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Gymnocranius indicus, a new large-eye seabream from the Indian Ocean

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Research Article

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Abstract

Gymnocranius indicus sp. nov. is described as a new species of the fish subfamily Monotaxinae (Sparoidea: Lethrinidae), a group of commercially important species distributed throughout the Indo-West Pacific, on the basis of 16 specimens collected from the Indian Ocean. The new species shares the following characters with its western Pacific sibling, the eyebrowed large-eye seabream, *G. superciliosus*: elongate body, distinctive and conspicuous dark patch above the eye, prominent forehead, moderately forked caudal fin, its lobes slightly convex inside, flank silvery, and reddish-to-red dorsal, pectoral, anal and caudal fins. However, principal component analysis based on seven morphological variables distinguished most specimens from the Indian Ocean from *G. superciliosus*. The most influential variable in the analysis was the eye diameter, significantly larger in the new species than in *G. superciliosus*. All specimens of the new species that were examined also lacked blue ornamentation on the snout and cheek. At the mitochondrial *cytochrome oxidase subunit-I* locus, the mean genetic *p*-distance between the two species was 0.039. With *Gymnocranius indicus* sp. nov., the genus now includes 12 valid nominal species; three additional species remain undescribed.

Introduction

The subfamily Monotaxinae of the actinopterygian fish family Lethrinidae comprises medium- to large-sized carnivorous species occurring in inshore waters over sandy or rubble substrates of coral reefs (Carpenter and Allen, 1989). Commonly known as large-eye seabreams, the monotaxines are important food fishes, which are sold fresh, frozen, or dried throughout the tropical Indo-West Pacific. With 11 currently recognized species, *Gymnocranius* Klunzinger, 1870 is the largest genus among the four valid genera within the Monotaxinae. The three other genera are *Gnathodentex* Bleeker 1873 (one species), *Monotaxis* Anonymous [Bennett], 1830 (two species), and *Wattsia* Chan & Chilvers, 1974 (one species) (Carpenter and Allen, 1989; Chen *et al.*, 2016, 2017; Chen and Borsa, 2020; Fricke *et al.*, 2022).

Fishes in the genus *Gymnocranius* are characterized by having an ovate, laterally compressed body, generally overall silvery in colour with a pattern of five to eight narrow, transverse dark bars along the body, particularly noticeable in juveniles and pre-adults; the eye is relatively large; the profile of the head in front of the eye is slightly to markedly convex, and the snout slope relatively steep (Carpenter and Allen, 1989). Largely due to the great similarity in shape and colour among the species, morphology-based species recognition has long been challenging (Sato, 1986). *Gymnocranius* has thus been considered one of the taxonomically most problematic tropical marine fish groups, and useful information such as life history and catch statistics have remained scant (Sato, 1986; Carpenter and Allen, 1989). An updated morphological key for 12 species including one undescribed species in this genus has been proposed by Chen *et al.* (2017). Several species including *G. frenatus* Bleeker, 1873, *G. grandoculis* (Valenciennes, 1830), *G. microdon* (Bleeker, 1851), *G. oblongus* Borsa *et al.*, 2010, *G. satoi* Borsa *et al.*, 2013, and *G. superciliosus* Borsa *et al.*, 2013 usually possess blue ornamentation on the snout and cheeks.

Large-eye seabream specimens morphologically similar to *G. superciliosus*, a species so far only reported from the tropical western Pacific (Borsa *et al.*, 2013; Miki *et al.*, 2014; Chen and Borsa, 2020), were noticed by the first author (WJC) at the Victoria fish market on Mahé Island in the Seychelles during a visit in April 2016. Other *Gymnocranius* species for sale at the Victoria fish market included *G. elongatus* Senta, 1973 and *G. microdon*. Like *G. superciliosus*, this large-eye seabream had a relatively elongate body with reddish pectoral, dorsal, and caudal fins and featured a distinctive eyebrow-like pattern above the eye, characters that together excluded all other large-eye seabreams then known (Carpenter and Allen, 1989; Borsa *et al.*, 2013; Chen *et al.*, 2017). Upon closer examination, however, the general body shape and proportions of these specimens seemed marginally different from *G. superciliosus*. Three specimens were purchased, measured, and photographed and one of them was preserved as voucher. A series of underwater pictures of large-eye seabreams from Reunion Island (Western Indian Ocean) taken by C. Schilling (GSM diving club,

Saint-Gilles-les-Bains) and posted online in June 2018 were seen by the last author (PB) and found to include the same fish. An additional specimen was collected in April 2019 by PB and WJC at fish stalls in Le Port, Reunion Island and kept as voucher. In June 2019, S. Paijo (BarCore project, Indonesia) looked for large-eye seabreams in the Peunayong and Lampulo fish markets in Banda Aceh (Andaman Sea) and sampled two *G. superciliosus*-like individuals (including one voucher specimen and a fin clip of another individual). Meanwhile, one of the co-authors, based in Mahé (JN) surveyed the Victoria fish market between 2013 and 2018, where he regularly sighted specimens of a species similar to *G. superciliosus*, of which photographs were retained and later examined in this study.

A recent multiple-gene study exploring the phylogeny and species diversity of the Monotaxinae (Chen and Borsa, 2020) has confirmed the validity of the 11 *Gymnocranius* species described so far and that of one undescribed species (*Gymnocranius* sp. D; Chen *et al.*, 2017); two additional species from the western Indian Ocean provisionally named *Gymnocranius* sp. F and *Gymnocranius* sp. G were reported, which formed a monophyletic group with *G. obesus* Chen *et al.*, 2017. The molecular analyses of the three large-eye seabream specimens sampled by WJC from the Seychelles in April 2016 designated them as of yet another distinct species, provisionally referred to as '*Gymnocranius* sp. H' (Chen and Borsa, 2020). *Gymnocranius* sp. H was placed within a separate clade mostly comprising *Gymnocranius* spp. with blue ornamentation on snout and cheek, and was resolved as the sister group of *G. superciliosus* (Chen and Borsa, 2020).

The objectives of the present paper are (1) to morphologically and genetically compare the *Gymnocranius* sp. H specimens from the Indian Ocean with the *G. superciliosus* material available to us; (2) to formally describe *Gymnocranius* sp. H as a new species.

