

## Redescriptions of *Ilisha melastoma* (Bloch & Schneider, 1801) and *Ilisha brachysoma* (Bleeker, 1852), two valid species of ilishas (Clupeiformes: Pristigasteridae)

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**Abstract.** *Ilisha brachysoma* (Bleeker, 1852), previously regarded as a junior synonym of *Ilisha melastoma* (Bloch & Schneider, 1801), is shown to be a valid species and is redescribed on the basis of seven specimens from Indonesian waters from Sumatra to Bali, including the previously designated holotype. Although *I. brachysoma* and *I. melastoma* share multiple morphological traits, including a deep body, the form of the swim bladder, the shape of the body scales and caudal fin, and almost same numbers of gill rakers and ventral scutes, *I. brachysoma* can be distinguished from *I. melastoma* by several features, including having a higher anal-fin ray count (total anal-fin rays 46 or 47 vs. 36–43 in *I. melastoma*) and a longer anal-fin base (40.1–43.4% of SL vs. 32.2–37.9%). In addition, both species differ from each other by a mean uncorrected mitochondrial COI genetic distance of 10.7%. In this study, we also examine and redescribe *I. melastoma*; we confirm that the species is widely distributed in the Indo-West Pacific from the Persian Gulf to Indonesia and Taiwan, and exhibits very low genetic differentiation throughout its distributional range, further suggesting reproductive separation from *I. brachysoma* despite shared morphology and limited contact between the populations on the northern coast of Indonesia. To stabilize the taxonomic status of nominal species related to *I. melastoma*, the holotype of “*Clupea*” *melastoma* is herein designated as the neotype for *Platygaster verticalis* Swainson, 1838, *Clupea* (*Pristigaster*) *indicus* Swainson, 1839, and *Pellona ditchoa* Valenciennes, 1847, the latter three nominal species becoming junior objective synonyms of *C. melastoma*.

**Key words.** Actinopterygii, *Ilisha striatula*, *Pellona ditchela*, Sunda Islands, taxonomy

### INTRODUCTION

The long-fin sardine genus *Ilisha* Richardson, 1846 (Clupeiformes: Pristigasteridae) is distributed circumglobally and is characterised by having dorsal and pelvic fins, moderately long anal fin with 34 to 53 fin rays, and a hypomaxilla without teeth (Whitehead, 1985; Munroe et al., 1999). The genus was taxonomically reviewed by Whitehead (1985) who recognized 14 valid species. Subsequently, two species, *Ilisha lunula* Kailola, 1986 and *Ilisha compressa* Randall, 1994 were described, bringing the number of valid species of *Ilisha* to 16. Among these fishes, specimens and populations exhibiting deep bodies, swim bladders with a pair of bilateral posterior extensions, body scales with grooves overlapping or meeting at scale-center, lower gill rakers on first gill arch 21–25, and caudal fins without extension, have

been regarded as a single species, *Ilisha melastoma* (Bloch & Schneider, 1801) (Fig. 1). A further five nominal species, *Platygaster verticalis* Swainson, 1838, *Clupea* (*Pristigaster*) *indicus* Swainson, 1839, *Pellona ditchoa* Valenciennes, 1847, *Pellona micropus* Valenciennes, 1847, and *Pellona brachysoma* Bleeker, 1852 have been reassigned as junior synonyms of *I. melastoma* (Whitehead, 1985; Munroe et al., 1999). However, *Ilisha melastoma* has been proposed as an invalid name by several researchers (Whitehead, 1967a, 1969; Kottelat, 2013).

Our re-examination of specimens identified as *I. melastoma*, including an assessment of the taxonomic status of all nominal species treated as synonyms of *I. melastoma* in previous studies, revealed two nominal species to be valid [true *I. melastoma* (Persian Gulf to Taiwan and Indonesia) and *I. brachysoma* (Sumatra to Bali)] and all other nominal taxa to be junior synonyms of *I. melastoma*. Molecular data are also presented for each of the two valid species to complement and reinforce the morphological observations.

### MATERIAL AND METHODS

Counts and measurements follow Hata & Motomura (2019). All measurements were made to the nearest 0.01 mm using digital calipers. “Pelvic scute” refers to a scute associated with the pelvic girdle, and “prepelvic scute” and “postpelvic

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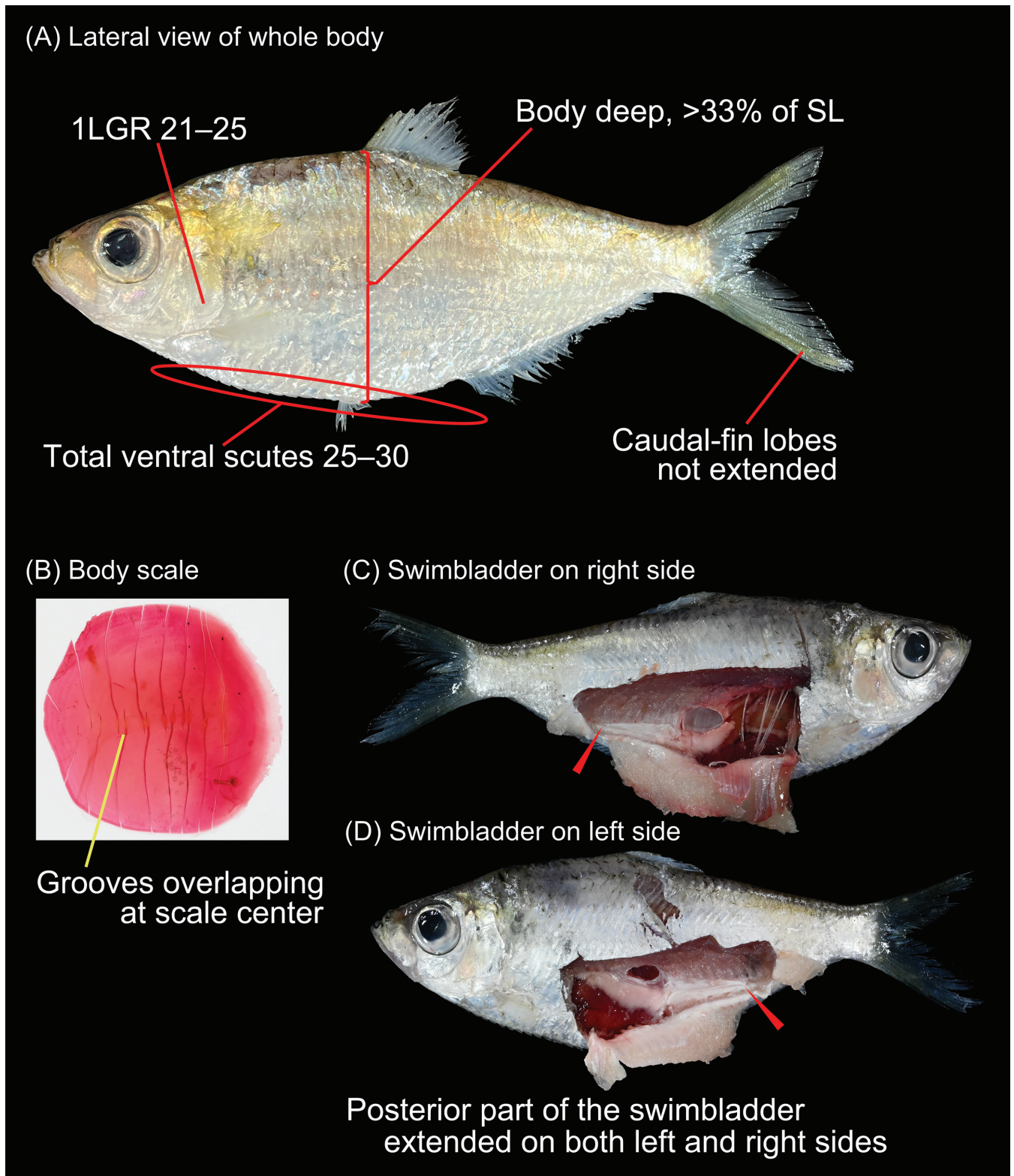


Fig. 1. Diagnostic characters of species previously identified as *Ilisha melastoma* [A, lateral view of whole body, B, scale on right side of body removed from just below dorsal-fin (left-right inverted); C, right side of dissected specimen (red triangle indicates posterior tip of swimbladder); D, left side of dissected specimen (red triangle indicates posterior tip of swim bladder). [A, USMFC (92) 00016, 122.5 mm SL, Penang, Malaysia; B, KAUM-I. 67324, 91.7 mm SL, Ha Long Bay, Vietnam (alizarin stain); C, D, USMFC (92) 00019, 111.7 mm SL, Penang, Malaysia]].

## RESULTS

***Ilisha melastoma* (Bloch & Schneider, 1801)**

(English name: Indian Ilisha)

(Figs. 1–3; Tables 1, 2, 4)

scute” to hard spine-like scutes anterior to the pelvic scute and posterior to the pelvic scute, respectively. Abbreviations are as follows—SL, standard length; UGR, LGR and TGR, upper limb, lower limb and total gill rakers, respectively, with associated numbers indicating the specific gill arch; D–P1, distance from dorsal-fin origin to pectoral-fin insertion; D–P2, distance from dorsal-fin origin to pelvic-fin insertion; D–A, distance between dorsal and anal fin origins; P1–P2, distance between pectoral- and pelvic-fin insertions; P2–A, distance from pelvic-fin insertion to anal-fin origin. Counts and measurements (expressed as percentages of SL) are given in Tables 1 and 2. Osteological characters were observed on soft X-ray photographs. Institutional codes follow Fricke & Eschmeyer (2025). The taxonomic statuses of *Pellona ditchela* Valenciennes, 1847 and *Ilisha striatula* Wongratana, 1983 follow Hata et al. (2025), which classified *P. ditchela* into the genus *Ilisha* and designated *Ilisha ditchela* as the senior synonym of *I. striatula*.

We inferred the genetic differentiation between *I. brachysoma* and *I. melastoma*, and their phylogenetic relationships within the family Pristigasteridae, by using the 651 base pair (bp) “barcode” fragment of the mitochondrial COI gene. The COI gene was newly sequenced for nine specimens of *I. melastoma* (Table 3). The new COI haplotypes were sequenced as described in Hata et al. (2019) using the same PCR and sequencing primers as above. All nine sequences generated in this study are deposited in the GenBank database (accession numbers provided in Table 3).

Mitochondrial COI data from the nine newly-sequenced specimens were combined with a selection of COI data from 34 specimens available in GenBank (Table 3), including four specimens of *Ilisha brachysoma*, 18 specimens of *Ilisha melastoma*, and 12 specimens of six other pristigasterid species. Three specimens of *I. brachysoma* used in the molecular part of this study were morphologically examined. Mitochondrial COI sequences were aligned by eye, with no indels required. Uncorrected pairwise genetic distances between species were calculated with MEGA v.11.0.13 (Tamura et al., 2021).

