Taiwanese waters, this species is known from Yeh Liu and Wang-li in New Taipei City, and Hengchung and Kenting in Pingtung County (Fig. 15). Specimens were collected from 0–2 m depth in Japan but are known from deeper (ca 20 m) in other areas. KK observed a small school of this species at Kuchinoerabu-jima Island (24 Aug. 2016).

Remarks. This species was described by Cuvier (1831), and the name *P. vanicolensis* has been used for several species, particularly from the Indian Ocean and the Red Sea. However, this species has only been collected from the Pacific Ocean and not from the Indian Ocean as shown in the present study. Jordan and Hubbs (1925) reported that the "*P. japonica*" documented by Snyder (1912) from Okinawa Island was a misidentification of *P. vanicolensis*. The early period of modern-day ichthyology in Japan probably followed Jordan and Hubbs (1952), and *P. vanicolensis* was recognized as "Minami-hatampo" in the species lists of Japanese waters (e.g., Okada 1938; Matsubara 1955). However, *P. vanicolensis* is very rare in Japan, and re-examination of Snyder's specimen (SU 22002) revealed that it was a misidentification of *P. schwenkii*, which is the most common species around Okinawa Island.

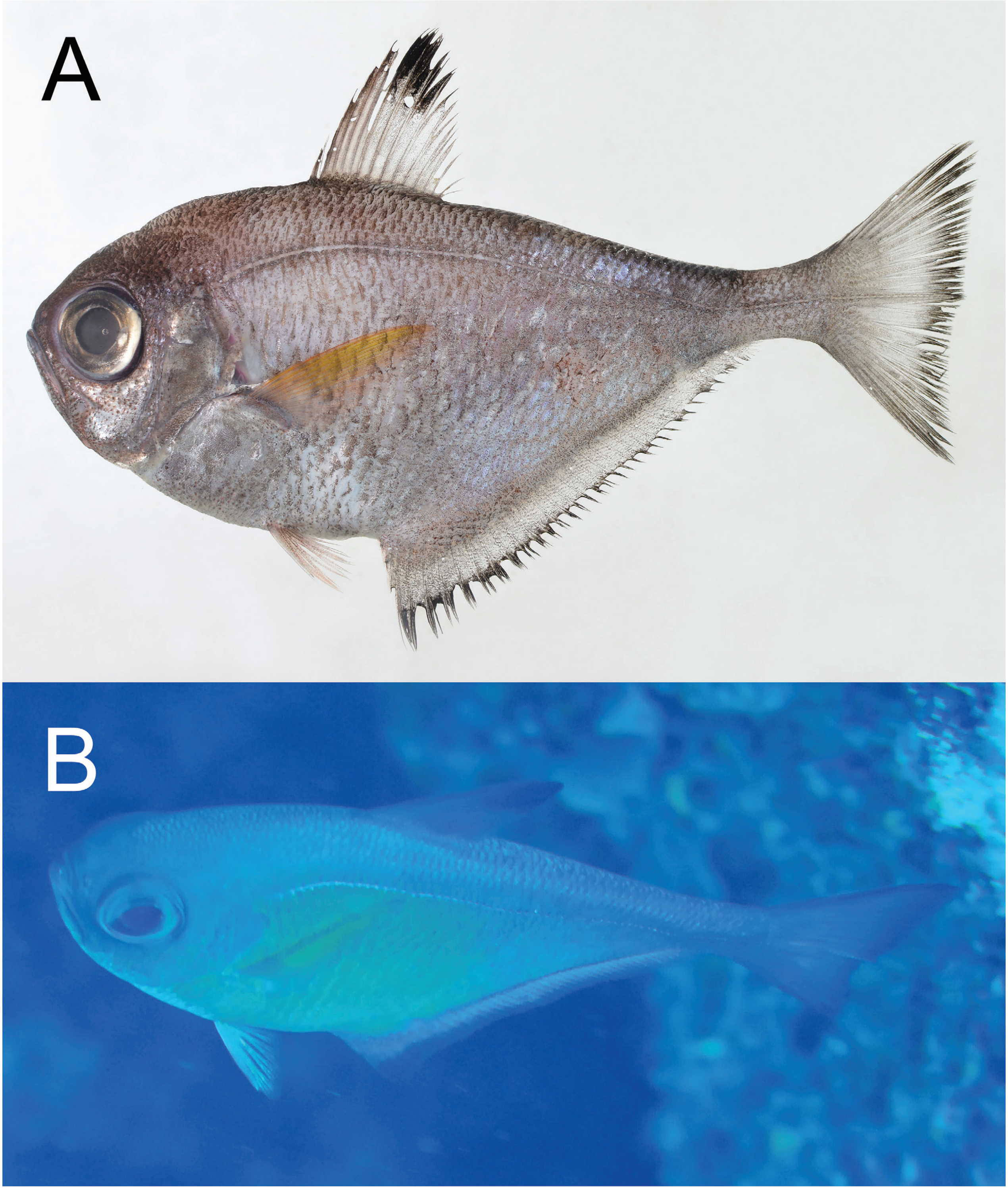

Figure 16. *Pempheris vanicolensis* **A** fresh specimen (KAUM–I. 65386, 132.7 mm SL, Hengchung, Pingtung, Taiwan) and underwater photograph (Palau).

Pempheris xanthoptera Tominaga, 1963

Figs 13, 17, Suppl. material 2
New standard Japanese name: Mizuho-hatampo

Pempheris xanthoptera Tominaga, 1963: 286, fig. 12 (type locality: Manazuri, Kanagawa Prefecture, Japan); Hiyama and Yasuda 1971: 204, fig. 440; Masuda et al. 1975: 199, pl. 33-C; Hayashi 1984: 160, pl. 151-D; Kohno 1986: 135, fig. 1; Randall et al. 1997: 35; Koeda et al. 2022: 11.

Pempheris molucca (not Cuvier, 1829): Temminck and Schlegel 1844: 85, pl. 44, fig. 3.

Pempheris oualensis (not Cuvier, 1831): Mochizuki 1995: 389, unnumbered fig. (in part).

Pempheris schwenkii (not Bleeker, 1855): Masuda and Kobayashi 1994: 180, fig. 6; Mochizuki 1995: 389, unnumbered fig.; Hatooka 1997 (in part): 380, unnumbered fig. (p. 381, lower left fig.); Hatooka 2002 (in part): 878; Takayama et al. 2003: 1317, fig. 2; Senou et al. 2006b: 463; Aramata 2007: 172, unnumbered figs; Yoshino 2008 (in part): 211; Takagi et al. 2010: 69, unnumbered figs; Kohno et al. 2011: 208, unnumbered fig.; Senou et al. 2012: 212; Hatooka and Yagishita 2013 (in part): 984; Koeda et al. 2013a: 237; Motomura et al. 2013 (in part): 168, unnumbered fig.; Kawano et al. 2014: 48; Koeda et al. 2014: 327; Ikeda and Nakabo 2015: 160, figs 1–3; Takeuchi et al. 2015: 8; Iwatsubo et al. 2016: 22, unnumbered figs; Kaburagi 2016: 98, lower fig. (without scientific name; indicated as “Minami-hatampo”); Kimura et al. 2017 (in part): 120, fig. 2; Koeda 2017a: 9, fig. 2 (middle); Koeda 2017b: 190, unnumbered fig.; Koeda and Motomura 2017a; Kagoshima City Aquarium Foundation 2018: 210, unnumbered fig.; Koeda 2018b: 298, unnumbered fig. (lower left fig.); Koeda 2018c: 343, unnumbered figs; Murase et al. 2019: 132, fig. 284; Koeda 2020a: 407, unnumbered figs; Murase et al. 2021: 166, fig. 340; Koeda 2022: 158, unnumbered fig.; Motomura 2023: 129 (in part).

Pempheris vanicolensis (not Cuvier, 1831): Okada 1938: 179 (in part); Okada and Matsubara 1938: 179 (in part); Matsubara 1955: 590 (in part); Abekawa and Nishi 1969: 24.

Pempheris japonica (not Döderlein, 1883): Nakamura 1993: 148, fig. 6.

Diagnosis. Counts of of holotype and paratypes are given in Table 2. Dorsal-fin rays VI–VII, 9; anal-fin rays III, 35–42; pectoral-fin rays 16–19; pored lateral-line scales 45–54; scale rows above lateral line 3 1/2; scale rows below lateral line 10–13; predorsal scales 23–28; circumpeduncular scales 12–14; gill rakers 7–9+18–21 = 25–27; head length 27.9–31.9%; body depth 39.3–45.4%; eye diameter 36.4–44.1%; upper jaw length 48.3–57.1%; maximum 137 mm SL; scales weakly ctenoid, very deciduous, thin, semicircular in shape, far wider than long (see Koeda et al. 2013a: fig. 2a); body golden in daytime, but silver in night time; no blackish blotch on; tip of dorsal fin distinctly blackish; anal-fin base zonal blackish, and margin very faintly blackish; caudal fin yellow (disappears in fixed specimens); pectoral and pelvic fin hyaline or pink; posterior margin of caudal fin dusky; body light brown to dark brown in fixed specimen; black pigmentation on each fins usually persistent; no blackish blotch on pectoral-fin base; posterior nostril usually open, not compressed; narrow band of villiform teeth in jaws; abdomen cross-sectional outline V-shaped.

Distribution. Endemic to the Northwest Pacific, recorded only from Japan, Jeju Island in Korea (Kim and Sakai 2004), and China. In Japanese waters, this species is known from Pacific coast (north to Boso Peninsula in Chiba Prefecture, south to Kagoshima Prefecture), Tsushima Island, East China Sea coast (north to Goto Islands in Nagasaki Prefecture, south to Kagoshima Prefecture), Izu-oshima, Miyake-jima and Hachijo-jima islands in Izu Islands, Chichi-jima,

Figure 17. Fresh specimen of *Pempheris xanthoptera*, KBF-I 00268, 123.0 mm SL, Amaji, Otsuki, Kochi.

Haha-jima, Ototo-jima islands in Ogasawara Islands, Tanega-shima, Yaku-shima, Kuchinoerabu-jima, Iou-jima and Take-shima islands in northern Ryukyu Archipelago (Fig. 13).

Remarks. Although Tominaga (1963) described *P. xanthoptera* based on its differences in fin color and distributional pattern from *P. schwenkii*, the former has been usually considered as a junior synonym of the latter in recent publications in Japan (see the synonym list) without any discussion. Our genetic analysis revealed apparent differences between these two species with high node support values (Fig. 3). The morphological comparison showed the additional small difference between these two species, such as *P. xanthoptera* has the posterior nostril usually open, not compressed (vs slit-like; see Koeda et al. 2014: fig. 8), and caudal fin yellow (vs pink to brown). The validity of *P. xanthoptera* was discussed in the remarks of *P. schwenkii*.

The standard Japanese name “Minami-hatampo” was used for both species and caused confusion, but this name should be adopted for *P. schwenkii* (see remarks of *P. schwenkii*). Therefore, a new standard Japanese “Mizuho-hatampo” is proposed for *P. xanthoptera*. “Mizuho” is an alternative name for Japan that frequently appears in ancient Japanese mythology and poetry, and it derives from the fact that the species is primarily distributed across the Japanese mainland.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: KK. Data curation: MBU, KK. Formal analysis: MBU, KK. Funding acquisition: KK, MBU. Project administration: KK. Validation: MBU. Visualization: KK. Writing - original draft: KK. Writing - review and editing: KK, MBU.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Preserved specimens of genus *Pempheris* examined in the present study

Authors: Keita Koeda, Manabu Bessho-Uehara

Data type: xlsx

Link: https://doi.org/10.3897/zookeys.1220.126762.suppl1

Supplementary material 2

requency distributions of pored lateral-line scales of species of *Pempheris* distributed in Japan and Taiwan, with *P. flavicycla* for comparison

Authors: Keita Koeda, Manabu Bessho-Uehara

Data type: xlsx

Link: https://doi.org/10.3897/zookeys.1220.126762.suppl2

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Research Article

A new species of the jawfish genus *Opistognathus* from Taiwan, northwestern Pacific Ocean (Perciformes, Opistognathidae)

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Abstract

A new species of jawfish genus *Opistognathus* is described based on a specimen collected from a beach in the Peng-hu Islands during a cold snap. The new species, *Opistognathus cryos* **sp. nov.**, differs from its congeners in having a rigid upper jaw, 10–11 + 1 + 19–22 = 31–33 gill rakers, 55 scale rows in lateral series, 10 + 16 = 26 vertebrae, the terminus of the lateral line at the base of the fourth segmented dorsal-fin ray (15th in total rays), the head, nape, dorsal-fin base above lateral line, throat, chest, and pectoral-fin base naked, dorsal fin with eight blotches along its entire base, body with five horizontal dark stripes, nape with two dark blotches in front of the dorsal-fin origin, and a caudal fin with five narrow, dark bands. A detailed description is provided and compared to its similar congeners.

Key words: Actinopterygii, biodiversity, ichthyology, morphology, taxonomy

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Introduction

The jawfish family Opistognathidae is a group of small to moderately sized fishes (up to 50 cm, but mostly less than 12 cm) that are distributed circumglobally, except for the Mediterranean Sea and the eastern Atlantic Ocean (Smith-Vaniz 1999, 2023). They are well known for their moth-brooding behavior, in which parents carry their sticky egg mass in their mouth until hatching (Smith-Vaniz 1999). They are bottom burrowers that inhabit sandy bottoms at depths of 2–30 m, with some Indo-West Pacific species down to 200 m (Smith-Vaniz 1999), and Caribbean species to at least 300 m (Smith-Vaniz 2017).

Currently, four genera are recognized as valid: *Anoptoplacus* Smith-Vaniz, 2017, *Lonchopisthus* Gill, 1862, *Opistognathus* Cuvier, 1816, and *Stalix* Jordan & Snyder, 1902. Among the four genera, *Opistognathus* can be discriminated from other genera in having the anterior dorsal-fin spines not transversely forked;

the posterior margin of upper jaw straight or rounded; dorsal-fin rays, X–XIII, 10–22; anal-fin rays II–III, 10–20; the caudal fin rounded, with 17–18 principal rays; and the infraorbital bones not plate-like (Smith-Vaniz 1999, 2003, 2017).

A recent revision of Indo-West Pacific *Opistognathus* by Smith-Vaniz (2023) recognized 60 species, including 18 new species. Moreover, he provided diagnostic characters and an identification key for all Indo-West Pacific species, and he noted that more undescribed species occur in this region. Thereafter, Fujiwara et al. (2023) and Fujiwara and Ikeda (2024) described *Opistognathus ctenion* Fujiwara, Shinohara & Motomura, 2023 and *Opistognathus abei* Fujiwara & Ikeda, 2024, respectively. Therefore, the total number of *Opistognathus* is 93, including 62 from the Indo-West Pacific, 17 from the western Atlantic, and 14 from the eastern Pacific (Smith-Vaniz 2023; Fujiwara and Ikeda 2024).

Penghu is a group of small islands in the Taiwan Strait off western Taiwan, with the Tropic of Cancer passing through it. In the historical records, several serious cold-related incidents have occurred along the northern coast during the winter seasons in Penghu, such as those in 1977, 2008, and 2022. The cold fronts brought low-temperature longshore currents from the north, causing the water temperature to drop below 14 °C. Consequently, many coral-reef fishes were frozen to death and washed ashore (Hsieh et al. 2012; Ho pers. observ.).

During the cold snap in 2022, many stranded fishes were collected and sent back to the lab. Among them, an apparently unnamed species of *Opistognathus* with a color pattern closely similar to *Opistognathus* sp. 1 of Smith-Vaniz (2023: fig. 103). The unnamed jawfish is here described as *O. cryos* and differs from other sympatric congeners in having a unique coloration and several morphological characters. A detailed description of the new species is provided and compared to its congeners.

Materials and methods

The specimen was fixed in 4% formaldehyde and subsequently transferred to 70% ethanol for preservation in the Pisces Collection of the National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (**NMMB-P**).

Terminology and methodology follow Smith-Vaniz (2023). Medial fin rays, vertebral formula, and both dorsal- and anal-fin interdigitation patterns were determined using X-radiographs taken by a digital X-ray machine set up in the National Museum of Marine Biology and Aquarium. The supraneural bones were abbreviated as “S” in the fin interdigitation patterns. Paired characters were expressed as left/right whenever available. Head pores were observed on both sides directly under a stereomicroscope (Olympus SZ51), with partial drying and adjusting light directions to enhance the detection. Illustrations of head pores were traced from magnified photographs using Adobe Photoshop.

Measurements were taken from the right side of the specimen using digital calipers rounding to the nearest 0.1 mm under a stereomicroscope. Morphometric data were expressed as ratios or percentages of standard length (**SL**) and head length (**HL**), except where otherwise indicated.

Results

Family Opistognathidae

***Opistognathus cryos* sp. nov.**

https://zoobank.org/8F808D49-8B17-4E9C-A4B8-E273BAC2742C
Figs 1–3, Tables 1, 2
New English name: Frozen jawfish
New Chinese name: 冷鋒後頜鱚

Opistognathus sp. 1: Smith-Vaniz 2023: 72, fig. 103.

Type locality. Taiwan, Peng-hu Islands, Chih-kan beach, ca 23°40'12"N, 119°36'10"E, 25 February 2022, H.-C. Ho leg.

Type specimen. Holotype: NMMB-P 36179, 65.1 mm SL.

Diagnosis. A species of *Opistognathus* differing from its congeners in having the following combination of characters: upper jaw rigid, without a distinct flexible lamina posteriorly; dorsal-fin rays XI, 11; anal-fin rays II, 10; gill rakers 10–11 + 1 + 19–22 = 31–33; scale rows in lateral series 55; vertebral formula 10 + 16 = 26; dorsal-fin interdigitation pattern S/S/1/1+1/1/; lateral-line ends at base of fourth segmented dorsal-fin ray (15th in total rays); head, nape, dorsal-fin base above lateral line, throat, chest, and pectoral-fin base scaleless; upper two preopercular and fifth mandibular pores bipored; vomer edentate; head mottled with small, dark blotches; dorsal fin with eight blotches along its base; distal portion of membrane between dorsal-fin spines white; body with five horizontal, dark stripes; nape with two dark blotches in front of dorsal-fin origin; and caudal fin with five narrow, dark bands.

Description. Meristic and morphometric data are provided in Tables 1, 2. Paired characters are presented as left/right whenever available.

Dorsal-fin rays XI, 11. Anal-fin rays II, 10. Pectoral-fin rays 19/19. Pelvic-fin rays I, 5/I, 5. Principal caudal-fin rays 8 + 8, with innermost 6 + 6 rays branched; procurrent caudal-fin rays 4 on both upper and lower lobes. Gill rakers 11 + 1 + 19 = 31/10 + 1 + 22 = 33. Scale rows in lateral series 55/55. Vertebrae 10+16=26. Dorsal-fin interdigitation pattern S/S/1/1+1/1/; anal-fin interdigitation pattern /1/1/1/1/1/.

Body slender, depth at anal-fin origin 4.2 in SL; both dorsal and ventral profiles of body flat. Head large, length 2.5 in SL; anterior profile of head rounded, gently curved to dorsal-fin origin. Eyes large, eye diameter 3.0 in HL. Two nostrils, anterior one a short tube with small flap; posterior one without flap, situated immediately in front of eye. Preoprecle and opercle covered by skin, their posterior margins without spines; single, small flap present on upper end of opercle.

Mouth lower in position, slightly oblique, forming ca 10° angle with body axis. Jaws terminal, with lower jaw slightly included. Upper-jaw length 1.5 in HL, its end exceeding 0.8 in eye diameter behind posterior margin of orbit; posterior margin of maxilla truncated, without distinct flexible lamina; its anterior margin without crenulae. Supramaxilla present, greatest width about one-third of maxilla. Premaxilla with two or three rows of small canine teeth anteriorly; posterior portion forming single row of conical teeth, their size decreasing posteriorly.

Table 1. Meristic characters of *Opistognathus cryos* sp. nov. and similar species. Paired characters are presented as left/right whenever available. Data of other species were retrieved from Smith-Vaniz (2023).

	***O. cryos* sp. nov.**	***O. asper***	***O. liturus***
	This study	**Smith-Vaniz (2023)**	**Smith-Vaniz (2023)**
	Holotype	**All types (*n* = 3)**	**Holotype**
Dorsal-fin rays	XI, 11	XI, 11–12	XI, 11
Pectoral-fin rays	19/19	19	19
Anal-fin rays	II, 10	II, 10	II, 10
Gill rakers	11 + 1+ 19 = 31/10 + 1 + 22 = 33	10–11 + 22–24 = 32–34	9 + 1 + 21 = 31
Scale rows in lateral series	55/55	42–44	44
Vertebrae	10 + 16 = 26	10 + 16 = 26	10 + 16 = 26
Dorsal-fin interdigitation anterior patterns	S/S/1/1+1/1/	S/S/1/1+1/1/	/ /1/1+1/1/
Lateral-line terminus total dorsal-fin rays	15/15	11–15	15

Table 2. Morphometric characters of *Opistognathus cryos* sp. nov. and similar species. Data of other species were retrieved from Smith-Vaniz (2023). Abbreviations: A = anal-fin; C = caudal-fin; D = dorsal-fin; HL = head length; SL = standard length; V = pelvic-fin.

	***O. cryos* sp. nov.**	***O. asper***	***O. liturus***
	This study	**Smith-Vaniz (2023)**	**Smith-Vaniz (2023)**
	Holotype	**All types (*n* = 3)**	**Holotype**
SL (mm)	65.1	34.4–50.2	55.3
%SL			
HL	39.5	37.0–40.3	37.8
Body depth at A origin	23.9	23.7–25.6	25.0
Postorbital length	23.5	20.6–21.4	21.9
Eye diameter	13.2	12.3–13.5	12.3
Upper-jaw length	26.3	24.3–26.2	26.2
Postorbital-jaw length	10.8	–	8.7
Predorsal length	35.7	36.9–40.8	35.8
Preanal length	62.3	61.8–66.9	63.3
Length of D base	57.5	60.0–64.2	59.7
Length of A base	24.9	23.3–27.8	27.3
V length	32.4	29.3–35.2	31.1
C length	28.9	30.2–43.0	30.6
Caudal-peduncle depth	14.1	13.5–15.1	14.8
%HL			
Postorbital length	59.4	52.7–57.4	57.9
Eye diameter	33.4	33.5–35.1	32.5
Upper-jaw length	66.6	65.0–67.7	69.4
Postorbital-jaw length	27.4	23.8–26.2	23.1

Dentary with small canine teeth forming two or three rows anteriorly and single row posteriorly. Vomer and palatine without teeth.

Body scales cycloid. Scales absent on head, nape, dorsal-fin base above lateral line, throat, chest, and pectoral-fin base (Fig. 2). Lateral-line terminus below 4th/4th or 15th/15th in soft ray or total elements of dorsal fin, respectively; lateral-line pores arranged in irregular series along embedded lateral-line canals. Cephalic sensory pores rather sparsely scattered (Fig. 2); upper-two preopercular pores bipored, others simple; fifth mandibular pore bipored, others simple.

Dorsal fin with long base, originated at vertical through upper end of gill slit; its distal nearly straight, with slight elevation on soft rays; no distinct notch between spines and soft rays. Pectoral-fin tip pointed; its origin at same horizontal through lower margin of eye; its tip reaching near vertical through anal-fin origin. Pelvic

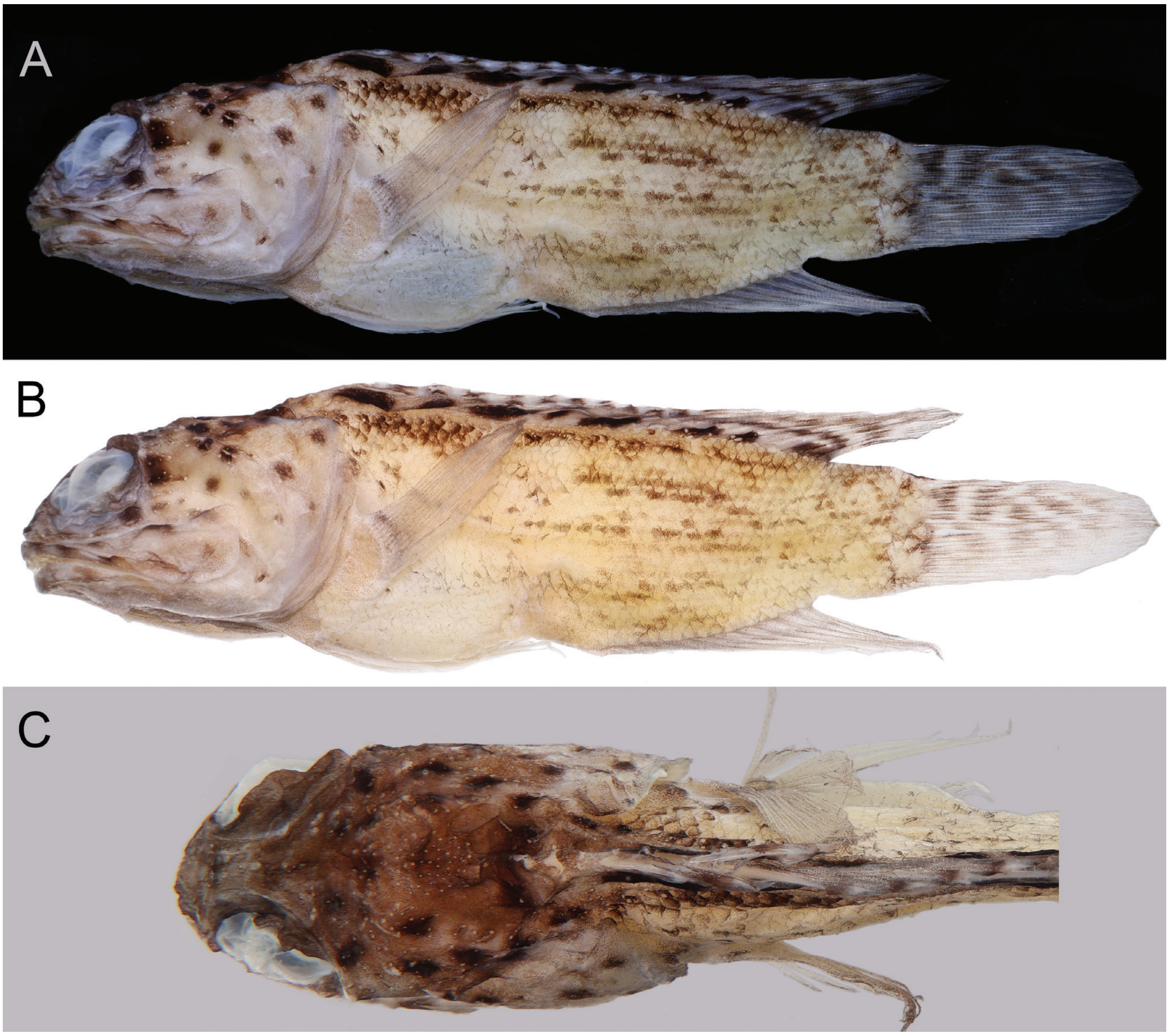

Figure 1. Preserved specimen of *Opistognathus cryos* sp. nov., holotype, NMMB-P 36179, 65.1 mm SL **A** on black background **B** on white background **C** dorsal view of nape. Photos by Y.-C. Hsu.

fin elongated, its origin below second dorsal-fin spine and in advance of pectoral fin; its tip reaching anal-fin origin when adpressed; outermost segmented ray not bounded to adjacent ray, with incision on interradial membrane. Anal-fin base moderately long, its posterior end slightly anterior to that of dorsal fin; its origin below first and second dorsal-fin soft rays (between 12th and 13th total dorsal-fin rays); fin rays gradually longer posteriorly; its distal margin nearly straight. Caudal fin rounded, slightly pointed; its length 1.4 in HL. Caudal peduncle broad, depth 2.8 in HL.

Coloration. When preserved (Fig. 1A, B), body pale, with one horizontal dark line near dorsal-fin base, and four rows of thinner dark lines on lateral side of body above anal-fin base. Head pale, scattered with irregularly sized dark blotches on operculum, upper and lower jaws, and infraorbital; their sizes smaller than pupil. Nape with two dark blotches in front of dorsal-fin origin (Fig. 1C). Dorsal fin dusky, with eight dark blotches along its base, slightly extending onto dorsum; distal end of fin spines white; soft rays with two horizontal, dark stripes. Caudal fin dusky, with five narrow, dark bands. Anal, pectoral, and pelvic fins dusky. Oral cavity, including underside of tongue pale.

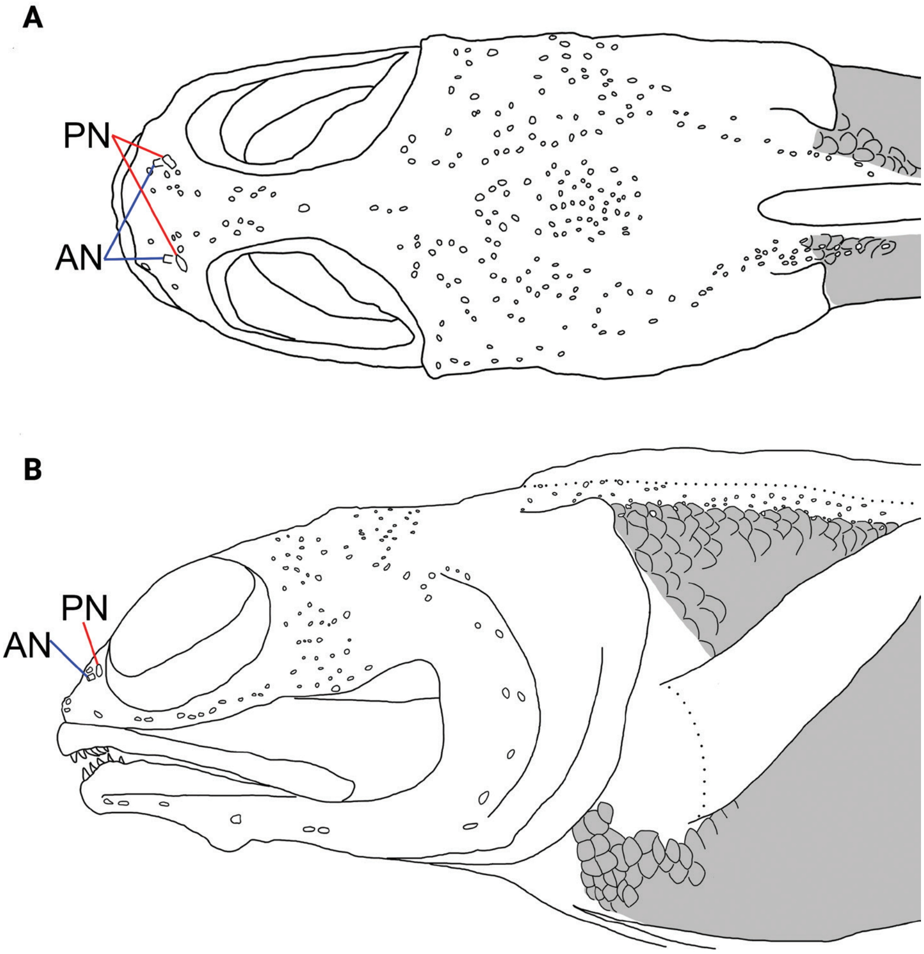

Figure 2. Head pores and adjacent area of *Opistognathus cryos* sp. nov., holotype, NMMB-P 36179, 65.1 mm SL, with scaled area shaded in gray **A** dorsal view **B** lateral view. Abbreviations: AN = anterior nostril; PN = posterior nostril. Dotted lines indicate dorsal- and pectoral-fin bases. Anterior to left. Figure not to scale.

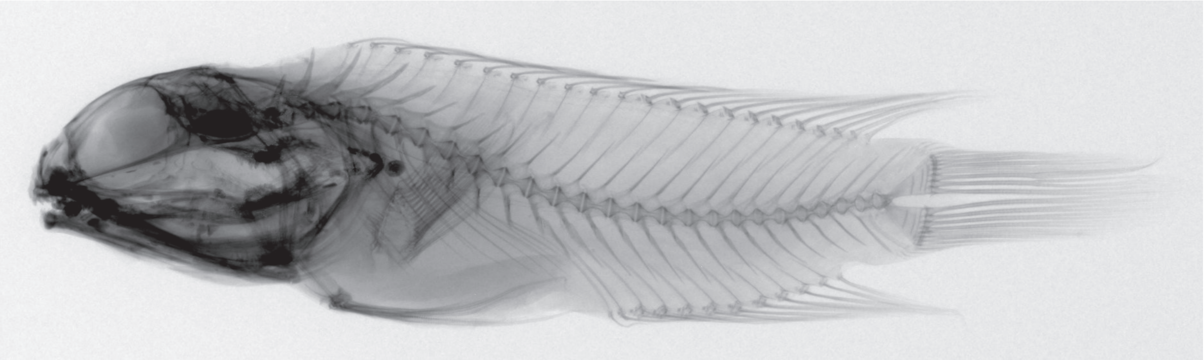

Figure 3. X-radiograph of *Opistognathus cryos* sp. nov., holotype, NMMB-P 36179, 65.1 mm SL.

Osteology. Pleural ribs present on fourth to tenth vertebra; epineurals present and epipleurals absent. Caudal skeleton consists of four plates, including three hypurals and one parhypural; hypural 1 and 2 fused; hypural 3 and 4 fused; hypural 5 present (Fig. 3).

Etymology. The specific name *cryos*, is from the Greek “κρύος” meaning cold or chilled, indicating that the holotype was collected during a cold snap in 2022. The common name “frozen jawfish” is also a reference to the fantasy film “Frozen” produced by Walt Disney Animation Studios.

Distribution. The holotype was collected ashore from the northern portion of the Peng-hu Islands, western Pacific Ocean. Another possible record from Japan (Smith-Vaniz 2023) may suggest a wide distribution in the northwestern Pacific Ocean.

Discussion

According to the key provided by Smith-Vaniz (2023), *Opistognathus cryos* sp. nov. mostly resembles *O. asper* Smith-Vaniz, 2023, a deep-water species from northwestern Australia; both species share a rigid upper jaw, its end without a flexible lamina, dark blotches on the dorsum extending onto the dorsal fin, and similar meristic counts. However, *O. cryos* can be discriminated from *O. asper* in having scales rows in horizontal series 55 (vs 42–44 in *O. asper*; Table 1); the upper two preopercular pore bipored and others simple (vs all bipored); the pectoral-fin base naked (vs scaly); eight dark blotches along the dorsal-fin base (vs 4–5); and nape with two dark blotches in front of the dorsal fin (Fig. 1C; blotch absent). Other differences in morphometric data (Table 2) need further study since the holotype of *O. cryos* is larger than all specimens of *O. asper* (65.1 mm SL vs 34.4–50.2 mm SL in *O. asper*).

Opistognathus cryos is also similar to *O. liturus* Smith-Vaniz & Yoshino, 1985, both occurring in the northwestern Pacific Ocean. However, *O. cryos* differs from the latter in having scale rows in horizontal series 55 (vs 44 in *O. liturus*; Table 1), dorsal-fin interdigitation anterior pattern S/S/1/1+1/1/ (vs / /1/1+1/1/), eight dark blotches along the entire dorsal-fin base (vs four blotches extending slightly onto fin base and terminated at middle); and the fifth mandibular pore bipored (vs simple).

Moreover, the combination of gill rakers 10–11 + 1 + 19–22 = 31–33, scale rows in lateral series 55, mottled head, and eight dark blotches along the dorsal-fin base readily distinguishes it from other Indo-Pacific congeners, including *O. ctenion* and *O. abei*, which were described subsequent to Smith-Vaniz (2023) (Fujiwara et al. 2023; Fujiwara and Ikeda 2024).

Species diversity of jawfishes in Taiwan

Table 3 listed species of jawfishes recorded from Taiwan historically, as well as the current museum specimens deposited in NMMB-P. Twelve species and two genera were recognized. Among them, *O. cryos* sp. nov., *O. flavidus* Smith-Vaniz, 2023, *O. microspilus* Smith-Vaniz, 2023, *O. variabilis* Smith-Vaniz, 2009, and *Stalix sheni* Smith-Vaniz, 1989 were described based on specimens collected from Taiwan. Moreover, the records of four species–*O. macrolepis* Peters, 1866, *O. microspilus*, and *O. solorensis* Bleeker, 1853–were based on a single voucher specimen from Taiwan.

Table 3. Checklist of opistognathids recorded from Taiwan.