Materials and methods

Material examined

Gymnocranius sp. H specimens to be chosen as type material of the new species included two specimens from the Western Indian Ocean preserved at the ichthyological collections of the National Taiwan University Museums in Taipei under collection nos. NTUM 12894 and NTUM 16756 and two specimens from Western Indonesia deposited in fish collections in Australia (NTM S.10771-004 and CSIRO H7306-13). Additional specimens from the Seychelles and Aceh (Table 1) were photographed and measured at their sampling site; fin clips were retained. Comparative material of *G. superciliosus* used for morphological examination included six specimens deposited at Muséum National d'Histoire Naturelle, Paris [MNHN ICOS-00715 (New Caledonia, voucher), MNHN 2009–0010 (New Caledonia, holotype), MNHN 2009-0011 to −0013 (New Caledonia and Fiji, paratypes)], six specimens deposited in the Miyazaki University Fisheries Science collections [MUFS 42021, MUFS 42771, MUFS 42776, MUFS 42785, MUFS 43073, and MUFS 43076 (Okinawa, vouchers)], as well as NTUM10729 (Marshall Islands, voucher), and United States National Museum, Washington DC USNM 443295 (South China Sea off Luzon, voucher). Another specimen from Aceh (Andaman Sea) was deposited in the Museum Zoologicum Bogoriense in Cibinong, Indonesia under collection no. MZB.26789. Preserved tissue samples of other individuals of the two species were also used for molecular examination. Three new sequences of the mitochondrial cytochrome c oxidase I (*COI*) gene and two new sequences of the nuclear early growth response protein 2B (*EGR2B*) gene were generated in this study according to the laboratory protocols and procedures of Ward *et al.* (2005) and Chen and Borsa (2020). Homologous *COI* gene sequences of *Gymnocranius* sp. H and *G. superciliosus* were searched in the GenBank (https://www.ncbi.nlm.nih.gov/genbank/; Benson *et al.*, 2017) and BOLD (www.boldsystems.org; Ratnasingham and Hebert, 2007) repositories. When such sequences were identified from the databases, we recorded the distribution information registered with the samples to further inform the distribution map of the two species (Figure 1). The list of all specimens used for the present work, together with sampling details and GenBank and BOLD accession numbers are provided in Table 1.

Measurements

The methods of measuring and counting and the terminology followed Carpenter and Allen (1989). Standard length (SL), largest body depth (BD), body depth at origin of first dorsal fin (BDd), body depth at origin of first anal fin (BDa), and pre-dorsal (PD), pre-pelvic (PP), and pre-anal (PA) lengths were measured to the nearest millimetre. Head length (HL), snout length [SN; measured without lips as in Carpenter and Allen (1989)], eye diameter (ED), inter-orbital width (IOW), and median ray of caudal fin length (MRC) were measured to the nearest half-millimetre using a vernier caliper. Box-plot distributions were calculated under R v. 4.2.2 (R Core Team, 2020). Colour patterns were recorded from the photographs of two live and 12 freshly caught specimens.

Data analysis

Nucleotide sequences were aligned manually with Se–Al v. 2.0 (Rambaut, 1996). The software PAUP* (Swofford, 2002) was used to compute *p*-distance, and to visualize the diagnostic characters at the *COI* gene and *EGR2B* gene loci within and between *Gymnocranius indicus* sp. nov. and *G. superciliosus*. We chose the uncorrected *p*-distance metric over other nucleotide distances because of its universality, its smaller variance, and its adequacy when nucleotide divergence is less than 10% (Kumar *et al.*, 1993).

Principal component analysis (PCA; Pearson, 1901) was run on a matrix of 29 *Gymnocranius* sp. H / *G. superciliosus* individuals (15 from the Indian Ocean, 14 from the Pacific Ocean), defined by seven morphological variables (BDd, ED, HL, PA, PD, SN, and depth of caudal peduncle) using FactoMineR v. 2.7 (Lê *et al.*, 2008) under R v. 4.2.2 (R Core Team, 2020). All measurements to be included in the PCA dataset were made on photographs (Borsa *et al.*, 2013; Miki *et al.*, 2014; Figure 2; Supplementary Plates S2–S4) so as to have all specimens measured in a standardized way, to enable meaningful comparisons. Morphological variables were expressed as percentages of standard length and these ratios were subjected to arcsine-square root transformation (Sokal and Rohlf, 1995). Clusters of individuals were defined by the agglomerative hierarchical clustering (Sneath and Sokal, 1973) algorithm implemented in FactoMineR (Husson *et al.*, 2010).

Results

Morphological measurements and meristic counts on vouchered *Gymnocranius* sp. H specimens are provided in Table 2, together with homologous data for the type material of *G. superciliosus*. *Gymnocranius* sp. H essentially differed from *G. superciliosus* by its larger eye. Eye diameter (ED) was about equal to the IOW (ratio of ED to IOW = 0.97–1.21) and always larger than MRC, with ratio of ED to MRC = 1.09–1.29, while eye diameter of *G. superciliosus* was smaller than both IOW and MRC. Other body proportions did not clearly differ between *Gymnocranius* sp. H (Table 2) and *G. superciliosus*: the ratio of SL to BD was 2.61–

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Table 1. List of specimens and sequences of *G. indicus* sp. nov. and *G. superciliosus* examined for the present work, with sampling location, sampling date when available (*NA* not acknowledged), and GenBank or BOLD accession nos. for *COI* gene sequences, and GenBank accession nos. for *EGR2B* gene sequences

