

Article

Taxonomic Status of Nominal Species of the Long-Fin Herring Genus *Ilisha* Previously Regarded as Synonyms of *Ilisha megalopectera* (Swainson, 1839) (Teleostei: Clupeiformes: Pristigasteridae)

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Abstract

Numerous specimens of long-fin herrings (ilishas), previously identified as *Ilisha megalopectera* (Swainson, 1839) because of their asymmetrical swimbladder, deep body, and few ventral scutes, were examined and found to represent three valid species: *Ilisha motius* (Hamilton, 1822) (frequently treated as a *nomen dubium*; distributed in rivers flowing into the Bay of Bengal), true *I. megalopectera* (eastern coast of India to Andaman Sea), and *Ilisha russellii* (Bleeker, 1852) (previously regarded as a junior synonym of *I. megalopectera*; distributed from Malacca Strait to Borneo). Each species is redescribed in detail based on specimens collected from throughout the range of each taxon. Due to the highly diverse shape of its swimbladder, the phylogenetic position of *I. motius* is still unclear. Reference COI “barcode” fragments are currently only available for *I. russellii*, preventing molecular confirmation.

Keywords: clupeomorpha; ganges; *Ilisha motius*; *Ilisha russellii*; swimbladder; taxonomy

1. Introduction

The genus *Ilisha* Richardson, 1846 (Clupeiformes: Pristigasteridae), a genus of long-fin herrings (ilishas) characterized by the presence of dorsal and pelvic fins, an anal fin with 53 or fewer fin rays, and a hypomaxilla without teeth, currently comprises 17 species (Wongratana 1983 [1]; Whitehead 1985 [2]; Kailola 1986 [3]; Randall 1994 [4]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]; this study). According to Whitehead (1985) [2], all specimens with asymmetrical swimbladders and 34 or more ventral scutes belong to a single species widely distributed in the Indo-West Pacific, *Ilisha megalopectera* (Swainson, 1839). However, taxonomic confusion is observed within *I. megalopectera*. Whitehead (1985) [1] regarded *Clupanodon motius* Hamilton, 1822 and *Platygaster macrophthalma* Swainson, 1838, nominal species described earlier than *I. megalopectera*, as a *nomen dubium* and a *nomen oblatum*, respectively, without sufficient discussion or application regarding these measures. In this study, we undertook an examination of specimens previously identified as *I. megalopectera* collected from throughout its wide-established range. The examination revealed that three allopatric species are included in what had previously been identified as *I. megalopectera* and the taxonomic status of all nominal species related to *I. megalopectera* was assessed and settled.



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2. Materials and Methods

Counts and measurements follow Hata and Motomura (2019) [7]. All measurements were made to the nearest 0.01 mm using digital calipers and were taken from all available specimens. The exception is the holotype of *Ilisha bleekeri* Bertin, 1941 (BMNH 1867.11.28.19), which was only accessible for standard length and some meristic data. “Pelvic scute” refers to a scute associated with the pelvic girdle, and “prepelvic scute” and “postpelvic scute” refer 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. Osteological characters were observed on soft X-ray photographs (duraSCAN 1417 made by Biosenstech, Yongin, Republic of Korea, and PXS5-927EA Microfocus X-Ray Source manufactured by ThermoFisher, Waltham, MA, USA). The pattern of grooves on body scales was observed after staining the scales with Alizarin Red S. The shape of the swimbladder was observed by making an incision in the lateral surfaces of the body just above the anal-fin origin. Institutional codes follow Fricke and Eschmeyer (2026) [8].