Species	Chinese name	Reference	Remarks
Opistognathus castelnaui Bleeker, 1859	卡氏後頜鰧	Mok 1993; Chen et al. 2010; Shen and Wu 2011; Tashiro 2019; Smith-Vaniz 2023	NMMB-P specimens: A total of 16 lots of 29 specimens.
O. cryos Su & Ho sp. nov.	冷峰後頜鰧	This study	
O. evermanni (Jordan & Snyder, 1902)	艾氏後頜鰧	Mok 1993; Shen and Wu 2011; Smith-Vaniz 2023	
O. flavidus Smith-Vaniz, 2023	金鰭後頜鰧	Shen et al. 1986; Mok 1993; Smith-Vaniz 2023	Three paratypes (NMMB-P35987, NTUM 6177 and 7112) were collected from Taiwan. Shen et al. (1986) reported as *O. fasciatus* and Mok (1993) reported as *O. evermanni*. NMMB-P specimens: NMMB-P 38449.
O. hongkongiensis Chan, 1968	香港後頜鰧	Mok 1993; Shen and Wu 2011; Tashiro 2019; Smith-Vaniz 2023	NMMB-P specimens: NMMB-P 4071; NMMB-P 11582; NMMB-P 23855; NMMB-P 40030.
O. hopkinsi (Jordan & Snyder, 1902)	霍氏後頜鰧	Smith-Vaniz 2023	Based on a specimen (ASIZP 61792) collected from northeastern Taiwan. NMMB-P specimens: NMMB-P 32936; NMMB-P 33923; NMMB-P34432.
O. macrolepis Peters, 1866	大鱗後頜鰧	Smith-Vaniz 2023	Based on a specimen (NTUM 15216) purchased at market of Taiwan and without precise locality.
O. microspilus Smith-Vaniz, 2023	小斑後頜鰧	Smith-Vaniz 2023	Only known from the holotype (NMMB-P13933) collected from Taiwan.
O. solorensis Bleeker, 1853	索洛後頜鰧	Smith-Vaniz 2016, 2023	Based on a specimen (SAIAB 27653) collected from Kenting National Park.
O. variabilis Smith-Vaniz, 2009	多彩後頜鰧	Smith-Vaniz 2009, 2023; Chen et al. 2010	Two paratypes (ASIZP 56989) were collected from Taiwan.
O. wassi Smith-Vaniz, 2023	瓦氏後頜鰧	Smith-Vaniz 2023	One paratype (ASIZP 56990) was collected from Spratly Islands, South China Sea.
Stalix sheni Smith-Vaniz, 1989	沈氏叉棘鰧	Smith-Vaniz 1989; Mok 1993; Shen and Wu 2011	Originally described from Taiwan.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: HCH. Formal analysis: YS. Funding acquisition: HCH. Supervision: HCH. Writing - original draft: YS. Writing - review and editing: HCH.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Checklist

An updated checklist of fishes of Dongsha Island, Taiwan, northern South China Sea

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Abstract

Dongsha Island, situated in the northern part of the South China Sea, is surrounded by coral reefs and deep-sea habitats. The coastal areas of the atoll, a marine protected area, serve as important nursery habitats for many reef fish species. At the same time, the offshore deep-sea continental slopes are historically important fishing grounds. Although previous inventories primarily focused on coral reef fishes within the atoll listing 652 species from 73 families, comprehensive surveys of fishes from deeper waters have been incomplete. In this study, the species composition of the fish fauna around Dongsha was updated by analyzing large volumes of frozen bycatch from commercial deep-sea trawlers operating in the area for the past four years and reviewing the existing literature. The species list increased to 1087 species belonging to 167 families, including several documented as new records and potentially undescribed species. This updated checklist also includes images of each species and most of their sagittal otoliths. This will assist further taxonomic work and significantly enhance understanding of marine biodiversity in the South China Sea.

Key words: Biodiversity, ichthyofauna, ichthyology, Pratas Island, taxonomy

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Introduction

The South China Sea is an arm of the western Pacific Ocean that borders the Southeast Asian mainland. Renowned for its significant marine biodiversity (Ng and Tan 2000; Liu 2013), the South China Sea also plays a crucial role in regional economic development and serves as a major fishing ground in bordering countries (Teh et al. 2019; Pauly and Liang 2020; Prince et al. 2023). Dongsha Island (also known as Dongsha Atoll or Pratas Island) is situated on the northern margin of the South China Sea, at the midpoint between Taiwan, Hong Kong, and

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* These authors contributed equally to this work.

Philippines. Dongsha is known for its coral reef ecosystems which support a diverse array of reef and seagrass-associated fishes (Chen et al. 1995; Lee et al. 2015). The island is governed by the Dongsha Atoll National Park of Taiwan and represents a critical marine biodiversity hotspot crucial for conservation and scientific studies (Dai 2004; Tkachenko and Soong 2017; Nieder et al. 2019).

Besides its coral reef ecosystems and associated fishes inhabiting Dongsha Atoll, the surrounding waters are also areas for commercial deep-sea fishing. Notably, the commercial trawl fishery, active in the deeper slope areas since the early 2000s, yields high volumes of deep-sea organisms. These catches, including a wide range of fish and invertebrate species (Komai et al. 2022, 2023), are highly diverse and are used primarily for aquaculture feeds. Despite their high biodiversity, research on these commercial species has only recently begun to receive substantial attention and there has been a rapid increase in the reporting of new fish species and records from these commercial trawl fishery sites in recent years (Ho and Lin 2022; Ho et al. 2023; Mediodia et al. 2024). However, new discoveries have overwhelmed current species lists, and there is a need to update these lists to accurately reflect the true baseline of fish diversity around Dongsha Island.

The purpose of this paper is to review and compile existing data and literature to provide a comprehensive overview of the fish fauna in and around Dongsha Island. While the list of coral and seagrass-associated fishes is derived from previous surveys outside of the marine protected area (Fig. 1), the list of deep-sea fish collected from the commercial trawl fishery is primarily based on our systematic sampling conducted over the past four years. In this updated checklist, we include records from both data sources but images of fresh specimens and otoliths are restricted to the deep-sea fishes. By updating this checklist, we aim to significantly enhance understanding of the region’s marine biodiversity, and make a crucial contribution to support the sustainable management of its marine resources.

Materials and methods

Our study used two distinct datasets: occurrence records from the literature on coral and seagrass-associated shallow-water fishes and newly collected occurrence data from deep-water fishes sampled via commercial bottom trawlers. Both datasets represent different ecological settings with distinct sampling techniques. For the former, we reviewed existing literature (Chen et al. 1995; Shao et al. 2008; Shao et al. 2011; Chang et al. 2012; Ebert et al. 2013; Xu et al. 2019) and validated nomenclatures (Fricke et al. 2024). From February to early July each year from 2021 to 2024, we obtained frozen samples from fishermen at Zhengbin fish port in Keelung, Taiwan that were collected from the commercial bottom trawlers operating in the waters off Dongsha Island at depths of approximately 300–600 meters (Fig. 1; coordinates 18°49'N to 20°45'N and 112°46'E to 116°15'E). These samples consisted mainly of fishes and other invertebrates and weighed approximately 30 kg each. The total samples ($n = 198$) processed collectively weighed more than 6,000 kg. We collected samples bi-monthly, carefully selecting specimens to ensure they represented the broadest possible diversity within the catch. These samples were then transferred to our lab and defrosted sequentially.

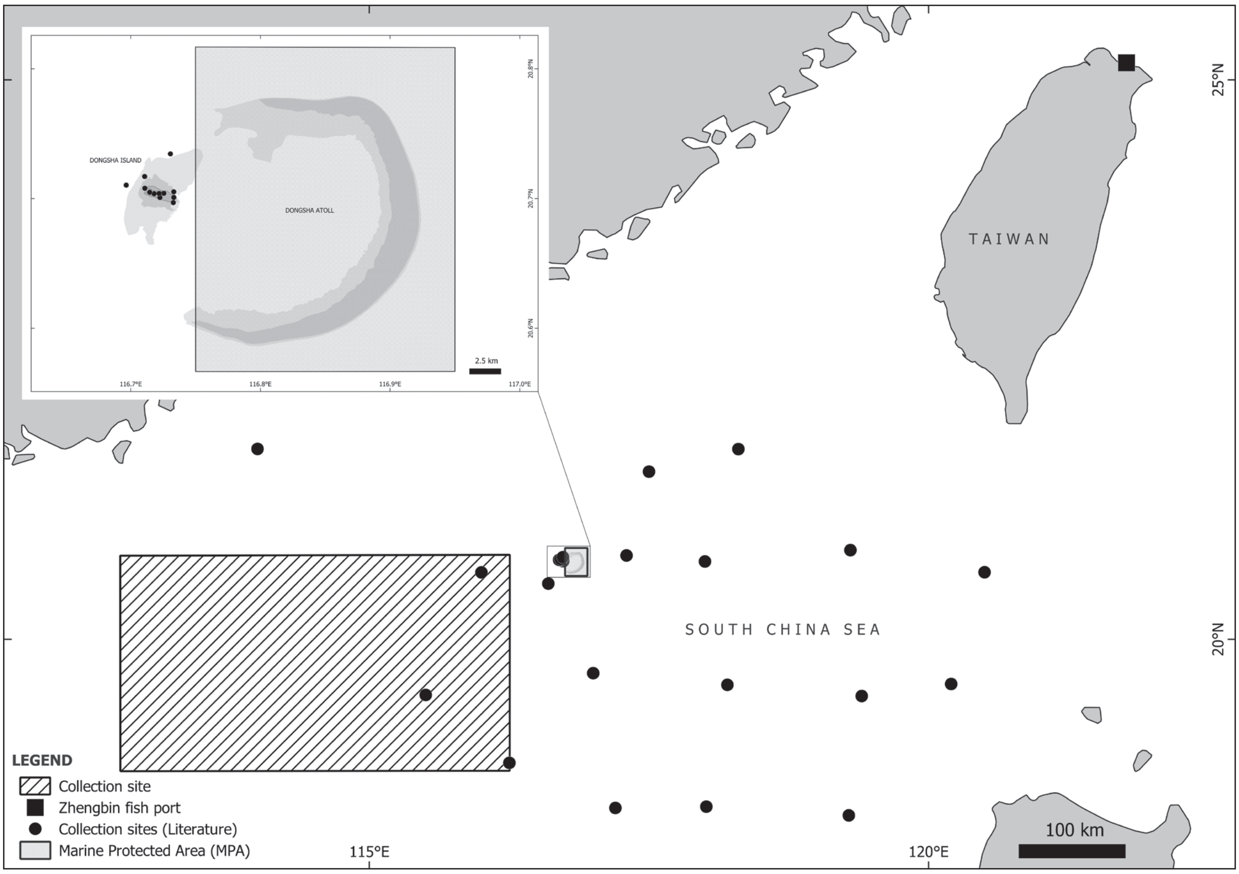

Figure 1. Map of Dongsha Atoll and the surrounding waters of the northern South China Sea showing the collection sites.

Each fish was measured for standard length (**SL**), total length (**TL**), and weight (**WT**), with preanal length (**PAL**) recorded when necessary. Specimens were photographed before muscle tissue was subsampled from the right caudal region. These tissue samples were preserved in 95% ethyl alcohol and deposited at the National Academy of Marine Research in Kaohsiung for future reference.

For images of teleostean otoliths, the left sagittal otoliths were primarily used; right otoliths were reversed for consistency and noted with an (**R**) in each caption (Lin and Chang 2012). These otoliths were coated with a thin layer of gold using an ion sputter machine (MCM-100P, Sec, South Korea) to enhance the visibility of the sulcus. In addition, images of small-sized otoliths were captured using a scanning electron microscope (JSM-7100FLV, Jeol, Japan). Otoliths were archived at the Marine Paleontology Lab, Biodiversity Research Center, Academia Sinica, registered under the code CHLOL. We follow Nelson et al. (2016) for general classification and incorporate recent modifications from newly published research (Smith et al. 2022; Near and Thacker 2024). Scientific names and taxonomic attributions adhere to the latest edition of the Catalog of Fishes (Fricke et al. 2024). Our remarks provide information on species distribution and abundance estimates around Dongsha Island.

Results

The occurrence dataset listed below was uploaded to the Global Biodiversity Information Facility (GBIF) and was published (Lin and Wu 2024). Representative fish specimens and their otoliths are presented in Figs 2–73.

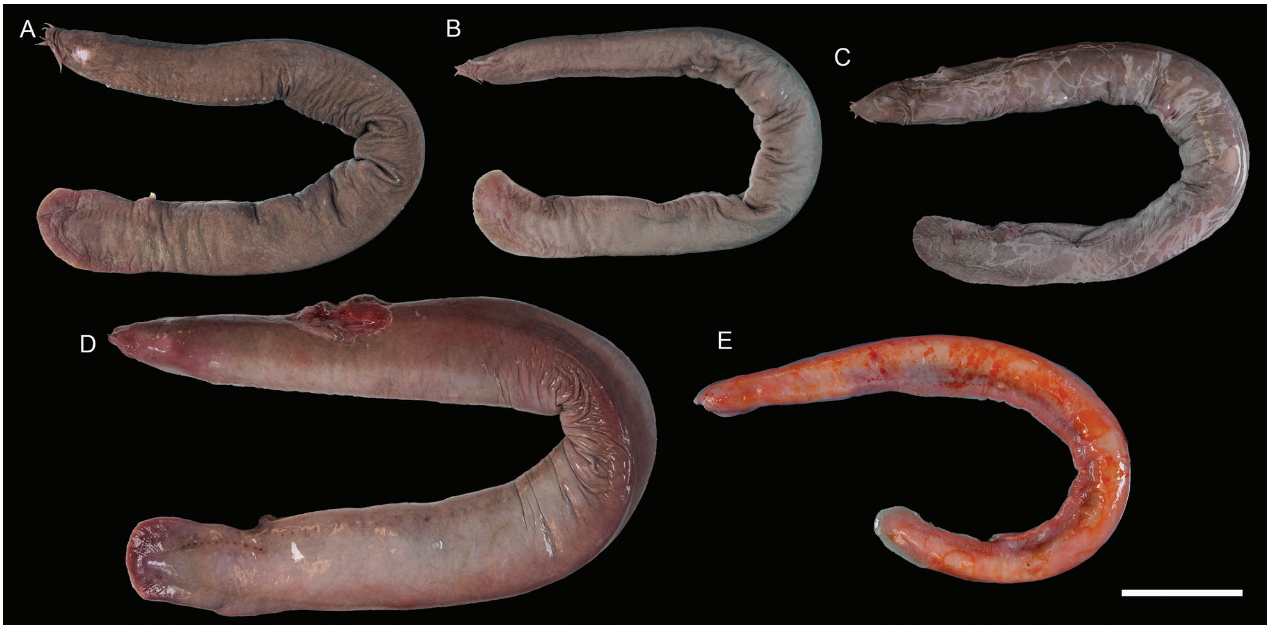

Figure 2. Images of fresh specimens collected around Dongsha Island **A** *Eptatretus okinoseanus*, 335.37 mm TL **B** *Eptatretus sheni*, 344.32 mm TL **C** *Eptatretus fernholmi*, 348.43 mm TL **D** *Eptatretus taiwanae*, 416.49 mm TL **E** *Rubicundus rubicundus*, 316.99 mm TL. Scale bar: 5 cm.

Species recently described, redescribed, or first recorded around Dongsha Island (2021–2024)

***Apristurus nakayai* Iglésias, 2012**
Fig. 4E

This species was originally described from New Caledonia, with one record from Papua New Guinea, and was recently recorded around Dongsha Island (Ng et al. 2023b). It is common in the area.

***Iago garricki* Fourmanoir & Rivaton, 1979**
Fig. 4J

This species is restricted to the tropical western Pacific, and is recently redescribed based on five specimens around Dongsha Island (Ng et al. 2022a).

***Etmopterus lii* Ng, Liu & Joung, 2024**
Fig. 5D

This species was recently described from the northern South China Sea, where we collected our samples. Juveniles are more common around Dongsha Island, while adults are rare, suggesting that the latter may inhabit deeper waters.

***Okamejei picta* Ng, Ho, Joung & Liu, 2023**
Fig. 3H

This species was described around Dongsha Island, based on two specimens (Ng et al. 2023a). No additional specimens were collected after the description.

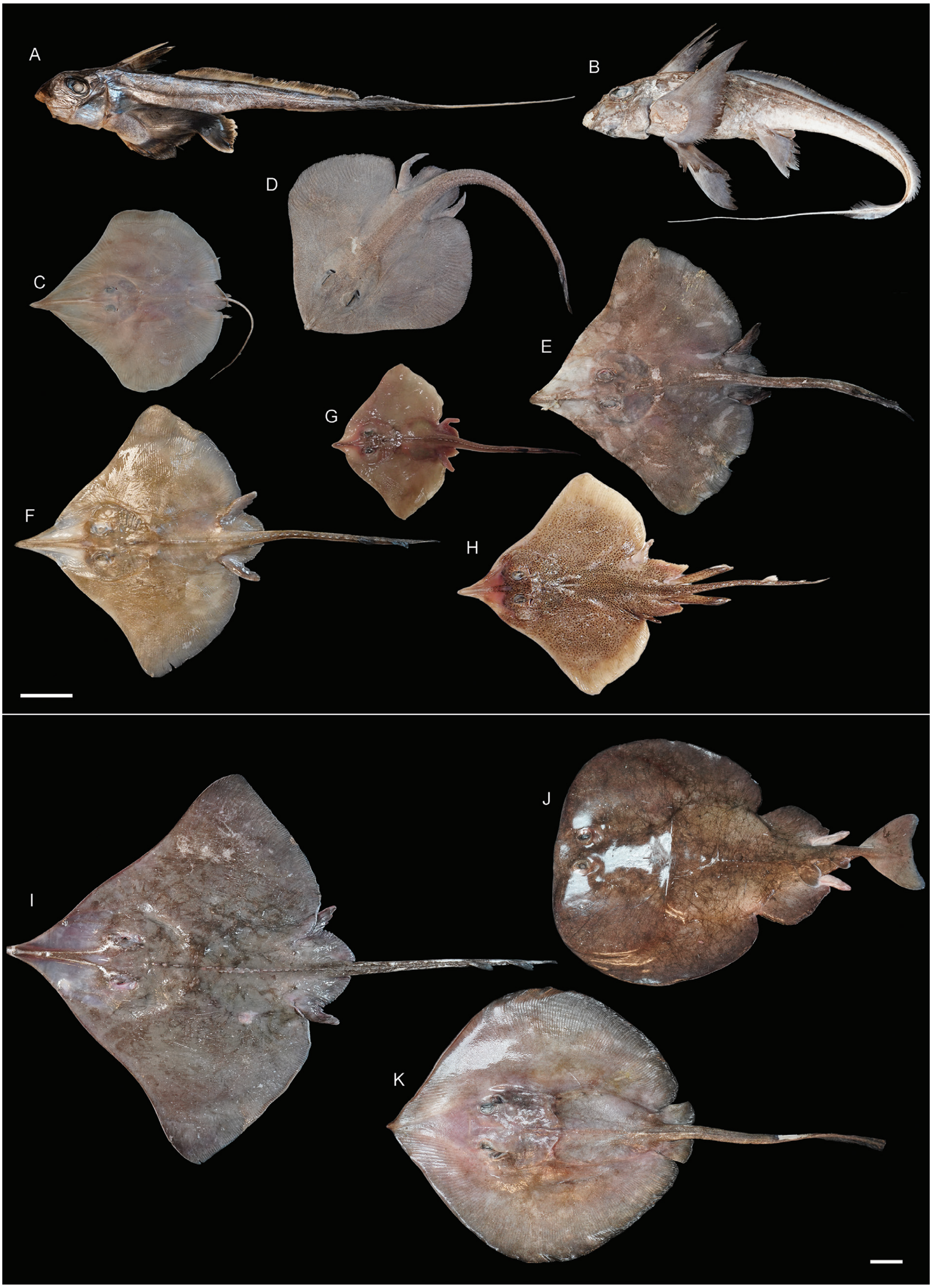

Figure 3. Images of fresh specimens collected around Dongsha Island **A** *Chimaera phantasma*, 511 mm TL **B** *Hydrolagus mitsukurii*, 633 mm TL **C** *Sinobatis borneensis*, 338 mm TL **D** *Notoraja tobitukai*, 448 mm TL **E** *Dipturus gigas*, 404 mm TL **F** *Dipturus tengu*, 400 mm TL **G** *Okamejei* sp., 266 mm TL **H** *Okamejei picta*, 429 mm TL **I** *Dipturus wuhanlingi*, 753 mm TL **J** *Tetronarce tokionis*, 576 mm TL **K** *Plesiobatis daviesi*, 801 mm TL. Scale bars: 5 cm.

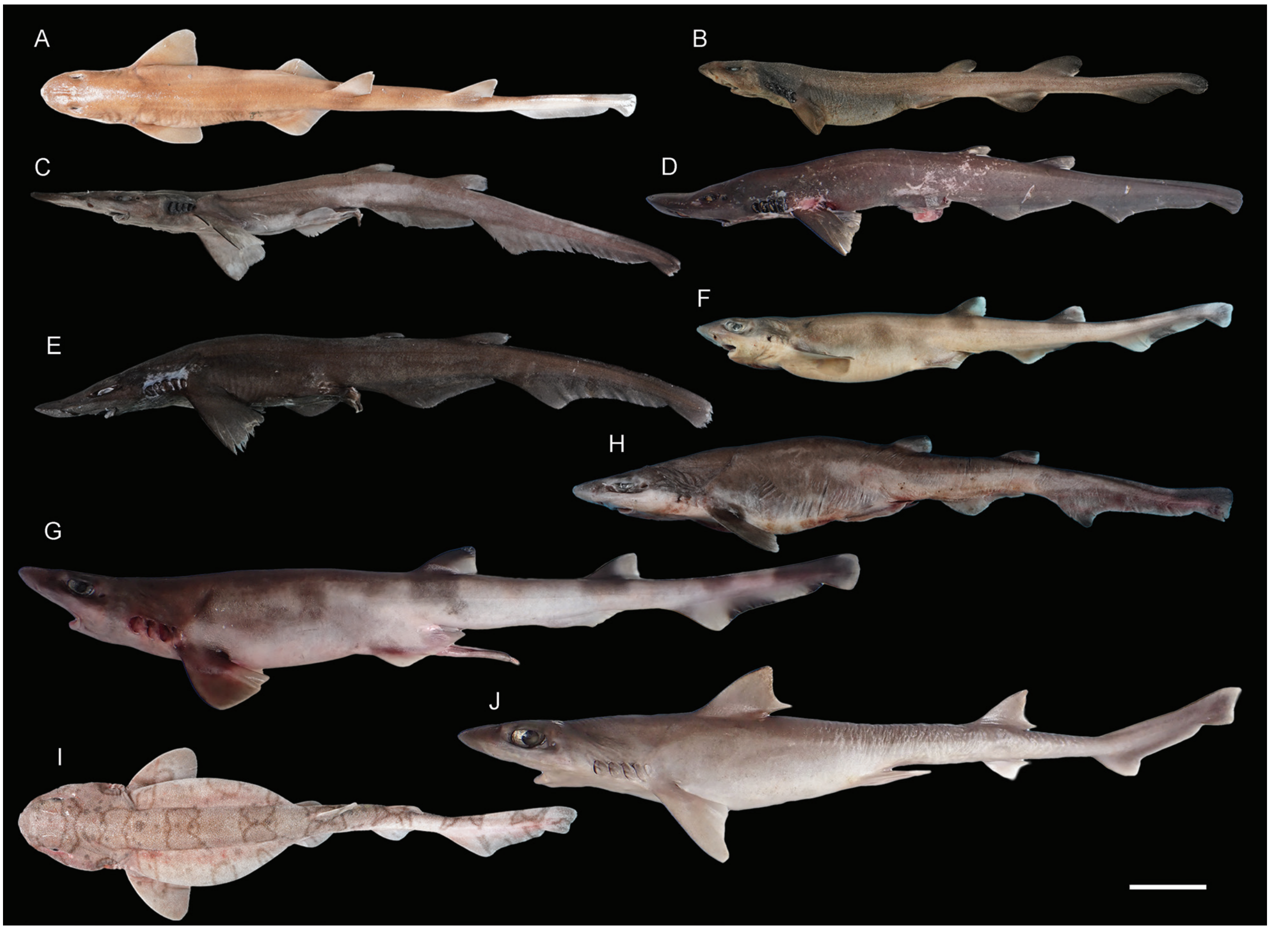

Figure 4. Images of fresh specimens collected around Dongsha Island **A** *Cirrhoscyllium formosanum*, 380 mm TL **B** *Dichichthys melanobranchus*, 320 mm TL **C** *Apristurus herklotsi*, 413 mm TL **D** *Apristurus macrostomus*, 361 mm TL **E** *Apristurus nakayai*, 421 mm TL **F** *Galeus eastmani*, 342 mm TL **G** *Galeus nipponensis*, 566 mm TL **H** *Galeus sauteri*, 408 mm TL **I** *Cephaloscyllium fasciatum*, 356 mm TL **J** *Iago garricki*, 515 mm TL. Scale bar: 5 cm.

Ophichthus kusanagi **Hibino, McCosker & Tashiro, 2019**
Fig. 9G

This species was described from Japan and reported around Dongsha Island (Ho et al. 2022). It is rare around Dongsha Island.

Ophichthus pratasensis **Ho, Ng & Lin, 2022**
Figs 9E, 10A

This species was described around Dongsha Island (Ho et al. 2022) and is rare in the area.

Congriscus maldivensis **(Norman, 1939)**
Figs 11B, 12B

This species is widespread in the Indo-West Pacific and was recently recorded by Huang et al. (in press.) around Dongsha Island. This species is common in the area but not found around Taiwan.

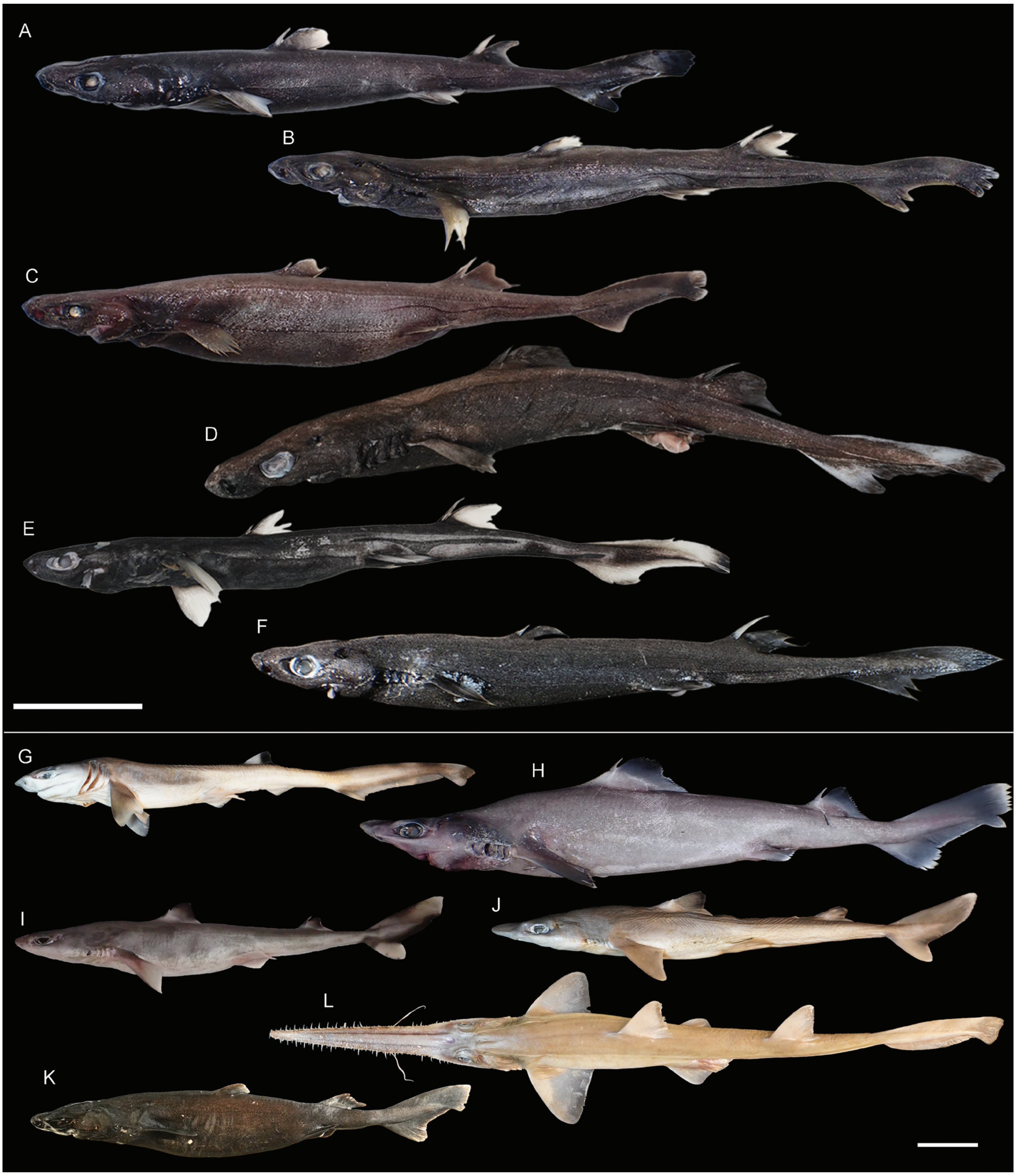

Figure 5. Images of fresh specimens collected around Dongsha Island **A** *Etmopterus bigelowi*, 261 mm TL **B** *Etmopterus brachyurus*, 268 mm TL **C** *Etmopterus decacuspidatus*, 270 mm TL **D** *Etmopterus lii*, 296 mm TL **E** *Etmopterus* cf. *molleri*, 264 mm TL **F** *Etmopterus lucifer*, 287 mm TL **G** *Heptranchias perlo*, 383 mm TL **H** *Centrophorus tessellatus*, 613 mm TL **I** *Squalus montalbani*, 371 mm TL **J** *Squalus japonicus*, 410 mm TL **K** *Zameus squamulosus*, 356 mm TL **L** *Pristiophorus japonicus*, 622 mm TL. Scale bars: 5 cm.

***Lestrolepis philippina* (Fowler, 1934)**
Figs 25G, 26F

This species was commonly misidentified as *Lestrolepis japonica* over the past few decades (e.g., Ho et al. (2019b), till Ho and Kawai (2024) verified their identities.

Kuronezumia macronema **(Smith & Radcliffe, 1912)**
Figs 34B, 37B

This species was originally described from the Philippines and was recorded around Dongsha Island (Ng et al. 2022b). No other specimen was collected after this record.

Amarsipus carlsbergi **Haedrich, 1969**
Figs 55E, 56B

This species is widespread in the Indo-West Pacific and was reported as a new record around Dongsha Island by Ho et al. (2023). It is very rare in the area.

Synagrops atrumoris **Mediodia & Lin, 2024**
Figs 57F, 58C

This recently described new species (Mediodia et al. 2024) is not common in our sampling, and it is often difficult to distinguish from its sympatric congener, *S. japonicus* (Döderlein, 1883).

Lophiodes lugubris **(Alcock, 1894)**
Figs 67B, 68D

This species is widely distributed in the Indo-West Pacific and was recently redescribed by Ho and Lin (2022).

Lophiodes triradiatus **(Lloyd, 1909)**
Figs 67E, 68F

This deepwater species was only found around Dongsha Island and was not recorded around Taiwan. Ho and Lin (2022) reported larger specimens from Dongsha Island, which are larger than those reported from other countries.

New records for Dongsha Island

Eptatretus sheni **(Kuo, Huang & Mok, 1994)**
Fig. 2B

This species was described from Taiwan. Though common around Taiwan, it was not reported in other regions. Our records around Dongsha Island show a substantial range extension. This species is rare around Dongsha Island.

Eptatretus taiwanae **(Shen & Tao, 1975)**
Fig. 2D

This species was described from Taiwan and is common in the area. It was recognized as endemic. Our first record around Dongsha Island suggests a broader distribution range. This species is rare around Dongsha Island.

Rubicundus rubicundus **(Kuo, Lee & Mok, 2010)**
Fig. 2E

This attractive cuskeel species was described from Taiwan and is considered endemic. The sole specimen we collected represents the first record around Dongsha Island. This species is very rare around Dongsha Island.

Centrophorus tessellatus **Garman, 1906**
Fig. 5H

Some species of the genus *Centrophorus* are very difficult to identify, including a long-snout species group. Within this group, two species occur in the northwestern Pacific, *C. tessellatus* and *C. isodon* Chu, Meng & Liu, 1981. We tentatively identified the long-snout specimens as *C. tessellatus*, which is not uncommon in southwestern Taiwan and is recorded in Japan. This species is uncommon around Dongsha Island, and most specimens are juveniles.

Etmopterus bigelowi **Shirai & Tachikawa, 1993**
Fig. 5A

This species is one of the circumglobal lanternshark species, yet records from the northwestern Pacific were limited to off Japan. Five specimens were collected in our study, confirming their occurrence around Dongsha Island, South China Sea.

Squalus montalbani **Whitley, 1931**
Fig. 5I

One of the widespread spurdog species, having records from northeastern Taiwan to northern Australia. Yet, no records are known from the South China Sea. This species is common around Dongsha Island. Large individuals are sold separately.

Atractodenchelys brevitrunca **Vo & Ho, 2020**
Figs 6I, 7I

This species was recently described in central Vietnam by Vo and Ho (2020). The novel record based on several specimens around Dongsha Island we examined suggests that this species has a broad distribution range in the South China Sea.

Dysomma polycatodon **Karrer, 1983**
Figs 6B, 7G

This species is widely distributed on continental shelf in the Indo-West Pacific, and is common around Taiwan. Only one specimen was recorded around Dongsha Island, suggesting the shallower habitat of this species.

Figure 6. Images of fresh specimens collected around Dongsha Island **A** *Aldrovandia affinis*, 188.65 mm TL **B** *Dysomma polycatodon*, 241.19 mm TL **C** *Dysomma anguillare*, 225.71 mm TL **D** *Dysommina orientalis*, 290.99 mm TL **E** *Dysomma dolichosomatum*, 290.86 mm TL **F** *Synaphobranchus kaupii*, 330.85 mm TL **G** *Synaphobranchus oligolepis*, 252.15 mm TL **H** *Synaphobranchus affinis*, 215.86 mm TL **I** *Atractodenchelys brevitrunca*, 605.05 mm TL. Scale bar: 5 cm.

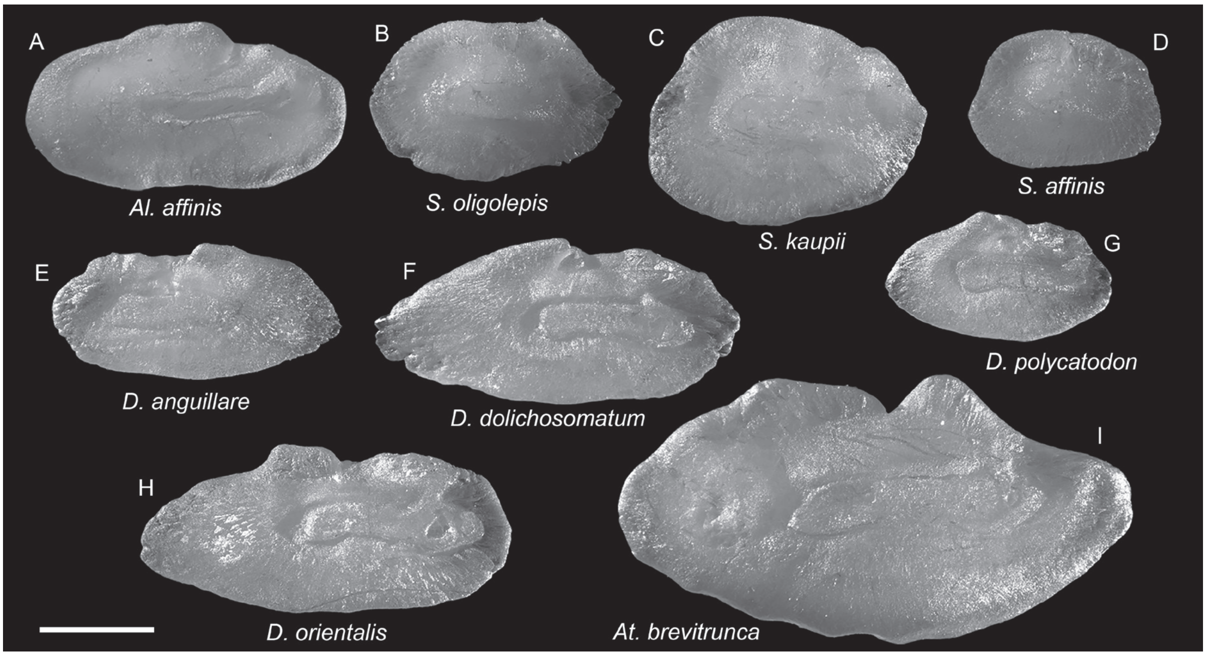

Figure 7. Otolith images of fresh specimens collected around Dongsha Island **A** *Aldrovandia affinis*, CHLOL 20601, 204.25 mm TL **B** *Synaphobranchus oligolepis*, CHLOL 23597, 275.98 mm TL **C** *Synaphobranchus kaupii*, CHLOL 23598, 330.85 mm TL (R) **D** *Synaphobranchus affinis*, CHLOL 26162, 215.86 mm TL **E** *Dysomma anguillare*, CHLOL 25422, 225.71 mm TL (R) **F** *Dysomma dolichosomatum*, CHLOL 20664, 322.95 mm TL **G** *Dysomma polycatodon*, CHLOL 9815, 241.19 mm TL **H** *Dysommina orientalis*, CHLOL 20492, 294.48 mm TL **I** *Atractodenchelys brevitrunca*, CHLOL 25213, 494.47 mm TL. Scale bar: 1 mm.