Species, Individual no.		Field no./other no.	Voucher no.	Sampling location	Collection date	GenBank/BOLD no. (*COI*)	GenBank no. (*EGR2B*)	Morphology
G. indicus sp. nov.								
1.	FSHMU407-14	F013-1	–	Baie du Cap, Mauritius	25 February 2010	MT888958	–	–
2.	BW-A10367	IN02295-PB324	CSIRO H 7306-13[a]	Pelabuhan Ratu, West Java	28 October 2010	FOAM404-10	–	Examined
3.	FSHMU330-12	F013-3	–	Flic en Flac, Mauritius	13 June 2012	MT888959	–	–
4.	LET1402	–	NTUM 12894	Victoria, Seychelles	16 April 2016	MT607095	MT607230	Examined
5.	LET1415	–	–	Victoria, Seychelles	20 April 2016	–	MT607231	Examined
6.	LET1416	–	–	Victoria, Seychelles	20 April 2016	–	–	Examined
7.	JN-1	1_01_Feb_17	–	Victoria, Seychelles	01 February 2017	–	–	Examined
8.	JN-7	7_10_Mar_17	–	Victoria, Seychelles	10 March 2017	–	–	Examined
9.	JN-8	8_10_Mar_17	–	Victoria, Seychelles	10 March 2017	–	–	Examined
10.	JN-10	10_24_Jun_17	–	Victoria, Seychelles	24 June 2017	–	–	Examined
11.	JN-25	25_20_Apr_18	–	Victoria, Seychelles	20 April 2018	–	–	Examined
12.	JN-26	26_11_May_18	–	Victoria, Seychelles	11 May 2018	–	–	Examined
13.	JN-30	30_05_Oct_18	–	Victoria, Seychelles	05 October 2018	–	–	Examined
14.	LET1546	–	NTUM 16756*	Le Port, Reunion Island	03 April 2019	OQ517983	–	Examined
15.	LET1612	PB-20190620-6	–	Peunayong, Aceh	20 June 2019	OQ517984	OR785721	Examined
16.	–	–	NTM S.10771-004[b]	Tanah Bala, West Sumatra	NA	–	–	Examined
G. cf. *superciliosus*								
17.[c]	LET1613	PB-20190622-1	MZB.26789	Lampulo, Aceh	22 June 2019	OQ517985	OR785722	Examined
G. superciliosus								
18.	–	–	MNHN ICOS-00715	New Caledonia	24 August 2002	–	–	Examined
19.	LET20	PB-z246	MNHN 2009–0010*	New Caledonia	21 January 2005	MT607085	MT607210	Examined
20.	LET21	PB-z269	MNHN 2009–0011	New Caledonia	02 March 2005	MT607086	MT607211	Examined
21.	LET23	PB-20080607 C	MNHN 2009–0012	New Caledonia	07 June 2008	–	MT607213	Examined
22.	LET54	PB- 20080919	MNHN 2009–0013	Viti Levu, Fiji	19 September 2008	–	MT607214	Examined
23.	LET971	PB-20101201	–	Boulouparis, New Caledonia	01 December 2010	MT607088	MT607220	–
24.	LET772	–	NTUM 10729	Marshall Islands	2012	MT607087	MT607218	Examined
25.	–	–	MUFS 42021	Tomariiyumachi, Okinawa	01 December 2012	–	–	Examined
26.	–	–	MUFS 42785	Tomariiyumachi, Okinawa	27 December 2012	–	–	Examined
27.	–	–	MUFS 42771	Tomariiyumachi, Okinawa	31 December 2012	–	–	Examined

(*Continued*)

Table 1. (*Continued.*)

Species, Individual no.	Field no./other no.	Voucher no.	Sampling location	Collection date	GenBank/BOLD no. (*COI*)	GenBank no. (*EGR2B*)	Morphology
28.	–	MUFS 42776	Tomariiyumachi, Okinawa	07 February 2013	–	–	Examined
29.	–	MUFS 42777	Tomariiyumachi, Okinawa	07 February 2013	–	–	Examined
30.	–	MUFS 43073	Yonashiro, Okinawa	13 April 2013	–	–	Examined
31.	–	MUFS 43076	Yonashiro, Okinawa	13 April 2013	–	–	Examined
32.	–	USNM 443295	South China Sea off Luzon	14 July 2016	–	–	Examined

Asterisk indicates holotype. *CSIRO* Australian National Fish Collection, Hobart; *MNHN*, Muséum national d'histoire naturelle, Paris; *MUFS*, University of Miyazaki, Fisheries Science, Japan; *MZB* Museum Zoologicum Bogoriense, Cibinong; *NTM* Museum and Art Gallery of the Northern Territory, Darwin; *NTUM*, National Taiwan University Museums, Taipei; *USNM* National Museum of Natural History, Washington DC.
[a]Same specimen as the one represented as '*Gymnocranius microdon*' in O'Neall *et al.* (2023) (J.J. Pogonoski, pers. comm.).
[b]Same specimen as the one represented as '*Gymnocranius* sp.' in Gloerfelt-Tarp and Kailola (2022) (B.C. Russell, pers. comm.).
[c]Individual morphologically identified as *G. superciliosus* but carrying *G. indicus* sp. nov. mitochondria and *EGR2B* alleles.

2.69 in *Gymnocranius* sp. H, *vs* 2.51–2.75 in *G. superciliosus*; the ratio of SL to HL was 2.79–3.10 in *Gymnocranius* sp. H, *vs* 3.02–3.40 in *G. superciliosus*. Also, the profile of the head in front of the eye was generally more prominent and the slope of the snout, steeper in *Gymnocranius* sp. H (Figure 2) than in *G. superciliosus*. No blue ornamentation on the snout and cheeks was visible in the *Gymnocranius* sp. H material examined (Figure 2; supplementary Plates S2, S3).

Two disjunct clusters of individuals were observed with PCA, and confirmed by hierarchical clustering (Figure 3). Principal component 1 represented over 45% of the total variance. One cluster included 12 of the 13 individuals sampled from the Indian Ocean; the other cluster consisted of all 14 individuals sampled from the tropical western Pacific, including the type material of *G. superciliosus*. The exception was individual MZB.26789 from Aceh, which clustered with *G. superciliosus* (thus morphologically identified as this species according to PCA) while possessing *Gymnocranius* sp. H mitochondria (Table 3) and nuclear *EGR2B* alleles (Table 4). Comparisons based on the arcsine-square root transformed foregoing measurements in *Gymnocranius* sp. H ($N = 12$) and *G. superciliosus* ($N = 15$) are presented as box-plot pairs in supplementary Plate S1. Among the most influential variables in the PCA was the arcsine-square root transformed ratio of ED to standard length, which was highly significantly larger in *Gymnocranius* sp. H than in *G. superciliosus* (supplementary Plate S1), confirming the quasi-diagnosticity of eye diameter to distinguish the two species. Other highly discriminant variables were the arcsine-square root transformed ratios of HL, PA, PD, and SN to standard length (Figure 3; supplementary Plate S1). Multivariate morphological analysis thus formally confirmed the morphological distinctness of the two species.