First, the phylogenetic relationships among Pristigasteridae were inferred by a maximum likelihood (ML) method using the Hasegawa–Kishino–Yano (HKY) model of sequence evolution and the software RAXML-NG (Kozlov et al. 2019) as implemented in the graphical interface raxmlGUI 2.0 (Edler et al., 2021). The phylogenetic matrix contained 16 specimens of eight species of Pristigasteridae and 651 nucleotide positions of the COI fragment. The phylogenetic tree was rooted with a specimen of *Coilia nasus* (family Engraulidae) and the robustness of each relationship determined by 1,000 bootstrap replicates.

The relationships amongst COI haplotypes of four specimens of *I. brachysoma* and 27 specimens of *I. melastoma* were inferred with an unrooted network constructed with the software package PopArt (Leigh & Bryant, 2015), using a median-joining algorithm (Bandelt et al., 1999) and default settings.

- Clupea melastoma* Bloch & Schneider, 1801: 427 (type locality: Coromandel coast, India)
- Platygaster verticalis* Swainson, 1838: 278 [original locality: Vizagapatham (currently Visakhapatnam), Andhra Pradesh, India, based on pl. CXCII (figure of “ditchoe”) of Russell, 1803; type locality: Coromandel, Tamil Nadu, India, based on the neotype, newly designated herein]
- Clupea (Pristigaster) indicus* Swainson, 1839: 294 [original locality: Vizagapatham (currently Visakhapatnam), Andhra Pradesh, India, based on pl. CXCII (figure of “ditchoe”) of Russell, 1803; type locality: Coromandel, Tamil Nadu, India, based on the neotype, newly designated herein]
- Pellona ditchoa* Valenciennes, 1847: 313 [original locality: Vizagapatham (currently Visakhapatnam), Andhra Pradesh, India, based on pl. CXCII (figure of “ditchoe”) of Russell, 1803; type locality: Coromandel, Tamil Nadu, India, based on the neotype, newly designated herein]; Günther, 1868 (in part): 455 (Java, Indonesia).
- Pellona micropus* Valenciennes, 1847 (in part): 320 [original locality: Coromandel coast of India and Bengal; type locality: Coromandel coast, India, based on the lectotype designated by Whitehead, 1967a]
- Pellona indica*: Day, 1876 (in part): 644 (India to Malay Archipelago); Day, 1889: 381 (British India).
- Pellona brachysoma* (not of Bleeker): Weber & de Beaufort, 1913 (in part): 87 (Singapore and British India).
- Ilisha micropus*: Whitehead, 1967a (in part): 115 (lectotype designation; Coromandel coast of India); Whitehead, 1967b: 246, fig. 24 [Singapore; Penang and Tanjong Dawai (currently Tanjung Dawai), Malaysia].
- Ilisha indica*: Fowler, 1941: 652 [Batavia, Java, Indonesia; Calicut (currently Kozhikode) and Bombay (Mumbai), India]; Nair, 1953: 123, fig. 10 (India); Whitehead, 1967b: 248, fig. 26 (Malaysia); Seshagiri Rao, 1972: 881 (Visakhapatnam, Andhra Pradesh, India); Misra, 1976 (in part): 80 (India); Kottelat, 2013 (in part): 49 (Southeast Asia).
- Ilisha melastoma*: Nair, 1953: 124 (India); Whitehead, 1969: 270 (description of holotype: Coromandel coast, India); Whitehead, 1972: 54, fig. 37 (India); Seshagiri Rao, 1973: 738 (Visakhapatnam, Andhra Pradesh, India); Misra, 1976 (in part): 76 (India); Wongratana, 1980 (Thailand); Jayaram, 1981: 46 (India, Sri Lanka, Pakistan, Burma, Malaysia, Thailand, Vietnam, and Hong Kong); Wongratana, 1983: 397 (eastern coast of India to Java Sea and Taiwan); Shen, 1984: 94, unnumbered fig. (southern and southwestern parts of Taiwan); Talwar & Kacker, 1984: 156, text-fig. 58 (Indian coast); ?Gloerfelt-Tarp & Kailola, 1984: 48 (Sumatra to Bali, Indonesia); Whitehead, 1985 (in part): 272, unnumbered fig. [Indian Ocean (Malabar coast to Kolkata); Java Sea (off Java); South China Sea (Singapore and Gulf of Thailand); and East China Sea (north to Taiwan)]; Kailola, 1986: 52 [Bolar, Mangalore (currently Mangaluru), Karnataka, India); Mok, 1993: 125, pl. 24-9 (Taiwan); De Bruin et al., 1994: 296, unnumbered fig. (Sri Lanka); Blaber et al., 1998: 499 (biology and life-history; Sarawak, Borneo, Malaysia); Munroe et al., 1999 (in part): 1764, unnumbered fig. [Indo-West Pacific from Malabar coast to Kolkata, Java Sea (off Java), South China Sea (Singapore and Gulf of Thailand), and East China Sea (north to Taiwan)]; Zhang, 2001: 110, fig. II-47 [Fujian Province (Dongshan County), Guangxi Province (Beihai), Guangdong



Table 1. Meristics of specimens of *Ilisha melastoma* and *Ilisha brachysoma*

	<i>Ilisha melastoma</i>				<i>Ilisha brachysoma</i>		
	Holotype of <i>Clupea</i> <i>melastoma</i>	Lectotype of <i>Pellona</i> <i>micropus</i>	Non-types		Holotype	Non-types	
	ZMB 3842	MNHN 3711	n = 118		BMNH 1867.11.28.16	n = 6	
Standard length (mm)	118.1	68.7	46.6–144.9	Modes	122.7	61.0–192.0	Modes
Unbranched dorsal-fin rays	damaged	4	3–4	3	3	4	4
Branched dorsal-fin rays	damaged	13	13–15	14	13	13	13
Total dorsal-fin rays	16	17	15–19	17	16	16–17	17
Unbranched anal-fin rays	damaged	4	3–4	4	4	4	4
Branched anal-fin rays	damaged	38	32–38	34	42	42–43	42
Total anal-fin rays	38	42	36–43	39	46	46–47	46
Unbranched pectoral-fin rays	1	1	1	1	1	1	1
Branched pectoral-fin rays	15	14	12–16	15	13	13–16	15
Total pectoral-fin rays	16	15	13–17	16	14	14–17	16
Unbranched pelvic-fin rays	1	1	1	1	1	1	1
Branched pelvic-fin rays	6	6	6	6	6	6	6
Total pelvic-fin rays	7	7	7	7	7	7	7
Caudal-fin rays	19	19	19	19	19	19	19
Upper gill rakers on 1st gill arch	11	11	10–14	11	12	10–12	12
Lower gill rakers on 1st gill arch	23	23	21–25	23	25	22–25	25
Total gill rakers on 1st gill arch	34	34	32–38	34	37	34–37	35
Upper gill rakers on 2nd gill arch	10	10	8–11	10	10	8–10	10
Lower gill rakers on 2nd gill arch	22	21	19–23	21	23	21–23	22
Total gill rakers on 2nd gill arch	32	31	28–34	31	33	30–33	30
Upper gill rakers on 3rd gill arch	9	8	6–10	8	8	7–9	8
Lower gill rakers on 3rd gill arch	15	15	13–17	15	16	14–16	15
Total gill rakers on 3rd gill arch	24	23	21–26	23	24	21–24	24
Upper gill rakers on 4th gill arch	8	7	6–9	7	6	6–7	6
Lower gill rakers on 4th gill arch	13	13	11–15	13	12	11–12	12
Total gill rakers on 4th gill arch	21	20	18–23	20	18	18–19	18
Gill rakers on posterior face of 3rd gill arch	6	6	3–7	5	5	4–5	4
Prepelvic scutes	18	21	18–22	20	18	19–20	19
Postpelvic scutes	9	8	7–10	9	7	8	8
Total pelvic scutes	27	29	25–30	28	25	27–28	27
Scale rows in longitudinal series	37	38	35–40	38	40	39–41	39
Transverse scales	11	12	11–13	12	12	12	11, 12
Pseudobranchial filaments	21	damaged	14–21	17	18	16–22	22
Pectoral-fin rays with melanophores	0	0	0–1	0	damaged	0–6	0



Table 2. Morphometrics of specimens of *Ilisha melastoma* and *Ilisha brachysoma*

	<i>Ilisha melastoma</i>				<i>Ilisha brachysoma</i>		
	Holotype of <i>Clupea</i> <i>melastoma</i>	Lectotype of <i>Pellona</i> <i>micropus</i>	Non-types		Holotype of <i>Pellona</i> <i>brachysoma</i>	Non-types	
	ZMB 3842	MNHN 3711	n = 118		BMNH 1867.11.28.16	n = 6	
Standard length (mm; SL)	118.1	68.7	46.6–144.9	Means	122.7	61.0–192.0	Means
As % SL							
Head length	27.6	28.0	25.7–30.3	28.3	24.7	24.3–25.9	25.1
Body depth	37.4	38.0	36.2–43.1	38.7	41.4	36.4–40.7	38.8
Pre-dorsal-fin length	47.9	47.0	45.6–52.0	48.5	47.0	46.4–48.6	47.4
Snout tip to pectoral-fin insertion	28.4	29.0	26.0–31.3	28.5	25.6	24.5–27.4	26.1
Snout tip to pelvic-fin insertion	46.3	50.2	46.3–52.5	49.0	46.5	45.4–48.3	46.5
Snout tip to anal-fin origin	63.9	63.8	61.4–68.7	65.1	60.0	59.2–61.3	60.7
Dorsal-fin base length	13.1	13.7	12.2–15.3	13.5	11.4	11.2–12.1	11.6
Anal-fin base length	35.3	damaged	32.2–37.9	34.7	43.3	40.1–43.4	41.6
Caudal-peduncle length	8.5	damaged	7.5–10.6	9.2	8.8	8.4–9.5	8.8
Caudal-peduncle depth	10.0	11.3	9.3–12.1	10.8	9.2	9.2–10.5	9.6
D–P1	36.0	35.2	35.0–39.3	37.1	36.3	36.1–36.9	36.6
D–P2	35.6	37.5	34.5–42.0	37.7	39.9	35.3–39.6	37.5
D–A	37.3	38.6	36.1–42.6	38.5	40.6	34.9–40.7	38.1
P1–P2	19.6	20.1	18.4–24.3	21.3	19.9	19.1–21.5	20.2
P2–A	20.4	17.9	15.5–21.3	18.7	15.9	15.3–17.9	16.5
Pectoral-fin length	damaged	damaged	18.8–22.8	20.5	damaged	19.8	19.8
Pelvic-fin length	damaged	damaged	6.7–7.8	7.0	damaged	6.3–6.7	6.5
Maxilla length	13.7	13.4	12.5–14.7	13.6	14.2	12.0–14.7	13.0
Mandibular length	14.4	14.3	12.5–15.7	14.3	13.5	12.2–14.3	13.1
Postorbital length	10.6	10.7	10.2–12.7	11.2	9.2	9.5–10.2	9.8