Synaphobranchus oligolepis **Ho, Hong & Chen, 2018**
Figs 6G, 7B

This species was recently described around Taiwan. It is common near the type locality but rare around Dongsha Island.

Coloconger maculatus **Ho & Tang, 2021**
Figs 8A, 10H

This species was recently described around Taiwan based on a single specimen. Our specimen collected around Dongsha Island is the second known specimen.

Coloconger raniceps **Alcock, 1889**
Figs 8C, 10I

This species is widespread in the Indo-West Pacific, but is not well presented in museums. It is rare around Dongsha Island.

Ophichthus megalops **Asano, 1987**
Figs 9H, 10B

This species was originally described from Japan. It is occasionally found in bycatches of bottom trawl around Taiwan, but it is rare around Dongsha Island.

Ophichthus obtusus **McCosker, Ide & Endo, 2012**
Figs 9C, 10E

This species is restricted to the northwestern Pacific and has records from Japan, Taiwan, and Vietnam. It is common around Dongsha Island and Taiwan.

Acromycter nezumi **(Asano, 1958)**
Figs 11F, 14A

This species is restricted to the northwestern Pacific. It is common around Dongsha Island but rare around Taiwan.

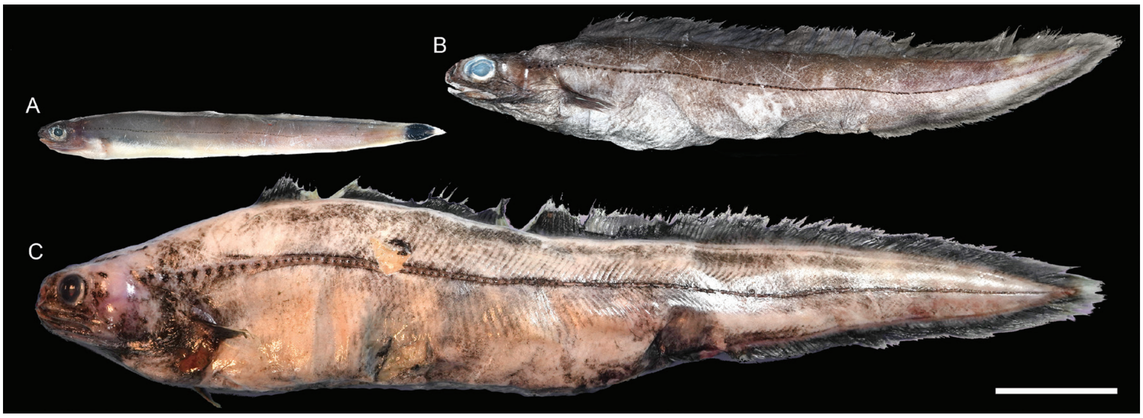

Figure 8. Images of fresh specimens collected around Dongsha Island **A** *Coloconger maculatus*, 171.06 mm TL **B** *Coloconger scholesi*, 274.87 mm TL **C** *Coloconger raniceps*, 461.33 mm TL. Scale bar: 5 cm.

Figure 9. Images of fresh specimens collected around Dongsha Island **A** *Pisodonophis boro*, 476.99 mm TL **B** *Neenchelys* sp., 311.24 mm TL **C** *Ophichthus obtusus*, 467.93 mm TL **D** *Ophichthus* sp., 448.31 mm TL **E** *Ophichthus pratasensis*, 860.23 mm TL **F** *Ophichthus urolophus*, 549.79 mm TL **G** *Ophichthus kusanagi*, 504.80 mm TL **H** *Ophichthus megalops*, 592.09 mm TL **I** *Nettastoma solitarium*, 557.13 mm TL. Scale bar: 5 cm.

***Ariosoma emmae* Smith & Ho, 2018**
Figs 11J, 12I

This species was described from southwestern Taiwan. It is rare around Dongsha Island.

***Bathycongrus bimaculatus* Smith & Ho, 2018**
Fig. 13D

This species was described from southwestern Taiwan. The sole specimen around Dongsha Island, suggests a broader distribution in the South China Sea.

***Bathycongrus bleekeri* Fowler, 1934**
Figs 12D, 13E

This species is restricted to the northwestern Pacific. It is rare around Dongsha Island.

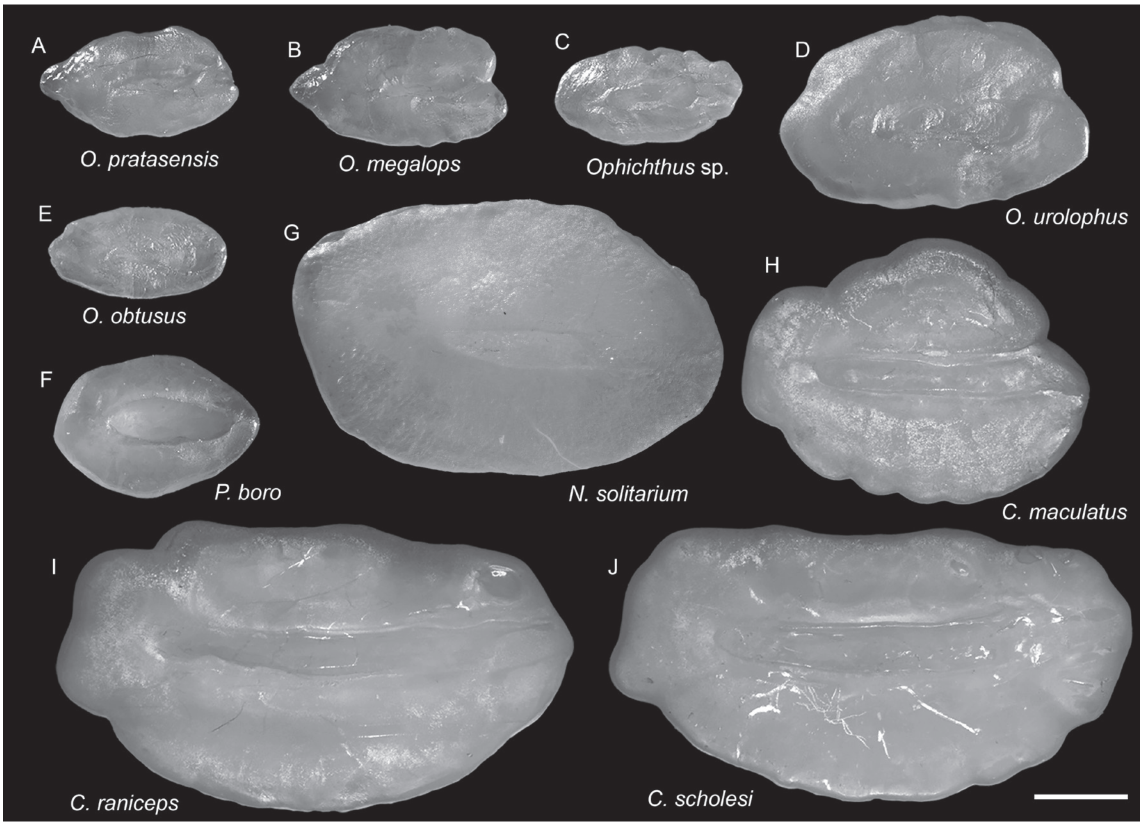

Figure 10. Otolith images of fresh specimens collected around Dongsha Island **A** *Ophichthus pratasensis*, CHLOL 20629, 495.21 mm TL **B** *Ophichthus megalops*, CHLOL 22042, 592.09 mm TL **C** *Ophichthus* sp., CHLOL 17929, 442.76 mm TL **D** *Ophichthus urolophus*, CHLOL 9821, 577.00 mm TL **E** *Ophichthus obtusus*, CHLOL 19481, 453.22 mm TL **F** *Pisodonophis boro*, CHLOL 21208, 476.99 mm TL **G** *Nettastoma solitarium*, CHLOL 29404, 648.86 mm TL **H** *Coloconger maculatus*, CHLOL 20620, 171.06 mm TL **I** *Coloconger raniceps*, CHLOL 27101, 207.50 mm TL **J** *Coloconger scholesi*, CHLOL 27100, 191.54 mm TL. Scale bar: 1 mm.

***Bathyuroconger parvibranchialis* (Fowler, 1934)**
Figs 13G, 14I

This species was originally described from the Philippines. It was recently documented in Taiwan by Ho et al. (2015) and redescribed by Smith et al. (2018). It is rare around Dongsha Island.

***Blachea xenobranchialis* Karrer & Smith, 1980**
Figs 11G, 14C

This species is widespread in the Indo-West Pacific and was previously reported from Taiwan by Ho and Shao (2010) based on a single specimen. We additionally collected two specimens around Dongsha Island, confirming its occurrence in the South China Sea.

***Congriscus megastoma* (Günther, 1877)**
Figs 11A, 12A

This species is restricted to the northwestern Pacific. It is not uncommon around Dongsha Island.

Figure 11. Images of fresh specimens collected around Dongsha Island **A** *Congriscus megastoma*, 348.09 mm TL **B** *Congriscus maldivensis*, 312.06 mm TL **C** *Nemichthys scolopaceus*, 507.37 mm TL **D** *Macrocephenchelys brachialis*, 461.81 mm TL **E** *Macrocephenchelys brevirostris*, 36.052 mm TL **F** *Acromycter nezumi*, 272.56 mm TL **G** *Blachea xenobranchialis*, 227.95 mm TL **H** *Gnathophis heterognathos*, 183.87 mm TL **I** *Ariosoma meeki*, 367.31 mm TL **J** *Ariosoma emmae*, 329.76 mm TL **K** *Gavialiceps taiwanensis*, 690.19 mm TL. Scale bar: 5 cm.

Macrocephenchelys brachialis **Fowler, 1934**

Figs 11D, 14D

This species is widespread in the Indo-West Pacific. It is common around Taiwan, yet only one specimen was collected around Dongsha Island.

Rouleina squamilatera **(Alcock, 1898)**

Figs 15E, 16D

This species has scattered distribution in the Indo-West Pacific. It is rare around Dongsha Island.

Diplophos vicinia **Koeda & Ho, 2019**

Figs 15C, 16C

This species was recently described from southern Taiwan and Papua New Guinea. The specimens we collected around Dongsha Island, suggest that this

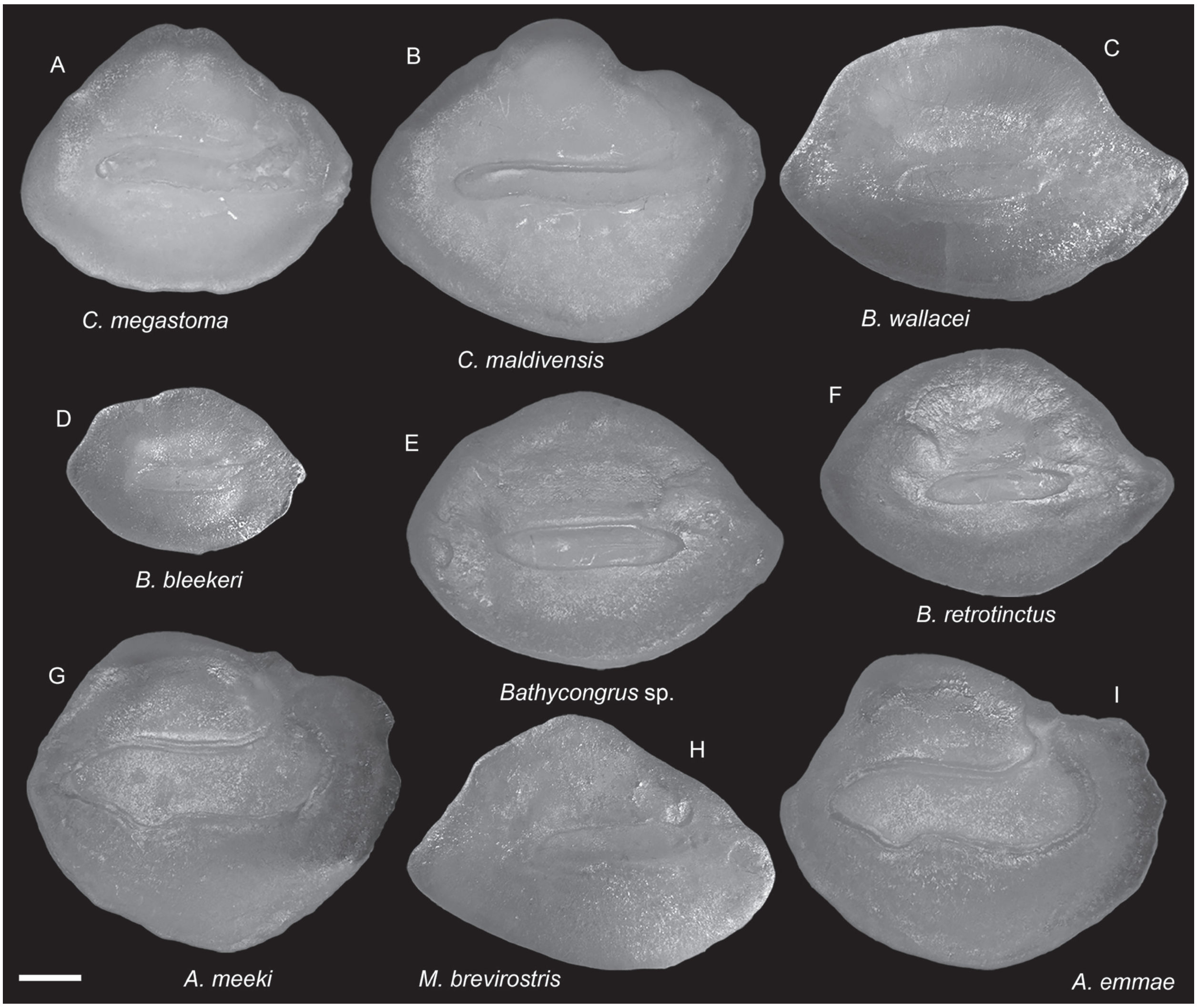

Figure 12. Otolith images of fresh specimens collected around Dongsha Island **A** *Congriscus megastoma*, CHLOL 27848, 307.35 mm TL **B** *Congriscus maldivensis*, CHLOL 27847, 217.73 mm TL **C** *Bathycongrus wallacei*, CHLOL 20479, 333.05 mm TL **D** *Bathycongrus bleekeri*, CHLOL 19487, 179.51 mm TL **E** *Bathycongrus* sp., CHLOL 20668, 315.03 mm TL **F** *Bathycongrus retrotinctus*, CHLOL 22039, 300.22 mm TL **G** *Ariosoma meeki*, CHLOL 20626, 326.77 mm TL **H** *Macrocephenchelys brevirostris*, CHLOL 9816, 360.52 mm TL **I** *Ariosoma emmae*, CHLOL 21649, 302.42 mm TL. Scale bar: 1 mm.

species is also found in the South China Sea and is sympatric with the morphologically similar congener *D. taenia*.

Polyipnus matsubarai **Schultz, 1961**
Figs 17A, 18A

This species has been reported from Japan and Hawaii (Emperor Seamounts). The occurrence around Dongsha Island suggests its broad distribution in the northwestern Pacific to Hawaii.

Polyipnus spinifer **Borodulina, 1979**
Figs 17B, 18B

This species is widespread in the western Pacific. It is not uncommon around Taiwan, especially in mid-water trawlers, but rare around Dongsha Island.

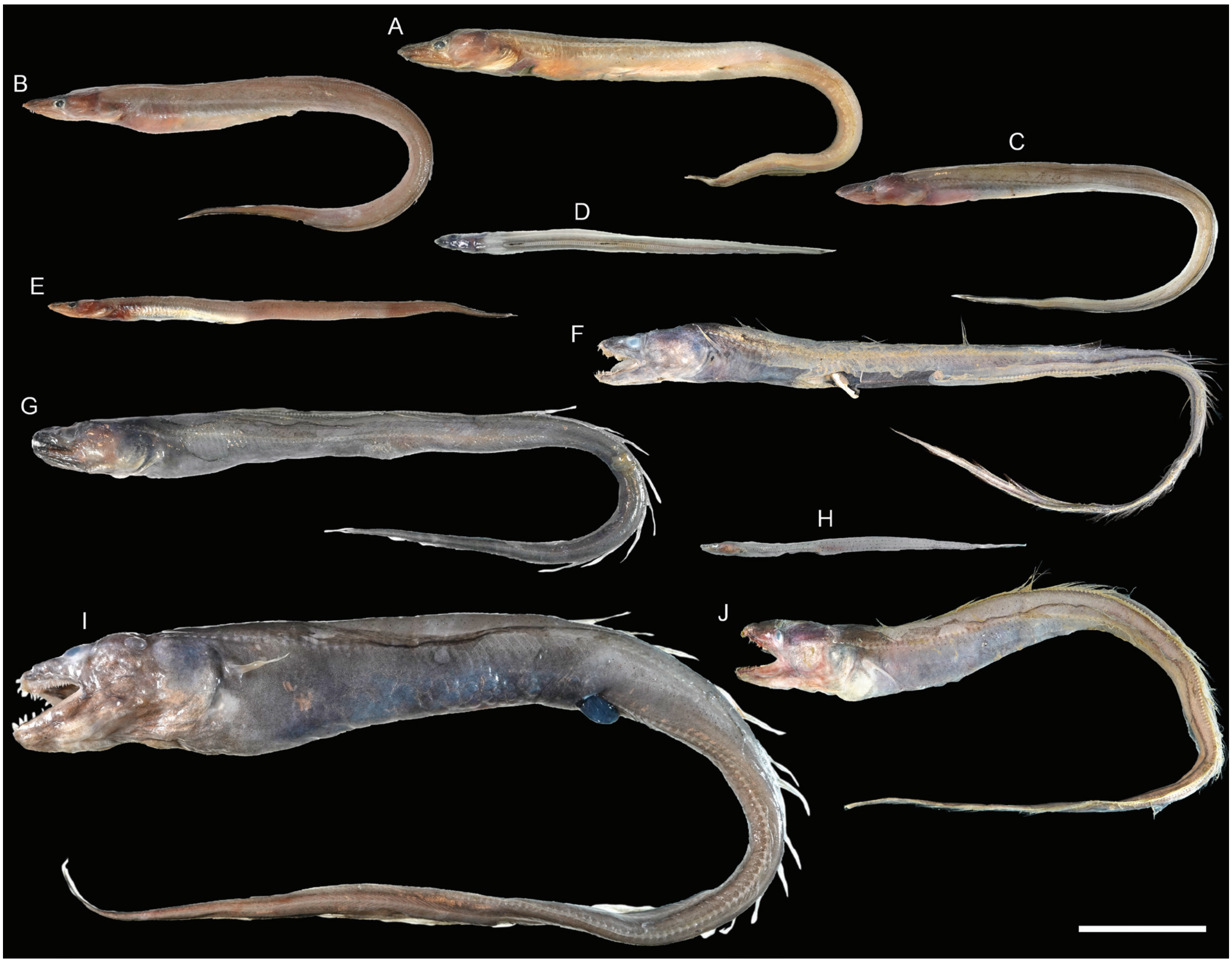

Figure 13. Images of fresh specimens collected around Dongsha Island **A** *Bathycongrus retrotinctus*, 254.48 mm TL **B** *Bathycongrus wallacei*, 273.51 mm TL **C** *Bathycongrus* sp., 275.39 mm TL **D** *Bathycongrus bimaculatus*, 153.61 mm TL **E** *Bathycongrus bleekeri*, 179.51 mm TL **F** *Bathyuroconger* cf. *vicinus*, 378.46 mm TL **G** *Bathyuroconger parvibranchialis*, 729.12 mm TL **H** *Bathyuroconger albus*, 127.79 mm TL **I** *Bathyuroconger* sp., 494.24 mm TL **J** *Bathyuroconger fowleri*, 375.93 mm TL. Scale bar: 5 cm.

Polymetme corythaeola **(Alcock, 1898)**
Figs 17I, 18H

This species can be found in the western Pacific. It is very common around Dongsha Island but rare around Taiwan.

Polymetme surugaensis **(Matsubara, 1943)**
Figs 17G, 18G

This species is widespread in the western Pacific. It is common in mid-water trawlers around Taiwan but rare around Dongsha Island.

Borostomias elucens **(Brauer, 1906)**
Figs 21A, 22G

While having circumglobal distribution in tropical and temperate oceans, this species is rare around Dongsha Island.

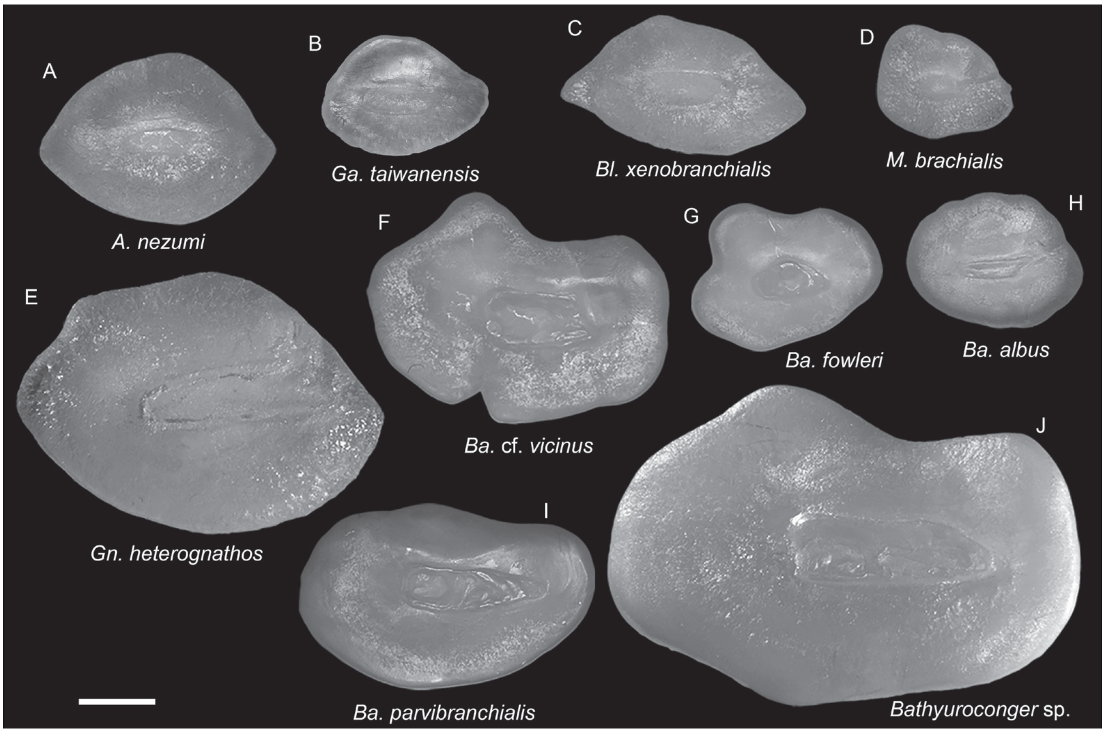

Figure 14. Otolith images of fresh specimens collected around Dongsha Island **A** *Acromycter nezumi*, CHLOL 20456, 208.92 mm TL **B** *Gavialiceps taiwanensis*, CHLOL 21638, 620.48 mm TL **C** *Blachea xenobranchialis*, CHLOL 22753, 257.88 mm TL **D** *Macrocephenchelys brachialis*, CHLOL 25636, 461.81 mm TL **E** *Gnathophis heterognathos*, CHLOL 9812, 183.87 mm TL **F** *Bathyuroconger* cf. *vicinus*, CHLOL 27098, 378.46 mm TL **G** *Bathyuroconger fowleri*, CHLOL 22668, 234.89 mm TL **H** *Bathyuroconger albus*, CHLOL 22038, 127.79 mm TL **I** *Bathyuroconger parvibranchialis*, CHLOL 22077, 729.12 mm TL **J** *Bathyuroconger* sp., CHLOL 16037, 494.24 mm TL. Scale bar: 1 mm.

Borostomias pacificus **(Imai, 1941)**
Figs 19I, 22H

This species is restricted to the northwestern Pacific and is rare around Dongsha Island.

Photostomias tantillux **Kenaley, 2009**
Figs 19G, 20C

This species is widespread in the Pacific. Only one specimen was collected around Dongsha Island.

Chlorophthalmus pectoralis **Okamaura & Doi, 1984**
Figs 23B, 24B

This species is found in the western Pacific. It is common around Dongsha Island but rare around Taiwan.

Dolichosudis fuliginosa **Post, 1969**
Figs 25I, 26A

This species is widely distributed in the Atlantic and Pacific. Ho et al. (2019a) reported this species from southern Taiwan. It is rare around Dongsha Island.

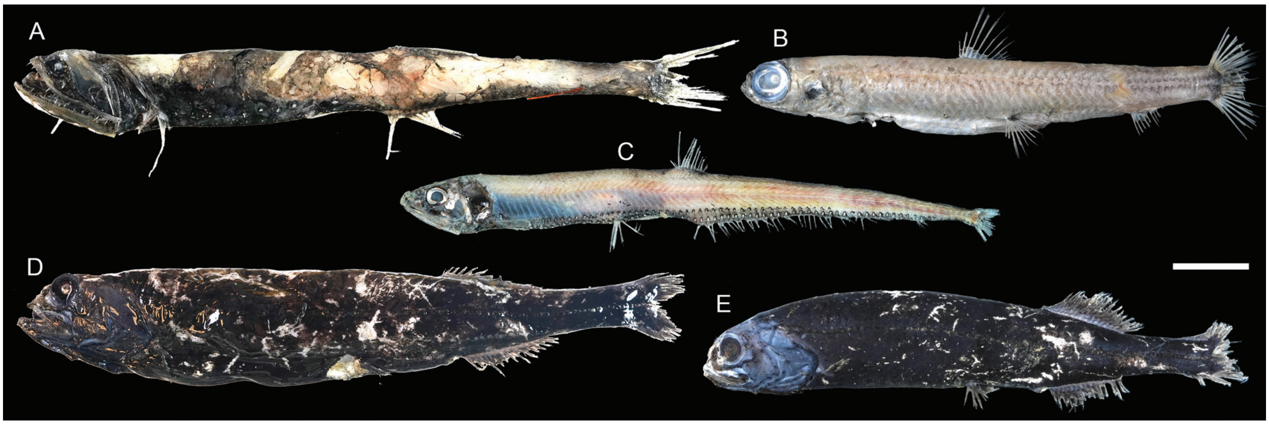

Figure 15. Images of fresh specimens collected around Dongsha Island **A** *Sigmops elongatus*, 146.75 mm SL **B** *Nansenia ardesiaca*, 187.71 mm SL **C** *Diplophos vicinia*, 138.84 mm SL **D** *Rouleina watasei*, 221.15 mm SL **E** *Rouleina squamilatera*, 202.20 mm SL. Scale bar: 3 cm.

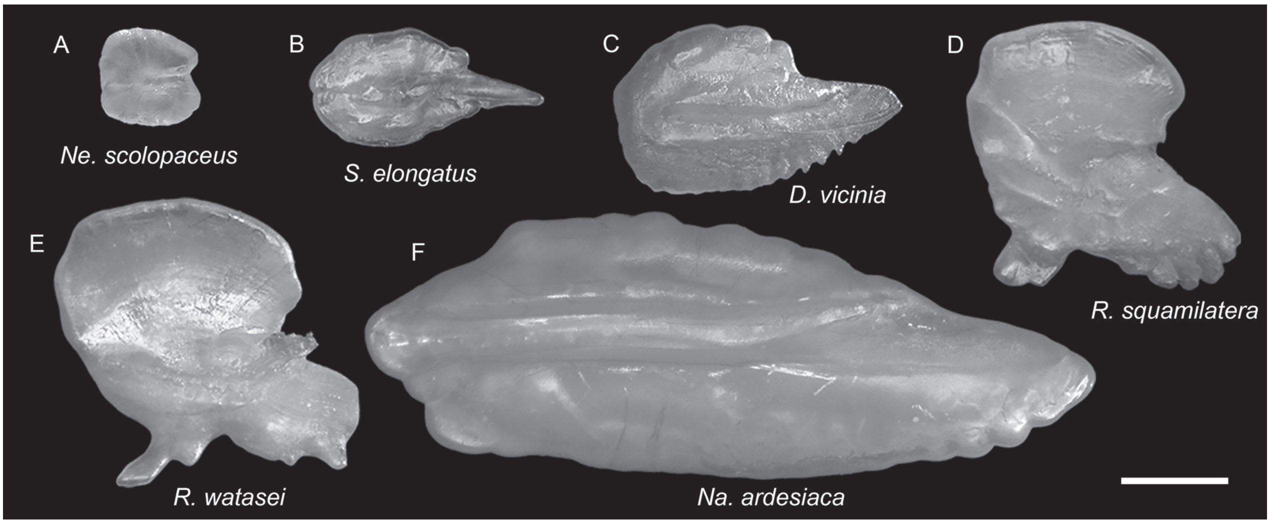

Figure 16. Otolith images of fresh specimens collected around Dongsha Island **A** *Nemichthys scolopaceus*, CHLOL 23020, 641.46 mm TL **B** *Sigmops elongatus*, CHLOL 15420, 146.75 mm SL **C** *Diplophos vicinia*, CHLOL 19048, 138.84 mm SL **D** *Rouleina squamilatera*, CHLOL 15938 166.50 mm SL **E** *Rouleina watasei*, CHLOL 16466, 221.15 mm SL **F** *Nansenia ardesiaca*, CHLOL 20443, 142.76 mm SL. Scale bar: 1 mm.

***Lestidium longilucifer* Ho, Graham & Russell, 2020**
Figs 25D, 26E

This species was recently described from southern Taiwan and Australia. It is rare around Dongsha Island and Taiwan.

***Lestidium orientale* Ho, Tsai & Li, 2019**
Figs 25F, 26C

This species, recently described around southwestern Taiwan, is restricted to the northwestern Pacific. It is rare around Dongsha Island, but common around Taiwan.

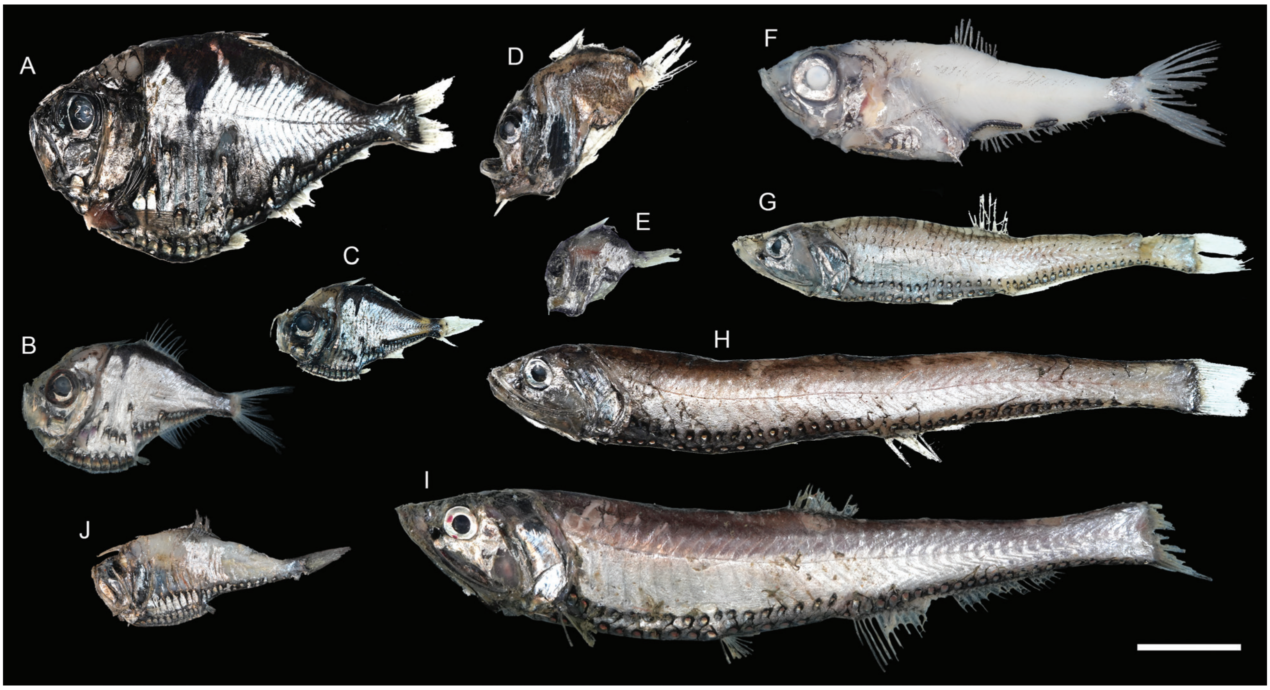

Figure 17. Images of fresh specimens collected around Dongsha Island **A** *Polyipnus matsubarai*, 79.97 mm SL **B** *Polyipnus spinifer*, 54.97 mm SL **C** *Polyipnus stereope*, 37.93 mm SL **D** *Sternoptyx pseudobscura*, 24.90 mm SL **E** *Sternoptyx diaphana*, 24.19 mm SL **F** *Argyripnus* sp., 87.00 mm SL **G** *Polymetme surugaensis*, 115.57 mm SL **H** *Polymetme elongata*, 124.14 mm SL **I** *Polymetme corythaeola*, 214.45 mm SL **J** *Argyropelecus affinis*, 46.60 mm SL. Scale bar: 3 cm.

Lestidium prolixum **Harry, 1953**
Figs 25E, 26D

This species is restricted to the northwestern Pacific. It is rare around Dongsha Island, but common around Taiwan (Ho et al. 2019b).

Stemonosudis rothschildi **Richards, 1967**
Figs 25B, 26H

This species is almost circumglobally distributed in tropical oceans, except eastern Pacific. Ho et al. (2019a, b) documented this species from the southern Taiwan Islands. It is common around Dongsha Island. However, it is necessary to compare the western Pacific population with their Atlantic siblings, there are significant differences between these two populations (H-CH, pers. obs.).

Dasyscopelus selenops **(Tåning, 1928)**
Figs 27G, 29I

This species is circumglobally distributed through tropical and warm temperate oceans, except eastern Pacific. It is rare around Dongsha Island, and was recently recorded off southwestern Taiwan (Ng et al. 2024).

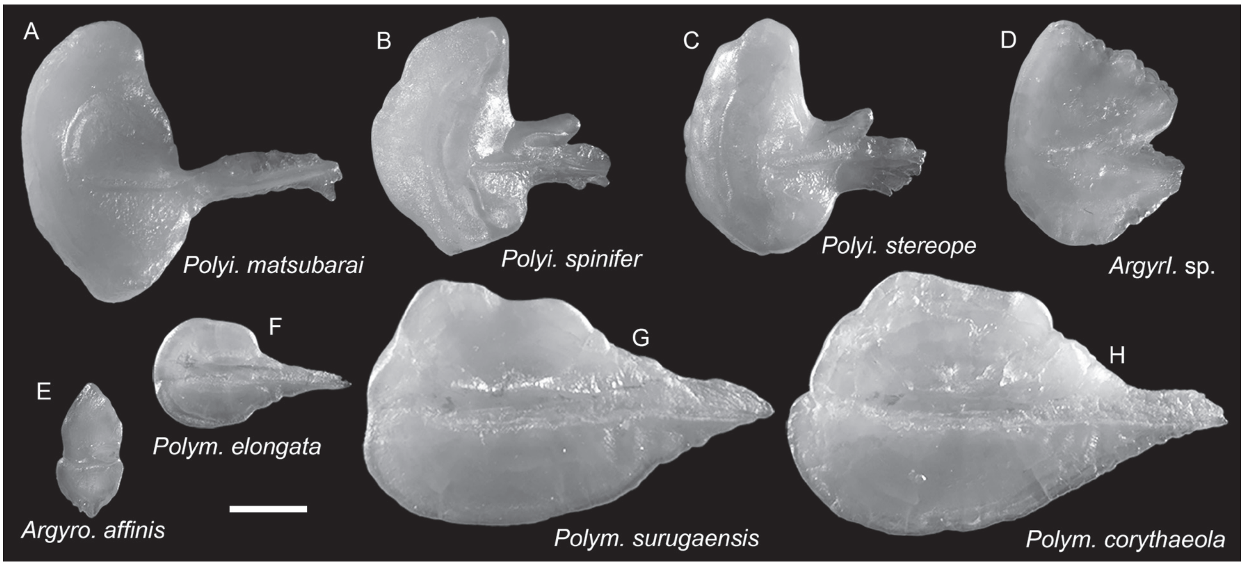

Figure 18. Otolith images of fresh specimens collected around Dongsha Island **A** *Polyipnus matsubarai*, CHLOL 16404, 79.97 mm SL **B** *Polyipnus spinifer*, CHLOL 21531, 52.83 mm SL **C** *Polyipnus stereope*, CHLOL 20639, 43.47 mm SL **D** *Argyripnus* sp., CHLOL 3446, 86.97 mm SL **E** *Argyropelecus affinis*, CHLOL 15486, 60.46 mm SL **F** *Polymetme elongata*, CHLOL 20610, 154.19 mm SL **G** *Polymetme surugaensis*, CHLOL 20580, 187.44 mm SL **H** *Polymetme corythaeola*, CHLOL 29482, 214.45 mm SL. Scale bar: 1 mm.