Genetic comparison at intra- and inter-specific levels of *Gymnocranius* sp. H and *G. superciliosus* was made at the *COI* and *EGR2B* loci (Tables 3 & 4). *Gymnocranius* sp. H was differentiated from its sibling *G. superciliosus* by 3.6–4.6% (mean = 3.9%) and 0.67–0.74% (mean = 0.67%) nucleotide sequence divergence at the *COI* and *EGR2B* loci, respectively. Genetic diversity at the *COI* locus appeared to be slightly higher within *G. superciliosus* (mean pairwise *p*-distance = 0.003) than in *Gymnocranius* sp. H (mean pairwise *p*-distance = 0.001; Table 3). Nucleotide sequences at locus *COI* nos. MT888958 and MT888959 in GenBank and FOAM404-10 in BOLD, all three labelled *G. microdon*, were characteristic of *Gymnocranius* sp. H.

Discussion

Morphological characters that might be useful for distinguishing species in other families of ray-finned fishes are remarkably uniform in *Gymnnocranius* spp. (Carpenter and Allen, 1989). As a matter of fact, the diagnosis of most species in the genus *Gymnocranius* involves body proportions, body and fin colours, and caudal fin shape (Sato, 1986; Carpenter and Allen, 1989; Chen *et al.*, 2017). Carpenter and Allen (1989) emphasized the importance of colour patterns as diagnostic characters for identification of species in Monotaxinae.

In a phylogenetic analysis based on four gene markers, we have previously referred to the new species described here as *Gymnocranius* sp. H, the Indian-Ocean sibling of *G. superciliosus* from the tropical western Pacific (Chen and Borsa, 2020). *Gymnocranius* sp. H fell under *G. superciliosus* according to the identification key of Chen *et al.* (2017: their table 3), except the blue dots on the cheek which were apparently absent. *Gymnocranius* sp. H has remained largely overlooked in the ichthyological literature. There is no mention of any *Gymnocranius* that match this species by external morphology and colour

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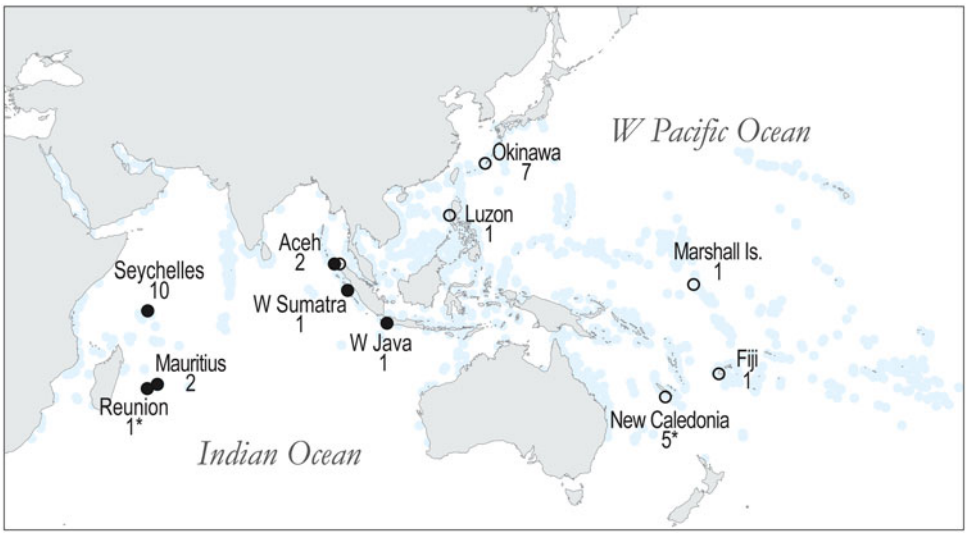

Figure 1. Map of the Indo-West Pacific showing the occurrence points of the material examined for the present study including material reported previously (Borsa *et al*., 2013; Miki *et al*., 2014; Chen and Borsa, 2020), including: *Gymnocranius indicus* sp. nov. (solid circles) and *G. superciliosus* (open circles). Asterisks (*) indicate type localities; numbers indicate sample sizes per locality; light-blue spots represent coral reefs. See Table 1 for additional details.

patterns in fish guides from the Western Indian Ocean or from the East Indian Ocean (Smith and Smith, 1963; Kyushin, 1977; Randall, 1992, 1995; Allen and Erdmann, 2012). An exception we found is the recently updated edition of Gloerfelt-Tarp and Kailola's compendium of trawled fishes of the northwestern Australia – southern Indonesia region. This guide includes a picture of a 195-mm long individual of this species (labelled '*Gymnocranius* sp.') captured off Tanah Bala Island off West Sumatra (Gloerfelt-Tarp and Kailola, 2022). A photograph of this species was published (as '*G. griseus*') in the IFREMer online identification sheets of marine species (Evano, 2016). Another photograph was published (as '*G. microdon*') in the fishIDER identification sheets for the commercial fishes of Indonesia (Proctor *et al*., 2018; O'Neill *et al*., 2023). This species was again reported (as *G.* cf. *superciliosus*) in the 'Sous les mers' online identification sheets for scuba divers at Reunion Island (Schilling, 2018). Another underwater picture of an individual of this species, erroneously labelled '*Gymnocranius microdon*', from off Utende, Tanzania in July 2021 has recently been posted in the iNaturalist community forum (https://forum.inaturalist.org/; page consulted 15 October 2023).

That an Andaman-Sea *G. superciliosus* individual (as identified by morphometrics) possesses *Gymnocranius* sp. H mitochondria and alleles at the nuclear marker scored in the present study suggests introgression of the genome of one of the two species by genetic material of the other species in this region of the Indo-West Pacific. Further investigation using a larger sample size of individuals and genome-wide locus sampling is warranted, as it will help address the phylogeographic structure and history of the two species in the Andaman Sea and adjacent regions.