Province (Zhao), Hainan Province (Xinyingzhen, Sanya, and Xincun), China]; Shao et al., 2008: 236 (Pintong County and Kaohsiung, Taiwan); Kimura, 2009: 24, unnumbered fig. (Andaman Sea in Thailand); Shen & Wu, 2011: 144, unnumbered fig. (Taiwan); Satapoomin, 2011: 49 (Andaman Sea); ?Mahmood et al., 2011: 516 (sex-ratio, maturation, and spawning season; off Pakistan); ?Mahmood et al., 2012: 71 (length-weight relationships; off Pakistan); Rainboth et al., 2012: pl. 12, fig. 237 (Ban Don Bay, Surat Thani, Gulf of Thailand, Thailand); Kimura, 2013: 29, unnumbered figs. (Gulf of Thailand, Thailand); Psomadakis et al., 2015: 161, unnumbered fig. (Pakistan); Ahmad et al., 2018: 36, unnumbered fig. (Southeast Asia); Kimura, 2018b: 48 (Ha Long Bay, northern Vietnam and Tanjong Sepat, Malaysia); Psomadakis et al., 2019: 303, unnumbered fig. (Myanmar); Hata, 2019: 198, unnumbered fig. (Ke-tzu-liao, southwestern Taiwan); Zainal Abidin et al., 2021a: 604, table 2 (Sungai Merbok, Kuala Kedah, Malaysia); Zainal Abidin et al., 2021b: 3, table

1 (Sungai Merbok, Kuala Kedah, Malaysia); Nagao Natural Environment Foundation, 2021: 62, figs. A and B (Vietnamese Mekong); ?Gloerfelt-Tarp & Kailola, 2022: 52. (Sumatra to Bali, Indonesia); Anderson, 2022: 162, unnumbered fig. (India); Hata et al., 2022: 25 (Tainan, Taiwan); Hata et al., 2024a: 66 (off Songkhla Province, Gulf of Thailand, Thailand); Hata et al., 2024b: 20, fig. 32 (Kochi, India; Andaman Sea coast of Thailand; Bali, Indonesia).

*Ilisha megaloptera* (not of Swainson): Rainboth et al., 2012: pl. 12, fig. 236 (Phuket, Thailand); Kimura, 2018a (in part): 47, middle fig. (Ha Long Bay, northern Vietnam); Ghosh & Vase, 2022: 1051, fig. 1 (Saurashtra Coast, Gujarat, India); Bampouri et al., 2024: 1, fig. 1 (northern part of Gulf of Oman).

**Holotype.** ZMB 3842, holotype of *Clupea melastoma* (also neotype of *Clupea indicus*, *Pellona ditchoa*, and *Platygaster verticalis*; see Remarks), 118.1 mm SL, Coromandel, Tamil Nadu, India.

Table 3. GenBank accession numbers of the COI nucleotide sequences (651bp) from 43 specimens of Pristigasteridae examined in this study along with respective specimen information. GenBank accession numbers (in bold text) indicate sequences determined in present study. Abbreviation: COI, cytochrome oxidase I.

Species	GenBank accession number	DNA tissue code	Museum registration number / BOLD entry	Origin
<i>Ilisha brachysoma</i>	HM902430	BW-A6909	CSIRO H 7696-28 / FOAJ059-09	off Pacitan, East Java, Indonesia (8°13'00.0"S, 111°04'01.2"E) (3 July 2008)
	PV664584	BW-A10186	CSIRO H 8581-05 / FOAM223-10	Jimbaran Bay, southern coast of Bali, Indonesia (8°45'S, 115°09'E) (6 August 2010)
	PV664585	BW-A10205	CSIRO H 8581-06 / FOAM242-10	Jimbaran Bay, southern coast of Bali, Indonesia (8°45'S, 115°09'E) (6 August 2010)
	PV664583	BW-A10206	MZB 28359 / FOAM243-10	Jimbaran Bay, southern coast of Bali, Indonesia (8°45'S, 115°09'E) (6 August 2010)
	MH325630	HH51	NMMBP-23499	Fish market, Dong-shi, Jiayi, Taiwan (25 October 2014)
<i>Ilisha melastoma</i>	MH325631	HH70	NMMBP not registered	off Ke-tzu-liao, Ziguang District, Kaohsiung, Taiwan (21 January 2015)
	<b>PV715800</b>	n2240	NMMBP-22957	Fish market, Donggang, Pintung, Taiwan (11 June 2015)
	<b>PV715801</b>	n2241	NMMBP-22957	Fish market, Donggang, Pintung, Taiwan (11 June 2015)
	MW498647	SP-20-1	USMFC (92) 00004 / DBMR022-19	Pasar Bisik Kuala Muda, Kuala Muda, Kedah, Malaysia (5°34'40.8"N, 100°20'27.6"E)
	MW498646	SP-20-2	USMFC (92) 00004 / DBMR023-19	Pasar Bisik Kuala Muda, Kuala Muda, Kedah, Malaysia (5°34'40.8"N, 100°20'27.6"E)
	MW498645	SP-20-3	USMFC (92) 00004 / DBMR024-19	Pasar Bisik Kuala Muda, Kuala Muda, Kedah, Malaysia (5°34'40.8"N, 100°20'27.6"E)
	MW498648	SP-20-4	USMFC (92) 00004 / DBMR025-19	Pasar Bisik Kuala Muda, Kuala Muda, Kedah, Malaysia (5°34'40.8"N, 100°20'27.6"E)
	MW498649	SP-20-5	USMFC (92) 00004 / DBMR026-19	Pasar Bisik Kuala Muda, Kuala Muda, Kedah, Malaysia (5°34'40.8"N, 100°20'27.6"E)
	MW498644	SP-60-1	USMFC (92) 00006 / DBMR027-19	Pompang Sg. Merbok, Merbok Kedah, Malaysia (5°39'50.4"N, 100°22'51.6"E)
	<b>PV715802</b>	MAY216	- / -	Kota Bharu, Kelantan, Malaysia
	<b>PV715803</b>	MAY217	- / -	Kota Bharu, Kelantan, Malaysia
	<b>PV715804</b>	MAY218	- / -	Kota Bharu, Kelantan, Malaysia
	<b>PV715805</b>	MAY220	- / -	Kota Bharu, Kelantan, Malaysia

Species	GenBank accession number	DNA tissue code	Museum registration number / BOLD entry	Origin
	<b>PV715806</b>	SI48	– / –	Sibu, Sarawak, Malaysia
	PQ817950	Ra24	– / –	Ranong fish market, Thailand
	PQ817951	Ra25	– / –	Ranong fish market, Thailand
	<b>PV715807</b>	Ra27	– / –	Ranong fish market, Thailand
	<b>PV715808</b>	Ra36	– / –	Ranong fish market, Thailand
	OK268103	Fish50-IRAN	– / –	Iran
	OK271436	Fish19-IRAN	– / –	Iran
	OK271439	Fish22-IRAN	– / –	Iran
	OL906113	Fish31-IRAN	– / –	Iran
	ON692700	Fish33-IRAN	– / –	Iran
	MN200469	– / –	DUZM_MF_88	Kuakata, Bangladesh (21°48'36.0"N, 90°E) (5 October 2018)
	MN200470	– / –	DUZM_MF_88_2	Kuakata, Bangladesh (21°48'36.0"N, 90°E) (5 October 2018)
	MN200471	– / –	DUZM_MF_88_3	Kuakata, Bangladesh (21°48'36.0"N, 90°E) (5 October 2018)
<i>Ilisha ditichela</i>	MH325643	Ra37	– / –	Ranong fish market, Thailand
	JQ928190	–	– / –	India
	PQ817946	n2404	– / –	Taiwan
	PQ817947	n2405	– / –	Taiwan
<i>Ilisha kampeni</i>	PQ817948	Ra89	– / –	Ranong fish market, Thailand
	PQ817949	Ra90	– / –	Ranong fish market, Thailand
<i>Ilisha megaloptera</i>	MH325638	MAY543	– / –	Sekinchan, Selangor, Malaysia
	MH325639	MAY544	– / –	Sekinchan, Selangor, Malaysia
<i>Opisthopterus tardore</i>	PQ817952	Ra20	– / –	Ranong fish market, Thailand
	PQ817953	Ra21	– / –	Ranong fish market, Thailand
<i>Raconda russeliana</i>	MH325626	KU02b	– / –	Kuching fish market, Sarawak, Malaysia
	MH325627	KU03b	– / –	Kuching fish market, Sarawak, Malaysia
<i>Coilia nasus</i> (outgroup)	AP009135	–	– / –	Japan



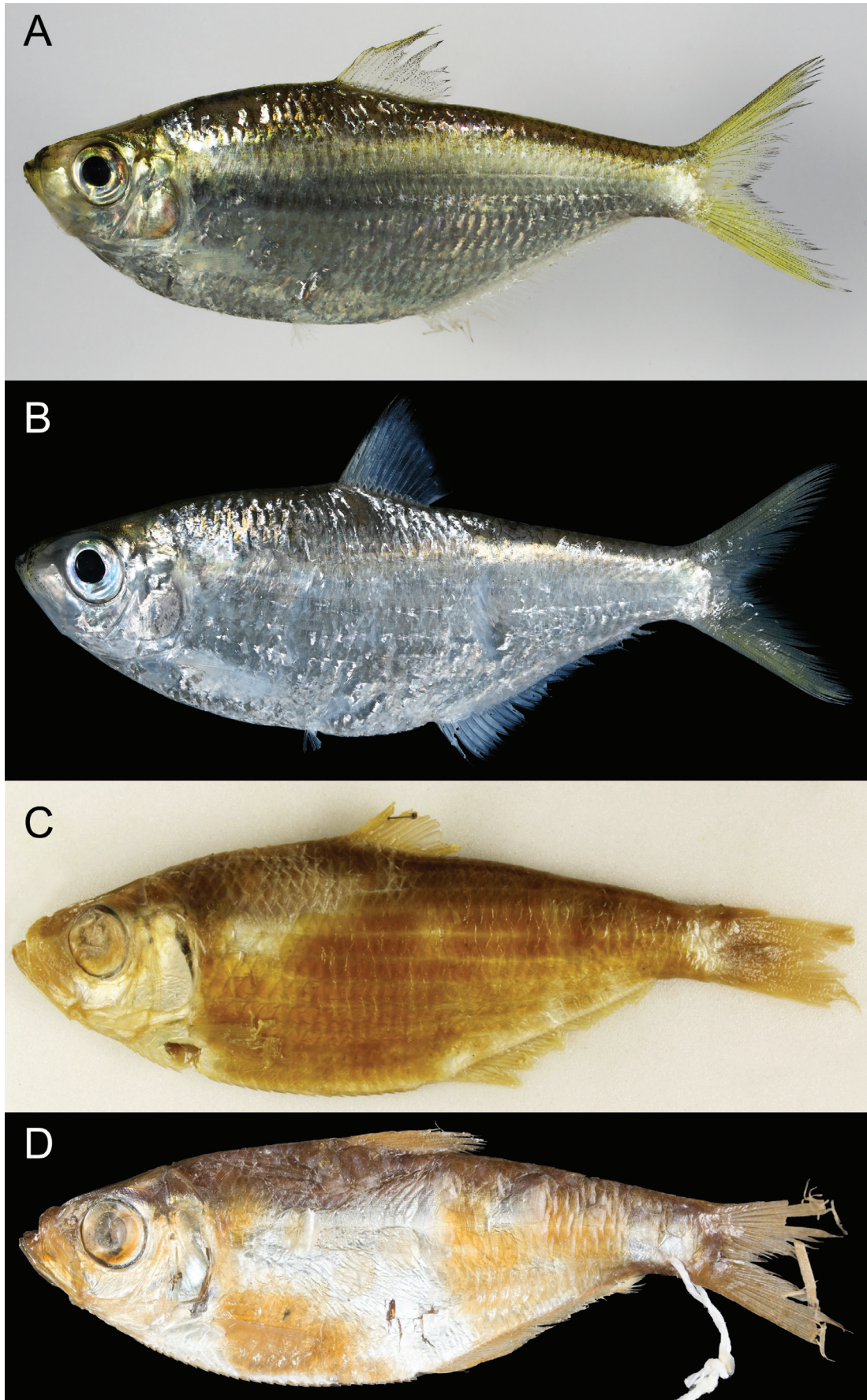


Fig. 2. A, B, Non-type specimens of *Ilisha melastoma*, fresh condition (A, KAUM-I. 67324, 91.7 mm SL, Ha Long Bay, Vietnam; B, MZB 29244, 112.5 mm SL, Java, Indonesia), C, holotype of *Clupea melastoma* (ZMB 3842, 118.1 mm SL, Coromandel, Tamil Nadu, India; also neotype of *Clupea indicus*, *Pellona ditchoa*, and *Platygaster verticalis*; photographed by The Trustees of the Museum für Naturkunde Berlin) and D, lectotype of *Pellona micropus* (MNHN 3711, 68.7 mm SL, Coromandel, Tamil Nadu, India; photographed by L. Randrihasipara, Muséum National d'Histoire Naturelle).