Figure 19. Images of fresh specimens collected around Dongsha Island **A** *Astronesthes lucifer*, 100.27 mm SL **B** *Astronesthes indica*, 84.31 mm SL **C** *Astronesthes chrysophekadion*, 96.90 mm SL **D** *Astronesthes indopacifica*, 129.70 mm SL **E** *Astronesthes trifibulata*, 123.68 mm SL **F** *Chauliodus sloani*, 176.27 mm SL **G** *Photostomias tantillux*, 105.26 mm SL **H** *Stomias nebulosus*, 76.28 mm SL **I** *Borostomias pacificus*, 113.63 mm SL **J** *Photonectes albipennis*, 191.94 mm SL. Scale bar: 3 cm.

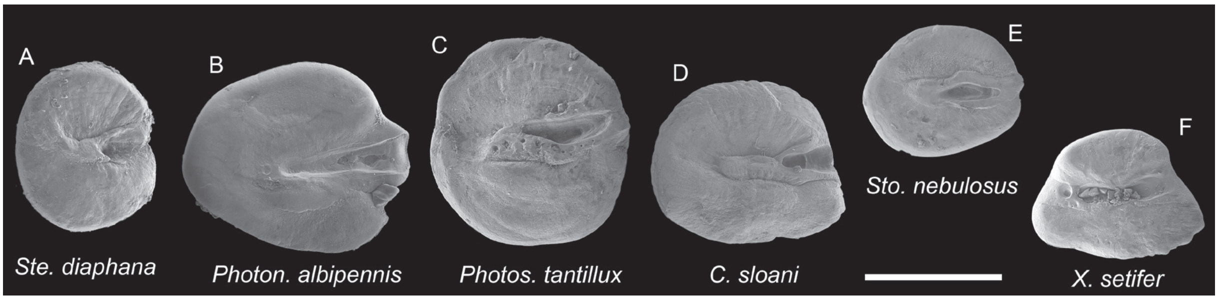

Figure 20. Otolith images of fresh specimens collected around Dongsha Island. Scanning electron microscope images of **A** *Sternoptyx diaphana*, CHLOL 21042, 24.19 mm SL **B** *Photonectes albipennis*, CHLOL 17271, 191.94 mm SL **C** *Photostomias tantillux*, CHLOL 20618, 105.26 mm SL **D** *Chauliodus sloani*, CHLOL 20056, 159.87 mm SL **E** *Stomias nebulosus*, CHLOL 29697 92.64 mm SL **F** *Xiphasia setifer*, CHLOL 26196, 312.83 mm TL. Scale bar: 0.5 mm.

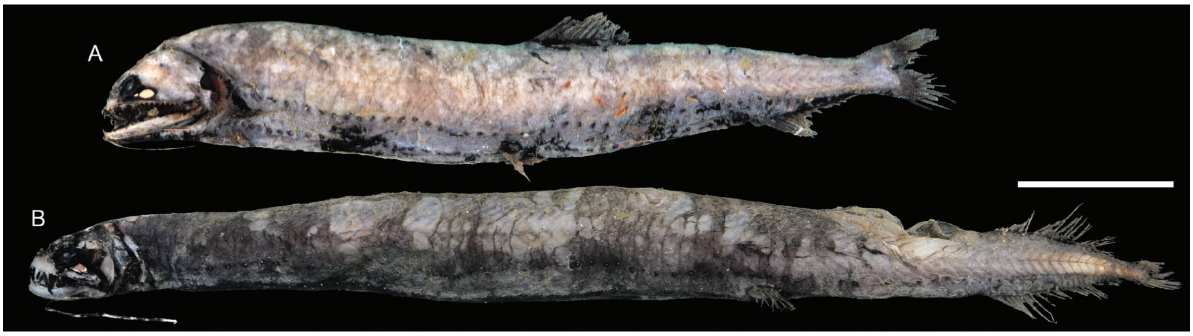

Figure 21. Images of fresh specimens collected around Dongsha Island **A** *Borostomias elucens*, 245.61 mm SL **B** *Leptostomias robustus*, 340.30 mm SL. Scale bar: 5 cm.

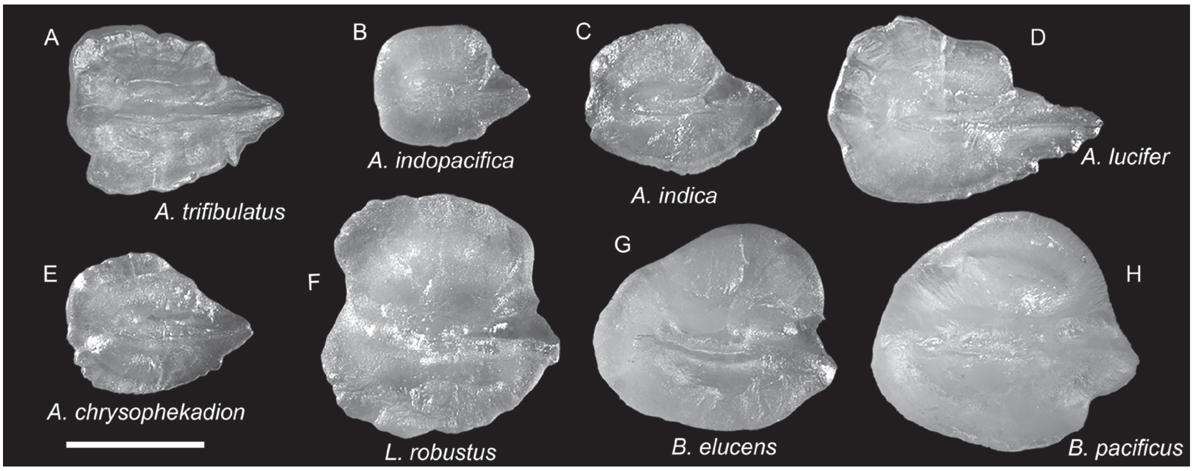

Figure 22. Otolith images of fresh specimens collected around Dongsha Island **A** *Astronesthes trifibulata*, CHLOL 15414, 123.68 mm SL **B** *Astronesthes indopacifica*, CHLOL 22771, 74.26 mm SL **C** *Astronesthes indica*, CHLOL 21597, 84.31 mm SL **D** *Astronesthes lucifer*, CHLOL 26368, 118.29 mm SL **E** *Astronesthes chrysophekadion*, CHLOL 23215, 96.90 mm SL **F** *Leptostomias robustus*, CHLOL 27092, 338.66 mm SL **G** *Borostomias elucens*, CHLOL 27093, 245.61 mm SL **H** *Borostomias pacificus*, CHLOL 28799, 223.81 mm SL. Scale bar: 1 mm.

Diaphus adenomus **Gilbert, 1905**

Figs 28K, 32A

Although widespread in the Pacific and Atlantic, this species has never been reported in the tropical northwestern Pacific. The two specimens collected in the present study represent the first record in the South China Sea.

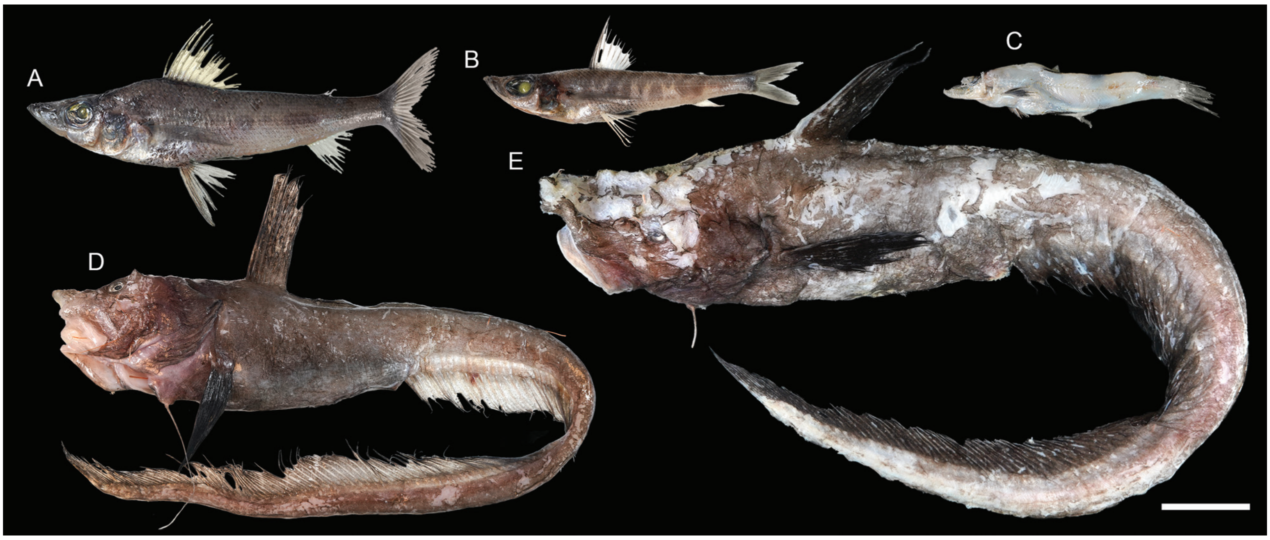

Figure 23. Images of fresh specimens collected around Dongsha Island **A** *Chlorophthalmus acutifrons*, 204.23 mm SL **B** *Chlorophthalmus pectoralis*, 145.18 mm SL **C** *Rosenblattichthys alatus*, 121.03 mm SL **D** *Ateleopus japonicus*, 621.62 mm TL **E** *Ijimaia dofleini*, 706.63 mm SL. Scale bar: 5 cm.

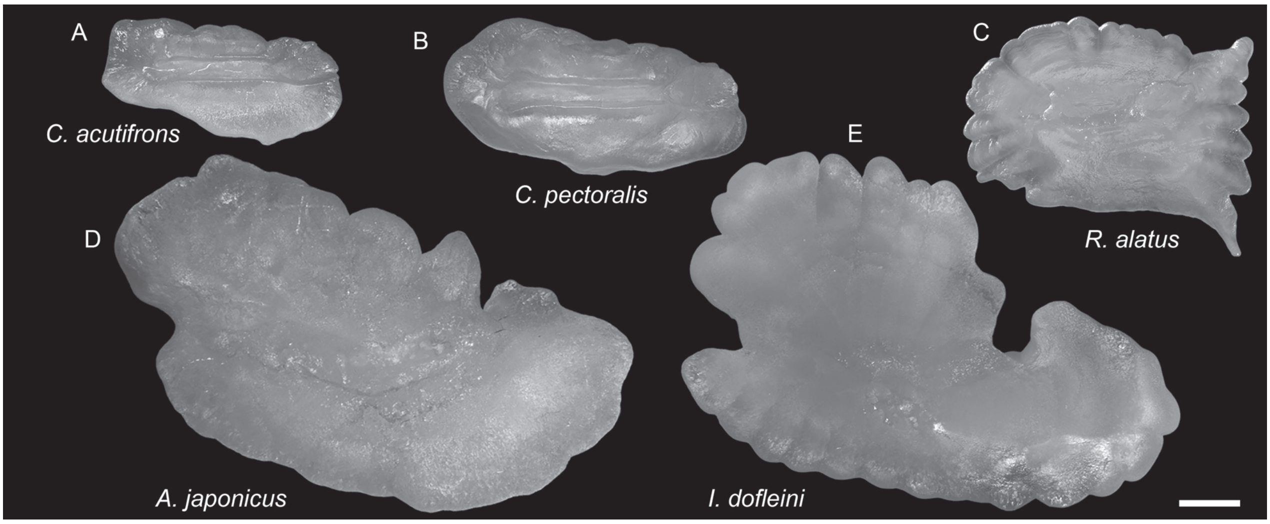

Figure 24. Otolith images of fresh specimens collected around Dongsha Island **A** *Chlorophthalmus acutifrons*, CHLOL 20303, 104.77 mm SL **B** *Chlorophthalmus pectoralis*, CHLOL 21197, 159.37 mm SL **C** *Rosenblattichthys alatus*, CHLOL 17910, 121.03 mm SL **D** *Ateleopus japonicus*, CHLOL 21595, 233.22 mm SL **E** *Ijimaia dofleini*, CHLOL 19918, 727.27 mm SL. Scale bar: 1 mm.

Zenion japonicum Kamohara, 1934
Figs 30I, 32N

This species is widespread in the Pacific. Only one specimen was collected around Dongsha Island, yet it appears to be more common around Taiwan.

Coelorinchus macrorhynchus Smith & Radcliffe, 1912
Figs 33E, 34H

This species is widespread from southwestern Taiwan to western Australia, but has never been recorded around Dongsha Island, until the present study. It is not uncommon around Dongsha Island, yet most of the specimens collected are small. The largest specimen examined was 302 mm TL.

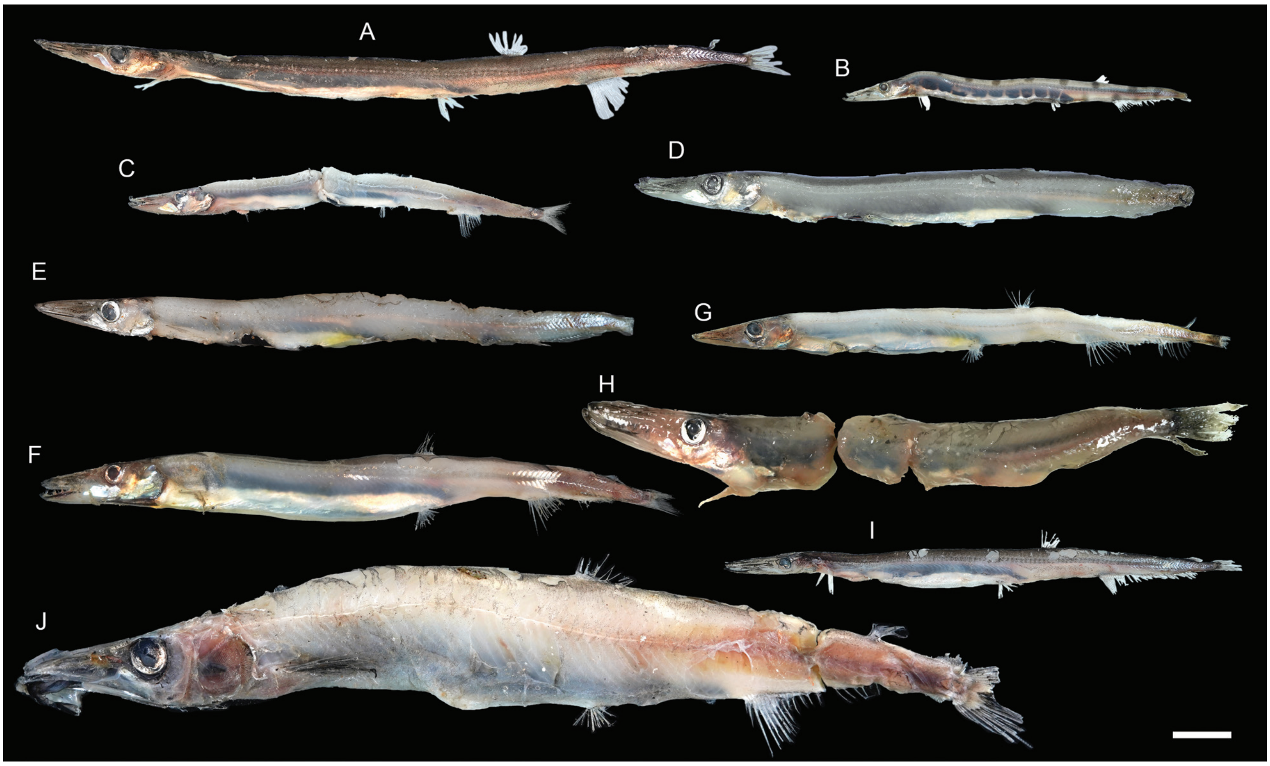

Figure 25. Images of fresh specimens collected around Dongsha Island **A** *Stemonosudis* cf. *siliquiventer*, 242.07 mm SL **B** *Stemonosudis rothschildi*, 172.22 mm SL **C** *Lestidiops* sp., 146.08 mm SL **D** *Lestidium longilucifer*, 190.84 mm TL **E** *Lestidium prolixum*, 209.71 mm SL **F** *Lestidium orientale*, 210.45 mm SL **G** *Lestrolepis philippina*, 191.77 mm SL **H** *Sudis* sp., 191.00 mm SL **I** *Dolichosudis fuliginosa*, 241.49 mm SL **J** *Magnisudis* sp., 318.06 mm SL. Scale bar: 3 cm.

Coelorinchus sheni **Chiou, Shao & Iwamoto, 2004**

Figs 33C, 34J

Only one specimen was collected from Dongsha Island. It is also very rare around Taiwan and Japan (Nakayama 2020). The present record is a distributional range extension from southeastern Taiwan. This species inhabits rocky bottoms in deep waters, where trawl fisheries rarely operate (Iwamoto et al. 2015).

Coelorinchus smithi **Gilbert & Hubbs, 1920**

Figs 33H, 34I

This species is widely distributed in the central Indo-West Pacific, and is rare around Dongsha Island and Taiwan. Nakayama (2020) noted different body colorations between specimens from the Philippines and Japan. The specimens around Dongsha Island resemble those from Japan, having the ventral side of the body distinctly paler than the lateral side.

Kuronezumia bubonis **Iwamoto, 1974**

Figs 34C, 37A

This species has a scattered distribution in the western Atlantic, western Indian Ocean, and the southwestern Pacific. Only one specimen was collected around Dongsha Island, representing the first record from the northwestern Pacific.

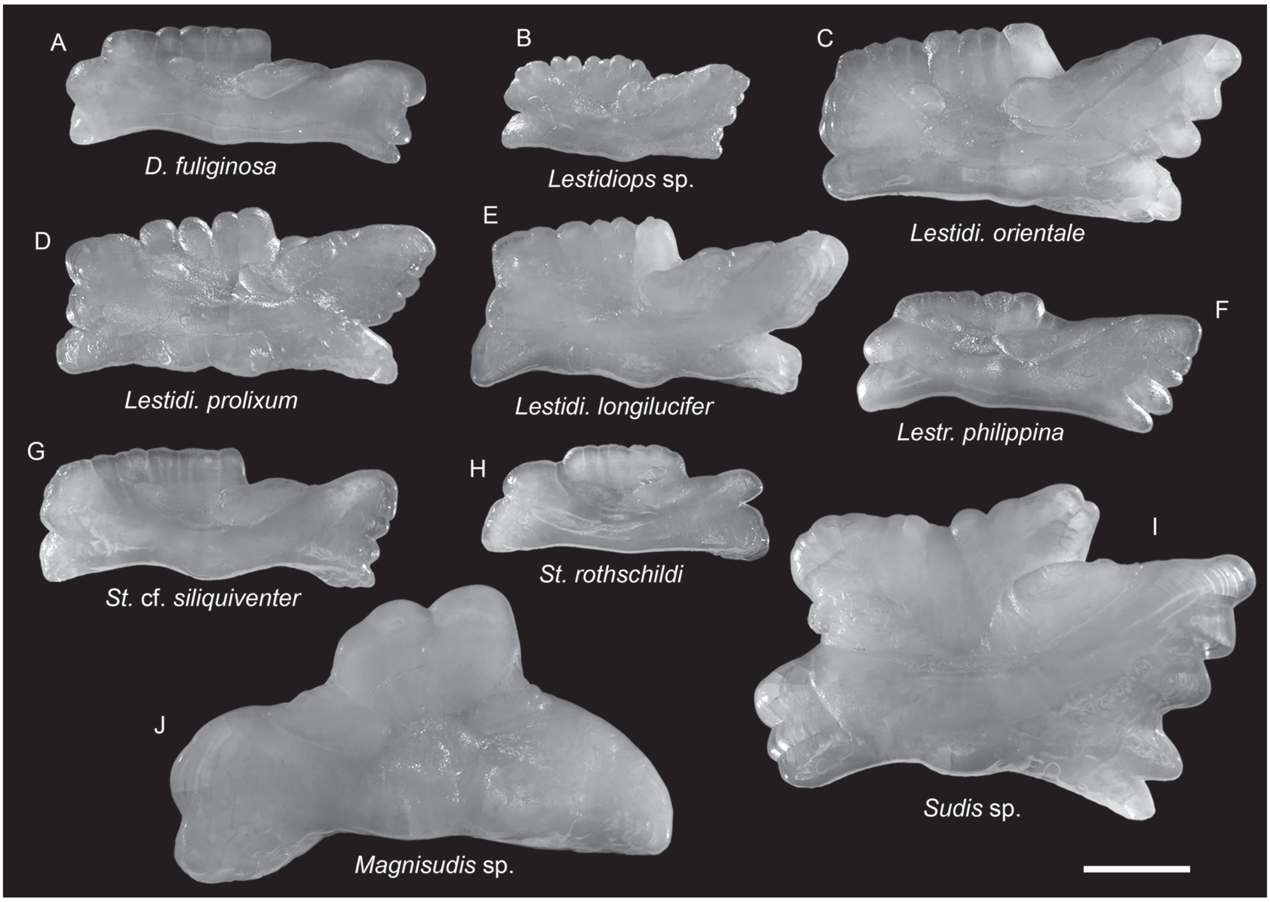

Figure 26. Otolith images of fresh specimens collected around Dongsha Island **A** *Dolichosudis fuliginosa*, CHLOL 18720, 249.25 mm SL **B** *Lestidiops* sp., CHLOL 16047, 146.08 mm SL **C** *Lestidium orientale*, CHLOL 24778, 227.03 mm SL (R) **D** *Lestidium prolixum*, CHLOL 22028, 222.87 mm SL (R) **E** *Lestidium longilucifer*, CHLOL 20615, 199.43 mm TL (R) **F** *Lestrolepis philippina*, CHLOL 20260, 191.46 mm SL (R) **G** *Stemonosudis* cf. *siliquiventer*, CHLOL 23015, 227.89 mm SL **H** *Stemonosudis rothschildi*, CHLOL 23330, 154.29 mm TL **I** *Sudis* sp., CHLOL 16187, 191.00 mm SL **J** *Magnisudis* sp., CHLOL22413, 294.11 mm SL. Scale bar: 1 mm.

Spicomacrurus kuronumai **(Kamohara, 1938)**
Figs 36L, 37K

This species was previously known only from Japan to Taiwan. The present record around Dongsha Island suggests its broad distribution in the northwestern Pacific.

Ventrifossa johnboborum **Iwamoto, 1982**
Figs 37D, 38A

This species is widespread in the central Indo-West Pacific and the southeastern Pacific. Only two small individuals were collected around Dongsha Island.

Gadella jordani **(Böhlke & Mead, 1951)**
Figs 39D, 40A

This species is widespread in the Indo-West Pacific and is one the most common species in deepwater trawl fisheries around Taiwan. However, this species appears to be less common around Dongsha Island.

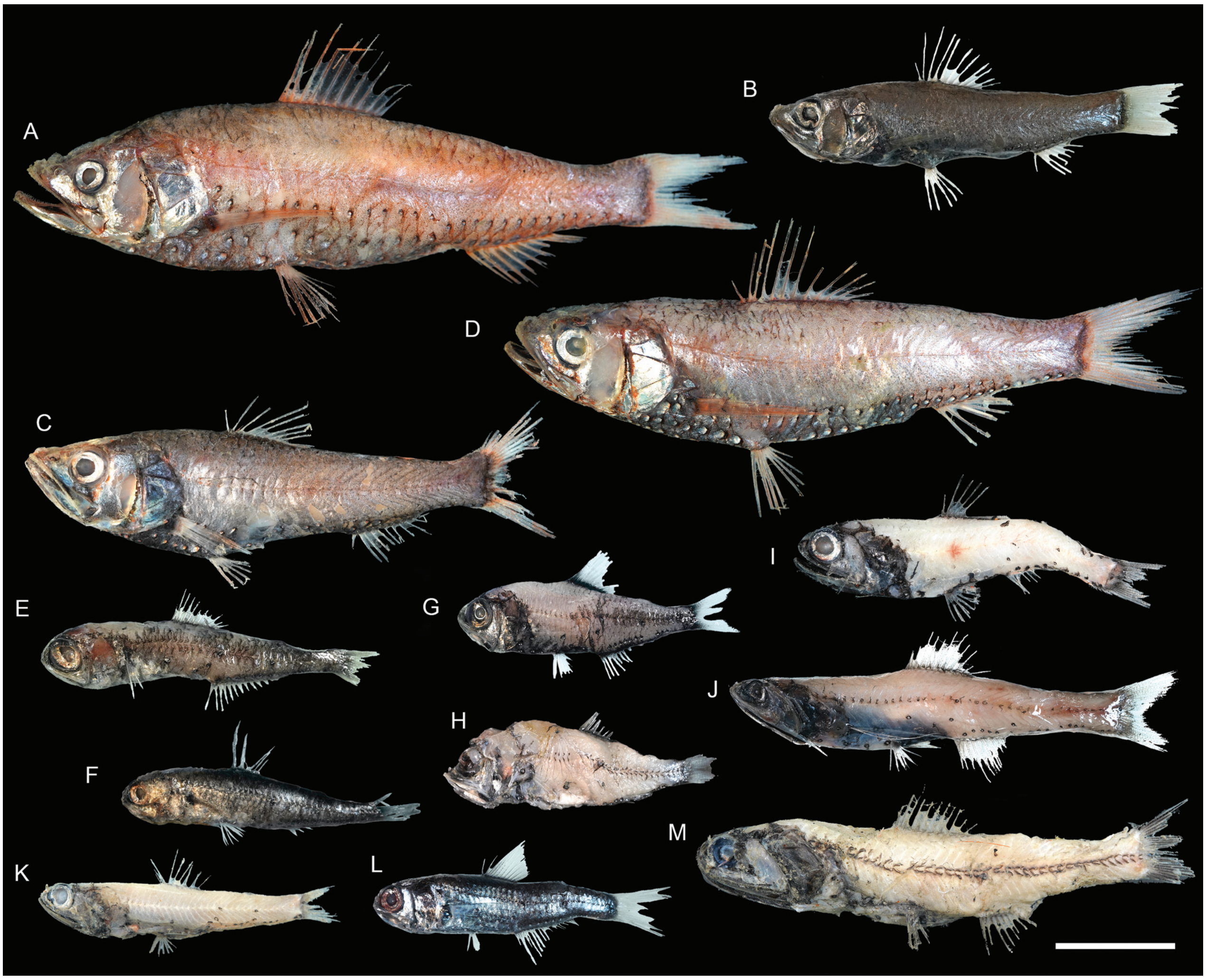

Figure 27. Images of fresh specimens collected around Dongsha Island **A** *Neoscopelus porosus*, 147.05 mm SL **B** *Neoscopelus microchir*, 87.87 mm SL **C** *Neoscopelus macrolepidotus*, 110.69 mm SL **D** *Neoscopelus* sp., 132.66 mm SL **E** *Dasyscopelus obtusirostris*, 75.20 mm SL **F** *Dasyscopelus asper*, 62.70 mm SL **G** *Dasyscopelus selenops*, 59.36 mm SL **H** *Electrona risso*, 57.32 mm SL **I** *Bolinichthys* sp., 72.95 mm SL **J** *Lampanyctus* sp., 97.39 mm SL **K** *Ceratoscopelus* sp., 63.30 mm SL **L** *Benthosema fibulatum*, 58.90 mm SL **M** *Lampadena luminosa*, 108.84 mm SL. Scale bar: 3 cm.

Laemonema robustum **Johnson, 1862**
Fig. 39F

This species has a circumglobal distribution in tropical and temperate oceans. It is known from one specimen captured by a deepsea longline fishery around Dongsha Island.

Physiculus chigodarana **Paulin, 1989**
Figs 39A, 40D

This species is restricted to the northwestern Pacific. It is common around Taiwan but rare around Dongsha Island. Based on our observations, this species usually occurs in shallower waters.

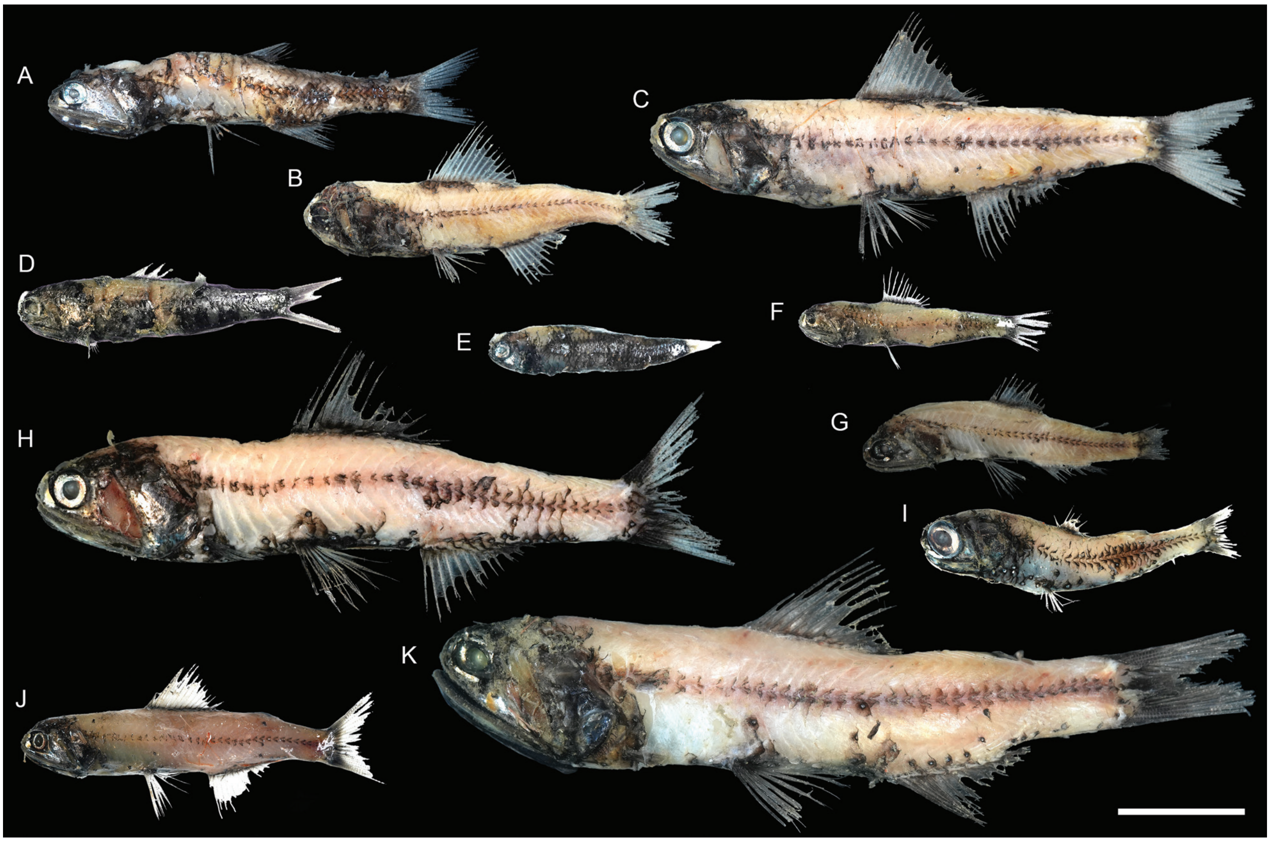

Figure 28. Images of fresh specimens collected around Dongsha Island **A** *Diaphus splendidus*, 83.65 mm SL **B** *Diaphus lucidus*, 77.38 mm SL **C** *Diaphus fragilis*, 118.97 mm SL **D** *Diaphus perspicillatus*, 63.58 mm SL **E** *Diaphus parri*, 47.04 mm SL **F** *Diaphus garmani*, 51.20 mm SL **G** *Diaphus suborbitalis*, 62.73 mm SL **H** *Diaphus watasei*, 132.33 mm SL **I** *Diaphus luetkeni*, 64.93 mm SL **J** *Diaphus problematicus*, 70.60 mm SL **K** *Diaphus adenomus*, 161.15 mm SL. Scale bar: 3 cm.

Hoplostethus roseus **Su, Lin & Ho, 2022**

Figs 41G, 42D

This species was recently described from Taiwan and is widespread in the central Indo-West Pacific. We found that this species is not uncommon around Dongsha Island, suggesting its broad distribution in the South China Sea.

Glyptophidium argenteum **Alcock, 1889**

Figs 43I, 44G

This species has a broad distribution in the Indo-West Pacific. It is rare around Taiwan and Dongsha Island, where only one specimen was collected.

Glyptophidium japonicum **Kamohara, 1936**

Figs 43G, 44E

Similar to the congeners, this species can be found in the Indo-West Pacific. It appears more common than the other sympatric congeners around Dongsha Island and Taiwan.

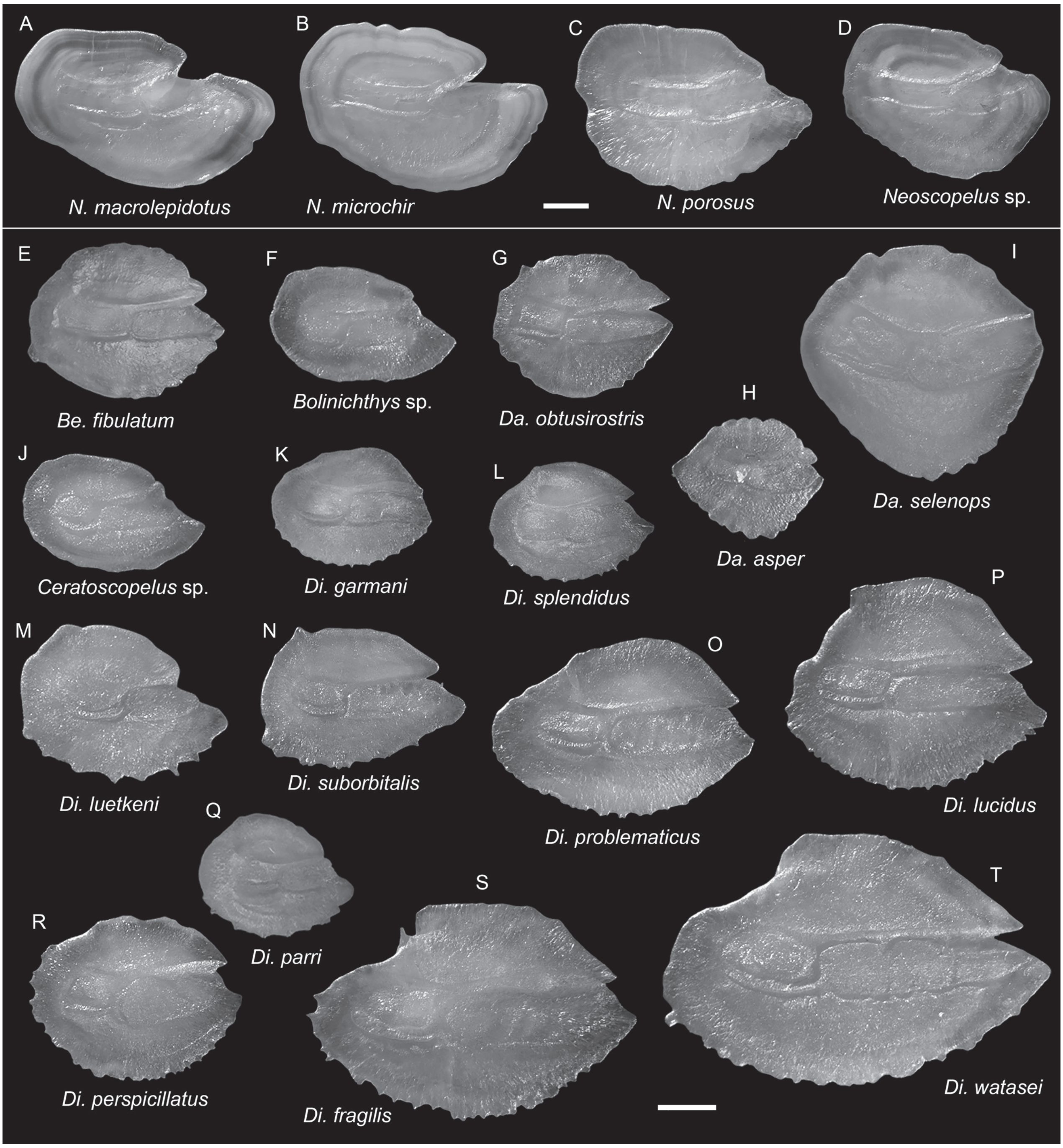

Figure 29. Otolith images of fresh specimens collected around Dongsha Island **A** *Neoscopelus macrolepidotus*, CHLOL 22410, 107.12 mm SL **B** *Neoscopelus microchir*, CHLOL 20187, 107.30 mm SL **C** *Neoscopelus porosus*, CHLOL 20608, 129.94 mm SL **D** *Neoscopelus* sp., CHLOL 20517, 83.60 mm SL **E** *Benthosema fibulatum*, CHLOL 9210, 57.15 mm SL **F** *Bolinichthys* sp., CHLOL 29700, 60.66 mm SL **G** *Dasyscopelus obtusirostris*, CHLOL 22678, 75.20 mm SL **H** *Dasyscopelus asper*, CHLOL 24112, 62.13 mm SL **I** *Dasyscopelus selenops*, CHLOL 20183, 63.61 mm SL **J** *Ceratoscopelus* sp., CHLOL 20651 61.32 mm SL **K** *Diaphus garmani*, CHLOL 22594, 48.91 mm SL **L** *Diaphus splendidus*, CHLOL 29230, 33.81 mm SL **M** *Diaphus luetkeni*, CHLOL 17523, 64.93 mm SL **N** *Diaphus suborbitalis*, CHLOL 22680, 73.40 mm SL **O** *Diaphus problematicus*, CHLOL 22774, 81.69 mm SL **P** *Diaphus lucidus*, CHLOL 16019, 91.21 mm SL **Q** *Diaphus parri*, CHLOL 20570, 47.04 mm SL **R** *Diaphus perspicillatus*, CHLOL 22485, 56.48 mm SL **S** *Diaphus fragilis*, CHLOL 20604, 108.61 mm SL **T** *Diaphus watasei*, CHLOL 3480, 114.45 mm SL. Scale bars: 1 mm.