Of the three species treated in this study, we were only able to collect tissue samples for genetic sequencing from four specimens of *Ilisha russellii* (Bleeker, 1852) collected in Malaysian marine waters. From these tissue samples, we generated reference “barcode” fragments (648 base-pairs) of the COI gene for this species. Genomic DNA was extracted from ethanol-preserved tissue fin clips. Polymerase chain reaction (PCR) amplification and sequencing of the COI gene followed standard protocols (Ward et al., 2005) [9], with annealing at 55 °C. Amplification of the partial COI gene used the following primers: forward COI_FishF1 (5'-TCA ACC AAC CAC AAA GAC ATT GGC AC-3') and reverse COI_FishR2 (5'-ACT TCA GGG TGA CCG AAG AAT CAG AA-3') (Ward et al., 2005) [9]. PCR products were sent to Apical Scientific Sdn. Bhd. (Selangor, Malaysia) for purification and bi-directional sequencing by Sanger Sequencing technology using the same PCR primers. Raw forward and reverse sequences were de novo assembled in MEGA 12.1 (Stecher et al., 2026) [10]. Consensus sequences generated in this study have been deposited in the GenBank database. The alignment of these four sequences was performed manually and did not require the introduction of indels; therefore, it resulted in an alignment of 648 nucleotide positions.

3. Results

3.1. *Ilisha motius* (Hamilton, 1822)

[New English name: Indian River Ilisha]

(Figures 1–3 and Tables 1–3)

Clupanodon motius Hamilton, 1822 [11]: 252 (original type locality: Brahmaputra River, Ganges branch, India; type locality: Pulta, West Bengal, India, based on the neotype designated in this study).

Clupea motius: Gray 1834 [12]: pl. 91, figures 3 and 4 (showing an illustration by F. Hamilton; Brahmaputra River, Ganges branch, India).

Clupea (Platygaster) parva Swainson, 1839 [13]: 294 [original locality: Brahmaputra River, Ganges branch, India, based on figure 3 in pl. 91 of Gray (1834) [12]; type locality: Pulta, West Bengal, India, based on the neotype designated in this study].

Pellona motius: Günther 1868 [14]: 456 (in part: Bengal); Day 1875 [15]: 643, figure 3 in pl. CLXV [Assam, Bengal and Odisha (currently Orissa), India]; Day 1889 [16]: 381 [Assam, Bengal and Orissa (Odisha), India].

Ilisha motius: Norman 1923 [17]: 5 (Assam and Bengal); Velappan Nair 1953 [18]: 124 (India); ?Misra 1976 [19]: 81 (Bay of Bengal).

Ilisha melastoma (not of Bloch and Schneider): Venkateswarlu and Menon 1979 [20]: 48 (Ganges).

Ilisha megaloptera: Whitehead 1985 [2]: 270 (in part: Bay of Bengal); Munroe et al., 1999 [5]: 1763 (in part Bay of Bengal).

Neotype. CAS-SU 35625, also neotype of *Clupea parva*, 71.7 mm SL, Pulta, West Bengal, India, 9 Apr. 1937, coll. A. W. Herre.

Other materials examined. 41 specimens, 60.8–77.0 mm SL. CAS 251386, 32 specimens, 60.8–76.7 mm SL, collected with the neotype; CAS 35716, 8 specimens, 65.0–77.0 mm SL, Pulta, Bengal, India, 9 Apr. 1937, coll. A. W. Herre; USNM 165088, 74.7 mm SL, Pulta, West Bengal, India.