Table 4. Frequency distribution of total anal-fin rays in *Ilisha melastoma* and *Ilisha brachysoma*.

		Total anal-fin rays											
		36	37	38	39	40	41	42	43	44	45	46	47
<i>Ilisha melastoma</i>	n = 115	8	6	17	33	25	16	9	1				
<i>Ilisha brachysoma</i>	n = 7											6	1

**Other materials examined.** 119 specimens: 46.6–144.9 mm SL. **TAIWAN:** ASIZP 59983, 2 specimens, 64.2–75.1 mm SL, Guandu, Taipei, 0–3 m depth; ASIZP 69736, 123.7 mm SL, off Tongxiao (24°32'24"N, 120°37'48"E), 30 m depth, bottom trawl; ASIZP 74487, 123.8 mm SL, off Miaoli; KAUM-I. 110319, 73.2 mm SL, KAUM-I. 110327, 84.8 mm SL, KAUM-I. 110328, 55.8 mm SL, KAUM-I. 113285, 144.9 mm SL, KAUM-I. 115198, 113.6 mm SL, KAUM-I. 115203, 126.1 mm SL, KAUM-I. 125060, 121.9 mm SL, NMMB-P28038, 123.8 mm SL, OISTICH 688, 111.6 mm SL, off Ke-tzu-liao, Ziguan District, Kaohsiung; NMMB-P22957 (tissue codes: n2240 and n2241), 112.5 mm SL, Donggang, Pintung; NMMB-P23120, 79.5 mm SL, Dong-shi, Jiayi; NMMB-P23499 (tissue code: HH51), 72.5 mm SL, Dong-shi, Jiayi. **VIETNAM:** KAUM-I. 67304, 87.0 mm SL, KAUM-I. 67324, 91.7 mm SL, KAUM-I. 72552, 89.3 mm SL, KAUM-I. 94542, 78.6 mm SL, KAUM-I. 94556, 85.2 mm SL, KAUM-I. 94574, 80.0 mm SL, KAUM-I. 94874, 85.0 mm SL, KAUM-I. 95108, 105.3 mm SL, KAUM-I. 95109, 115.2 mm SL, Ha Long Bay, Ha Long; NSMT-P 66266, 114.8 mm SL, NSMT-P 68381, 109.3 mm SL, Long Chau Bay. **THAILAND:** ANSP 60596, 87.5 mm SL, Bangkok; ANSP 61765, 99.2 mm SL, Paknam, Samut Prakan Province; ANSP 87388, 59.1 mm SL, Krabi; ANSP 89418, 2 of 17 specimens, 74.4–84.2 mm SL, Tachin, Samut Sakhon Province; KAUM-I. 23881, 77.5 mm SL, KAUM-I. 32855, 99.0 mm SL, KAUM-I. 44231, 84.4 mm SL, KAUM-I. 44232, 80.1 mm SL, KAUM-I. 44233, 98.6 mm SL, KAUM-I. 44234, 83.3 mm SL, Gulf of Thailand, Thailand (obtained at fish market in Mahachai, Mueang Samut Sakhon District); NSMT-P 23081, 73.0 mm SL, Songkhla; NSMT-P 66057, 90.9 mm SL, OCF-URM-P 12644, 108.0 mm SL, OCF-URM-P 30860, 107.3 mm SL, Phuket; OCF-URM-P 14246, 77.9 mm SL, OCF-URM-P 14247, 76.7 mm SL, OCF-URM-P 14248, 80.0 mm SL, OCF-URM-P 14249, 87.5 mm SL, Ranong; PMBC 6694, 96.1 mm SL, Yao Yai Island, Phang-nga; PMBC 9958, 109.0 mm SL, Bang Rong, Phuket (mangrove area); PMBC 20600, 2 specimens, 81.1–81.9 mm SL, Yao Yai Island, Phang-nga; PMBC 20626, 89.7 mm SL, Yao Yai Island, Phang-nga; PMBC 25613, 87.2 mm SL, Tha Lane Bay, Krabi; PMBC 26082, 94.7 mm SL, Phang-nga Bay (8°04'57"N, 98°40'09"E), 21 m depth, otter trawl, THNHM-F 12517, 100.3 mm SL, Ban Ta Klang Pear, Suk Samaran, Ranong; THNHM-F 23143, 103.7 mm SL, THNHM-F 23144, 108.3 mm SL, THNHM-F 23274, 107.8 mm SL, THNHM-F 23275, 103.2 mm SL, THNHM-F 23307, 112.3 mm SL, THNHM-F 23308, 110.6 mm SL, Wat Ton Son Market, Ban Laem, Phetchaburi Province; THNHM-F 23328, 115.8 mm SL, fishing village near mouth of Bang Tabun River estuary,



Fig. 3. Stained scale removed from right side of midbody (above anal fin) of *Ilisha melastoma*, KAUM-I. 210219, 117.6 mm SL, Johor, Malaysia (left-right inverted).

Ban Laen District, Phetchaburi Province; USMFC uncat.-Bangkok, 87.8 mm SL, Bangkok. **MALAYSIA:** KAUM-I. 189904, 105.0 mm SL, KAUM-I. 189905, 96.5 mm SL, off Kuantan, Pahang (3°42'22.8"N, 103°21'03.0"E; obtained at Pasar Nelayan Pantai Sepat); KAUM-I. 210080, 91.2 mm SL, KAUM-I. 210104, 72.0 mm SL, eastern part of Johor Strait, Johor (1°27'01.2"N, 104°01'26.4"E), 18 m depth; KAUM-I. 210218, 100.4 mm SL, KAUM-I. 210219, 117.6 mm SL, eastern part of Johor Strait, Johor (1°24'05.4"N, 104°06'11.4"E), 3–4 m depth, trawl; NSMT-P 93944, 81.7 mm SL, OCF-URM-P 44356, 97.0 mm SL, OCF-URM-P 44357, 99.3 mm SL, OCF-URM-P 46279, 59.1 mm SL, Port Dickson, Negeri Sembilan; OCF-URM-P 44369, 111.9 mm SL, Tanjung Sepat, Selangor; USMFC (92) 00016 (code specimen: BM-24-16), 122.5 mm SL, obtained at Batu Maung fish market, Penang State; USMFC (92) 00019 (code specimen: BM-25-12), 111.7 mm SL, obtained at Batu Maung fish market, Penang State; USMFC (92) 00013, 2 specimens (code specimen: ME-24-09), 104.1 mm SL, (code specimen: ME-24-18), 101.4 mm SL, Kuala Muda Whispering Market (Pasar Bisik), Kuala Kedah, Kedah State (05.578°N, 100.341°E); USMFC (92) 00004, 5 specimens (code specimen: SP-20-1), 102.5 mm SL, (code specimen: SP-20-2), 98.2 mm SL, (code specimen: SP-20-3), 93.4 mm SL, (code specimen: SP-20-4), 99.3 mm SL, (code specimen: SP-20-5), 101.1 mm SL, Kuala Muda Whispering Market (Pasar Bisik), Kuala Kedah, Kedah State (05.578°N, 100.341°E); ZRC 24442, 91.6 mm SL, Mersing Jetty, Johor. **SINGAPORE:** ANSP 53494, 2 specimens, 75.4–81.8 mm SL, Clyde Terrace Market; LSUMZ 16523, 108.3 mm



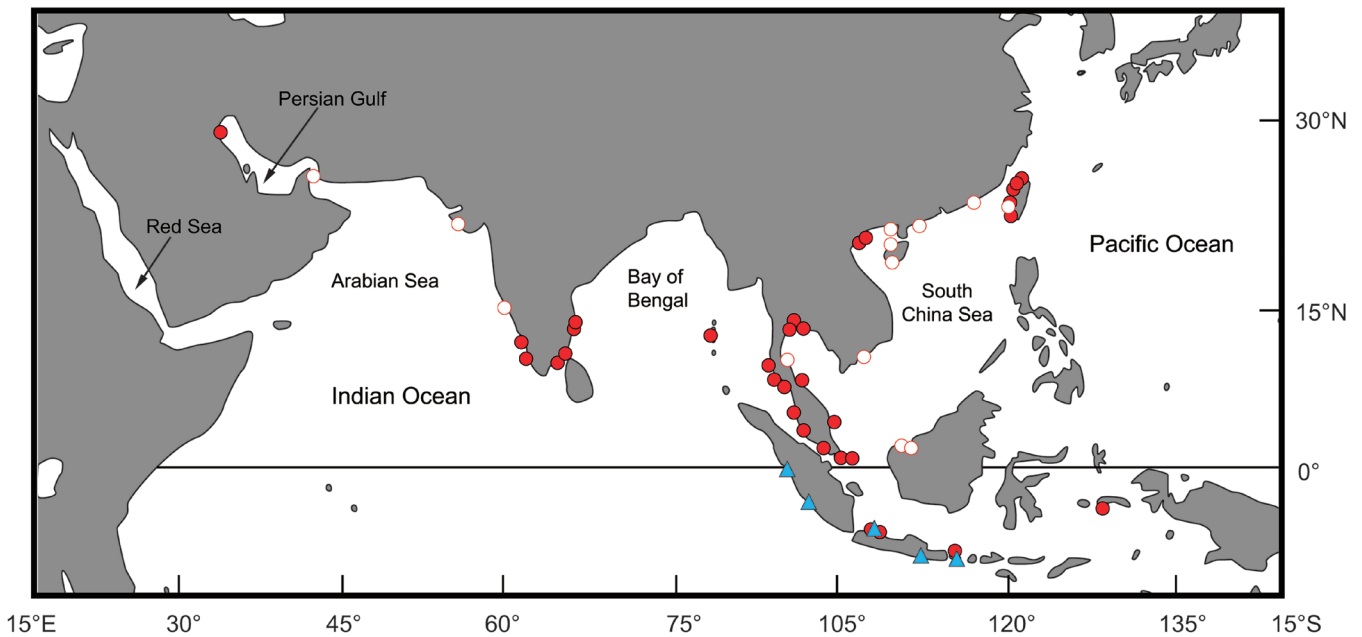


Fig. 4. Distributional records of *Ilisha melastoma* (red circles) and *Ilisha brachysoma* (blue triangles). Solid and open symbols represent specimens examined in this study and in literature respectively.