Large-eye sea breams of the genus *Gymnocranius* are fishes of high commercial interest throughout the tropical Indo-West Pacific (Coleman, 1981; Carpenter and Allen, 1989). The discovery of a new *Gymnocranius* species is therefore significant. *Gymnocranius* sp. H was just one of four potentially undescribed *Gymnocranius* species included in Chen and Borsa's (2020) phylogeny of the Monotaxinae. The three other species have been provisionally referred to as *Gymnocranius* sp. D, *Gymnocranius* sp. F and *Gymnocranius* sp. G. The description of the Indo-West Pacific distributed *Gymnocranius* sp. D is currently in preparation. The two other species, both possibly endemic to the Western Indian Ocean, remain to be investigated in more depth.

Taxonomy

Gymnocranius indicus *sp. nov*

ZooBank no. urn:lsid:zoobank.org:act:3CD85B8F-19F8-4EBA-B8DE-CB4AE4C818FC. Proposed vernacular names: Indian-Ocean eyebrowed large-eye seabream (English); empereur à sourcils de l'océan Indien (French); ikan kakap putih alis Samudera Hindia (Indonesian); capitaine sourcil (Mascarene Islands); kapten blan grolizye (Seychelles). See Tables 2–4; Figures 2 & 3; supplementary Plates S2, S3. Previously reported as *Gymnocranius* sp. (Gloerfelt-Tarp and Kailola, 2022), *Gymnocranius* sp. H (Chen and Borsa, 2020) and *Gymnocranius* cf. *superciliosus* (Schilling, 2018). Misidentifications: *Gymnocranius microdon* (non Bleeker, 1851) (O'Neill *et al*., 2023); *Gymnocranius griseus* (non Temminck and Schlegel, 1843) (Evano, 2016; upper photograph).

Type material

Holotype: NTUM 16756 (Table 2; Figure 2A), 281 mm SL, Reunion Island, Western Indian Ocean, 3 April 2019. The specimen was captured using baited bottom handline by ca. 20 m depth on Reunion Island's western shore. Paratypes: NTUM 12894 (Table 2; Figure 2B), 291 mm SL, Victoria, Seychelles, 16 April 2016; NTM S.10771-004 (Gloerfelt-Tarp and Kailola, 2022: 210; Table 2), off West Sumatra, Eastern Indian Ocean; CSIRO H7306-13 (Table 2), Pelabuhan Ratu, West Java, Eastern Indian Ocean.

Nucleotide sequences of the type material of *Gymnocranius indicus* sp. nov. deposited in GenBank have the following registration numbers. Holotype: OQ517983 (*COI* gene); paratype from Seychelles: MT607095 (*COI* gene), MT606910 (*cytochrome b* gene), MT607230 (*early growth response protein 2B* gene), and MT607051 (*rhodopsin* gene). The partial nucleotide sequence of the *COI* gene of the paratype from West Java has been deposited in BOLD (as '*G. microdon*') under accession no. FOAM404-10.

Other specimens examined

Gymnocranius indicus sp. nov.: specimen nos. 1–3, 5–13, 15 and 16 listed in Table 1. *Gymnocranius superciliosus*: specimen nos. 17–32 listed in Table 1, including type material of this species.

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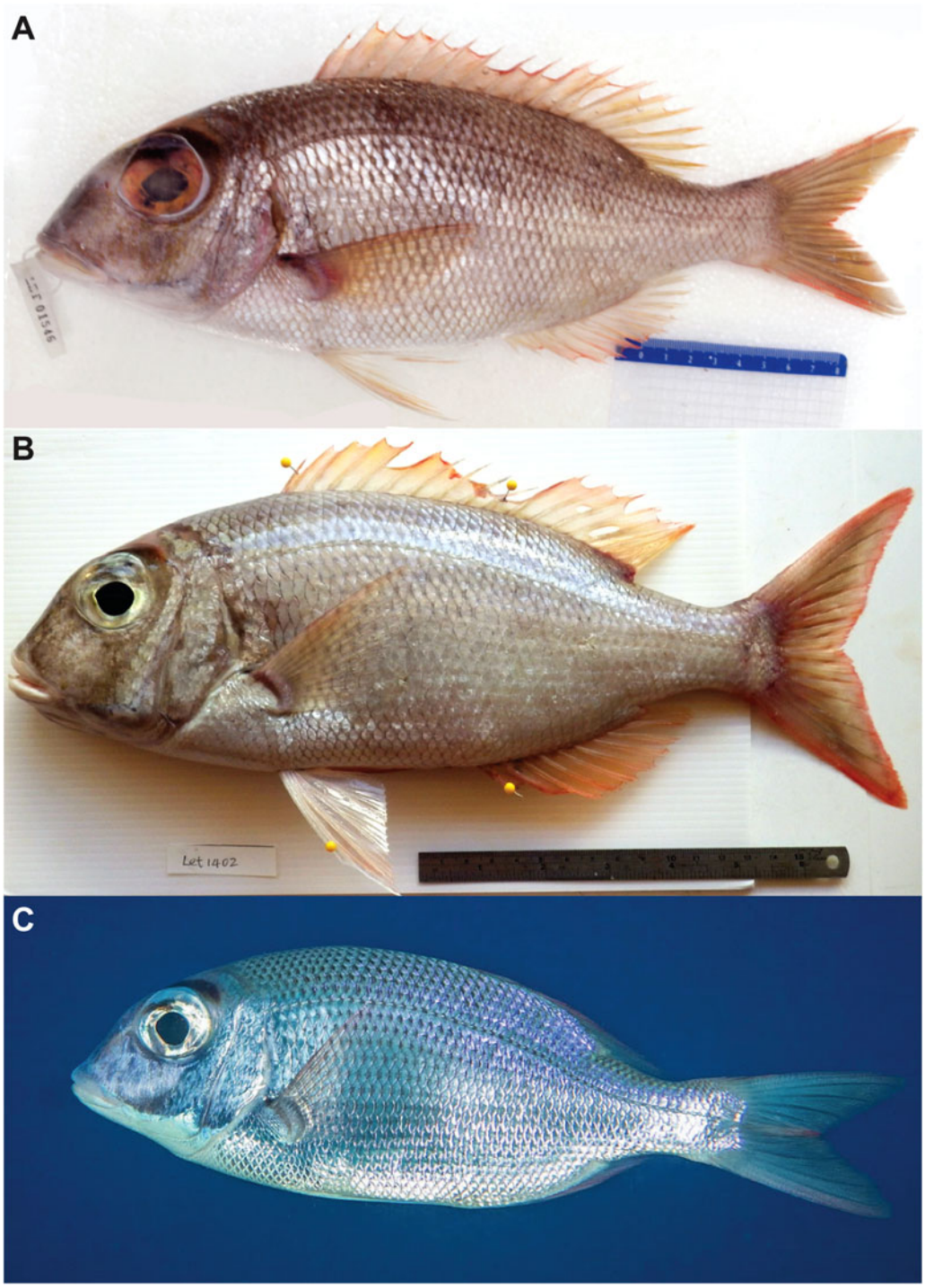