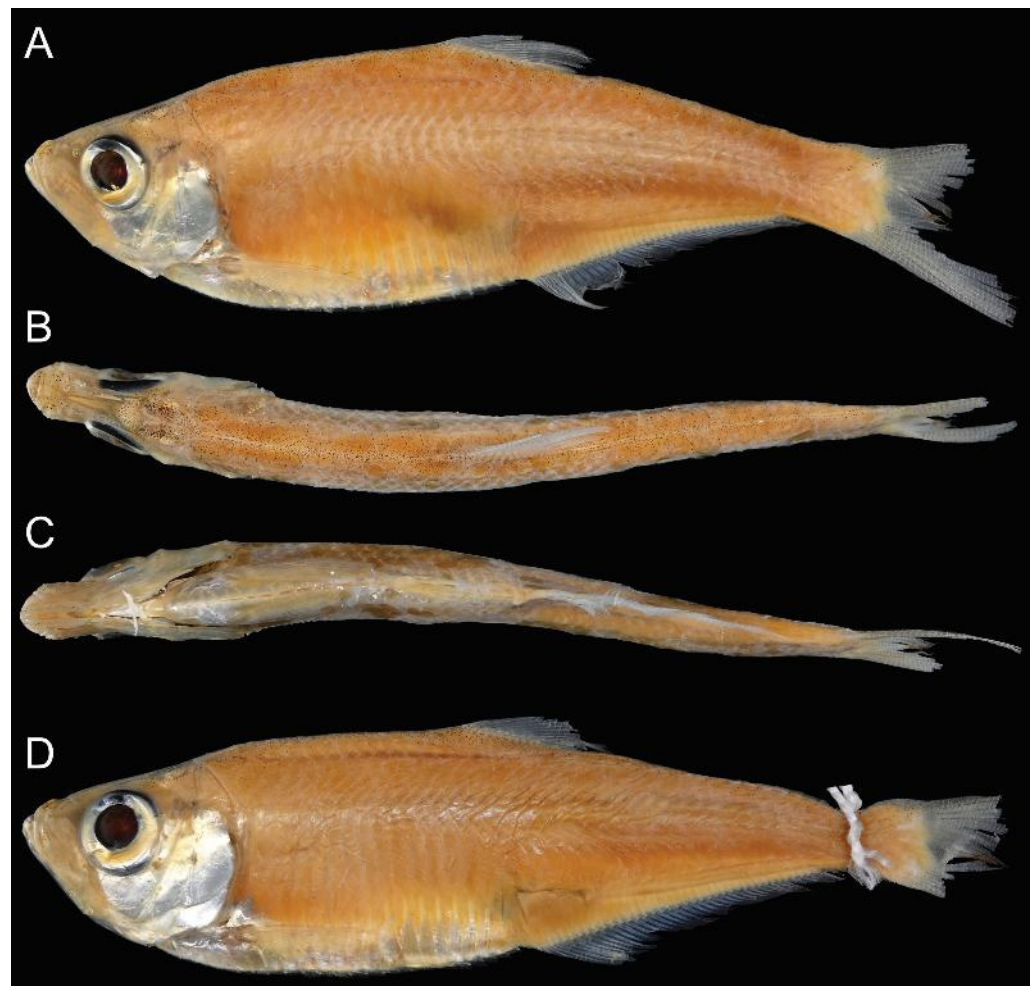


Figure 1. (A) Lateral, (B) dorsal, and (C) ventral views of neotype of *Clupanodon motius* (CAS-SU 35625, 71.7 mm SL, Pulta, West Bengal, India; also neotype of *Clupea parva*) and (D) lateral view of non-type specimen (CAS 251386, 74.5 mm SL, Pulta, West Bengal, India).



Figure 2. Stained scale removed from right side of midbody (above anal fin) of neotype of *Ilisha motius* (CAS-SU 35625, 71.7 mm SL, Pulta, West Bengal, India; left-right inverted).

Diagnosis. A species of *Ilisha* with the following combination of characters: body somewhat elongated, 27.0–31.5% of SL, distance between dorsal-fin origin and pelvic-fin insertion 27.5–31.9% of SL, distance between origins of dorsal and anal fins 27.0–30.8% of SL; head short, 24.5–27.1% of SL; postorbital length short, 9.3–10.9% of SL; abdomen covered with 17–20 + 7–9 = 24–28 scutes; dorsal fin with 15–17 rays, its base short, 10.1–11.3% of SL; anal fin with 36–43 rays, its base short, 32.1–35.4% of SL; scales rows in longitudinal series 37–40; pectoral fin long, 18.1–19.8% of SL, with 13–15 rays; pelvic fin short, 7.6–8.5% of SL, its posterior tip posteriorly not reaching to vertical through dorsal-fin origin when depressed; maxilla short, 11.3–13.1% of SL, without distinct lobe; lower jaw somewhat short, 12.8–14.1% of SL; caudal peduncle long, 8.5–10.1% of SL; grooves on body scales not overlapping at center; 1UGR 10–13, 1LGR 23–26, 1TGR 34–37; 2UGR 8–9, 2LGR 21–23, 2TGR 29–32; pseudobranchial filaments 13–17; shape of swimbladder variable, with (or without) single (or double) tube; maximum standard length approx. 8 cm.