SL, west of Pulau Ubin ( $1^{\circ}25'06.6''\text{N}$ ,  $103^{\circ}55'43.3''\text{E}$ ). **INDONESIA:** MZB 29099, 116.9 mm SL, MZB 29104, 122.1 mm SL, off Tanjung Pasir, Java (obtained at Tanjung Pasir Fish Market); MZB 29244, 112.5 mm SL, off Rawa Saban, Tangerang, Java (obtained at Cituis Fish Market, Pakuhaji, Tangerang, Banten); NMW 1879, 106.0 mm SL, Amboina, Moluccas; OCF-URM-P 43193, 46.6 mm SL, Pulau Bintan, Riau Archipelago; PMBC 37410, 105.8 mm SL, Bali; USNM 72511, 2 specimens, 115.3–123.7 mm SL, Java. **INDIA:** ANSP 74849, 79.1 mm SL, Kozhikode, Kerala; MNHN 3711, lectotype of *Pellona micropus*, 68.7 mm SL, Coromandel; NMW 4333, 109.5 mm SL, Andaman Islands; PMBC 3575, 99.4 mm SL, Kochi, Kerala; USNM 276415, 102.9 mm SL, Vellar River estuary, Porto Novo, Tamil Nadu; USNM 276416, 2 specimens, 86.4–95.1 mm SL, Kirakarai, Tamil Nadu; USNM 276417, 110.7 mm SL, Mysore, Mysore District, Karnataka; USNM 276419, 3 specimens, 103.6–107.9 mm SL, Mandapam, Chennai, Ramanathapuram District, Tamil Nadu; USNM 283218, 111.5 mm SL, Puducherry. **KUWAIT:** LSUMZ 17439, 10 specimens, 67.7–83.7 mm SL, LSUMZ 17450, 3 specimens, 75.1–87.6 mm SL, Kuwait.

**Diagnosis.** A species of *Ilisha* with the following combination of characters: body deep, 36.2–43.1% of SL; abdomen covered with  $18-22 + 7-10 = 25-30$  scutes; anal fin with 36–43 fin rays, its base short, 32.2–37.9% of SL; pelvic fin long, 6.7–7.8% of SL, its posterior tip posteriorly beyond vertical through dorsal-fin origin (reaching to 3rd–8th dorsal-fin ray origin) when depressed; grooves on body scales overlapping at center; 1UGR 10–14, 1LGR 21–25, 1TGR 32–38; 2UGR 8–11, 2LGR 19–23, 2TGR 28–34; 3UGR 6–10, 3LGR 13–17, 3TGR 21–26; 4UGR 6–9, 4LGR 11–15, 4TGR 18–23; pectoral fin with scattered melanophores restricted to uppermost fin ray or absent; swim bladder with double tubes passing posteriorly into muscles on both sides of haemal spines; no distinct lobe on maxilla; head

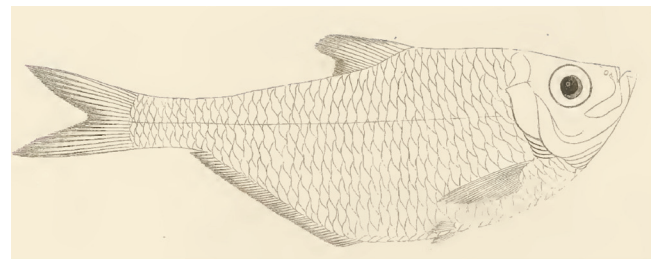


Fig. 5. Illustration of specimen shown in Russell (1803 “ditchoe” on pl. CXCII, the basis of *Platygaster verticalis* Swainson, 1838, *Clupea indicus* Swainson, 1839, and *Pellona ditchoa* Valenciennes, 1847; source: Biodiversity Heritage Library)

rather long, 25.7–30.3% of SL; distances from snout tip to pectoral-fin long, 26.0–31.3% of SL; distance from snout to pelvic-fin insertion long, 46.3–52.5% of SL; distance from snout to anal-fin origin long, 61.4–68.7% of SL; distance from pelvic-fin insertion to anal-fin origin rather long, 15.5–21.3% of SL; dorsal-fin base long, 12.2–15.3% of SL; postorbital length long, 10.2–12.7% of SL.

**Description.** Counts and measurements (expressed as percentages of SL) are shown in Tables 1 and 2. Data for holotype “*Clupea*” *melastoma* given in parentheses (if different). Body strongly compressed, deep, deepest at dorsal-fin origin. Dorsal contour of head and body gradually elevated from snout tip to dorsal-fin origin thereafter gently decreased to uppermost point of caudal-fin base. Ventral contour of head and body lowering from lower-jaw tip to pelvic-fin insertion and subsequently rising to lowermost point of caudal-fin base. Abdomen covered with 18 or 22 (20) and 7–10 (9) scutes from isthmus to pelvic scute, and pelvic scute to anus, respectively. Abdomen scutes hard, sharp, and projected backwards. Pectoral-fin insertion anterior to posterior margin of opercle and lower than lower margin of eye; dorsal, posterior, and ventral profile nearly straight;



posterior tip pointed, reaching to or slightly not to vertical through pelvic-fin insertion; uppermost fin ray unbranched, others branched. Pelvic-fin insertion anterior to dorsal-fin origin; posterior tip of depressed fin (posterior part of pelvic fin broken in most specimens including holotype of *C. melastoma*) reaching to vertical through 3rd to 8th dorsal-fin ray origin, not to anus; anterior-most fin ray unbranched, other rays branched; outer profiles of fin nearly straight. Dorsal fin nearly triangular, outer profiles of fin nearly straight; fin origin located near midpoint of body; initial three or four rays unbranched, others branched (distal part of dorsal fin of holotype damaged). Anal-fin origin posterior to 10th dorsal-fin ray origin, sometimes posterior to dorsal-fin base end (just below origin of 15th dorsal-fin ray); initial three or four rays unbranched, other rays branched (distal part of anal fin of holotype damaged). Caudal fin forked and bifurcate, but not lunate; both lobes without extended tips; outer profile of each lobe nearly straight. Anus just anterior to anal-fin origin. Lower jaw projecting anteriorly than maxilla tip. Single rows of conical teeth on premaxilla, maxilla and anterior margin of lower jaw, but not on hypomaxilla. Several rows of fine conical teeth on palatine. Band of fine teeth presenting on pterygoid. Small conical teeth patch on ectopterygoid and tongue. No teeth on vomer. Mouth large, posterior tip of maxilla beyond vertical through anterior margin of eye. Eye large, round, covered with adipose eyelid, laterally on head and dorsal to horizontal through pectoral-fin insertion, visible in dorsal view; pupil round; orbit round. Interorbital space flat, width less than eye diameter. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle convex, without serrations. Gill membrane without serrations. Pseudobranchial filaments exposed, length of longest filament less than eye diameter. Gill rakers long, slender, and rough. Scales on body cycloid, thin, deciduous. Several vertical grooves on body scales; posterior-most groove crossing scale; grooves on central part meeting or overlapping at center of scale; posterior part somewhat denticulated (Fig. 3). No scales on head and fins. Axillary scales located on insertions of pectoral and pelvic fins. Posterior part of swim bladder forming a pair of extensions on left and right sides.

**Colouration of fresh specimens.** Body uniformly silver, upper part yellowish or greenish. Dorsum dark brown (in individuals in which scales on body have fallen off, body uniformly whitish silver and dorsum to upper part light brown. Melanophores densely scattered on upper part of body). Region around cleithrum yellow. No band on lateral surface of body. Dorsal surface of head and both jaw-tips blackish. Pectoral, dorsal, and caudal fins yellow. Pelvic and anal fins whitish. Melanophores scattered along fin rays of dorsal and caudal fins. No melanophores scattered on pectoral, pelvic, and anal fins. Iris silver, pupil black.

**Colouration of preserved specimens.** Body uniformly pale, light ivory, or silver (silver in holotype). Melanophores densely scattered on dorsum to lateral surface of body, reaching to level of center of eye, sometimes beyond level of pectoral-fin insertion (difficult to see when guanine remains on body surface). Melanophores scattered along fin rays of dorsal and caudal fins but not on fin rays of pelvic and anal

fins. Pectoral fin without melanophores (rarely scattered on only 1st pectoral-fin ray). Melanophores scattered on gill rakers, first gill arch, inner surfaces of hyoid arch and preopercle and opercle. Iris silver, pupil black.

**Distributional records and ecological notes.** *Ilisha melastoma* is widely distributed in the Indo-West Pacific from the Persian Gulf to the Moluccan Islands and Taiwan (Fig. 4). The species is distributed over a range of 85 degrees in longitude, making it the species with the widest distribution in the genus *Ilisha*. According to Blaber et al. (1998), which reported the ecology and life history of a population of *I. melastoma* in Sarawak, the species is found only in coastal waters and the lower reaches of estuaries, and it mainly feeds on molluscs, especially scaphopods. Both males and females of the species mature at approximately 100 mm SL and the majority live for less than 2 years. Although Mahmood et al. (2011, 2012) recorded sex-ratio, maturation, spawning season, and length-weight relationship of supposed *I. melastoma* obtained off the coast of Pakistan, they did not provide any clear identification, and we cannot exclude the possibility that their samples contained *I. ditchela*, a species similar in appearance to *I. melastoma* and distributed in the northern Indian Ocean (Wongratana, 1983; Whitehead, 1985; this study).