Figure 2. *Gymnocranius indicus* sp. nov. (A) Photograph of holotype, no. NTUM 16756 from Reunion Island (NTUM /W.-J. Chen). (B) Photograph of paratype, no. NTUM 12894 from Victoria, Seychelles (NTUM /W.-J. Chen). (C) Photograph of individual sighted underwater at ca. 18 m depth at Pierre-du-Préfet off Saint-Gilles, Reunion Island (C. Schilling, 31 March 2022).

Description

The description of the new species is based on 16 specimens, using discriminant morphometric and genetic approaches (Tables 2–4; Figure 3). *Gymnocranius indicus* sp. nov., as all species in the genus *Gymnocranius*, is characterized by a continuous dorsal fin with ten spines and ten to 11 soft rays (ten spines and ten soft rays in *Gymnocranius indicus* sp. nov.); anal fin with three spines and nine to ten soft rays (three spines and ten soft rays in *Gymnocranius indicus* sp. nov.); pectoral fin rays 14; rear part of cheek with three to five transverse scale rows (four in *Gymnocranius indicus* sp. nov.); remainder of cheek, preorbital, snout, and interorbital region scaleless; inner surface of pectoral fin base scaleless; body laterally compressed and ovate; profile of the head in front of the eye convex, slope of the snout relatively steep; adult specimens often develop a bony ridge on the nape and a bony shelf above the anterior part of the eye; mouth small, posterior part of the jaw usually anterior to the level of the anterior edge of the eye; each jaw with two or three slender canines at the front, conical teeth on the sides, and a range of numerous villiform teeth behind the front teeth; eye relatively large, a pair of close-set, round nasal openings on each side of the snout in front of the eyes, usually a thin flap of skin on the rear edge of the anterior opening.

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Table 2. Measurements on the type material of *Gymnocranius indicus* sp. nov. and comparison with type material of *G. superciliosus*

	G. indicus sp. nov.				*G. superciliosus*	
	NTUM16756	CSIRO H 7306-13	NTM S.10771-004	NTUM12894	MHNH 2009-0010	MHNH 2009-0011 to −0013
Measurement	Holotype	Paratype	Paratype	Paratype	Holotype[a]	Paratypes[a]
Standard length (SL) (mm)	281	225	186	291	323	220–311
Body depth (BD) (mm)[b]	105	85.6	71.2	108	124	80–118
BD at dorsal-fin origin (BDd) (mm)	104	84.3	69.8	107	118	77–106
BD at anal-fin origin (mm)	92	77.3	63.4	97	110	77–99
Head length (HL) (mm)	92	80.8	66.6	94	105	70–96
Snout length without lip (mm)[b]	27.5	29.1	26.5	29	30.5	18.5–29
Eye diameter (ED) (mm)	36	27.8	26.4	35	29	22–27
Inter-orbital width (IOW) (mm)	35	26.1	21.8	36	36	25–36
Predorsal length (mm)	103	99.9	81.4	104	118	79–113
Prepelvic length (mm)	103	91.6	78.6	106	114	76–107
Preanal length (mm)	175	147.5	122.3	176	202	137–196
Median caudal ray (MRC) (mm)	28	21.0	20.6	32	37.5	27.4–35.0
Dorsal fin spines, rays (count)	X, 10	X, 10	X, 10	X, 10	X, 10	X, 10
Anal fin spines, rays (count)	III, 10	III, 10	III, 10	III, 10	III, 10	III, 10
Pored scales on lateral line (count)	49	48	49	48	48	48–49
SL/BD	2.68	2.69	2.61	2.69	2.60	2.51–2.75
SL/BDd	2.70	2.72	2.66	2.72	2.74	2.65–2.86
SL/HL	3.05	3.10	2.79	3.10	3.08	3.02–3.24
ED/SL	0.13	0.12	0.14	0.12	0.09	0.09–0.10
ED/HL	0.39	0.37	0.40	0.37	0.28	0.28–0.31
ED/IOW	1.03	0.98	1.21	0.97	0.81	0.75–0.90
ED/MRC	1.29	1.09	1.28	1.09	0.77	0.77–0.98

CSIRO Australian National Fish Collection, Hobart; *MNHN*, Muséum national d'histoire naturelle, Paris; *NTM* Museum and Art Gallery of the Northern Territory, Darwin; *NTUM*, National Taiwan University Museums, Taipei.
[a]From Borsa *et al.* (2013), except BD and SL.
[b]Measured as in Carpenter and Allen (1989).