Figure 30. Images of fresh specimens collected around Dongsha Island **A** *Parazen pacificus*, 89.49 mm SL **B** *Polymixia longispina*, 64.33 mm SL **C** *Polymixia berndti*, 115.2 mm SL **D** *Cyttomimus affinis*, 75.63 mm SL **E** *Xenolepidichthys* cf. *dalgleishi*, 90.42 mm SL **F** *Xenolepidichthys dalgleishi*, 51.16 mm SL **G** *Cyttopsis rosea*, 147.47 mm SL **H** *Zenion* sp., 42.07 mm SL **I** *Zenion japonicum*, 61.92 mm SL **J** *Zu cristatus*, 216.98 mm SL. Scale bar: 3 cm.

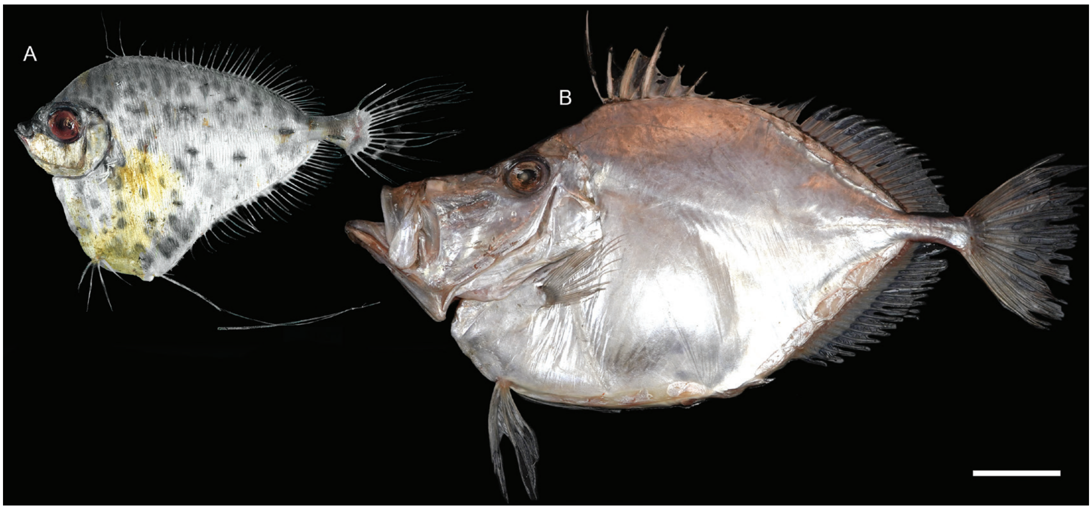

Figure 31. Images of fresh specimens collected around Dongsha Island **A** *Grammicolepis brachiusculus*, 159.37 mm SL **B** *Zenopsis nebulosa*, 378.54 mm SL. Scale bar: 3 cm.

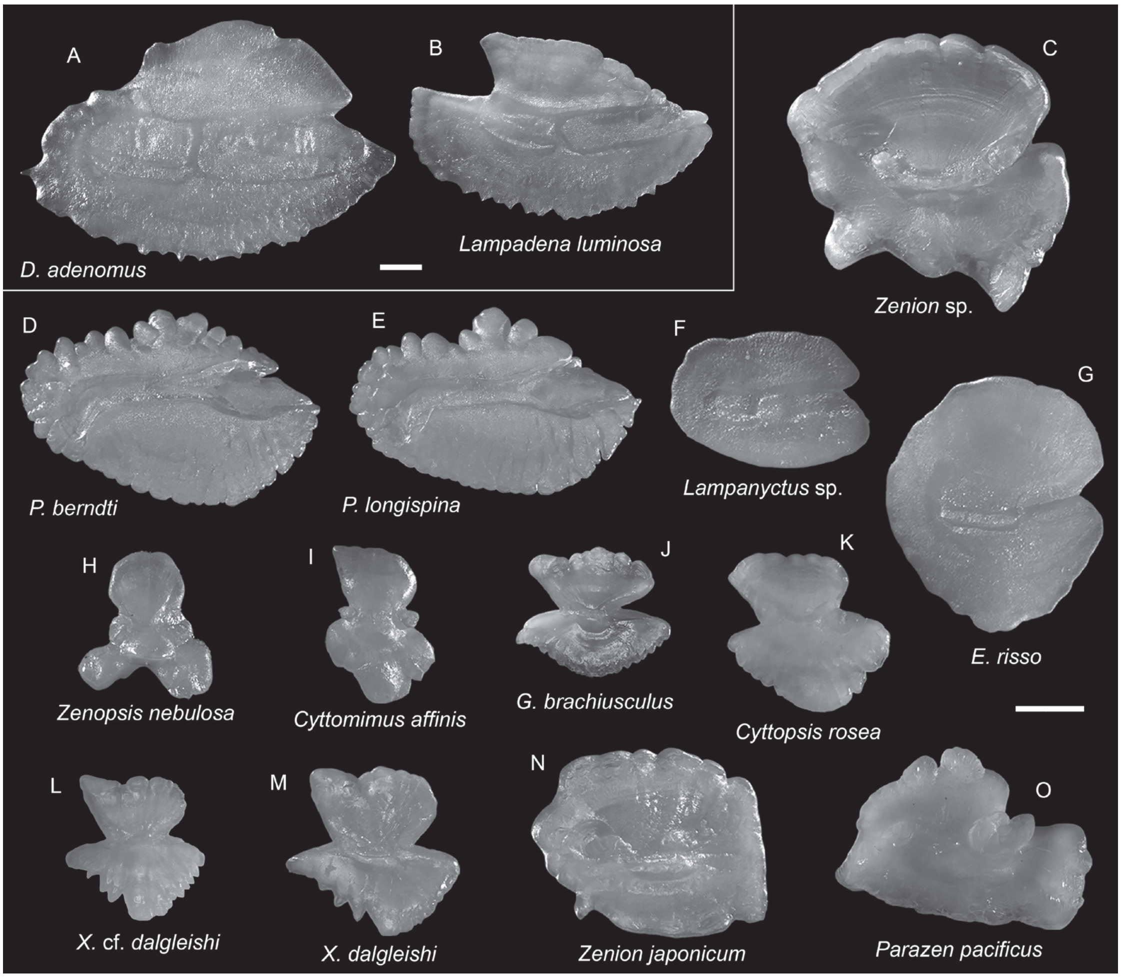

Figure 32. Otolith images of fresh specimens collected around Dongsha Island **A** *Diaphus adenomus*, CHLOL 29085, 161.15 mm SL **B** *Lampadena luminosa*, CHLOL 17521, 89.71 mm SL **C** *Zenion* sp., CHLOL 30182, 82.69 mm SL (R) **D** *Polymixia berndti*, CHLOL 29480, 71.65 mm SL **E** *Polymixia longispina*, CHLOL 20312, 76.05 mm SL **F** *Lampanyctus* sp., CHLOL 18810, 97.39 mm SL (R) **G** *Electrona risso*, CHLOL 16387, 57.32 mm SL **H** *Zenopsis nebulosa*, CHLOL 5787, 378.54 mm SL **I** *Cyttomimus affinis*, CHLOL 23366, 56.18 mm SL **J** *Grammicolepis brachiusculus*, CHLOL 20638, 140.27 mm SL **K** *Cyttopsis rosea*, CHLOL 29192, 99.27 mm SL **L** *Xenolepidichthys* cf. *dalgleishi*, CHLOL 17498, 97.39 mm SL **M** *Xenolepidichthys dalgleishi*, CHLOL 21836, 104.22 mm SL **N** *Zenion japonicum*, CHLOL 30180, 61.92 mm SL (R) **O** *Parazen pacificus*, CHLOL 18765, 122.83 mm SL. Scale bars: 1 mm.

Glyptophidium oceanium Smith & Radcliffe in Radcliffe, 1913

Figs 43J, 44H

As in other congeners, this species is widespread in the Indo-West Pacific. It is rare around Dongsha Island and around Taiwan.

Neobythites bimaculatus Nielsen, 1997

Figs 43E, 44O

Being widespread in the central Indo-West Pacific, this species is very common around Dongsha Island, but less common around Taiwan. It is especially similar to *N. macrops* Günther, 1887 described from the Philippines. However, *N. macrops* has not been reported in the South China Sea before. Therefore, all specimens are identified as *N. bimaculatus*.

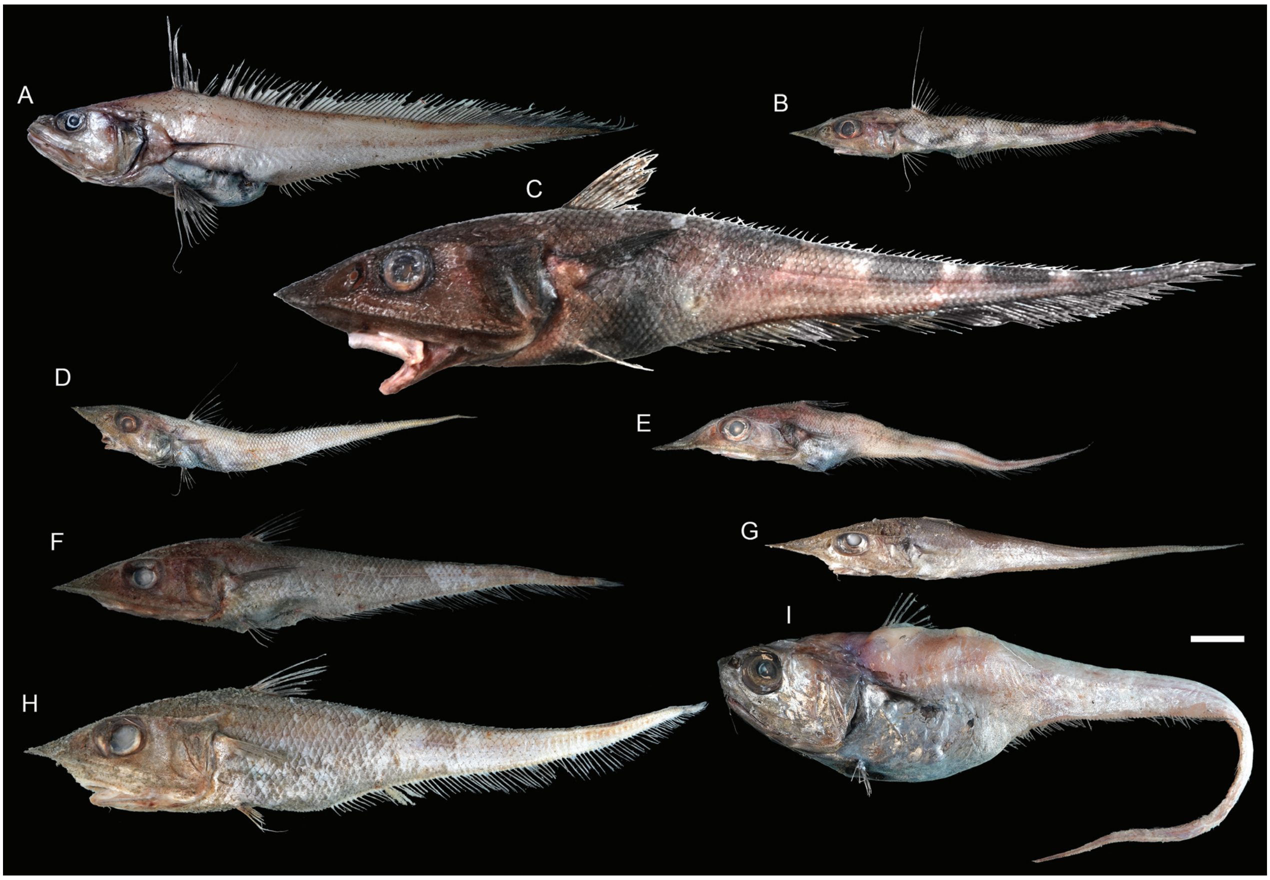

Figure 33. Images of fresh specimens collected around Dongsha Island **A** *Gadomus colletti*, 114.77 mm PAL **B** *Coelorinchus cingulatus*, 88.53 mm PAL **C** *Coelorinchus sheni*, 184.66 mm PAL **D** *Coelorinchus brevirostris*, 76.92 mm PAL **E** *Coelorinchus macrorhynchus*, 80.41 mm PAL **F** *Coelorinchus* sp., 125.80 mm PAL **G** *Coelorinchus longissimus*, 95.10 mm PAL **H** *Coelorinchus smithi*, 138.37 mm PAL **I** *Malacocephalus nipponensis*, 100.03 mm PAL. Scale bar: 3 cm.

Neobythites unimaculatus Smith & Radcliffe in Radcliffe, 1913
Figs 43F, 44N

This species is widespread in the central Indo-West Pacific. It is known only from one specimen around Dongsha Island but appears to be more common around the shallower waters of Taiwan. The depth record around Dongsha Island appears to be the lower depth limit of this species.

Cataetyx lepidogenys (Smith & Radcliffe, 1913)
Figs 45F, 46G

This species is restricted to the northwestern Pacific. While it is common off southwestern Taiwan, we only collected a few specimens around Dongsha Island.

Pseudonus squamiceps (Lloyd, 1907)
Figs 45D, 46C

This species is found in the central Indo-West Pacific. Although poorly presented in museums, we found that it is not uncommon around Dongsha Island.

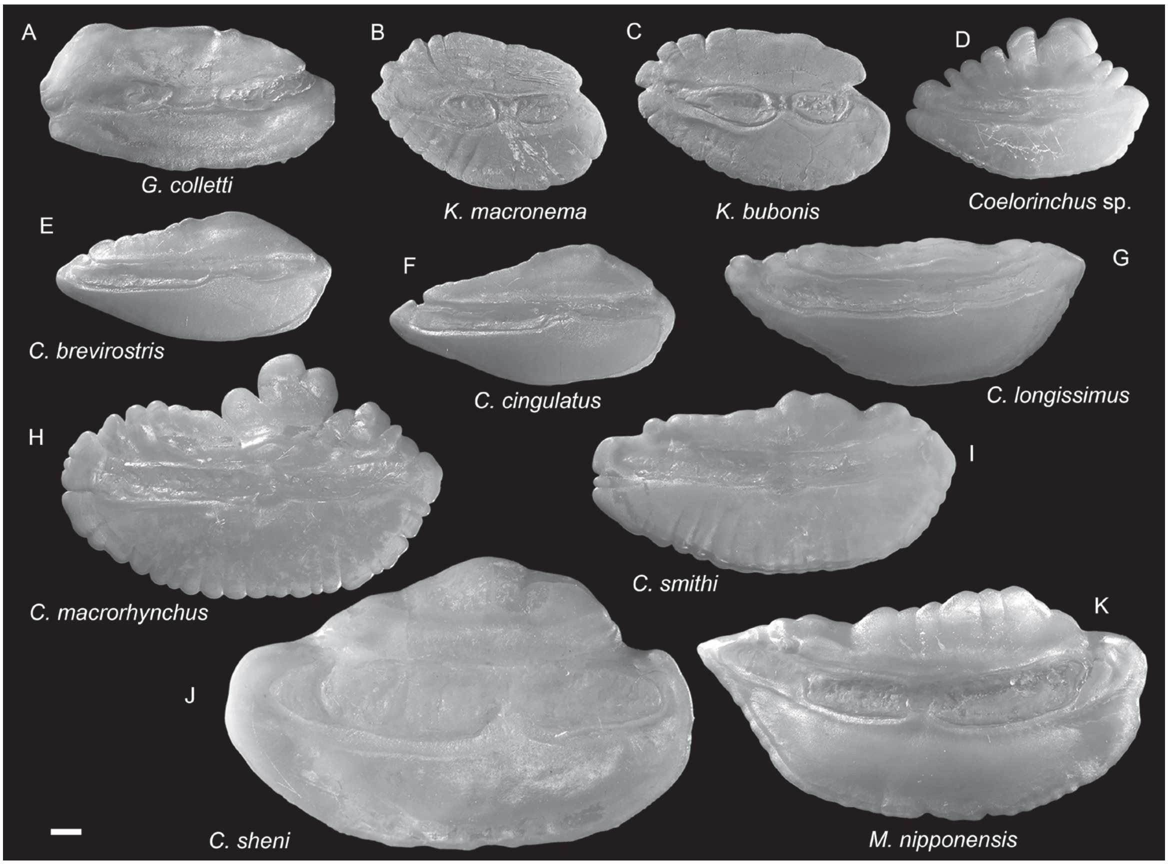

Figure 34. Otolith images of fresh specimens collected around Dongsha Island **A** *Gadomus colletti*, CHLOL 20823, 103.93 mm PAL **B** *Kuronezumia macronema*, CHLOL 27490, 208.00 mm TL (R) **C** *Kuronezumia bubonis*, CHLOL 27491, 51.66 mm PAL **D** *Coelorinchus* sp., CHLOL 20068, 112.86 mm PAL **E** *Coelorinchus brevirostris*, CHLOL 15969, 83.09 mm PAL **F** *Coelorinchus cingulatus*, CHLOL 17475, 79.90 mm PAL **G** *Coelorinchus longissimus*, CHLOL 15397, 105.80 mm PAL **H** *Coelorinchus macrorhynchus*, CHLOL 15763, 126.55 mm PAL **I** *Coelorinchus smithi*, CHLOL 17376, 125.91 mm PAL **J** *Coelorinchus sheni*, CHLOL 19815, 214.53 mm PAL **K** *Malacocephalus nipponensis*, CHLOL 28535, 106.91 mm PAL. Scale bar: 1 mm.

Saccogaster horrida **Nielsen, Schwarzhans & Cohen, 2012**
Figs 45E, 46A

This species was known only from western Australia. The sole specimen collected around Dongsha Island in the present study suggests a potential broad distribution in the central Indo-West Pacific.

Barathronus maculatus **Shcherbachev, 1976**
Figs 45B, 46D

This species is widespread in the Indo-West Pacific. It is rare around Dongsha Island, as it usually occurs in much deeper waters (e.g. Nielsen and Machida 1985; Yeh et al. 2009).

Cubiceps pauciradiatus **Günther, 1872**
Figs 55D, 56D

This species has circumglobal distribution in tropical and temperate oceans. It is very rare around Dongsha Island, known only from one specimen.

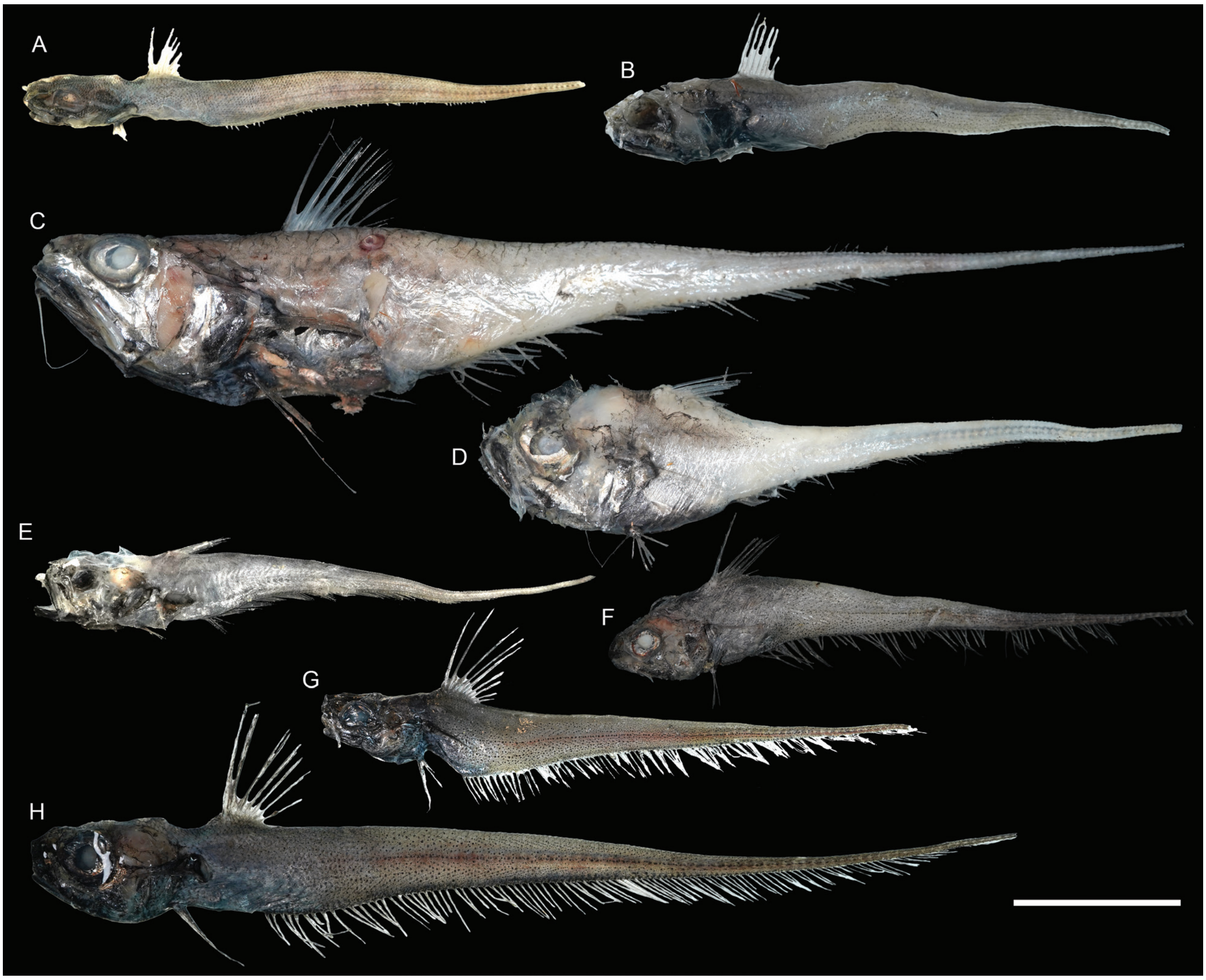

Figure 35. Images of fresh specimens collected around Dongsha Island **A** *Sphagemacrurus pumiliceps*, 23.47 mm PAL **B** *Hymenocephalus lethonemus*, 37.27 mm PAL **C** *Hymenocephalus longibarbis*, 199.32 mm TL **D** *Hymenocephalus striatissimus*, 39.66 mm PAL **E** *Pseudocetonurus* cf. *septifer*, 25.13 mm PAL **F** *Kumba gymnorhynchus*, 22.12 mm PAL **G** *Kumba japonica*, 18.44 mm PAL **H** *Kumba punctulata*, 21.27 mm PAL. Scale bar: 3 cm.

***Cubiceps whiteleggii* (Waite, 1894)**
Figs 55C, 56C

Although widely distributed in the Indo-West Pacific, this species has not been recorded around Dongsha Island. Here, we found that this species is very abundant in the area, outnumbering the congeners.

***Champsodon longipinnis* Matsubara & Amaoka, 1964**
Figs 55B, 56I

This species is widespread in the Indo-West Pacific, and is common off southwestern Taiwan. However, only one specimen was collected around Dongsha Island, which suggests that this species may prefer shallower waters.

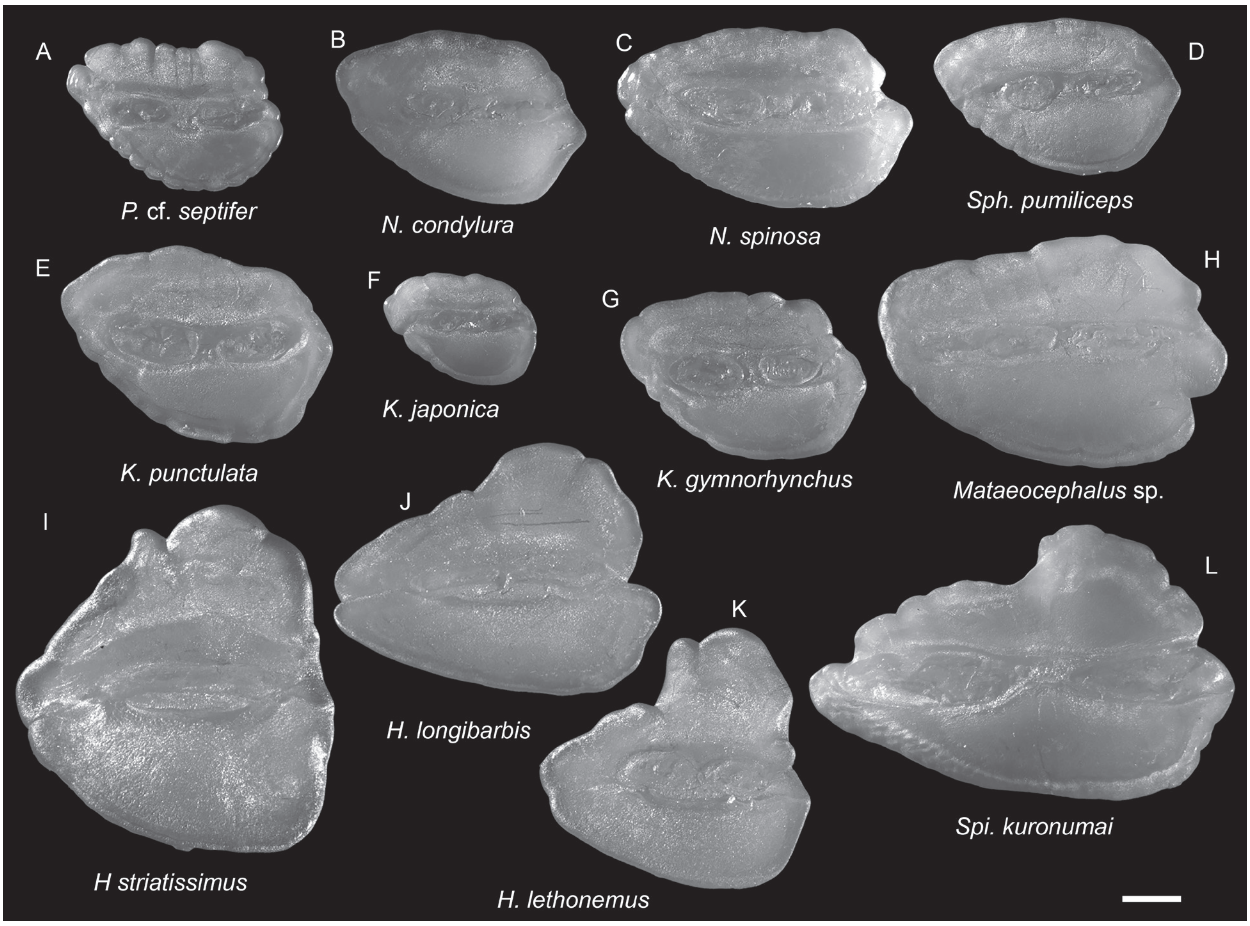

Figure 36. Otolith images of fresh specimens collected around Dongsha Island **A** *Pseudocetonurus* cf. *septifer*, CHLOL 22917, 25.13 mm PAL **B** *Nezumia condylura*, CHLOL 28936, 27.50 mm PAL **C** *Nezumia spinosa*, CHLOL 28000, 38.12 mm PAL **D** *Sphagemacrurus pumiliceps*, CHLOL 20138, 23.13 mm PAL **E** *Kumba punctulata*, CHLOL 20826, 34.22 mm PAL **F** *Kumba japonica*, CHLOL 29704, 15.49 mm PAL **G** *Kumba gymnorhynchus*, CHLOL 27679, 22.12 mm PAL **H** *Mataeocephalus* sp., CHLOL 28763, 156.82 mm TL **I** *Hymenocephalus striatissimus*, CHLOL 20135, 33.43 mm PAL **J** *Hymenocephalus longibarbis*, CHLOL 20012, 58.81 mm PAL **K** *Hymenocephalus lethonemus*, CHLOL 20137, 39.68 mm PAL **L** *Spicomacrurus kuronumai*, CHLOL 23002, 52.10 mm PAL. Scale bar: 1 mm.

Malakichthys elegans Matsubara & Yamaguti, 1943

Figs 57D, 58H

This species is widespread in the central Indo-West Pacific, and is one of the most abundant species in bottom trawl fisheries in Taiwan. However, only one specimen was collected around Dongsha Island, possibly due to a much deeper sampling depth.

Parascombrops serratospinosus (Smith & Radcliffe, 1912)

Figs 57B, 58A

This species is found in the western Pacific. Although common off southwestern Taiwan, the species is very rare around Dongsha Island, which suggests that it usually occurs in shallower waters.

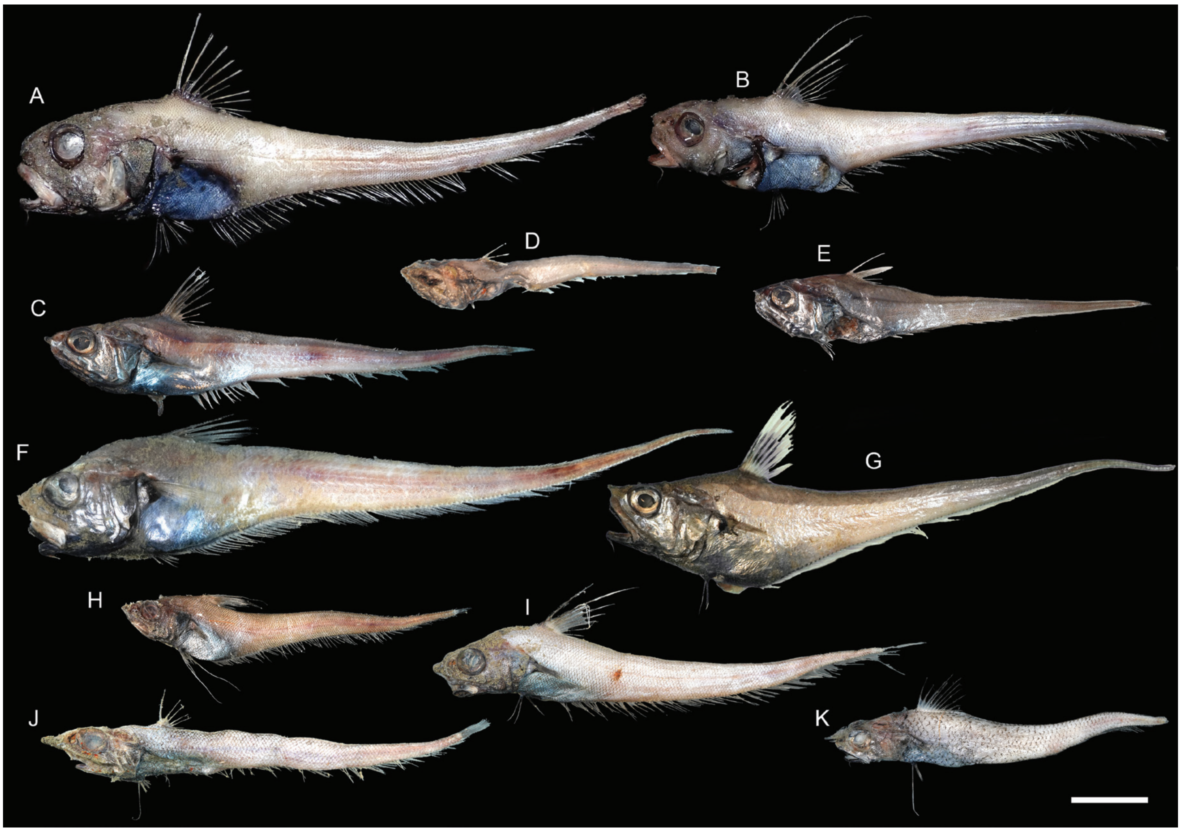

Figure 37. Images of fresh specimens collected around Dongsha Island **A** *Kuronezumia bubonis*, 51.66 mm PAL **B** *Kuronezumia macronema*, 208 mm TL **C** *Ventrifossa longibarbata*, 41.13 mm PAL **D** *Ventrifossa johnboborum*, 35.24 mm PAL **E** *Ventrifossa sazonovi*, 166.76 mm TL **F** *Ventrifossa divergens*, 56.05 mm PAL **G** *Ventrifossa* cf. *longibarbata*, 52.96 mm PAL **H** *Nezumia condylura*, 30.56 mm PAL **I** *Nezumia spinosa*, 45.92 mm PAL **J** *Mataeocephalus* sp., 54.96 mm PAL **K** *Spicomacrurus kuronumai*, 37.02 mm PAL. Scale bar: 3 cm.

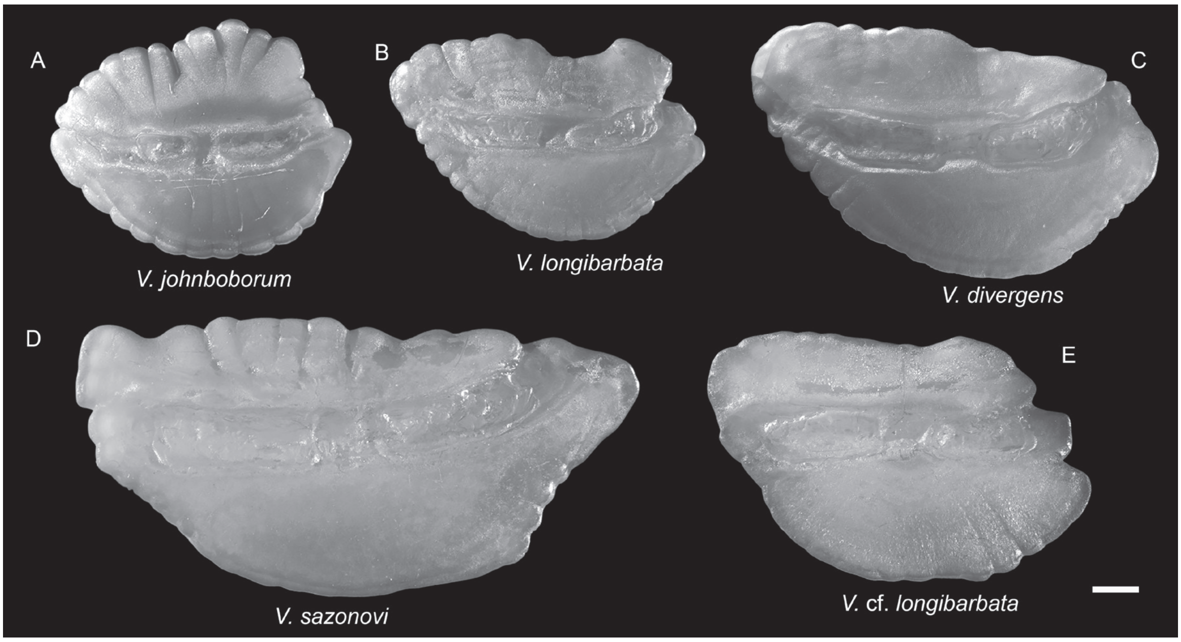

Figure 38. Otolith images of fresh specimens collected around Dongsha Island **A** *Ventrifossa johnboborum*, CHLOL 27105, 35.24 mm PAL **B** *Ventrifossa longibarbata*, CHLOL 22754, 48.88 mm PAL **C** *Ventrifossa divergens*, CHLOL 25656, 69.58 mm PAL **D** *Ventrifossa sazonovi*, CHLOL 20707, 56.86 mm PAL **E** *Ventrifossa* cf. *longibarbata*, CHLOL 17064, 47.15 mm PAL. Scale bar: 1 mm.

Figure 39. Images of fresh specimens collected around Dongsha Island **A** *Physiculus chigodarana*, 211.21 mm TL **B** *Physiculus* sp. 1, 129.64 mm TL **C** *Physiculus japonicus*, 203.06 mm TL **D** *Gadella jordani*, 192.16 mm TL **E** *Physiculus* sp. 2, 195.32 mm TL **F** *Laemonema robustum*, 391.00 mm TL. Scale bar: 3 cm.