Because the taxonomy of the genus *Ilisha* is still confused and identification methods for each species are not well developed, species of the genus including *I. melastoma* have been frequently misidentified. In particular, *I. melastoma* has often been confused with *Ilisha megaloptera* (Swainson, 1839). Dehadrai (1960) reported on the swim bladder morphology of *I. indica* (regarded as a junior synonym of *I. melastoma* in this study) but without the diagnostic posterior extension on the left side. Therefore, the individual illustrated in Dehadrai (1960) is likely to be another species of *Ilisha*, such as *I. megaloptera* (posterior extension only on right side) or *Ilisha sirishae* Seshagiri Rao, 1975 (swim bladder without extension on both sides; Whitehead, 1985; Munroe et al., 1999). Rainboth et al. (2012) reported a color photograph of a pristigasterid fish collected from Phuket, Thailand, as *I. megaloptera*. However, the specimen has a distinctly deep body and is therefore identified as *I. melastoma*. Kimura (2018a) showed a color photograph of a pristigasterid fish (KAUM-I. 67304) collected from Ha Long Bay, northern Vietnam as *I. megaloptera*, however the specimen is reidentified as *I. melastoma* in this study. Kimura (2018a) also showed another pristigasterid fish from the Johor Strait, Malaysia (bottom fig. on p. 47), as *I. megaloptera*, this specimen is herein considered to be *I. megaloptera* due to its more slender body. Jaafar (2021) showed a color photograph of a pristigasterid fish collected from Kuantan, eastern coast of the Malay Peninsula, Malaysia as *I. melastoma*. However, the photographed specimen, being not very deep-bodied, is probably *I. megaloptera*. Ghosh & Vase (2022) studied the reproduction and diet of *I. megaloptera* from the Saurashtra coast, northeastern Arabian Sea, but the photographed fish shown in fig. 1 probably belongs to *I. melastoma* because of its distinct deep body. The individuals used in Ghosh & Vase (2022) were very large, ranging from 18.4 to 35.2 cm

in SL (*I. melastoma* determined in this study <15 cm SL), and lengths at sexual maturity (50%) were estimated at 24.21 cm and 24.92 cm SL for females and males, respectively (fig. 4 in Ghosh & Vase, 2022), which is a large difference from the maturity size of *I. melastoma* (approx. 100 mm SL) given by Blaber et al. (1998; fig. 2). Therefore, whereas the individual shown in fig. 1 is *I. melastoma*, the biological research of Ghosh & Vase (2022) appears to be based on a population of *I. megaloptera*. Bampouri et al. (2024) examined minerals and trace elements contained in various body parts of *I. megaloptera* obtained from northern part of the Gulf of Oman. However, the pristigasterid fish shown in fig. 1 has a distinct deep body and it could belong to *I. melastoma*.

**Comparisons.** *Ilisha melastoma* can be distinguished from all other congeners except for *Ilisha brachysoma*, *Ilisha lunula* Kailola, 1986, and *I. ditchela*, by having a deeper body (> 35% of SL), two tubes from posterior ends of swimbladder extending and passing back into muscles on either side of haemal spines, ventral scutes 30 or less (Whitehead, 1985; Randall, 1994; Munroe et al., 1999; this study). Furthermore, *I. melastoma* differs from *I. lunula* in having more gill rakers (1LGR 21 or more in *I. melastoma* vs. 20 or less in *I. lunula*) and caudal fin without extended tips (vs. caudal fin deeply forked and strongly lunate, both lobes extended) (Kailola, 1986; Munroe et al., 1999; this study). *Ilisha melastoma* differs from *I. ditchela* by having scales with grooves overlapping at their center (Fig. 3 vs. not meeting at center of scales; fig. 277 on Whitehead, 1985, as *I. striatula*) and no longitudinal band on lateral surface of body (vs. a faint dark longitudinal band present on lateral surface of body) (Wongratana, 1983; Whitehead, 1985; Munroe et al., 1999; this study). Detailed comparisons of *I. melastoma* with *I. brachysoma* are given under Remarks for the latter.

**Remarks.** *Ilisha melastoma* was originally described by Bloch & Schneider (1801) as *Clupea melastoma* based on a specimen collected from Coromandel Coast, Tamil Nadu, India (ZMB 3842; Fig. 2C). After that, the nominal species was not used as a valid name for a long time, and until the mid-20th century, specimens of *I. melastoma*, as determined in this study, were often treated as *I. brachysoma* or *I. indica* (see synonym list). Whitehead (1967a, 1969) considered *C. melastoma* to be a senior synonym of *P. ditchela* and suggested that *C. melastoma* should be regarded as a nomen oblitum. Although Whitehead (1967a, 1969) stated that an application for suppression would be made in due course, this was never done and in Whitehead (1972, 1985)—published subsequently—both *P. ditchela* and *I. melastoma* were treated as valid species. Even if *I. melastoma* was conspecific with *P. ditchela*, *I. melastoma* has now been used in many publications in the 21st century and does not meet the requirements of ICZN for suppression (1999: 23.9.1.1); therefore *C. melastoma* must not be considered a nomen oblitum.

*Platygaster verticalis* Swainson, 1838, *Pellona ditchoa* Valenciennes, 1847, and *Clupea (Pristigaster) indicus* Swainson, 1839 are all described based on a figure of

“ditchoe” in Russell (1803: pl. CXCII; Fig. 5). Russell (1803)’s “ditchoe” (local name for the fish) was described based on a specimen collected from Visakhapatnam, Andhra Pradesh, India. The meristics of “ditchoe” shown in Russell (1803: p. 74) generally matched those of *I. melastoma* determined in this study. According to the figure of “ditchoe” in Russell (1803), the fish has a deep body and pelvic fins nearly reaching vertical through dorsal-fin origin. Among the species of the genus *Ilisha* recorded from the Indian Ocean, only two species, *I. melastoma* as determined in this study, and *I. ditchela*, have these characters (Wongratana, 1983; Whitehead, 1985; Kailola, 1986; Whitehead et al., 1988; Randall, 1994; Munroe et al., 1999; Hata et al., 2025; this study). Of these two species, *I. ditchela* is distinguished by its greater number of anal fin rays (40–47; Wongratana, 1983; Whitehead, 1985; Munroe et al., 1999) than “ditchoe” (37), and therefore “ditchoe” is conspecific with *I. melastoma*. Consequently, *Platygaster verticalis*, *Pellona ditchoa*, and *Clupea (Pristigaster) indicus* are regarded here as junior synonyms of *I. melastoma*. Because the specimen on which the illustration of “ditchoe” in Russell (1803) was based has not been preserved, the holotype of *Clupea melastoma* [ZMB 3842, 118.1 mm SL, collected from Coromandel, Tamil Nadu, India; Fig. 2C] is herein designated as the neotype of *C. indicus*, *P. ditchoa*, and *P. verticalis*; the three names are therefore reassigned as junior objective synonyms of *C. melastoma*.

*Pellona micropus* was described by Valenciennes (1847) based on two specimens, one collected from Coromandel Coast of India and the other from the Bengal Region. Subsequently, Whitehead (1967a), who treated this nominal species as a valid name *Ilisha micropus*, designated MNHN 3711 (Fig. 2D), the specimen collected from Coromandel, as the lectotype of the nominal species. Because characters of the lectotype were a good match for those of *I. melastoma* determined in this study, *P. micropus* is herein considered as a junior synonym of *I. melastoma*, as in Whitehead (1985) and Munroe et al. (1999). In addition, the paralectotype of *P. micropus* was indicated as a different species from *I. melastoma* and designated as the paratype of *Ilisha obfuscata* by Wongratana (1983).

### *Ilisha brachysoma* (Bleeker, 1852)

(English name: Indonesian *Ilisha*)

(Figs. 6, 7; Tables 1, 2, 4)

*Pellona brachysoma* Bleeker, 1852: 22 [type locality: Batavia (currently Jakarta), Java, Indonesia]; Günther, 1868: 456 (Java and Sumatra, Indonesia); Weber & de Beaufort, 1913 (in part): 87 (Java and Sumatra, Indonesia).

*Ilisha brachysoma*: Fowler, 1941: 653 (Padang, Sumatra, Indonesia); Whitehead et al., 1966: 100 (holotype description; Jakarta, Java, Indonesia).

*Ilisha melastoma* (not of Bloch & Schneider): ?Gloerfelt-Tarp & Kailola, 1984: 48, unnumbered fig. (Sumatra to Bali, Indonesia); Whitehead, 1985 (in part): 272 (Java Sea); Munroe et al., 1999 (in part): 1764 (Java Sea); White et al., 2013: 78, fig. 9.1 (southern Bali, Indonesia); ?Gloerfelt-Tarp & Kailola, 2022: 52, unnumbered fig. (Sumatra to Bali, Indonesia).

*Ilisha indica* (not of Swainson): Kottelat, 2013 (in part): 49 (Jakarta, Java, Indonesia).



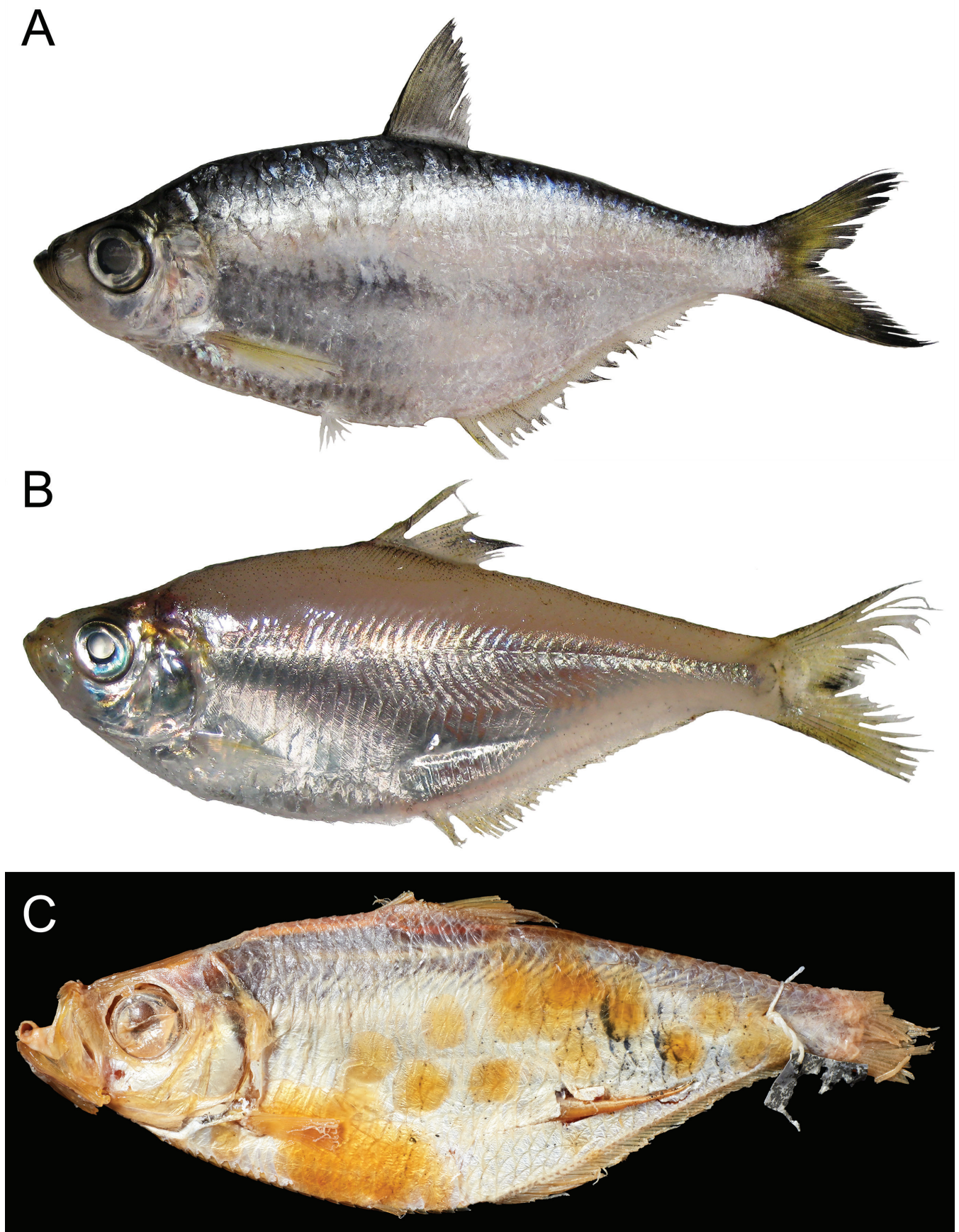


Fig. 6. A, B, Non-type specimens of *Ilisha brachysoma*, fresh condition (A, CSIRO H 8581-05, Jimbaran Bay, southern coast of Bali, Indonesia; B, CSIRO H 7696-28, 61.0 mm SL, off Pacitan, East Java, Java, Indonesia) and C, holotype of *Pellona brachysoma* (BMNH 1867.11.28.16, 122.7 mm SL, Jakarta, Java, Indonesia; (photographed by The Trustees of the Natural History Museum, London).