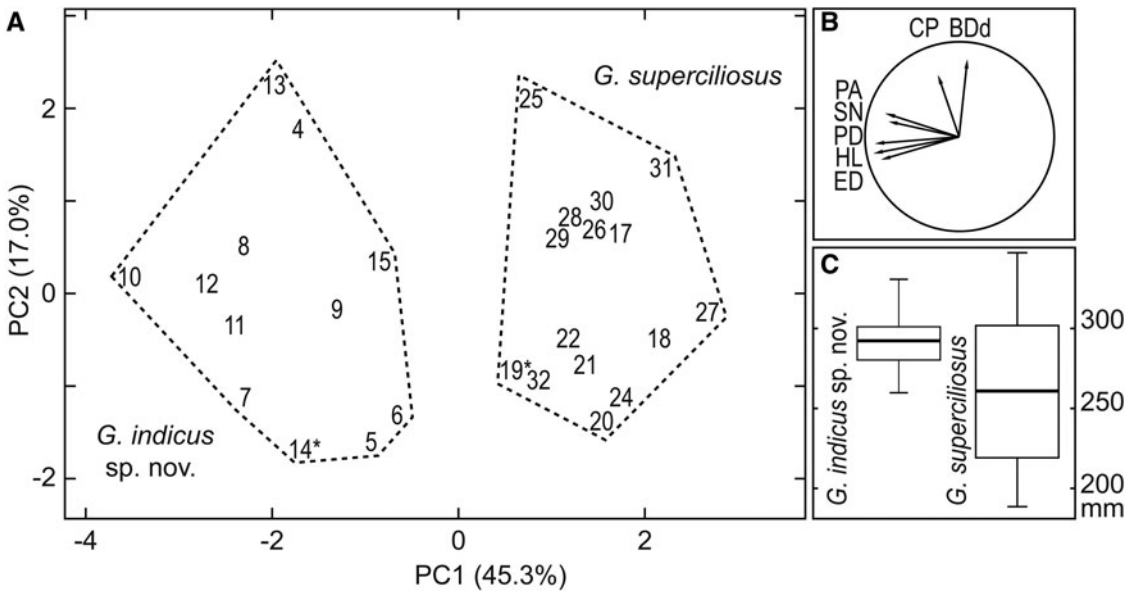

Figure 3. Principal component analysis (PCA) based on seven morphological measurements as defined in text. (A) Principal plane of PCA; envelopes delimit the two main clusters identified by hierarchical clustering; specimen numbers as in Table 1, first column. Asterisks designate holotypes. (B) Correlation circle; *BDd* body depth at origin of dorsal fin; *CP* depth of caudal peduncle; *ED*, eye diameter; *HL*, head length; *PA*, pre-anal length; *PD*, pre-dorsal length; *SN*, snout length. (C) Boxplots representing the distribution of standard length in each cluster.

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Table 3. Matrix of pairwise genetic distances (*p*-distance) at the *COI* locus, deduced from the nucleotide sequences sampled in 11 individuals morphologically identified as *Gymnocranius indicus* sp. nov. (*GspH*) or *G. superciliosus* (*Gsup*)

Individual					Individual no.										
No.	ID	GenBank/BOLD	Species	Locality	1.	2.	3.	4.	14.	15.	17.[a]	19.	20.	23.	24.
1.	F013 1	MT888958	GspH	Mauritius	–										
2.	BW-A10367	FOAM404_10	GspH	W Java	0.000	–									
3.	F013 3	MT888959	GspH	Mauritius	0.005	0.005	–								
4.	Let1402	MT607095	GspH	Seychelles	0.000	0.000	0.005	–							
14.	LET1546	OQ517983	GspH	Reunion	0.000	0.000	0.005	0.000	–						
15.	LET1612	OQ517984	GspH	Aceh	0.000	0.000	0.005	0.000	0.000	–					
17.[a]	LET1613	OQ517985	Gsup	Aceh	0.000	0.000	0.005	0.000	0.000	0.000	–				
19.	LET20	MT607085	Gsup	New Caledonia	0.036	0.036	0.040	0.036	0.036	0.037	0.037	–			
20.	LET21	MT607086	Gsup	New Caledonia	0.036	0.037	0.041	0.037	0.037	0.036	0.036	0.000	–		
23.	LET971	MT607088	Gsup	New Caledonia	0.038	0.038	0.043	0.038	0.038	0.038	0.038	0.002	0.002	–	
24.	LET772	MT607087	Gsup	Marshall Is.	0.041	0.041	0.046	0.041	0.041	0.041	0.041	0.005	0.005	0.006	–

Sample numbers as in Table 1, first column.
[a]Individual morphologically identified as *G. superciliosus* but carrying *G. indicus*-like mitochondria.

Table 4. Matrix of pairwise genetic distances (*p*-distance) at the *EGR2B* locus, deduced from exon 1 to intron region nucleotide sequences (450 bp) sampled in ten individuals morphologically identified as *Gymnocranius indicus* sp. nov. (*GspH*) or *G. superciliosus* (*Gsup*)

Individual					Individual no.									
no.	ID	GenBank/BOLD	Species	Locality	4.	5.	15.	17.[a]	19.	20.	21.	22.	23.	24.
4.	Let1402	MT607230	GspH	Seychelles	–									
5.	LET1415	MT607231	GspH	Seychelles	0.000	–								
15.	LET1612	XX000000	GspH	Aceh	0.000	0.000	–							
17.[a]	LET1613	XX000000	Gsup	Aceh	0.000	0.000	0.000	–						
19.	LET20	MT607210	Gsup	New Caledonia	0.007	0.007	0.007	0.007	–					
20.	LET21	MT607211	Gsup	New Caledonia	0.007	0.007	0.007	0.007	0.000	–				
21.	LET23	MT607213	Gsup	New Caledonia	0.007	0.007	0.007	0.007	0.000	0.000	–			
22.	LET54	MT607214	Gsup	Fiji	0.007	0.007	0.004	0.007	0.000	0.000	0.000	–		
23.	LET971	MT607220	Gsup	New Caledonia	0.007	0.007	0.007	0.007	0.000	0.000	0.000	0.000	–	
24.	LET772	MT607218	Gsup	Marshall Is.	0.007	0.007	0.007	0.007	0.000	0.000	0.000	0.000	0.000	–

Sample numbers as in Table 1, first column.
[a]Individual morphologically identified as *G. superciliosus* but genetically characterized as *G. indicus* sp. nov.

The specimens of the new species possess the following combination of characters: body elongated, 2.7–2.9 times in standard length (2.7 in holotype); pored scales on lateral line 47–49; forehead prominent; lower edge of eye slightly above a line from tip of snout to middle of caudal fin; presence of distinctive and conspicuous dark patch above eye; eyes protruding and large, the eye diameter (ED) reaching 37–40% of head length (39% in holotype), usually close to or slightly smaller than inter-orbital width (IOW) with an ED/IOW ratio of 0.91–1.21 (1.03 in holotype); caudal fin moderately forked, its lobes slightly convex inside, the median rays nearly shorter than ED with an ED/MRC ratio of 1.09–1.38 (1.29 in holotype); body colour silvery, sides without visible transversal dark bars in adults, blackish spot at basis of scales forming longitudinal rows on back; pectoral, dorsal, and caudal fins reddish to red; front row of six pre-dorsal scales, arranged in a 'V' pointed backwards (Figure 2; supplementary Plates S2, S3).