***Epigonus denticulatus* Dieuzeide, 1950**
Figs 58F, 59L

This species has a circumglobal distribution in tropical and temperate oceans. It is uncommon around Dongsha Island and Taiwan.

***Epigonus megalops* (Smith & Radcliffe, 1912)**
Figs 58E, 59K

This species is restricted to the Philippines. The sole specimen we recognized around Dongsha Island reflects a broad distribution in the South China Sea.

***Epigonus pectinifer* Mayer, 1974**
Figs 58D, 59J

Although widespread circumglobally in tropical and temperate oceans, this species is rare around Dongsha Island and Taiwan.

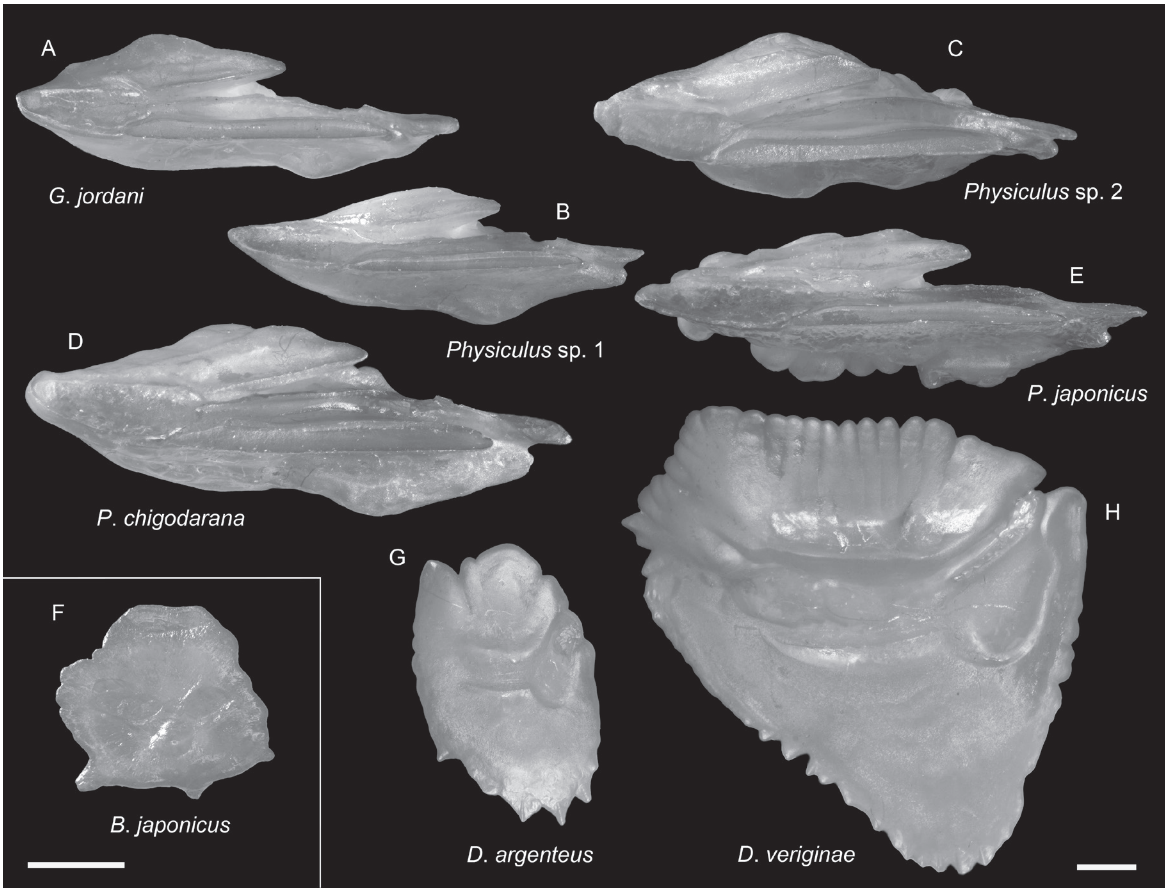

Figure 40. Otolith images of fresh specimens collected around Dongsha Island **A** *Gadella jordani*, CHLOL 27463, 205.96 mm SL (R) **B** *Physiculus* sp. 1, CHLOL 27649, 112.77 mm SL **C** *Physiculus* sp. 2, CHLOL 4203, 56.27 mm PAL **D** *Physiculus chigodarana*, CHLOL 22372, 168.71 mm SL **E** *Physiculus japonicus*, CHLOL 18348, 57.47 mm PAL **F** *Bregmaceros japonicus*, CHLOL 15755, 62.54 mm SL **G** *Diretmus argenteus*, CHLOL 22570, 52.10 mm SL. **H** *Diretmoides veriginae*, CHLOL 18692, 118.47 mm SL Scale bars: 1 mm.

Neobathyclupea gracilis **(Fowler, 1938)**
Figs 58I, 59B

This genus was established by Prokofiev (2014), and the species were extensively revised. It is widespread in the Indo-West Pacific, and is the most abundant bathyclupeid species around Dongsha Island and Taiwan.

Neobathyclupea japanotaiwana **(Prokofiev, 2014)**
Figs 58J, 59C

This species has a narrower distribution than its congeners, known only from Japan and Taiwan. However, this species is not uncommon around Dongsha Island, suggesting a broad distribution in the northwestern Pacific.

Neobathyclupea malayana **(Weber, 1913)**
Figs 58K, 59A

Although widespread in the Indo-West Pacific, this species is rare around Dongsha Island. It is also more prominent in body size than the two sympatric congeners.

Figure 41. Images of fresh specimens collected around Dongsha Island **A** *Diretmoides veriginae*, 157.03 mm SL **B** *Diretmus argenteus*, 51.84 mm SL **C** *Bregmaceros japonicus*, 82.38 mm SL **D** *Encheliophis* sp., 165.00 mm SL **E** *Beryx mollis*, 118.03 mm SL **F** *Hoplostethus melanopus*, 174.52 mm SL **G** *Hoplostethus roseus*, 110.34 mm SL **H** *Hoplostethus* sp., 107.77 mm SL **I** *Hoplostethus robustispinus*, 213.97 mm SL. Scale bar: 3 cm.

Brama dussumieri **Cuvier, 1831**

Figs 59I, 61B

This species can be found in tropical and warm temperate oceans. The two specimens from our collection are the first record of this species around Dongsha Island.

Brama orcini **Cuvier, 1831**

Figs 59H, 61C

This species is widespread in the Indo-West Pacific. It is common around Taiwan, but only one specimen was collected around Dongsha Island.

Owstonia aurora **Liao, Reyes & Shao, 2022**

Figs 59G, 61G

This species was recently described from the Philippines. Our present record, represented by one specimen around Dongsha Island, suggests its broad distribution in the South China Sea.

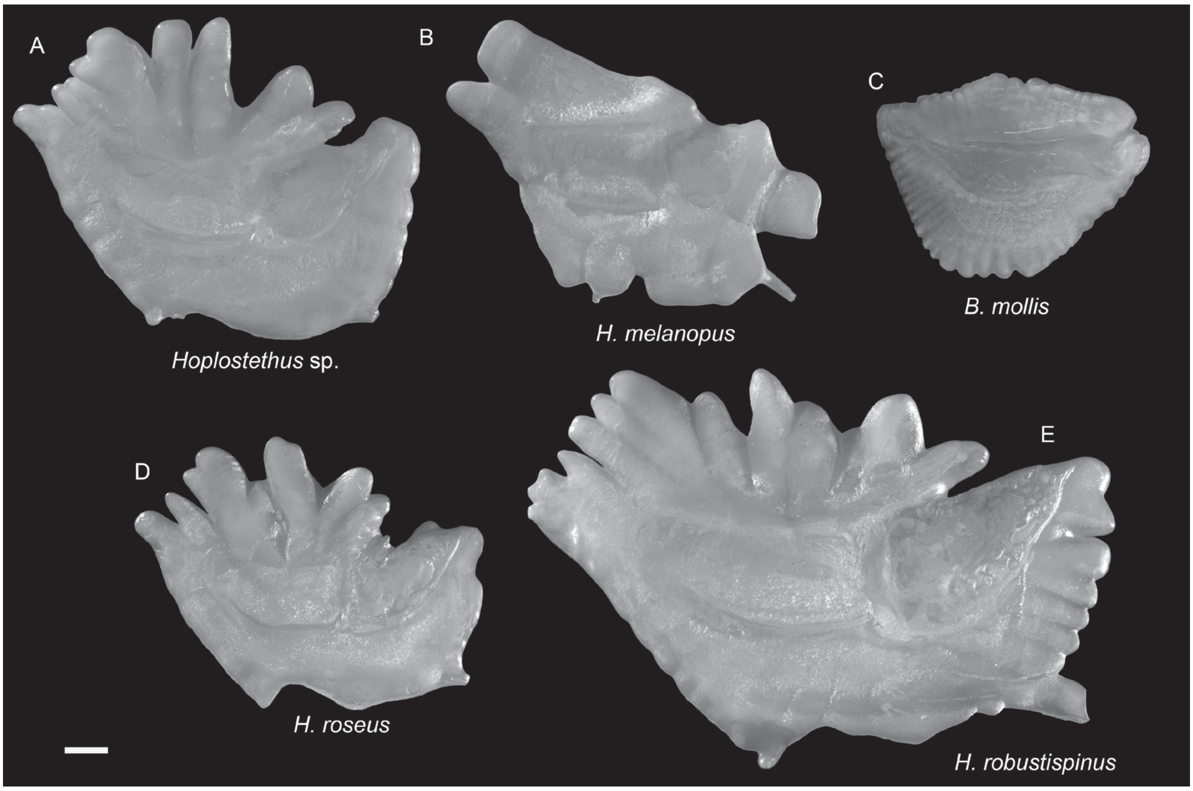

Figure 42. Otolith images of fresh specimens collected around Dongsha Island **A** *Hoplostethus* sp., CHLOL 29039, 140.17 mm SL **B** *Hoplostethus melanopus*, CHLOL 20387, 157.22 mm SL **C** *Beryx mollis*, CHLOL 20633, 122.49 mm SL **D** *Hoplostethus roseus*, CHLOL 22715, 110.74 mm SL **E** *Hoplostethus robustispinus*, CHLOL 22731, 213.97 mm SL. Scale bar: 1 mm.

Owstonia grammodon **(Fowler, 1934)**
Figs 59F, 61F

This species has scattered records in Indonesia and Taiwan. The two specimens collected around Dongsha Island confirm its broader distribution in the tropical Indo-West Pacific.

Lythrichthys cypho **(Fowler, 1938)**
Figs 60H, 62F

This species was recently revised by Wada et al. (2021). It is widely distributed in the Indo-West Pacific, and is common around Dongsha Island.

Lythrichthys eulabes **Jordan & Starks, 1904**
Figs 60I, 62C

Being revised together with *L. cypho*, this species is also widespread in the Indo-West Pacific. It is very common around Dongsha Island and Taiwan.

Setarches guentheri **Johnson, 1862**
Figs 60F, 62A

This species has circumglobal distribution in tropical and subtropical oceans. It is not uncommon around Dongsha Island and Taiwan.

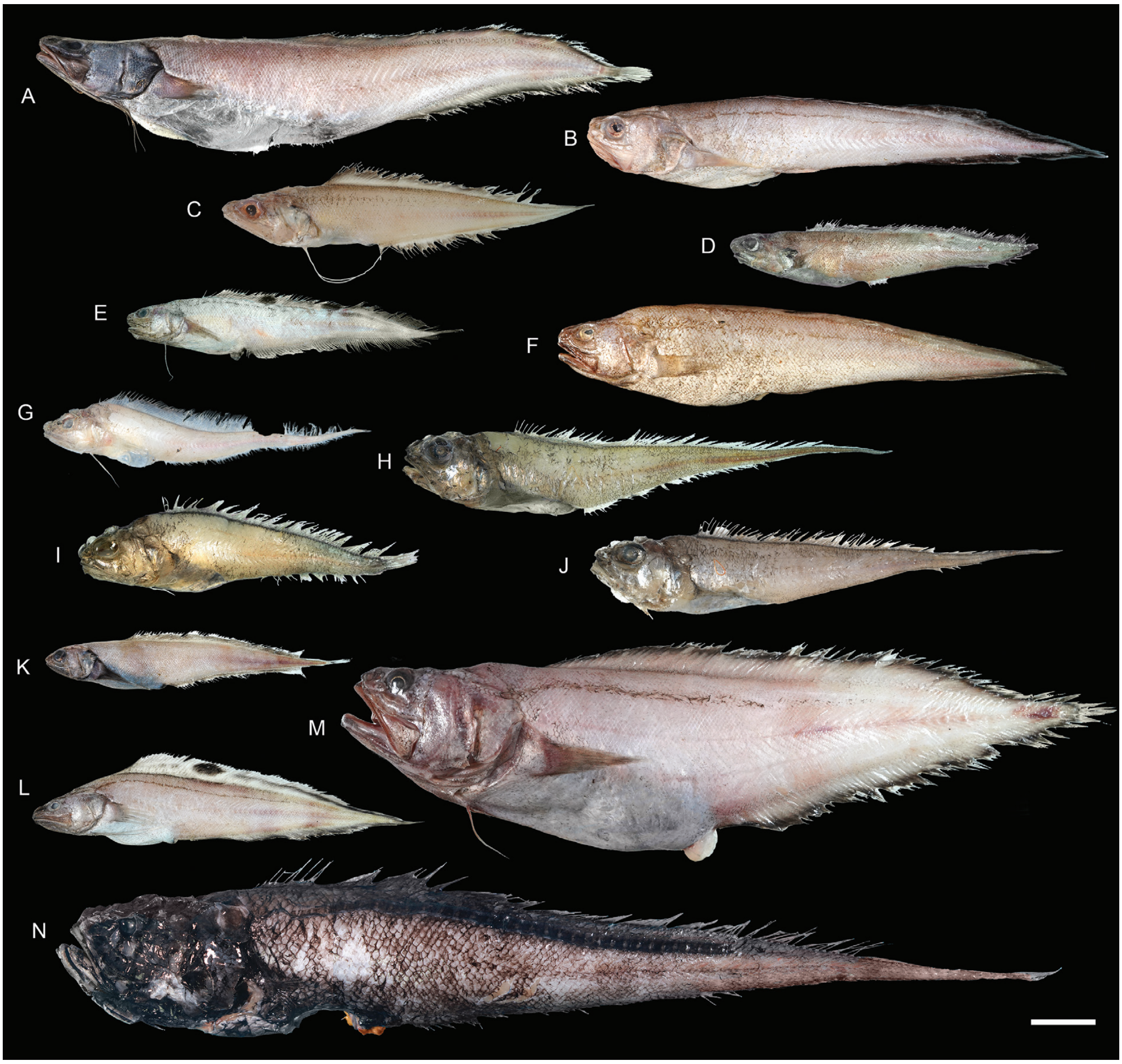

Figure 43. Images of fresh specimens collected around Dongsha Island **A** *Luciobrotula bartschi*, 133.17 mm PAL **B** *Hoplobrotula armata*, 81.73 mm PAL **C** *Homostolus acer*, 68.27 PAL **D** *Monomitopus* sp., 58.58 mm PAL **E** *Neobythites bimaculatus*, 50.38 mm PAL **F** *Neobythites unimaculatus*, 96.75 mm PAL **G** *Glyptophidium japonicum*, 56.51 mm PAL **H** *Glyptophidium lucidum*, 74.65 mm PAL **I** *Glyptophidium argenteum*, 65.90 mm PAL **J** *Glyptophidium oceanium*, 77.92 mm PAL **K** *Dicrolene tristis*, 51.33 PAL **L** *Neobythites longipes*, 51.33 mm PAL **M** *Pycnocraspedum microlepis*, 142.31 mm PAL **N** *Lamprogrammus brunswigi*, 440.00 mm TL. Scale bar: 3 cm.

Lepidotrigla pectoralis Fowler, 1938
Figs 63F, 64F

This species is possibly endemic to the northwestern Pacific, and is rare around Dongsha Island.

Pterygotrigla cajorarori Richards & Yato, 2012
Figs 63B, 64H

Although widespread in the Indo-West Pacific, this species appears to be uncommon around Dongsha Island.

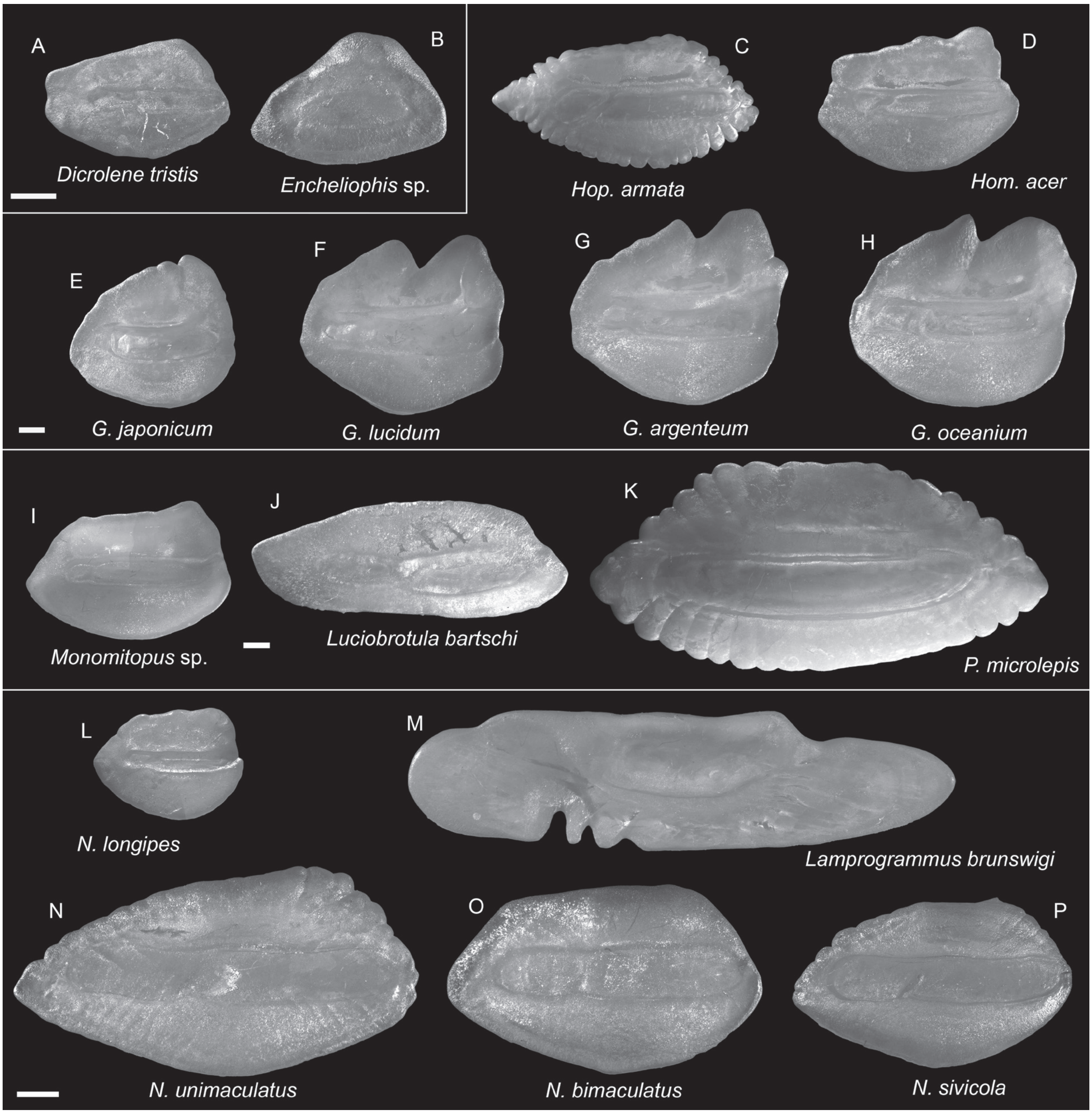

Figure 44. Otolith images of fresh specimens collected around Dongsha Island **A** *Dicrolene tristis*, CHLOL 20052, 63.84 mm PAL **B** *Encheliophis* sp., CHLOL 4101, 165.00 mm TL **C** *Hoplobrotula armata*, CHLOL 24857, 196.93 mm SL **D** *Homostolus acer*, CHLOL 20168, 73.17 mm PAL **E** *Glyptophidium japonicum*, CHLOL 29128, 56.51 mm PAL **F** *Glyptophidium lucidum*, CHLOL 23426, 58.25 mm PAL **G** *Glyptophidium argenteum*, CHLOL 22281, 65.90 mm PAL **H** *Glyptophidium oceanium*, CHLOL 19990, 77.92 mm PAL. **I** *Monomitopus* sp., CHLOL 22272, 59.58 mm PAL **J** *Luciobrotula bartschi*, CHLOL 20829, 231.74 mm SL **K** *Pycnocraspedum microlepis*, CHLOL 15786, 142.31 mm PAL. **L** *Neobythites longipes*, CHLOL 22758, 68.89 mm SL **M** *Lamprogrammus brunswigi*, CHLOL 17964, 440.00 mm TL **N** *Neobythites unimaculatus*, CHLOL 6266, 88.86 mm PAL **O** *Neobythites bimaculatus*, CHLOL 9881, 57.53 mm PAL **P** *Neobythites sivicola*, CHLOL 27431, 48.80 mm PAL. Scale bars: 1 mm.

Paraheminodus murrayi **(Günther, 1880)**
Figs 63C, 64D

This species is widely distributed in the Indo-West Pacific, and is common around Dongsha Island, but rare around Taiwan.

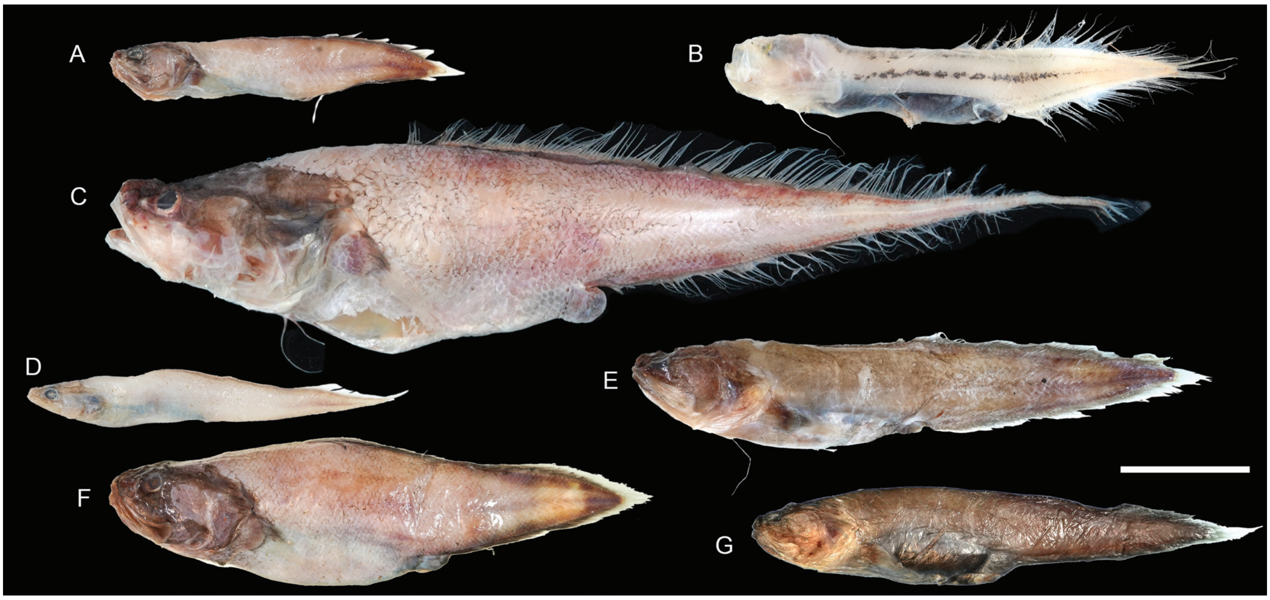

Figure 45. Images of fresh specimens collected around Dongsha Island **A** Bythitidae indet., 42.50 mm PAL **B** *Barathronus maculatus*, 69.18 mm PAL **C** *Diplacanthopoma* sp., 103.86 mm PAL **D** *Pseudonus squamiceps*, 41.47 mm PAL **E** *Saccogaster horrida*, 58.20 mm PAL **F** *Cataetyx lepidogenys*, 71.10 mm PAL **G** *Saccogaster tuberculata*, 59.34 mm PAL. Scale bar: 3 cm.

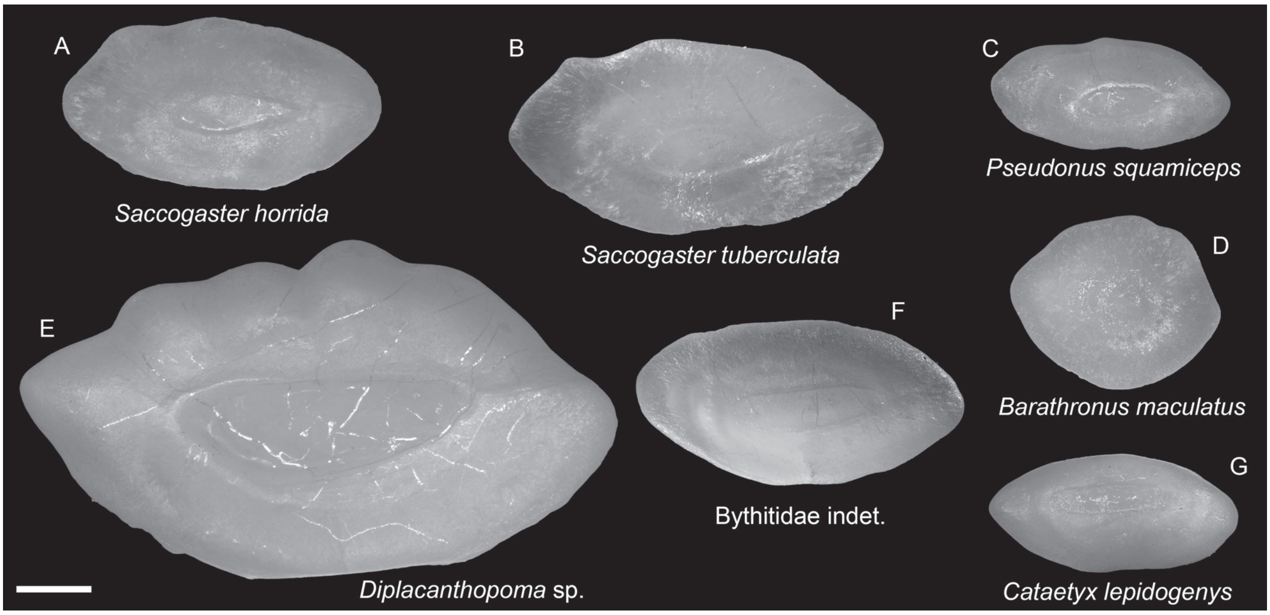

Figure 46. Otolith images of fresh specimens collected around Dongsha Island **A** *Saccogaster horrida*, CHLOL 18127, 55.20 mm PAL **B** *Saccogaster tuberculata*, CHLOL 22284, 59.34 mm PAL **C** *Pseudonus squamiceps*, CHLOL 19987, 37.55 mm PAL **D** *Barathronus maculatus*, CHLOL 25717, 69.18 mm SL **E** *Diplacanthopoma* sp., CHLOL 19402, 76.62 mm PAL **F** Bythitidae indet., CHLOL 19985, 42.50 mm PAL (R) **G** *Cataetyx lepidogenys*, CHLOL 18149, 71.10 mm PAL. Scale bar: 1 mm.

Satyrichthys milleri **Kawai, 2013**
Figs 63N, 64C

This species is widely distributed in the central Indo-West Pacific. It is common off southwestern Taiwan but rare around Dongsha Island.

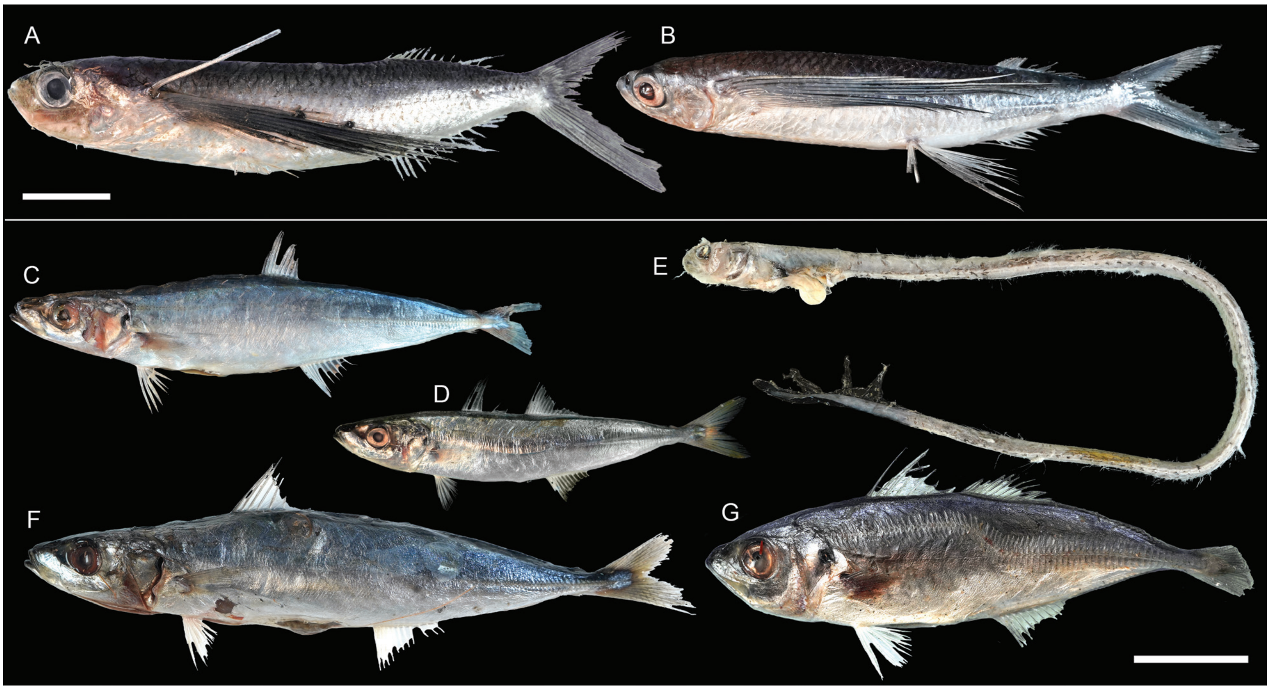

Figure 47. Images of fresh specimens collected around Dongsha Island **A** *Exocoetus monocirrhus*, 144.25 mm SL **B** *Hirundichthys oxycephalus*, 211.01 mm TL **C** *Decapterus macrosoma*, 124.06 mm SL **D** *Decapterus tabl*, 91.56 mm SL **E** *Xiphasia setifer*, 312.83 mm TL **F** *Decapterus macarellus*, 174.18 mm TL **G** *Trachurus japonicus*, 125.57 mm SL. Scale bars: 3 cm.

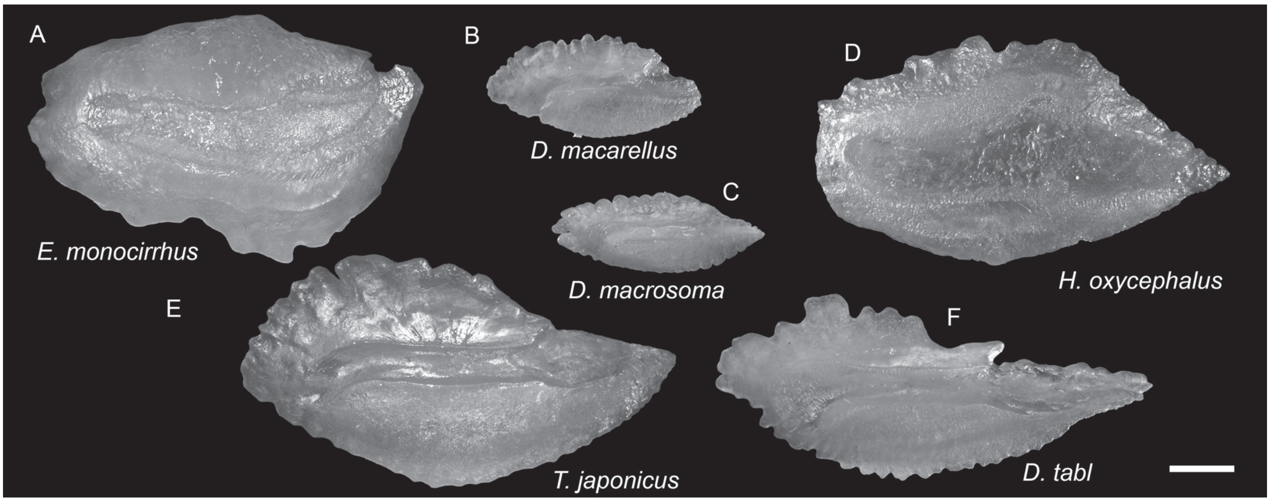

Figure 48. Otolith images of fresh specimens collected around Dongsha Island **A** *Exocoetus monocirrhus*, CHLOL 19408, 144.25 mm SL **B** *Decapterus macarellus*, CHLOL 20653, 174.18 mm TL **C** *Decapterus macrosoma*, CHLOL 17765, 124.06 mm SL (R) **D** *Hirundichthys oxycephalus*, CHLOL 15698, 211.01 mm TL **E** *Trachurus japonicus*, CHLOL 24117, 104.79 mm SL **F** *Decapterus tabl*, CHLOL 22730, 251.70 mm SL. Scale bar: 1 mm.

Hoplichthys filamentosus **Matsubara & Ochiai, 1950**

Figs 63L, 66C

This species is widespread in the central Indo-West Pacific. It is common around Taiwan, but rare around Dongsha Island.

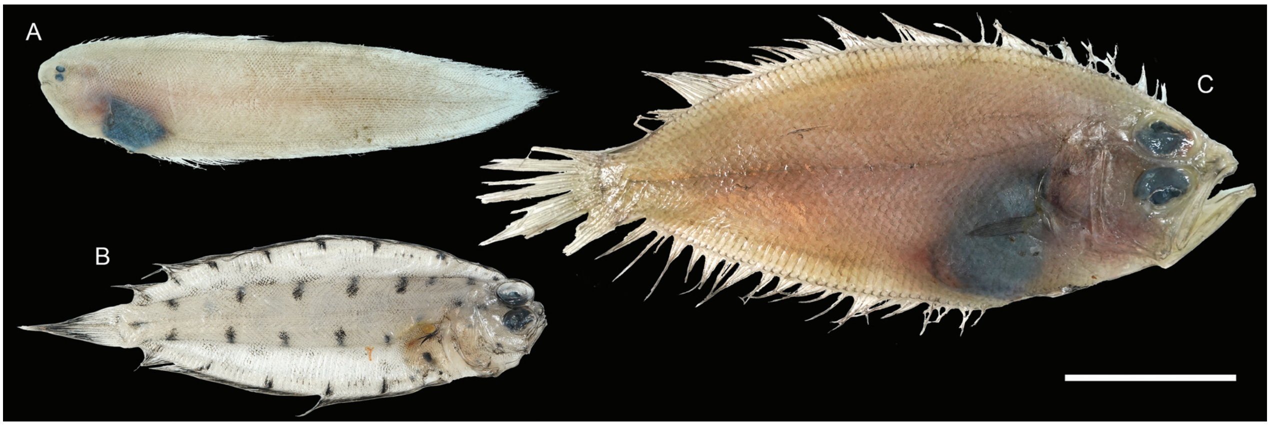

Figure 49. Images of fresh specimens collected around Dongsha Island **A** *Symphurus orientalis*, 85.62 mm SL **B** *Poecilopsetta plinthus*, 75.68 mm SL **C** *Lepidoblepharon ophthalmolepis*, 108.77 mm SL. Scale bar: 3 cm.

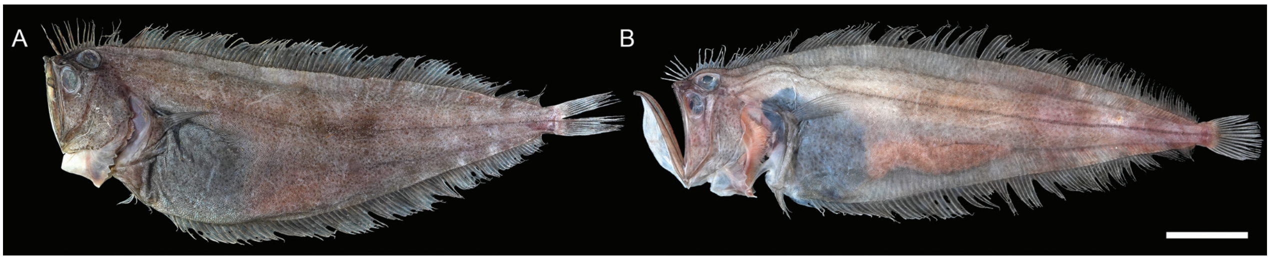

Figure 50. Images of fresh specimens collected around Dongsha Island **A** *Chascanopsetta lugubris*, 315.02 mm SL **B** *Chascanopsetta prognatha*, 334.43 mm SL. Scale bar: 5 cm.