**Holotype.** BMNH 1867.11.28.16, holotype of *Pellona brachysoma*, 122.7 mm SL, Jakarta, Java, Indonesia.

**Non-type specimens.** 6 specimens: 61.0–192.0 mm SL, all specimens collected from Indonesia. ANSP 27441, 110.7 mm SL, Padang, Sumatera Barat, Sumatra, Indonesia; CSIRO H 7696-28 (code tissue: BW-A6909), 61.0 mm SL, off Pacitan, East Java, Java, Indonesia (obtained at Pacitan Fish Market); CSIRO H 8581-05 (code tissue: BW-A10186), 192.0 mm SL, Jimbaran Bay, southern coast of Bali, Indonesia (obtained at Kedonganan Fish Market); CSIRO H 8581-06 (code tissue: BW-A10205), 171.0 mm SL, Jimbaran Bay, southern coast of Bali, Indonesia (obtained at Kedonganan Fish Market); MZB 28359, 186.8 mm SL, Jimbaran Bay, southern coast of Bali, Indonesia (obtained at Kedonganan Fish Market); USNM 87976, 66.4 mm SL, Bengkulu, Sumatra, Indonesia.

**Diagnosis.** A species of *Ilisha* with the following combination of characters: body deep, 36.4–41.4% of SL; abdomen covered with  $18-20 + 7-8 = 25-28$  scutes; anal fin with 46 or 47 fin rays, its base long, 40.1–43.4% of SL; pelvic fin long, 6.3–6.7% of SL, its posterior tip posteriorly beyond vertical through dorsal-fin origin (reaching to 4–5th dorsal-fin ray origin) when depressed; grooves on body scales overlapping at center; 1UGR 10–12, 1LGR 22–25, 1TGR 34–37; 2UGR 8–10, 2LGR 21–23, 2TGR 30–33; 3UGR 7–9, 3LGR 14–16, 3TGR 21–24; 4UGR 6 or 7, 4LGR 11 or 12, 4TGR 18 or 19; melanophores scattered on 3rd to 6th pectoral-fin rays from uppermost ray (in specimens > 170 mm SL); swim bladder with double tubes passing posteriorly into muscles on both sides of haemal spines; no distinct lobe on maxilla; head rather short, 24.3–25.9% of SL; distances from snout tip to pectoral-fin short, 24.5–28.4% of SL; distance from snout to pelvic-fin insertion short, 45.4–48.3% of SL; distance from snout to anal-fin origin short, 59.2–61.2% of SL; distance from pelvic-fin insertion to anal-fin origin short, 15.3–17.9% of SL; dorsal-fin base short, 11.2–12.1% of SL; postorbital length short, 9.2–10.2% of SL.

**Description.** Data for holotype given in parentheses (if different). Counts and measurements, expressed as percentages of SL are shown in Tables 1 and 2. Data for holotype given in parentheses (if different). Body strongly compressed, deep, deepest at dorsal-fin origin. Dorsal contour of head and body gradually elevated from snout tip to dorsal-fin origin, hump on occiput region. Dorsal contour subsequently lowering to uppermost point of caudal-fin base. Ventral contour of head and body lowering from lower-jaw tip to pelvic-fin insertion or anal-fin origin (to pelvic-fin insertion in holotype), subsequently increasing to lowermost point of caudal-fin base. Abdomen covered with 18–20 (18) and 7 or 8 (7) scutes from isthmus to pelvic scute, and pelvic scute to anus, respectively. Abdomen scutes hard, sharp, and projecting backwards. Pectoral-fin insertion anterior to posterior margin of opercle and lower than lower margin of eye; dorsal, posterior, and ventral profiles nearly straight; posterior tip pointed, reaching to or slightly not to vertical through pelvic-fin insertion (pectoral fin damaged in holotype); uppermost fin ray unbranched, others branched. Pelvic-fin insertion anterior to dorsal-fin origin;



Fig. 7. Stained scale removed from right side of midbody (above anal fin) of *Ilisha brachysoma*, CSIRO H 8581-05, 192.0 mm SL, Jimbaran Bay, southern coast of Bali, Indonesia (left-right inverted).

posterior tip of depressed fin reaching to vertical through 4th or 5th dorsal-fin ray origin, not to anus; anteriormost fin ray unbranched, other rays branched; outer profiles of fin nearly straight (pelvic fin damaged in holotype). Dorsal fin nearly triangular, outer profiles of fin nearly straight; fin origin located near midpoint of body; initial three or four (three) rays unbranched, others branched. Anal-fin origin located just below 9th to 13th (9th) dorsal-fin ray origin; initial four rays unbranched, other rays branched. Caudal fin forked and bifurcate, but not lunate; both lobes without extended tips; outer profile of each lobe nearly straight. Anus just anterior to anal-fin origin. Lower jaw projecting anteriorly than maxilla tip. Single rows of conical teeth on premaxilla, maxilla and anterior margin of lower jaw, but not on hypomaxilla. Several rows of fine conical teeth on palatine. Band of fine teeth presenting on pterygoid. Small conical teeth patch on ectopterygoid and tongue. No teeth on vomer. Mouth large, posterior tip of maxilla beyond vertical through anterior margin of eye. Eye large, round, covered with adipose eyelid, laterally on head and dorsal to horizontal through pectoral-fin insertion, visible in dorsal view; pupil round; orbit round. Interorbital space flat, width less than eye diameter. Nostrils close to each other, anterior to orbit. Posterior margins of preopercle and opercle convex, without serrations. Gill membrane without serrations. Pseudobranchial filaments exposed, length of longest filament less than eye diameter. Gill rakers long, slender, and rough. Scales on body cycloid, thin, deciduous. Several vertical grooves on body scales; posteriormost groove crossing scale; grooves on central part meeting or overlapping at center of scale; posterior part somewhat denticulated (Fig. 7). No scales on head and fins. Axillary scales located on

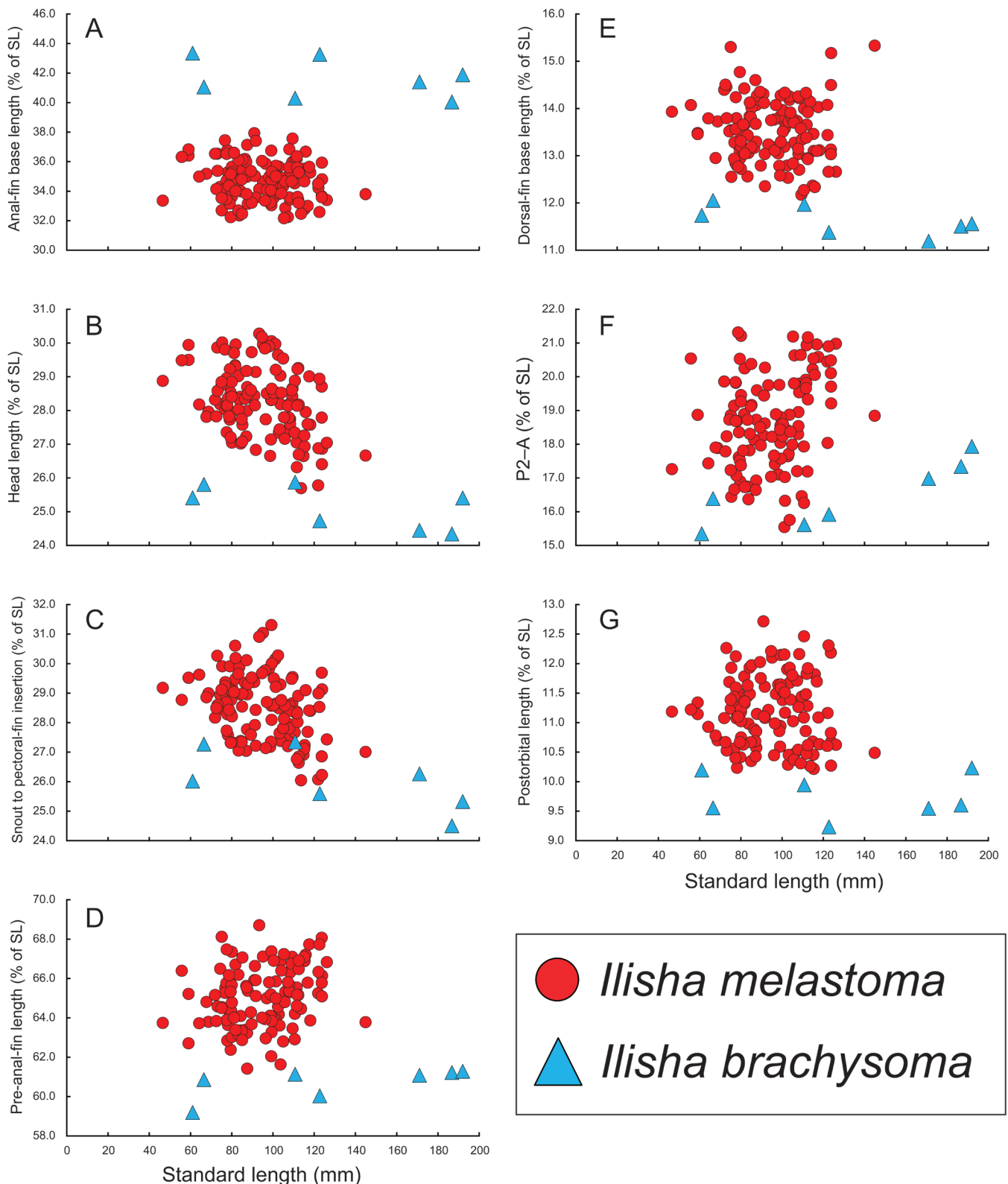


Fig. 8. Relationships of selected measurements relative to standard length (SL) versus SL in *Ilisha melastoma* (red circles) and *I. brachysoma* (blue triangles). A, anal-fin base length; B, head length; C, distance from snout to pectoral-fin insertion; D, preanal-fin length; E, dorsal-fin base; F, distance between pelvic-fin insertion and anal-fin origin (P2–A; as % of SL); and G, postorbital length.

insertions of pectoral and pelvic fins. Posterior part of swim bladder forming a pair of extensions on left and right sides.