Nucleotide sequences at the *COI* locus that can be used as DNA barcodes to identify *Gymnocranius indicus* sp. nov. are available from the GenBank sequence repository under accession nos. MT607095, MT888958, MT888959, OQ517983, and OQ517984; and from the BOLD repository under record no. FOAM404-10. Similarly, nucleotide sequences at the *EGR2B* locus are available from GenBank under accession nos. MT607230, MT607231, OR785721, and OR785722.

Diagnosis

The specimens of *Gymnocranius indicus* sp. nov. possess the same combination of morphological traits that distinguishes *G. superciliosus* from all other known *Gymnocranius* spp. in Chen *et al.*'s (2017) key to species of this genus: general body shape oblong to elongate, SL/BDd ratio 2.7–3.1, forehead prominent; caudal fin large, moderately forked with a subtle middle notch, its lobes slightly convex inside; flanks silvery; anal fin, caudal fin, dorsal fin, and pectoral fin reddish to red; distinctive dark patch above eye. Protruding, large eyes (eye diameter reaching 37–40% of head length) is the main distinctive trait to diagnose *Gymnocranius indicus* sp. nov. from *G. superciliosus*. The PCA graph (Figure 3) demonstrated complete separation of two clusters along PC1, one including the type material of *G. superciliosus*, the other one including type material of the new species. The size of the specimens examined in this analysis ranged from 189 to 341 mm. Therefore, the combination of quasi-diagnostic characters ED, HL, PA, PD, and SN measured in the present study was diagnostic all over this range of size.

Along the *COI* gene, the following apomorphic sites have unique nucleotides shared by all seven *Gymnocranius indicus* sp. nov. sequences examined so far, that distinguish it from all other species in the genus *Gymnocranius*: nos. 360 (T *vs* C), 405 (T *vs* C), 453 (T *vs* C) and 477 (C *vs* A or G), where the numbering of nucleotide sites starts from the first nucleotide of the gene. These genetic characters remain diagnostic for individuals of any size, from egg to adult, except for possible hybrids or introgressed individuals which would, for example, possess the mitochondrial type of the female ancestor. They are also diagnostic for body parts, including fillets, offal, scales, blood, mucus, etc. DNA sequences are indeed powerful characters for identifying individuals to species, valid for any age and a wide array of preservation conditions, potentially including stuffed and alcohol-preserved specimens.

Habitat and distribution

The type locality is Reunion Island in the Western Indian Ocean. *Gymnocranius indicus* sp. nov. was recorded (as either '*G. superciliosus*' or '*Gymnocranius* sp. H') from Reunion Island and the Seychelles in the western Indian Ocean (Schilling, 2018; Chen and Borsa, 2020). Based on these and additional records from the present study, its distribution range extends from the western Indian Ocean (Tanzania, Seychelles, Reunion, and Mauritius) to the Andaman Sea (Aceh) and to the eastern Indian Ocean off West Sumatra and West Java (Figure 1; Table 1). Underwater sightings of solitary individuals have been made by C. Schilling at ca. 18 m to ca. 25 m depth on the outer slope of the reef off Saint-Gilles on the western coast of Reunion Island, above a bottom constituted by sand, lava boulders, and sparse coral colonies (supplementary Plate S3A). An additional underwater sighting has been reported from off Tanzania.

Etymology

Epithet *indicus* is the latin translation of 'Indian', a reference to the geographic distribution of this species, as inferred from the available records.

Remarks

As reported above, *Gymnocranius indicus* sp. nov. has previously been confused with *G. microdon* and *G. griseus*. The inferred multigene phylogeny revealed that *Gymnocranius indicus* sp. nov. is closely related to neither *G. microdon* or *G. griseus* (Chen and Borsa, 2020). Morphologically, *Gymnocranius indicus* sp. nov. differs from *G. microdon* in general body shape (oblong in *Gymnocranius indicus* sp. nov. *vs* oblong to elongate in *G. microdon*), in snout shape (more protruding and steeper in *G. microdon* than in *Gymnocranius indicus* sp. nov.) and in the shape of caudal fin (moderately forked with parenthesis-shaped edge in *Gymnocranius indicus* sp. nov. *vs* forked and concave in *G. microdon*). *Gymnocranius indicus* sp. nov. differs from *G. griseus* by the following suite of characters: (i) body shape oblong to elongate (high-bodied to oblong in *G. griseus*; Chen *et al.*, 2017); (ii) silvery, mostly immaculate flanks (*vs* several transversal dark bars *in G. griseus*; Chen *et al.*, 2017); (iii) number of pre-dorsal scales in front row (six in *Gymnocranius indicus* sp. nov. *vs* nine to 11 in *G. griseus*; Chen *et al.*, 2017). Moreover, based on the genetically validated records available, the geographic distributions of *Gymnocranius indicus* sp. nov. and *G. griseus* are disjunct, as *G. griseus* is confined to the southern Japanese archipelago and Taiwan, where *G. indicus* sp. nov. is absent (Chen *et al.*, 2017; Chen and Borsa, 2020).

Notice

The present article in portable document (.pdf) format is a published work in the sense of the International Code of Zoological Nomenclature [International Commission on Zoological Nomenclature (ICZN), 2012] or ICZN Code. Hence, the new name contained in the present article is effectively published under the ICZN Code. The present article and the new nomenclatural act it contains have been registered in the online registration system for the ICZN, ZooBank (http://zoobank.org/). The online version of this article is available from the *JMBA* journal website (https://www.cambridge.org/core/journals/journal-of-the-marine-biological-association-of-the-united-kingdom/), and from the HAL (https://cnrs.hal.science/; Daphy and Ha–Duong, 2010) repository.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315424000274.

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Data availability. All nucleotide sequences were deposited in the GenBank-Nucleotide open-access repository (https://www.ncbi.nlm.nih.gov/nucleotide/). Pictures of all specimens examined are provided in this article or in its supplementary material. Other data not included in this article, or in its supplementary material, or in open-access repositories will be made available upon reasonable request.

Author contributions. Designed the study: PB, WJC; contributed reagents or materials or analysis tools: PB, WJC, RM, JN; analysed and interpreted the data: PB, WJC; wrote the paper: PB, WJC; read, edited, and approved the final draft: PB, WJC, RM, JN.

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Ethical standards. All specimens examined were obtained from fish markets. No live specimen was manipulated.

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