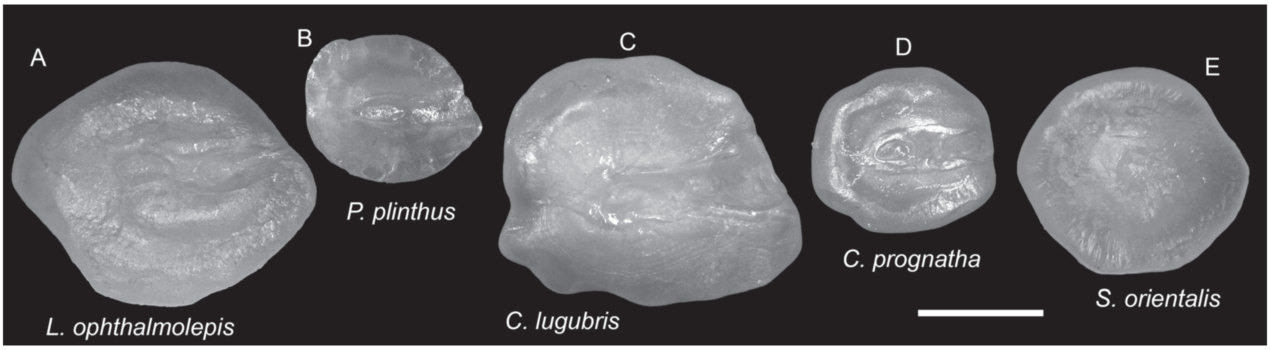

Figure 51. Otolith images of fresh specimens collected around Dongsha Island **A** *Lepidoblepharon ophthalmolepis*, CHLOL 22379, 67.13 mm SL **B** *Poecilopsetta plinthus*, CHLOL 23359, 69.60 mm SL **C** *Chascanopsetta lugubris*, CHLOL 14976, 230.17 mm SL **D** *Chascanopsetta prognatha*, CHLOL 15675, 194.29 mm SL **E** *Symphurus orientalis*, CHLOL 18684, 87.69 mm SL. Scale bar: 1 mm.

Stlengis distoechus Bolin, 1936

Figs 65B, 66E

This species was formerly restricted to Japan. The present record around Dongsha Island suggests its broader distribution in the northwestern Pacific.

Figure 52. Images of fresh specimens collected around Dongsha Island **A** *Nesiarchus nasutus*, 430.94 mm SL **B** *Nealotus tripes*, 143.09 mm SL **C** *Rexea bengalensis*, 241.14 mm SL **D** *Rexea prometheoides*, 235.74 mm SL **E** *Promethichthys prometheus*, 267.82 mm SL **F** *Scombrolabrax heterolepis*, 161.77 mm SL **G** *Neoepinnula orientalis*, 193.94 mm SL **H** *Gempylus serpens*, 506.87 mm SL **I** *Ruvettus pretiosus*, 211.29 mm SL **J** *Thyrsitoides marleyi*, 386.84 mm SL. Scale bar: 5 cm.

Psychrolutes macrocephalus **(Gilchrist, 1904)**
Figs 65C, 66D

This species has a widespread distribution in the Indo-West Pacific. Only a few specimens were collected around Dongsha Island.

Lophiodes iwamotoi **Ho, Séret & Shao, 2011**
Figs 67A, 68B

This species was originally described from off Society Islands. A few specimens were collected around Dongsha Island, representing a substantial range extension.

Chaunax apus **Lloyd, 1909**
Figs 69D, 71B

This species is widespread in the Indo-West Pacific. Although not previously recorded from Dongsha Island, we found it very common in the area but rare around Taiwan.

Chaunax breviradius **Le Danois, 1978**
Figs 69C, 71C

This species is common around Taiwan and is restricted to the South China Sea. It has never been recorded around Dongsha Island before, until the present study.

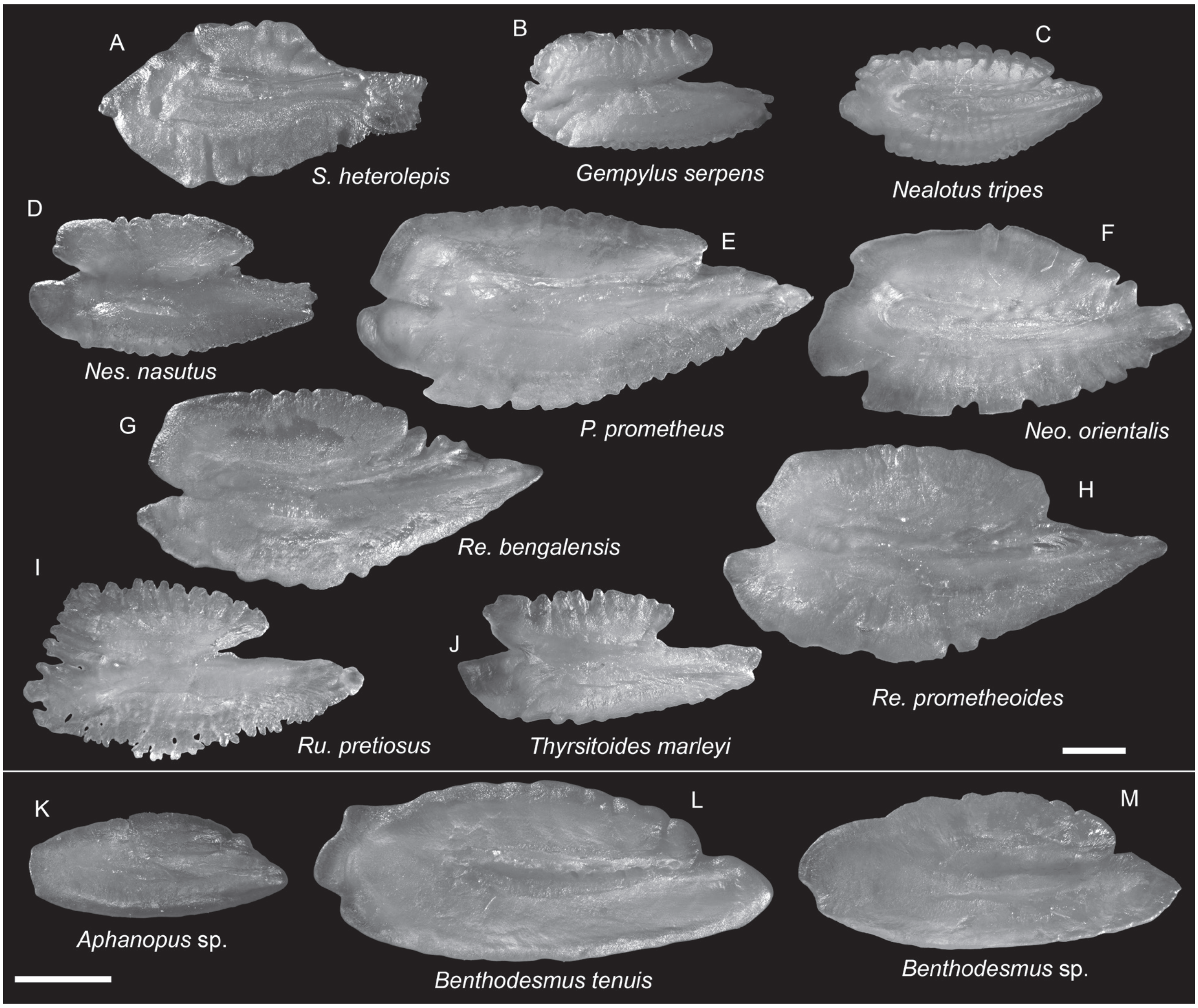

Figure 53. Otolith images of fresh specimens collected around Dongsha Island **A** *Scombrolabrax heterolepis*, CHLOL 21499, 161.77 mm SL **B** *Gempylus serpens*, CHLOL 21292, 506.87 mm SL **C** *Nealotus tripes*, CHLOL 18041, 143.09 mm SL **D** *Nesiarchus nasutus* CHLOL 23266, 389.39 mm SL **E** *Promethichthys prometheus*, CHLOL 21502, 292.37 mm SL **F** *Neoepinnula orientalis*, CHLOL 20027, 185.78 mm SL **G** *Rexea bengalensis* CHLOL 5395, 241.14 mm SL **H** *Rexea prometheoides*, CHLOL 5394, 235.80 mm SL **I** *Ruvettus pretiosus*, CHLOL 22035, 292.42 mm SL **J** *Thyrsitoides marleyi*, CHLOL 24722, 390.60 mm SL **K** *Aphanopus* sp., CHLOL 28066, 437.53 mm SL (R) **L** *Benthodesmus tenuis*, CHLOL 22846, 510.72 mm SL **M** *Benthodesmus* sp., CHLOL 16539, 665.63 mm SL. Scale bars: 1 mm.

Figure 54. Images of fresh specimens collected around Dongsha Island **A** *Aphanopus* sp., 437.53 mm SL **B** *Benthodesmus* sp., 665.63 mm SL **C** *Benthodesmus tenuis*, 523.03 mm TL. Scale bar: 5 cm.

Figure 55. Images of fresh specimens collected around Dongsha Island **A** *Champsodon snyderi*, 90.06 mm SL **B** *Champsodon longipinnis*, 127.54 mm SL **C** *Cubiceps whiteleggii*, 163.50 mm SL **D** *Cubiceps pauciradiatus*, 115.74 mm SL **E** *Amarsipus carlsbergi*, 146.27 mm SL **F** *Psenes pellucidus*, 229.58 mm SL **G** *Psenes cyanophrys*, 141.89 mm SL **H** *Psenes arafurensis*, 123.44 mm SL **I** *Cubiceps baxteri*, 265.12 mm SL **J** *Psenopsis anomala*, 76.07 mm SL. Scale bar: 3 cm.

Halieutopsis echinoderma **Ho, 2021**
Figs 70A, 71K

This species was recently described from Taiwan and the Coral Sea, and one specimen was collected around Dongsha Island, suggesting its broad distribution in the central Indo-West Pacific.

Halieutopsis nasuta **Alcock, 1891**
Figs 70B, 71L

Although being widespread in the Indo-West Pacific, this species is very rare around Dongsha Island, known only from a few specimens. The present record confirms its appearance in the South China Sea.

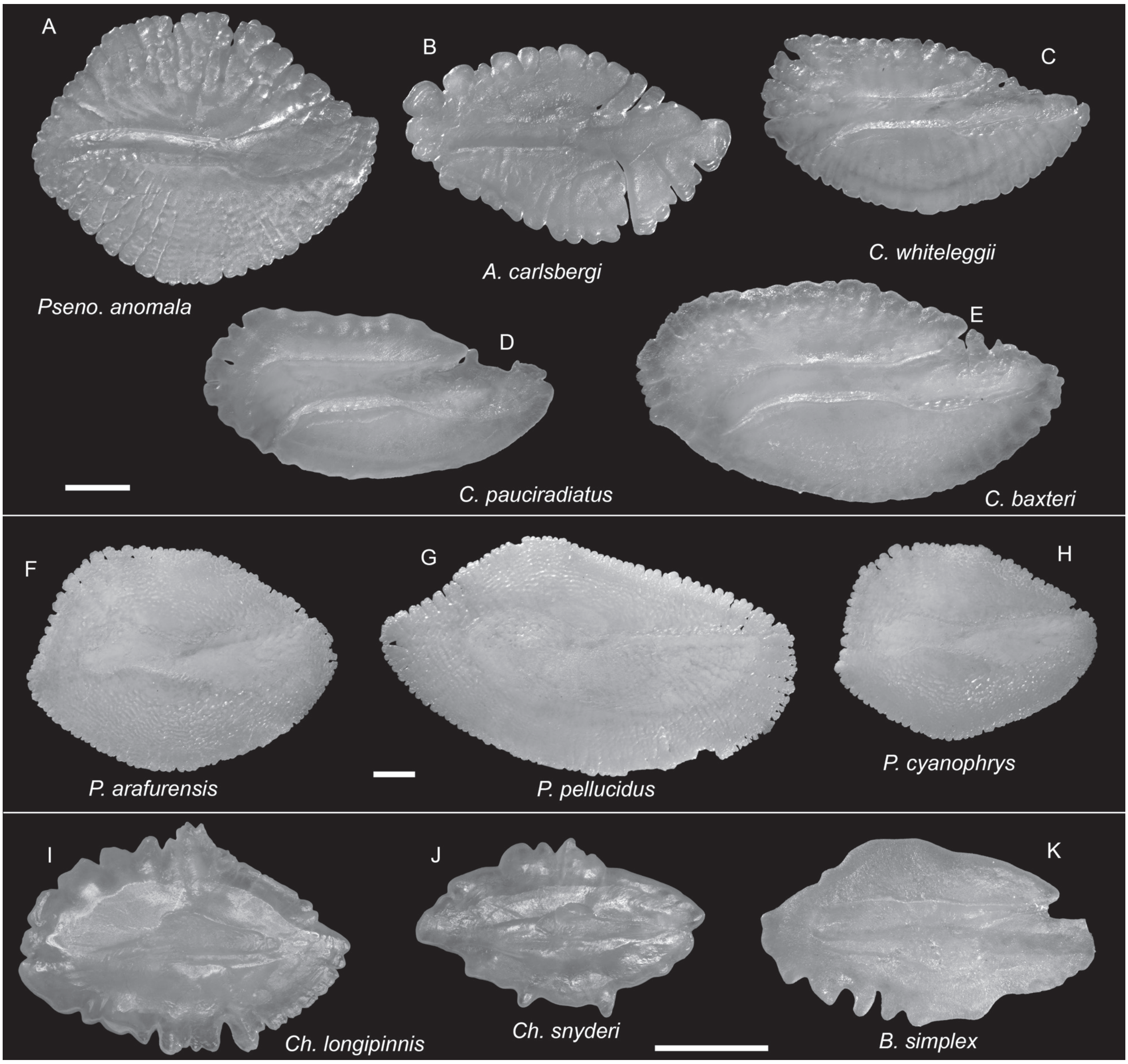

Figure 56. Otolith images of fresh specimens collected around Dongsha Island **A** *Psenopsis anomala*, CHLOL 26057, 76.07 mm SL **B** *Amarsipus carlsbergi*, CHLOL 29706, 146.27 mm SL **C** *Cubiceps whiteleggii*, CHLOL 21285, 112.40 mm SL **D** *Cubiceps pauciradiatus*, CHLOL 24988, 115.74 mm SL **E** *Cubiceps baxteri*, CHLOL 20390, 119.10 mm SL **F** *Psenes arafurensis*, CHLOL 24971, 132.51 mm SL **G** *Psenes pellucidus*, CHLOL 20622, 213.19 mm SL **H** *Psenes cyanophrys*, CHLOL 27368, 123.32 mm SL. **I** *Champsodon longipinnis*, CHLOL 24121, 127.54 mm SL **J** *Champsodon snyderi*, CHLOL 21520, 90.06 mm SL **K** *Bathysphyraenops simplex*, CHLOL 15774, 69.53 mm SL. Scale bars: 1 mm.

Malthopsis kobayashii **Tanaka, 1916**

Figs 70G, 71H

This species was originally described from Japan and resurrected by Ho and Shao (2010), with additional information provided in Ho and Koeda (2019). Although it is widespread in the Indo-West Pacific and common around Taiwan, it is rare around Dongsha Island.

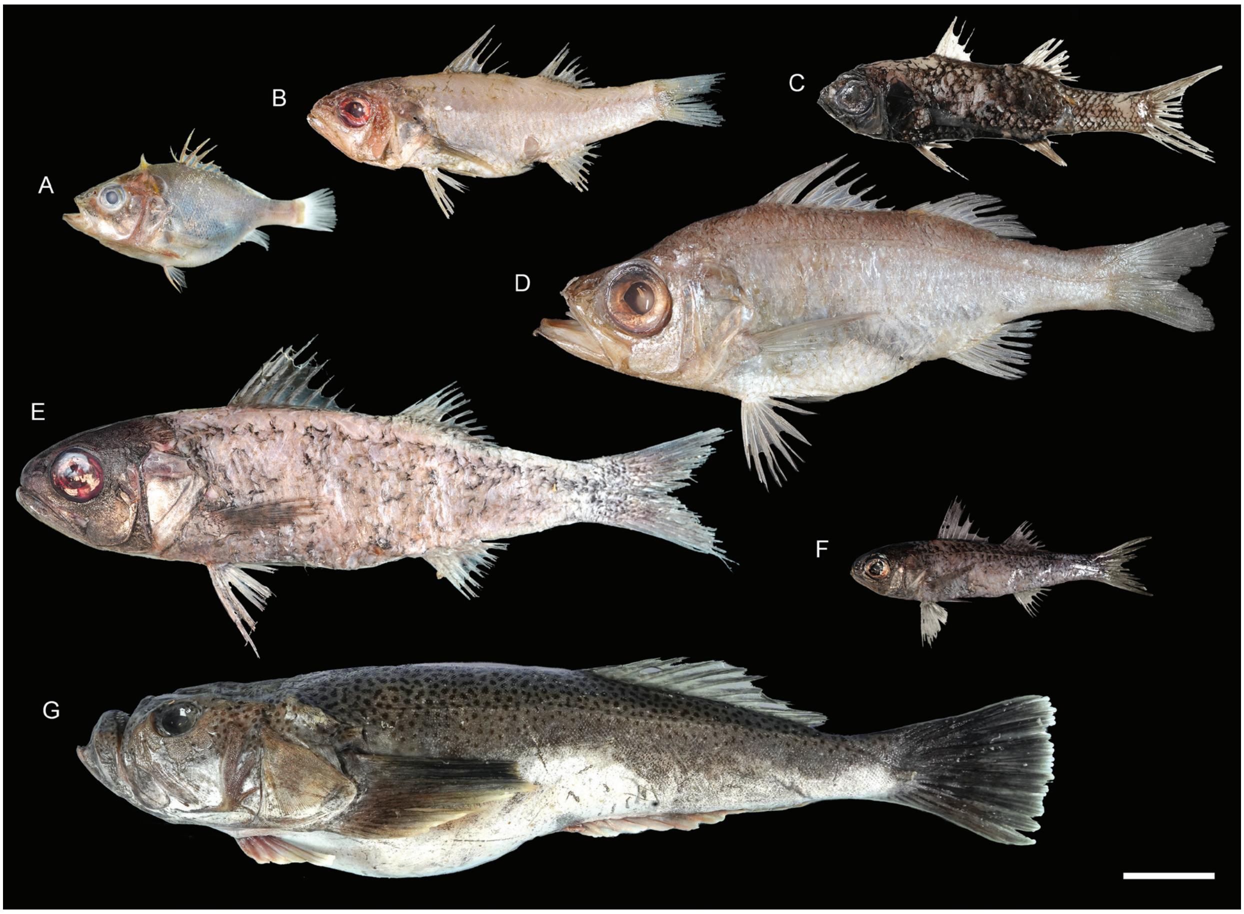

Figure 57. Images of fresh specimens collected around Dongsha Island **A** *Ostracoberyx dorygenys*, 73.53 mm SL **B** *Parascombrops serratospinosus*, 107.83 mm SL **C** *Bathysphyraenops simplex*, 69.53 mm SL **D** *Malakichthys elegans*, 170.51 mm SL **E** *Synagrops japonicus*, 220.42 mm SL **F** *Synagrops atrumoris*, 132.91 mm SL **G** *Xenocephalus elongatus*, 219.48 mm SL. Scale bar: 5 cm.

Species that were not identified to specific level

***Okamejei* sp.**
Fig. 3G

This sole neonate specimen is light yellow on the dorsal side and white on the ventral side, without any blotches or patterns. This species is under investigation by SLN.

***Mobula* spp.**

Several large specimens were observed at the landing site but were dissected, making specific identification impossible. Nevertheless, this record shows the existence of *Mobula* species in the deep waters around Dongsha Island.

***Neenchelys* sp.**
Fig. 9B

This sole specimen belongs to *Neenchelys* but morphologically does not resemble any members.

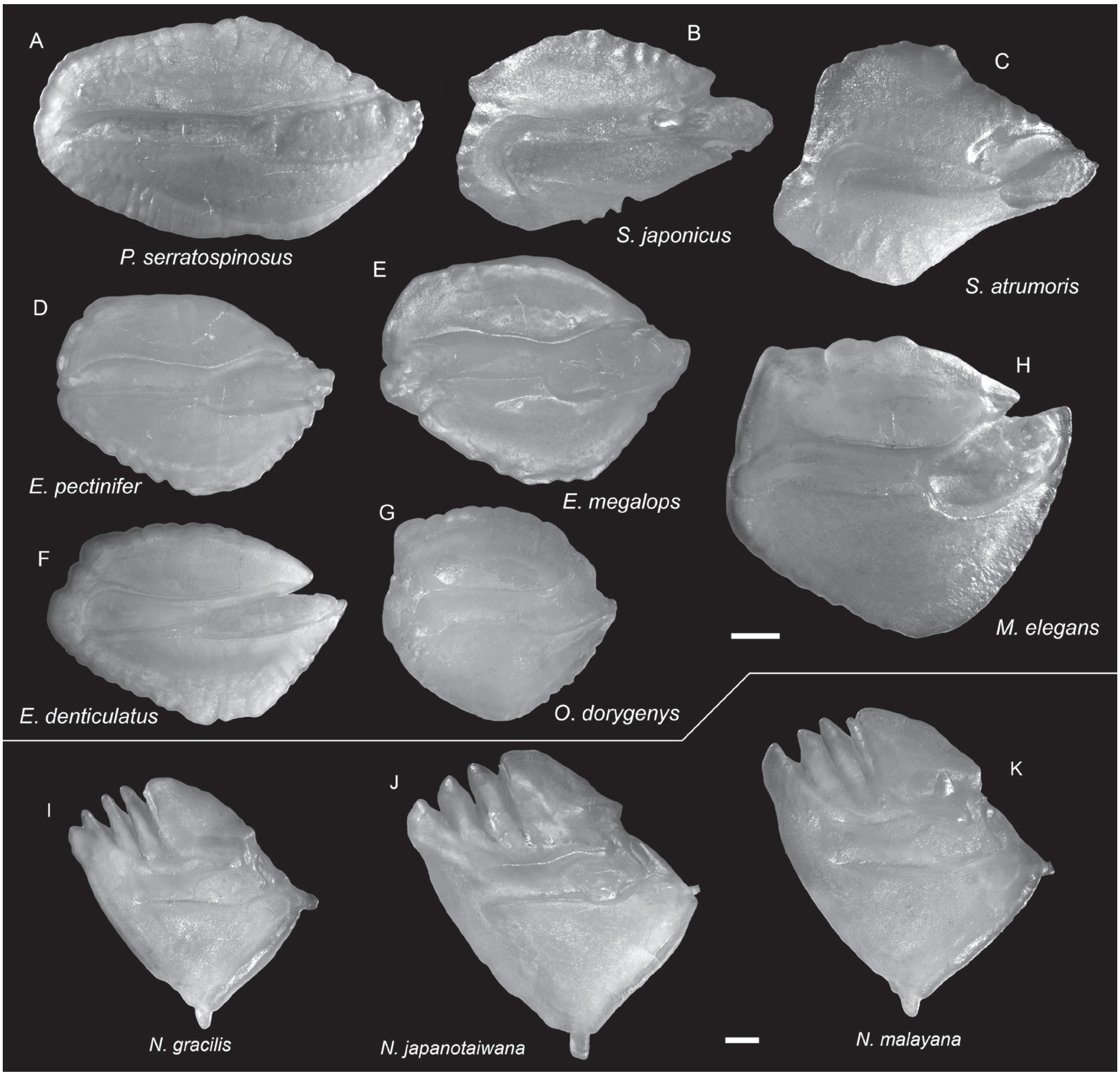

Figure 58. Otolith images of fresh specimens collected around Dongsha Island **A** *Parascombrops serratospinosus*, CHLOL 5589, 92.81 mm SL **B** *Synagrops japonicus*, CHLOL 24379, 203.28 mm SL **C** *Synagrops atrumoris*, CHLOL 26169, 129.07 mm SL **D** *Epigonus pectinifer*, CHLOL 22798, 97.02 mm SL **E** *Epigonus megalops*, CHLOL 22100, 102.02 mm SL (R) **F** *Epigonus denticulatus*, CHLOL 27481, 103.79 mm SL **G** *Ostracoberyx dorygenys*, CHLOL 28712, 103.95 mm SL **H** *Malakichthys elegans*, CHLOL 24712, 122.29 mm SL (R). **I** *Neobathyclupea gracilis*, CHLOL 17470, 159.61 mm SL **J** *Neobathyclupea japanotaiwana*, CHLOL 22536, 194.90 mm SL **K** *Neobathyclupea malayana*, CHLOL 22087, 187.50 mm SL. Scale bars: 1 mm.

***Ophichthus* spp.**
Figs 9D, 10C

These specimens belong to *Ophichthus*. More specimens without precise identification are found in the collection.

***Bathycongrus* sp.**
Figs 12E, 13C

This species has certain differences in morphology from other congeners. It is common around Dongsha Island.

Figure 59. Images of fresh specimens collected around Dongsha Island **A** *Neobathyclupea malayana*, 229.75 mm SL **B** *Neobathyclupea gracilis*, 179.90 mm SL **C** *Neobathyclupea japanotaiwana*, 181.32 mm SL **D** *Pentaceros japonicus*, 100.59 mm SL **E** *Priacanthus zaiserae*, 124.10 mm SL **F** *Owstonia grammodon*, 183.01 mm SL **G** *Owstonia aurora*, 111.14 mm SL **H** *Brama orcini*, 102.62 mm SL **I** *Brama dussumieri*, 142.96 mm SL **J** *Epigonus pectinifer*, 94.61 mm SL **K** *Epigonus megalops*, 161.37 mm SL **L** *Epigonus denticulatus*, 169.85 mm SL. Scale bar: 3 cm.

Bathyuroconger* cf. *vicinus
Figs 13F, 14F

The sole specimen resembles *B. vicinus*, but has a longer dorsal fin and more elongated body.

***Bathyuroconger* sp.**
Figs 13**I**, 14J

This species is most similar to *B. albus*, but its otoliths are distinctly different from those of the congeners.

***Argyripnus* sp.**
Figs 17F, 18D

This species represents the first record of the genus in the South China Sea. However, the specimen was partially damaged and was not retained.

Figure 60. Images of fresh specimens collected around Dongsha Island **A** *Bembrops caudimacula*, 165.04 mm SL **B** *Lioscorpius longiceps*, 139.94 mm SL **C** *Ectreposebastes imus*, 56.56 mm SL **D** *Plectrogenium kamoharai*, 43.27 mm SL **E** *Phenacoscorpius megalops*, 65.03 mm SL **F** *Setarches guentheri*, 126.15 mm SL **G** *Erisphex pottii*, 62.07 mm SL **H** *Lythrichthys cypho*, 53.30 mm SL **I** *Lythrichthys eulabes*, 137.08 mm SL. Scale bar: 3 cm.

***Lestidiops* sp.**

Figs 25C, 26B

One specimen with a partially damaged body was identified at a generic level. This species is the only representative of the genus from our collection.

***Magnisudis* sp.**

Figs 25J, 26I

This species is uncommon around Dongsha Island. Most of the individuals are severely damaged.

Stemonosudis cf. *siliquiventer*

Figs 25A, 26G

This species is rare around Dongsha Island but common around Taiwan (Ho et al. 2019a). The morphology of these specimens is slightly different from the Atlantic population.

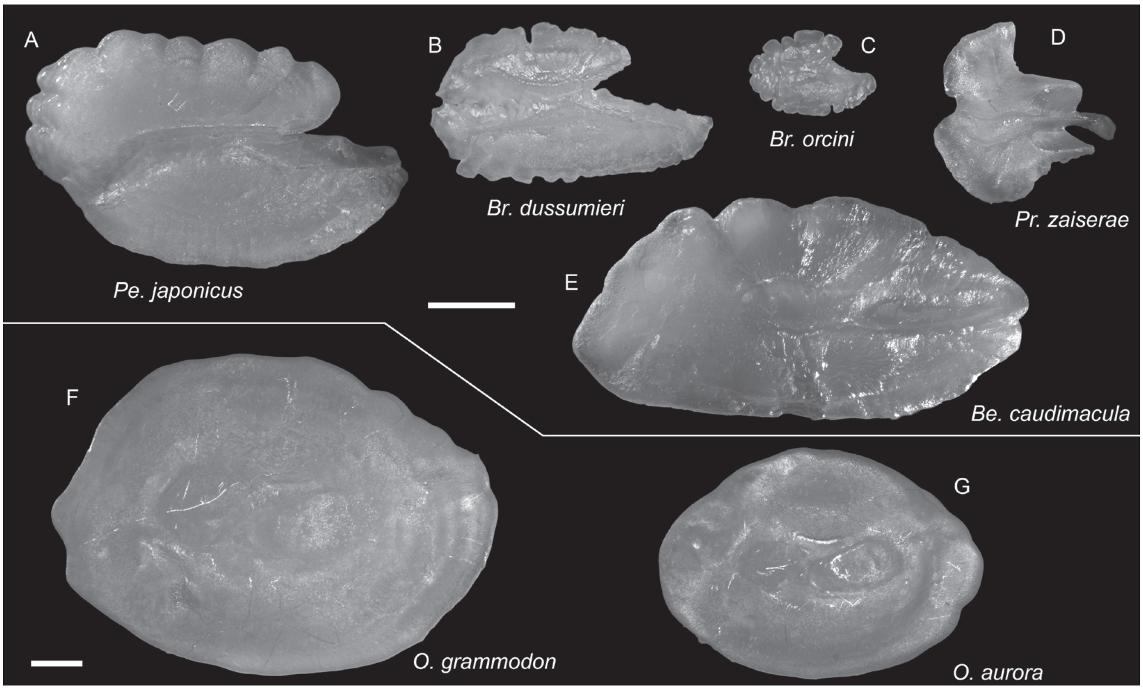

Figure 61. Otolith images of fresh specimens collected around Dongsha Island **A** *Pentaceros japonicus*, CHLOL 26254, 100.59 mm SL **B** *Brama dussumieri*, CHLOL 25658, 142.96 mm SL **C** *Brama orcini*, CHLOL 15403, 56.19 mm SL **D** *Priacanthus zaiserae*, CHLOL 5243, 124.10 mm SL (R) **E** *Bembrops caudimacula*, CHLOL 22142, 165.04 mm SL **F** *Owstonia grammodon*, CHLOL 24036, 183.01 mm SL **G** *Owstonia aurora*, CHLOL 20621, 111.14 mm SL. Scale bars: 1 mm.

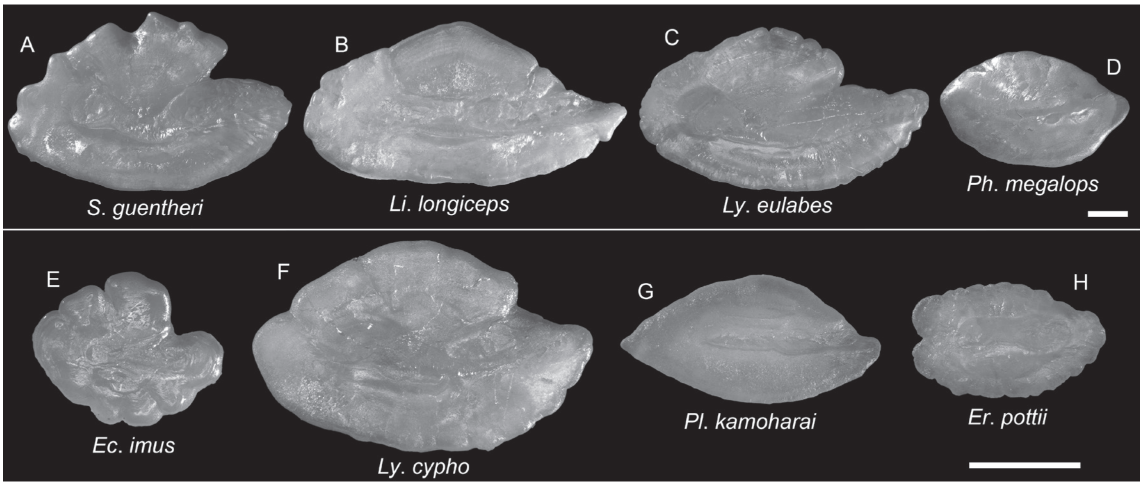

Figure 62. Otolith images of fresh specimens collected around Dongsha Island **A** *Setarches guentheri*, CHLOL 24292, 131.63 mm SL **B** *Lioscorpius longiceps*, CHLOL 22373, 136.03 mm SL **C** *Lythrichthys eulabes*, CHLOL 24508, 120.40 mm SL **D** *Phenacoscorpius megalops*, CHLOL 24396, 62.60 mm SL **E** *Ectreposebastes imus*, CHLOL 28795, 47.71 mm SL **F** *Lythrichthys cypho*, CHLOL 24502, 47.83 mm SL **G** *Plectrogenium kamoharai*, CHLOL 9880, 49.42 mm SL **H** *Erisphex pottii*, CHLOL 29164, 62.07 mm SL. Scale bars: 1 mm.

***Sudis* sp.**

Figs 25H, 26J

A single specimen was collected from Dongsha Island. Although both species under *Sudis* were predicted to be circumglobal, our specimen represents the first record of the genus in the South China Sea.

Figure 63. Images of fresh specimens collected around Dongsha Island **A** *Pterygotrigla macrorhynchus*, 179.11 mm SL **B** *Pterygotrigla cajorarori*, 225.51 mm SL **C** *Paraheminodus murrayi*, 193.98 mm SL **D** *Heminodus philippinus*, 248.83 mm SL **E** *Lepidotrigla* sp., 115.30 mm SL **F** *Lepidotrigla pectoralis*, 127.46 mm SL **G** *Peristedion riversandersoni*, 158.52 mm SL **H** *Peristedion orientale*, 128.99 mm SL **I** *Scalicus hians*, 165.47 mm SL **J** *Hoplichthys gilberti*, 288.42 mm SL **K** *Hoplichthys fasciatus*, 78.74 mm SL **L** *Hoplichthys filamentosus*, 184.54 mm SL **M** *Scalicus orientalis*, 129.56 mm SL **N** *Satyrichthys milleri*, 265.63 mm SL **O** *Chelidonichthys spinosus*, 132.61 mm. Scale bar: 3 cm.

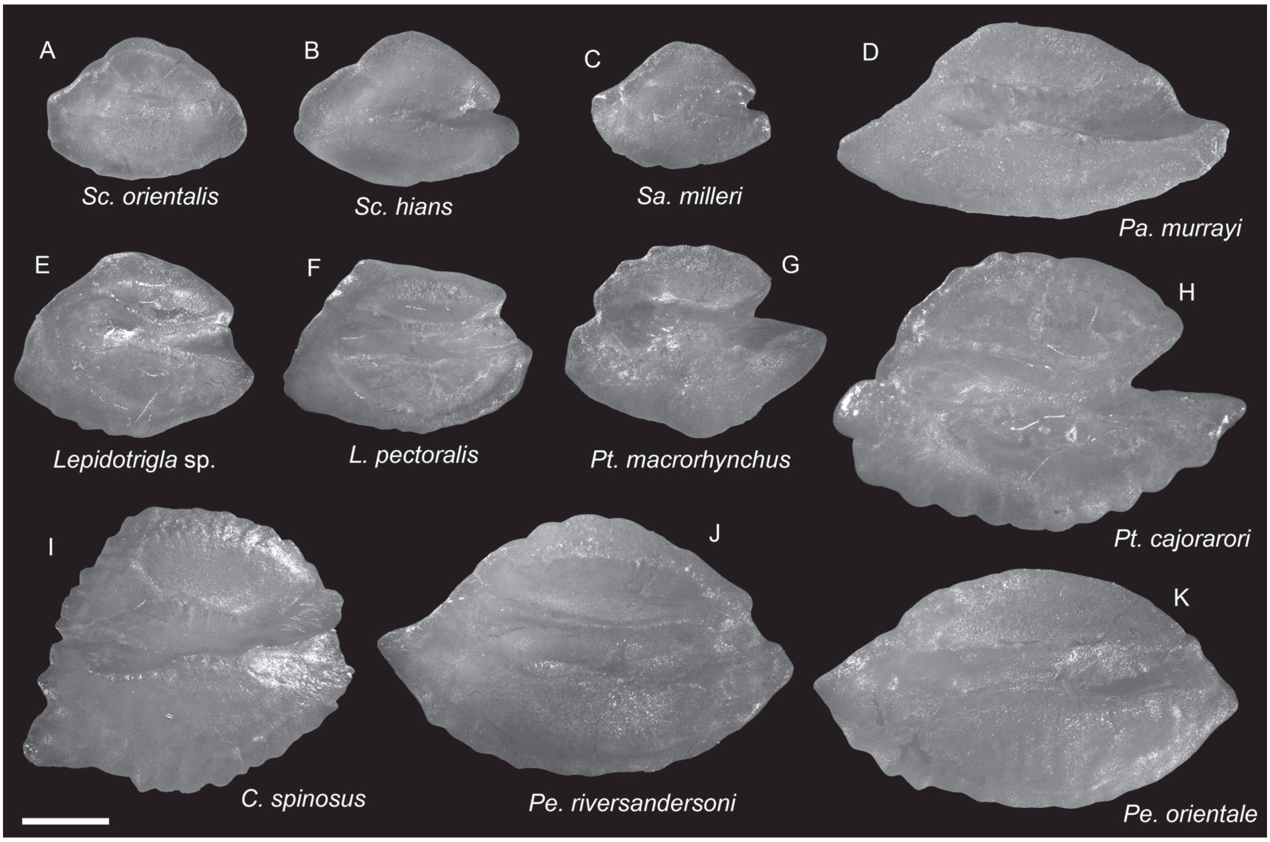

Figure 64. Otolith images of fresh specimens collected around Dongsha Island **A** *Scalicus orientalis*, CHLOL 27465, 128.73 mm SL **B** *Scalicus hians*, CHLOL 29478, 165.47 mm SL **C** *Satyrichthys milleri*, CHLOL 20905, 103.55 mm SL **D** *Paraheminodus murrayi*, CHLOL 20864, 245.67 mm SL **E** *Lepidotrigla* sp., CHLOL 23056, 115.30 mm SL **F** *Lepidotrigla pectoralis*, CHLOL 29737, 124.66 mm SL **G** *Pterygotrigla macrorhynchus*, CHLOL 8397, 155.76 mm SL **H** *Pterygotrigla cajorarori*, CHLOL 23058, 171.52 mm SL **I** *Chelidonichthys spinosus*, CHLOL 29166, 212.35 mm SL (R) **J** *Peristedion riversandersoni*, CHLOL 23051, 164.13 mm SL **K** *Peristedion orientale*, CHLOL 21074, 151.57 mm SL. Scale bar: 1 mm.