**Colouration of fresh specimens.** (Based on a color photograph of CSIRO H 8581-05, 192.2 mm SL; Fig. 6A) Body uniformly whitish silver, upper part greyish. Dorsum

bluish black. Faint dark longitudinal band on lateral surface of body from cleithrum to just below dorsal fin. Pectoral fin whitish, upper part yellow; melanophores scattered on upper part of fin. Pelvic fin whitish. Dorsal fin dusky black, upper part yellowish; anterior margin black; basally whitish. Anal fin whitish yellow, melanophores scattered on entire fin,

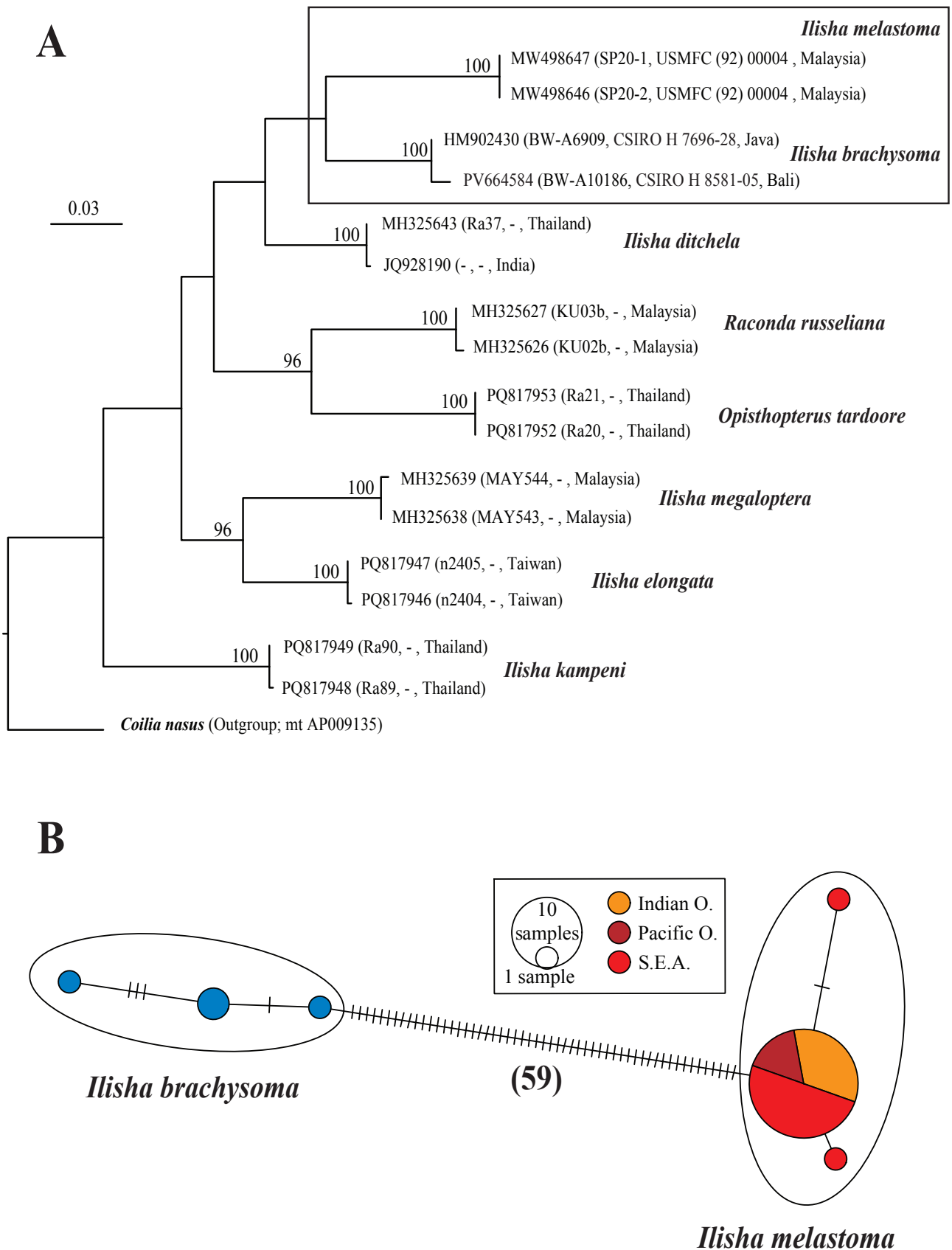


Fig. 9. A, Maximum-likelihood phylogenetic tree of eight species of Pristigasteridae (including *Ilisha brachysoma* and *Ilisha melastoma*), based on partial cytochrome oxidase I (COI) gene (651 characters). Each specimen of Pristigasteridae is identified by the GenBank number of its COI sequence followed, in parentheses, by its tissue code, voucher Museum catalogue number, and country/region of origin. Tree rooted with *Coilia nasus*. Branch lengths proportional to number of nucleotide changes (Scale bar represents the number of nucleotide changes per site); numbers above the corresponding nodes indicate bootstrap proportions (when above 75%). B, Median-joining network showing relationships among 31 mitochondrial DNA (COI) haplotypes of *Ilisha brachysoma* (blue dots [Java and Bali]) and *Ilisha melastoma* (red [Southeast Asia (S.E.A.)], deep red [Pacific Ocean (Pacific O.)] and orange [Indian Ocean (Indian O.)] dots). Each circle represents a unique haplotype, with size proportional to total frequency. Each cross-bar on branches represents a single nucleotide change.



but not on posterior part. Caudal fin blackish yellow, outer margin of fin jet black. Iris silver, pupil black. In juvenile (based on a color photograph of CSIRO H 7696-28, 61.0 mm SL; Fig. 6B), body uniformly silver, dorsum yellowish pale. Melanophores sparsely scattered on dorsum and both jaws. Posteroventral part of lateral surface of body (just above anal fin) semi-transparent, yellowish pale. Snout and both jaws semi-transparent, yellowish. Opercle uniformly silver. Cleithrum yellowish. Pectoral fin transparent, upperpart yellow. Pelvic fin translucent, colorless. Dorsal fin yellowish, melanophores scattered along fin rays. Anal fin semi-transparent, marginally yellowish; melanophores scattered on anterior and ventral margin of fin. Caudal fin yellow, upper, lower, and posterior margins of fin black.

**Colouration of preserved specimens.** Body uniformly pale, light ivory, or silver (silver in holotype). Melanophores densely scattered on dorsum to lateral surface of body, reaching to level of center of eye, sometimes beyond level of pectoral-fin insertion (difficult to see when guanine remains on body surface including holotype). Melanophores scattered along fin rays of dorsal and caudal fins but not on fin rays of pelvic and anal fins. Melanophores scattered on 3rd to 6th pectoral-fin rays from uppermost ray in specimens > 170 mm SL (not scattered specimens < 110 mm SL). Melanophores scattered on gill rakers, first gill arch, inner surfaces of hyoid arch and preopercle and opercle. Iris silver, pupil black.

**Distribution.** *Ilisha brachysoma* is currently known only from southern Indonesian waters from Sumatra to Bali. Most examined specimens were collected from the Indian Ocean side (Fig. 4).

**Morphological comparisons.** *Ilisha brachysoma* can be distinguished from *I. melastoma* by having more anal-fin rays (total anal-fin rays 46–47 in *I. brachysoma* vs. 36–43 in *I. melastoma*; Tables 1, 4), longer anal-fin base (40.1–43.4% of SL vs. 32.2–37.9%), shorter head (24.3–25.9% of SL vs. 25.7–30.3%), distance from snout to pectoral-fin insertion (24.5–27.4% of SL vs. 26.0–31.1%), preanal-fin length (59.2–61.1% of SL vs. 61.4–68.7%), dorsal-fin base (11.2–12.1% of SL vs. 12.2–15.3%), distance between pelvic-fin insertion and anal-fin origin (15.4–17.9% of SL vs. 15.5–21.3%), and postorbital length (9.2–10.2% of SL vs. 10.2–12.7%) (Fig. 8).

**Molecular comparisons.** Our maximum likelihood phylogenetic tree recovers a sister-group relationship between *I. brachysoma* and *I. melastoma* (Fig. 9A). Both species are separated from each other by a mean uncorrected mitochondrial COI genetic distance of 10.7%. This is well-above the commonly used intra- versus inter-specific threshold of 2–3% in fishes (e.g., April et al., 2011). The unrooted median-joining network (Fig. 9B) shows the relationships among the COI haplotypes of both species. The haplotypes of the two species are separated by a minimum of 59 nucleotide differences. The 27 COI sequences of *Ilisha melastoma* comprise only three unique haplotypes, with the most common one shared from Indian Ocean to the

Pacific Ocean, evidencing low geographical differentiation throughout the distribution of this species.

**Remarks.** *Ilisha brachysoma* was originally described by Bleeker (1852) as *Pellona brachysoma* based on a specimen collected from Jakarta, Java, Indonesia. Since Whitehead (1972) considered the nominal species as a junior synonym of *I. melastoma*, many studies have followed this (e.g., Talwar & Kacker, 1984; Munroe et al., 1999; Kottelat, 2013; Anderson, 2022), however, the validity of *I. brachysoma* is confirmed in the present study. Although Gloerfelt-Tarp & Kailora (1984, 2022) reported an illustration of a pristigasterid specimen collected from the Indonesian coast (the area between Sumatra and Bali) as *Ilisha melastoma*, they showed its anal-fin ray count as 35–48, therefore their *I. melastoma* probably includes *I. brachysoma*. In this study, *I. melastoma* was not observed along the southern coast of Indonesia where most populations of *I. brachysoma* are recorded, suggesting either ecological competitive exclusion or the presence of a geographic barrier. *Ilisha brachysoma* and *I. melastoma* perhaps originated from an allopatric or peripatric speciation event. In addition, *I. melastoma* is distributed over a very wide area in the Indo-Pacific, while *I. brachysoma* is distributed only in a localized area (Fig. 4), which may reflect differences in the reproductive strategies of the two species. However, there is no biological or life history information available on *I. brachysoma*, and further investigation is required.

**Comparative material examined.** *Ilisha lunula* (5 specimens: 67.8–161.6 mm SL): ANSP 122297, 67.8 mm SL, estuary of Byone River, Gulf of Carpentaria, Queensland, Australia; CSIRO B4111, holotype of *Ilisha lunula*, 137.8 mm SL, south of Wessel Islands, Northern Territory, Australia (11°41'S, 136°20'E); CSIRO H 7690-03, 105.4 mm SL, northeast of Broad Sound, Queensland, Australia (21°54'52.2"S, 150°01'58.2"E), 21 m depth; CSIRO H 8827-05, 137.3 mm SL, Kerema Bay, Gulf of Papua, Papua New Guinea (8°02'07.2"S, 145°45'21.0"E), 14 m depth; CSIRO H 8845-10, 105.4 mm SL, off Purari, Gulf of Papua, Papua New Guinea (7°55'06.6"S, 145°03'52.2"E), 16 m depth. *Ilisha ditchela*: BMNH 1968.8.26.2, neotype of *Pellona ditchela* (also holotype of *Ilisha striatula*), 135.8 mm SL, off Pakistan, Arabian Sea (25°11'N, 66°20'E).

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