***Neoscopelus* sp.**
Figs 27D, 29D

This species is currently known only around Dongsha Island, and is abundant. It differs from other congeners by the unique photophore pattern and the pinkish coloration and is recognized as undescribed.

***Bolinichthys* spp.**
Figs 27I, 29F

The specimens are easily recognizable as *Bolinichthys* by having a whitish crescent on the posterior edge of the eye. However, almost all specimens are partially damaged and lack diagnostic photophores; thus, species-level identification is impossible. They are very common around Dongsha Island.

***Ceratoscopelus* sp.**
Figs 27K, 29J

Ceratoscopelus warmingii (Lütken, 1892) is the only species previously reported in the South China Sea (Randall and Lim 2000). However, almost all

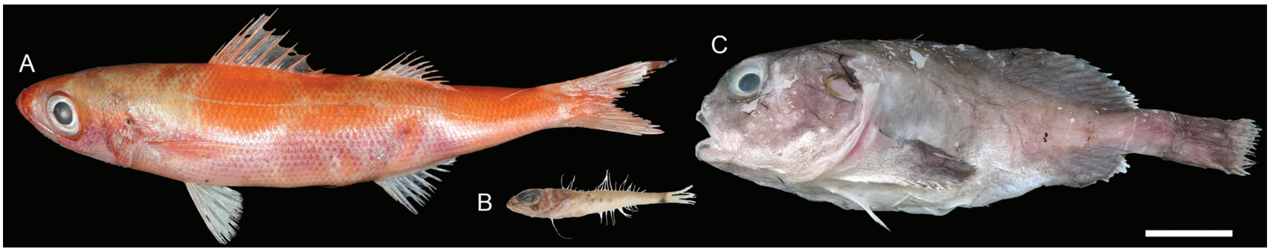

Figure 65. Images of fresh specimens collected around Dongsha Island **A** *Erythrocles schlegelii*, 177.46 mm SL **B** *Stlengis distoechus*, 48.45 mm SL **C** *Psychrolutes macrocephalus*, 155.12 mm SL. Scale bar: 3 cm.

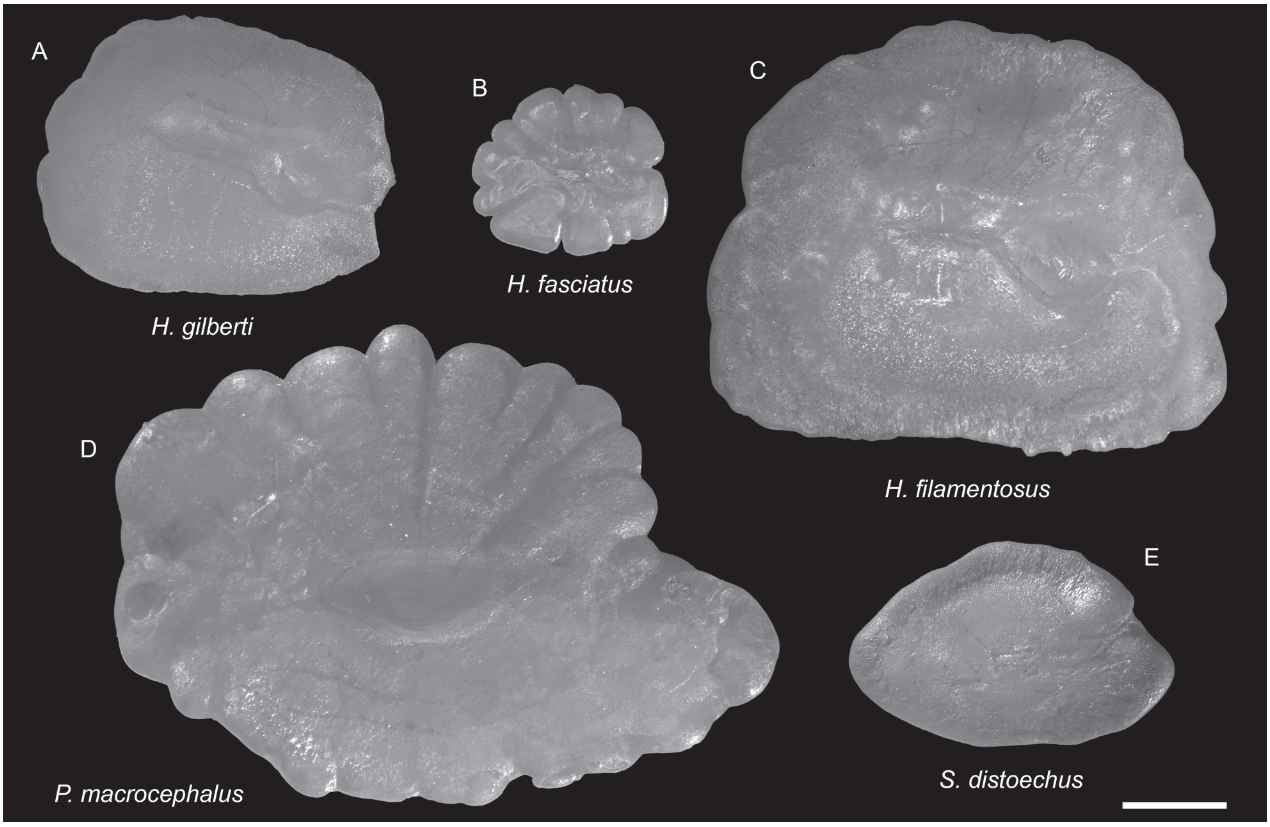

Figure 66. Otolith images of fresh specimens collected around Dongsha Island **A** *Hoplichthys gilberti*, CHLOL 9890, 89.80 mm SL **B** *Hoplichthys fasciatus*, CHLOL 24449, 78.74 mm SL **C** *Hoplichthys filamentosus*, CHLOL 22098, 204.66 mm SL **D** *Psychrolutes macrocephalus*, CHLOL 25008, 172.17 mm SL **E** *Stlengis distoechus*, CHLOL 24045, 48.77 mm SL. Scale bar: 1 mm.

specimens are partially damaged, lacking the diagnostic photophores, making them difficult to identify. In addition, the relationship between *C. warmingii* and the circumglobal *C. townsendi* (Eigenmann & Eigenmann, 1889) is also unclear (Badcock and Araújo 1988; dos Santos et al. 2024). This species is common around Dongsha Island.

***Lampanyctus* spp.**
Figs 27J, 32K

This genus has a complicated taxonomic history and is especially difficult to identify. All specimens are conservatively identified at a generic level. This genus is uncommon around Dongsha Island.

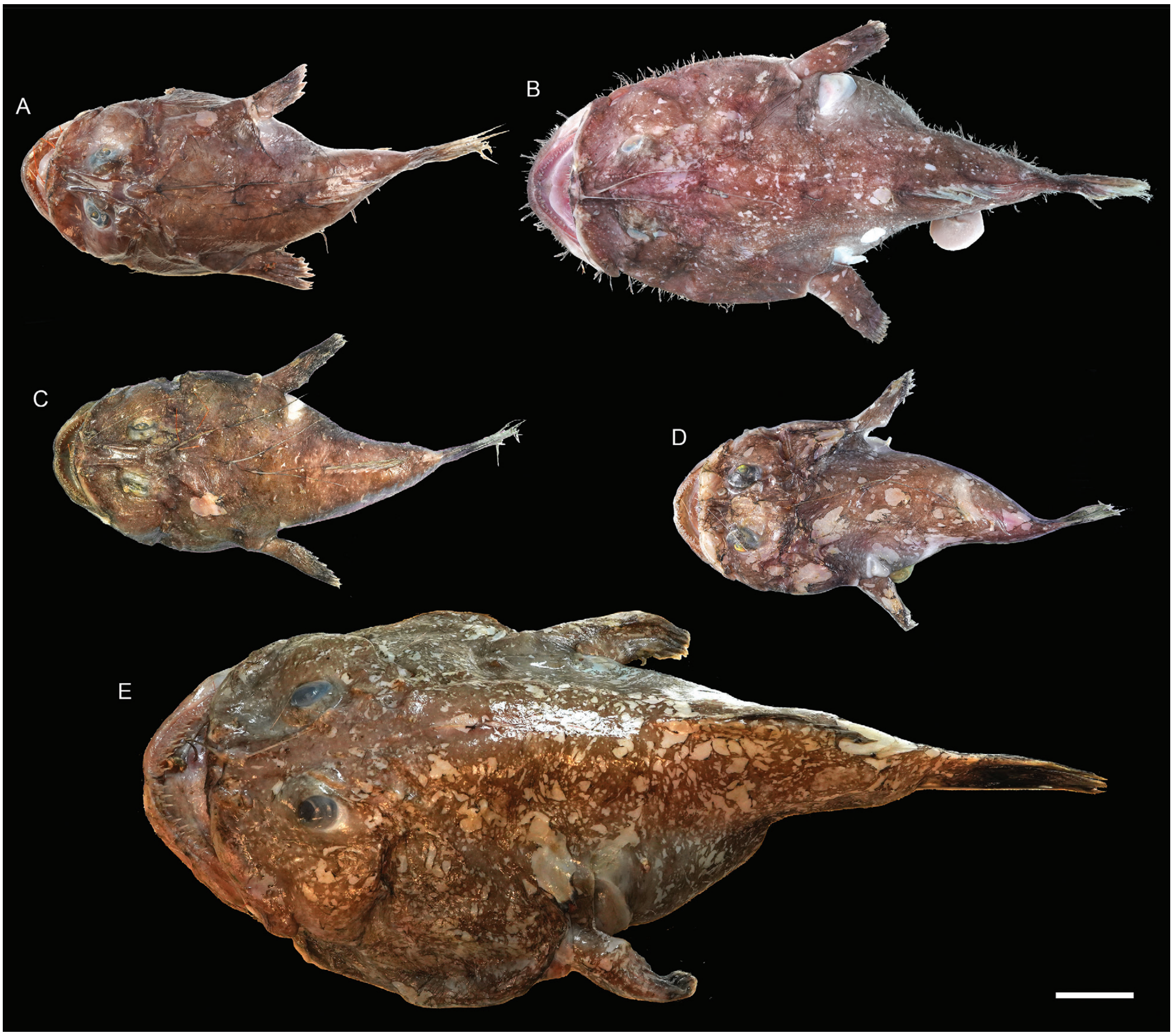

Figure 67. Images of fresh specimens collected around Dongsha Island **A** *Lophiodes iwamotoi*, 228.40 mm SL **B** *Lophiodes lugubris*, 313.96 mm SL **C** *Lophiodes naresi*, 231.87 mm SL **D** *Lophiodes mutilus*, 180.04 mm SL **E** *Lophiodes triradiatus*, 513.12 mm SL. Scale bar: 5 cm.

***Zenion* sp.**
Figs 30H, 32C

This common species is currently known only from Dongsha Island. It is similar to *Z. japonicum*, but differs in the dorsal-fin morphology and some body morphometrics. It is recognized as undescribed. and is currently under investigation by YTL in the special issue.

Xenolepidichthys* cf. *dalgleishi
Figs 30E, 32L

These specimens are similar to *X. dalgleishi* in all aspects, but without the conspicuous black blotches on the body.

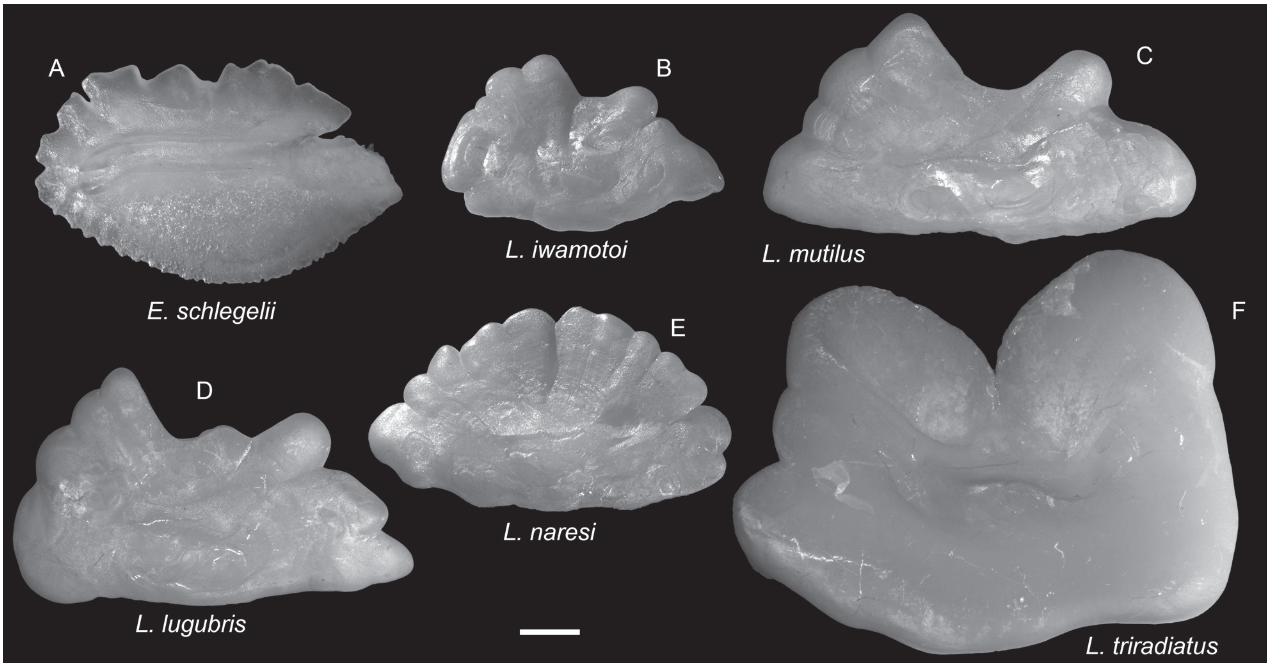

Figure 68. Otolith images of fresh specimens collected around Dongsha Island **A** *Erythrocles schlegelii*, CHLOL 21498, 177.46 mm SL (R) **B** *Lophiodes iwamotoi*, CHLOL 23849, 109.84 mm SL **C** *Lophiodes mutilus*, CHLOL 23149, 250.73 mm SL **D** *Lophiodes lugubris*, CHLOL 23262, 265.64 mm SL **E** *Lophiodes naresi*, CHLOL 9768, 185.84 mm SL **F** *Lophiodes triradiatus*, CHLOL 20515, 437.17 mm SL. Scale bar: 1 mm.

Coelorinchus **sp.**
Figs 33F, 34D

This species is similar to *C. smithi*, but differs from the morphology of the occipital scale and body morphometrics. It is the most abundant macrourid species collected around the studied area and is possibly restricted to the South China Sea.

Mataeocephalus **sp.**
Figs 36H, 37J

This species differs from the two sympatric species, *M. cristatus* Sazonov, Shcherbachev & Iwamoto, 2003 and *M. hyostomus* (Smith & Radcliffe, 1912), by having the underside of snout largely naked (Iwamoto et al. 2015). However, as most specimens are small and not intact, a generic-level identification is given conservatively. It is common around Dongsha Island.

Pseudocetonurus **cf.** ***septifer***
Figs 35E, 36A

The sole specimen collected around Dongsha Island resembles the Taiwanese specimen listed in Nakayama (2020). This species may be an undescribed species.

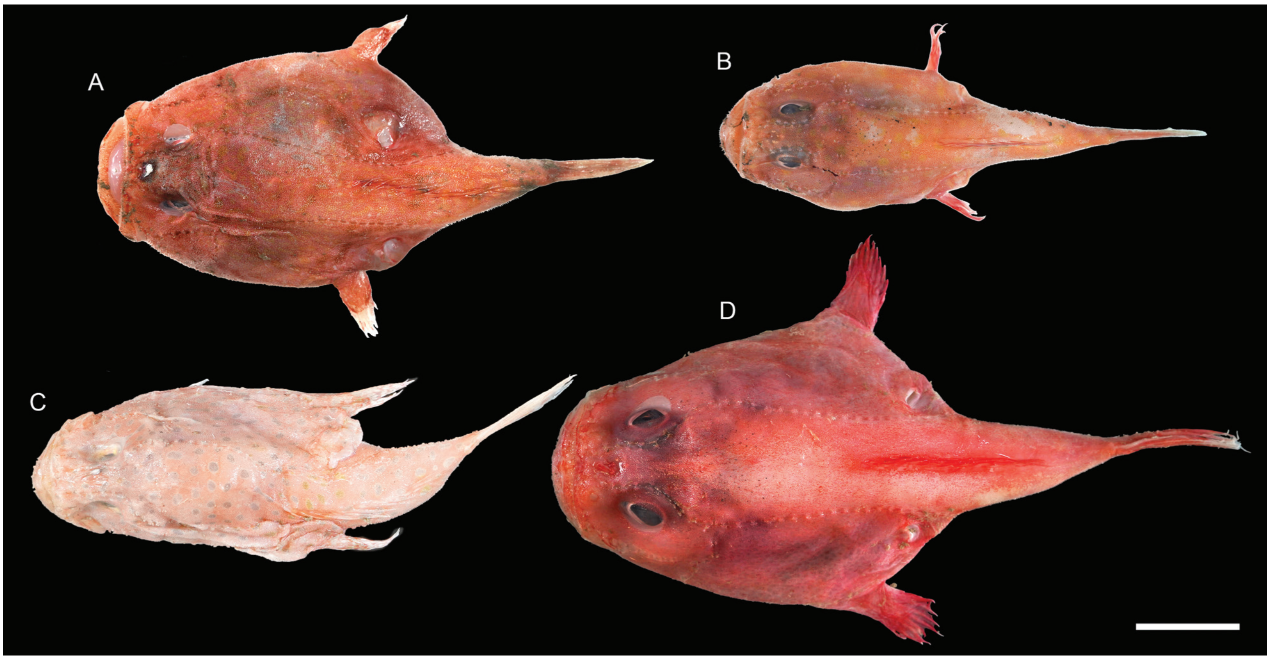

Figure 69. Images of fresh specimens collected around Dongsha Island **A** *Chaunax penicillatus*, 108.89 mm SL **B** *Chaunax* sp., 103.01 mm SL **C** *Chaunax breviradius*, 131.88 mm SL **D** *Chaunax apus*, 124.73 mm SL. Scale bar: 3 cm.

Ventrifossa* cf. *longibarbata
Figs 37G, 38E

This species differs from *V. longibarbata* by having fewer transverse scale rows, body morphometrics, and having distinct black blotch on the first dorsal fin. The status of the species is currently under investigation by SLN. It is common around Dongsha Island.

***Physiculus* sp. 1**
Figs 39B, 40B

This species resembles the *Physiculus* sp. 1 in Koeda and Ho (2019), which is uncommon around Taiwan and rare around Dongsha Island.

***Physiculus* sp. 2**
Figs 39E, 40C

This species resembles the *Physiculus* sp. 3 in Koeda and Ho (2019), which is common in southwestern Taiwan. We only collected one specimen around Dongsha Island.

***Hoplostethus* sp.**
Figs 41H, 42A

This species is similar to *H. roseus*, but differs from the latter by having the gular region covered with scales and the oral cavity pale (Su et al. 2022).

Figure 70. Images of fresh specimens collected around Dongsha Island **A** *Halieutopsis echinoderma*, 64.26 mm SL **B** *Halieutopsis nasuta*, 54.01 mm SL **C** *Halieutaea coccinea*, 65.84 mm SL **D** *Halieutopsis* sp., 53.07 mm SL **E** *Malthopsis annulifera*, 85.54 mm SL **F** *Malthopsis mitrigera*, 55.29 mm SL **G** *Malthopsis kobayashii*, 75.44 mm SL **H** *Malthopsis tiarella*, 66.21 mm SL **I** *Halicmetus ruber*, 86.79 mm SL **J** *Halicmetus* cf. *ruber*, 56.29 mm SL **K** *Halicmetus reticulatus*, 77.90 mm SL **L** *Coelophrys micropus*, 64.00 mm SL. Scale bar: 3 cm.

***Encheliophis* sp.**
Figs 41D, 44B

Known only from two specimens in rather poor condition around Dongsha Island. We conservatively identified the specimens to a generic level. This is the first record of this genus in the area.

***Monomitopus* sp.**
Figs 43D, 44I

Members of this genus are exceptionally similar to each other, thus making it difficult to identify. A comprehensive taxonomic revision of all the members is needed. This species is common around Dongsha Island.

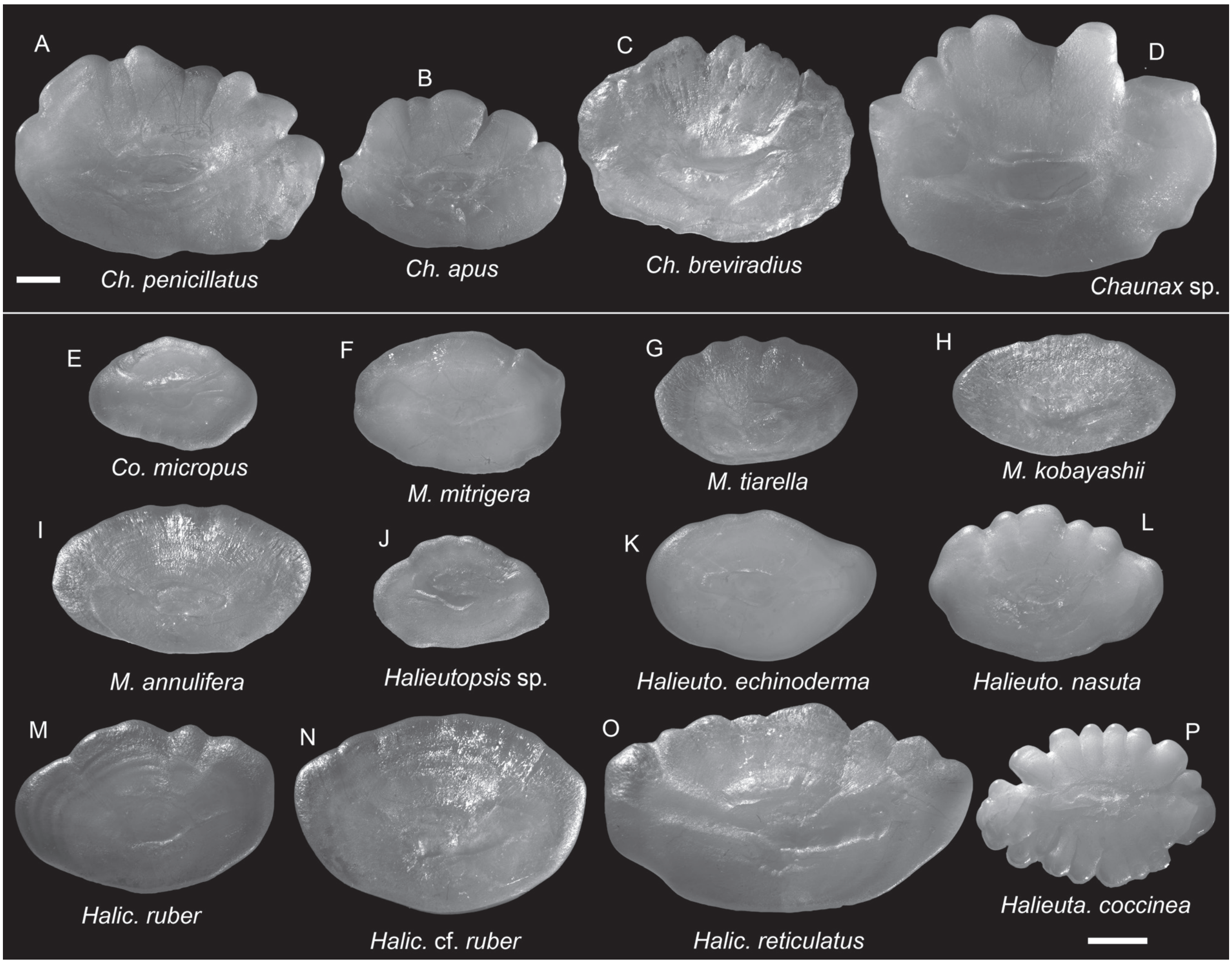

Figure 71. Otolith images of fresh specimens collected around Dongsha Island **A** *Chaunax penicillatus*, CHLOL 20309, 127.92 mm SL **B** *Chaunax apus*, CHLOL 20308, 95.51 mm SL **C** *Chaunax breviradius*, CHLOL 5399, 131.88 mm SL **D** *Chaunax* sp., CHLOL 15746, 160.97 mm SL **E** *Coelophrys micropus*, CHLOL 27454, 64.00 mm SL **F** *Malthopsis mitrigera*, CHLOL 17434, 55.29 mm SL **G** *Malthopsis tiarella*, CHLOL 4394, 58.70 mm SL **H** *Malthopsis kobayashii*, CHLOL 6852, 61.09 mm SL **I** *Malthopsis annulifera*, CHLOL 3678, 85.54 mm SL **J** *Halieutopsis* sp., CHLOL 18748, 46.37 mm SL **K** *Halieutopsis echinoderma*, CHLOL 29043, 64.26 mm SL **L** *Halieutopsis nasuta*, CHLOL 25666, 73.65 mm SL **M** *Halicmetus ruber*, CHLOL 21065, 65.15 mm SL **N** *Halicmetus* cf. *ruber*, CHLOL 24204, 64.74 mm SL **O** *Halicmetus reticulatus*, CHLOL 20910, 101.23 mm SL **P** *Halieutaea coccinea*, CHLOL 27444, 65.84 mm SL. Scale bars: 1 mm.

Bythitidae indet.
Figs 45A, 46F

This specimen resembles members of the genus *Cataetys*, but it has a more slender body. Due to the limited knowledge of the taxonomy of the bythihtids in this region, we conservatively assigned this specimen to the familial level.

***Diplacanthopoma* sp.**
Figs 45C, 46E

This genus is poorly studied, and it is uncertain how many species are valid. As a result, all specimens are identified to a generic level. This species is uncommon around Dongsha Island.

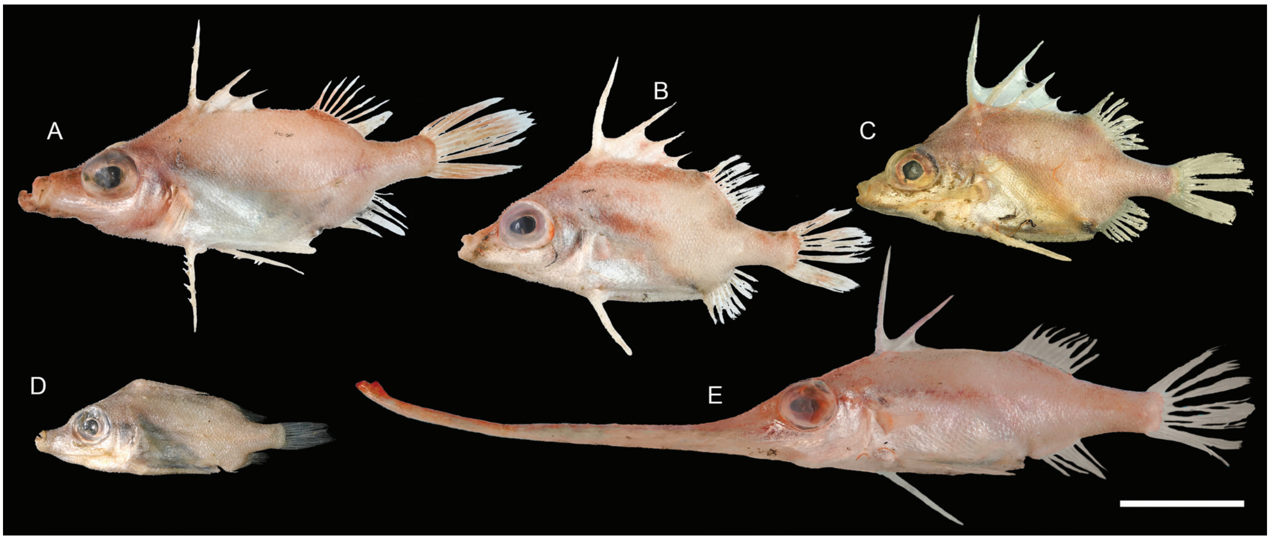

Figure 72. Images of fresh specimens collected around Dongsha Island **A** *Tydemania navigatoris*, 95.54 mm SL **B** *Triacanthodes anomalus*, 76.52 mm SL **C** *Paratriacanthodes retrospinis*, 70.23 mm SL **D** *Bathyphylax bombifrons*, 58.07 mm SL **E** *Halimochirurgus alcocki*, 185.04 mm SL. Scale bar: 3 cm.

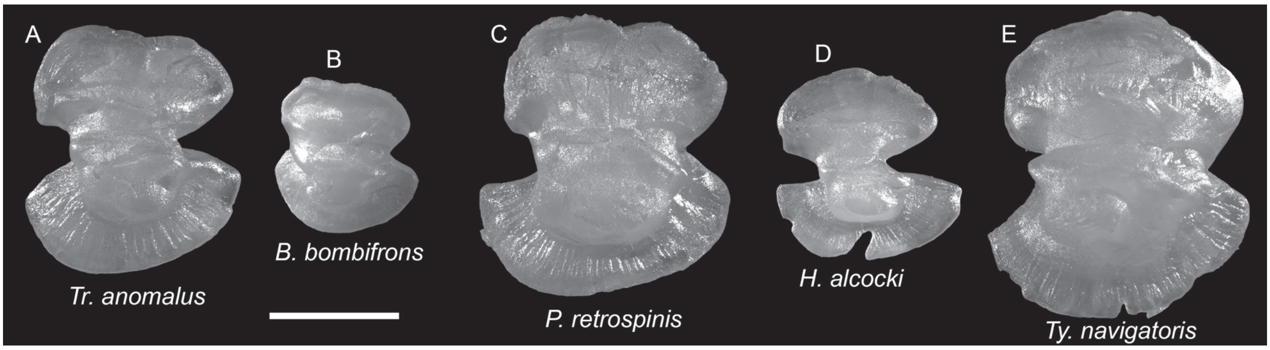

Figure 73. Otolith images of fresh specimens collected around Dongsha Island **A** *Triacanthodes anomalus*, CHLOL 22706, 73.57 mm SL **B** *Bathyphylax bombifrons*, CHLOL 12732, 43.93 mm SL **C** *Paratriacanthodes retrospinis*, CHLOL 23527, 90.30 mm SL (R) **D** *Halimochirurgus alcocki*, CHLOL 22698, 143.53 mm SL (R) **E** *Tydemania navigatoris*, CHLOL 22702, 110.20 mm SL (R). Scale bar: 1 mm.

***Aphanopus* sp.**
Figs 53K, 54A

The sole specimen represents the first record of the genus *Aphanopus* around Taiwan and the South China Sea. The status of the species if under investigation by YTL.

***Benthodesmus* sp.**
Figs 53M, 54B

This species is uncommon around Dongsha Island. It is similar to *B. tenuis* in morphological aspects but with a dense black body coloration and a shorter orbital length.

***Lepidotrigla* sp.**
Figs 63E, 64E

This species resembles *Lepidotrigla* sp. sensu Yamada and Yagishita (2013) in morphological aspects. It is rare around Dongsha Island.

***Chaunax* sp.**
Figs 69B, 71D

This species is morphologically distinct from other known *Chaunax* species. It is not uncommon around Taiwan but rare around Dongsha Island.

Halicmetus* cf. *ruber
Figs 70J, 71N

This species is similar to, yet distinct from *H. ruber*. This is also common around Dongsha Island.

***Halieutopsis* sp.**
Figs 70D, 71J

This species, represented by a few specimens, is recognized as undescribed.

Discussion

The earliest record of the ichthyofauna around Dongsha Island was a report by Chen et al. (1995), which was later incorporated by Randall and Lim (2000) into a comprehensive checklist of South China Sea fishes. Despite updates by Shao et al. (2008, 2011) in their checklists for southern Taiwan and the northern South China Sea, there has until now been no concerted effort to synthesize new data from subsequent studies. Our study presents the most exhaustive inventory to date, utilizing existing literature and newly sampled fish collections conducted between 2021 and 2024. More importantly, this is the first attempt to target samples derived from commercial fisheries, which operate with much higher fishing effort, generate larger catches using bigger fishing gear, and more broadly cover deeper and remote areas compared to typical scientific research vessels. Thus, our results provide novel insights and deeper knowledge of the fish fauna around Dongsha Island, especially for the less explored western waters off the atoll.

In this study, we cataloged a total of 1087 species across 167 families, and our recent efforts alone identified 337 species from 93 families (Suppl. material 1). Thirteen species have been described from 2021 to 2024 around Dongsha Island, and 89 species have been newly recorded in this study, with 35 species still undescribed and requiring further investigation. We revised the scientific names of previously reported species in literature following Fricke et al. (2024) from the families Torpedinidae, Rajidae, Dasyatidae, Congridae, Apogonidae, Gobiidae, Pomacentridae, Exocoetidae, Belonidae, Carangidae, Syngnathidae, Nomeidae, Mullidae, Kyphosidae, Anthiadidae, Epinephelidae, Haemulidae, Plectrogeniidae, Peristediidae, Platycephalidae, and Ostraciidae. We also categorized the families of each taxon following Fricke et al. (2024). Additionally, this study provides actual images and otoliths of the fishes from Dongsha Island, offering a tool for species identification.

The updated checklist not only enriches our understanding of marine biodiversity but also serves as a critical resource for future research and conservation initiatives. Notably, based on the IUCN Red List of Threatened Species (IUCN 2012), there were two fish species recorded in Dongsha Island that were considered Critically Endangered: the Reticulated Swellshark (*Cephaloscyllium fasciatum*) and the Oceanic Whitetip Shark (*Carcharhinus longimanus*). Nine species are listed as Endangered: *Aetobatus narinari*, *Centrophorus granulosus*, *Centrophorus squamosus*, *Centrophorus tessellatus*, *Cheilinus undulatus*, *Eptatretus taiwanae*, *Negaprion acutidens*, *Squalus japonicus*, and *Squatina nebulosa*; ten as Vulnerable: *Benthobatis yangi*, *Carcharhinus limbatus*, *Chimaera phantasma*, *Cirrhoscyllium formosanum*, *Eptatretus fernholmi*, *Istiophorus platypterus*, *Nebrius ferrugineus*, *Pateobatis fai*, *Squalus montalbani*, and *Taeniurops meyeni*; and six as Near Threatened: *Deania calcea*, *Dipturus gigas*, *Dipturus tengu*, *Eptatretus burgeri*, *Heptranchias perlo*, and *Hydrolagus mitsukurii*. However, most species were categorized as Least Concern or Data Deficient, highlighting the need for continued research and conservation efforts to ensure sustainable fishing practices in the region.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Checklist of fishes around Dongsha Island

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Data type: docx

Explanation note: **table S1.** Checklist of fishes around Dongsha Island based on the literature and our collection. Species recorded and described around Dongsha Island for the first time (in this study) are in bold font.

Link: https://doi.org/10.3897/zookeys.1220.131100.suppl1