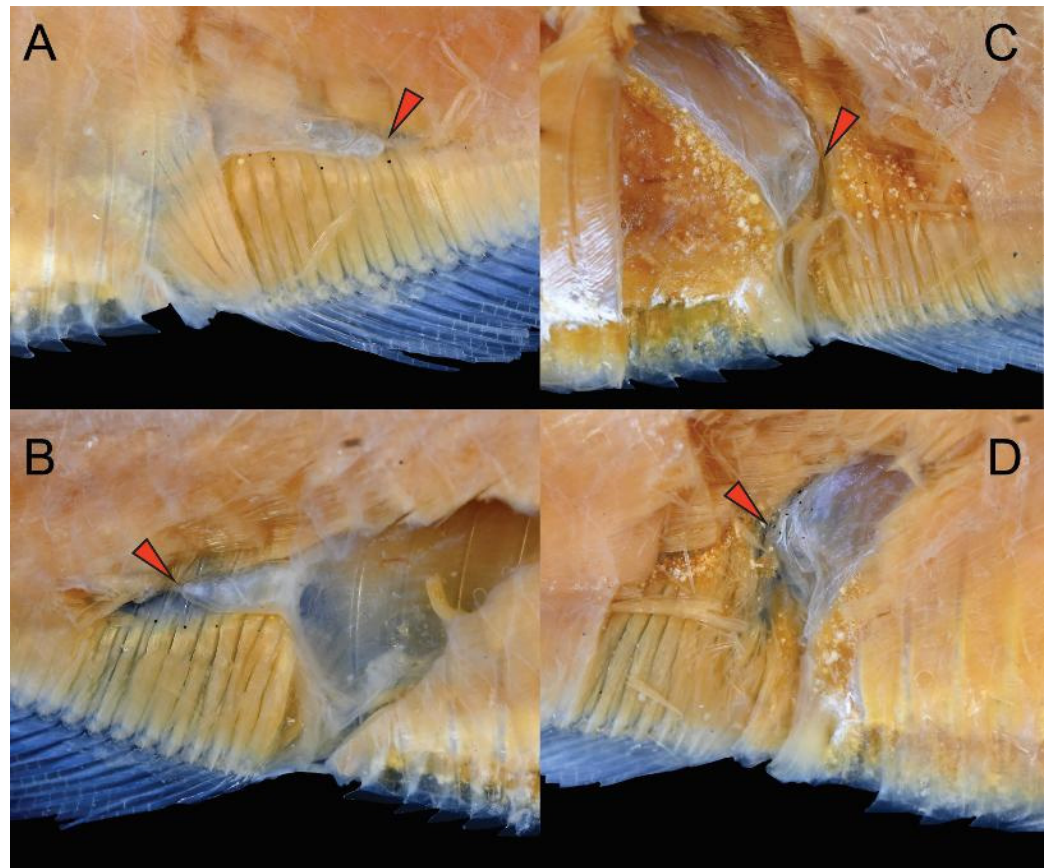


Figure 3. Variation in form of swimbladder of preserved specimens of *Ilisha motius* (red triangle indicating posterior tip of swimbladder): (A) left and (B) right sides of CAS 251386, 60.8 mm SL, Pulta, West Bengal, India (posterior portion of both sides extended); (C) left and (D) sides of CAS 251386, 75.1 mm SL, Pulta, West Bengal, India (posterior portion of both sides without extension).

Description. Counts and measurements (expressed as percentages of SL) are shown in Tables 1 and 2. Data for neotype of *Clupanodon motius* (also neotype of *Clupea parva*) given in parentheses (if different). Body strongly compressed, somewhat deep, deepest at dorsal-fin origin. Dorsal contour of body gradually elevated from snout tip to dorsal-fin origin thereafter gently decreased to uppermost point of caudal-fin base. Ventral profile of body lowering from lower-jaw tip to pelvic-fin insertion and subsequently rising to lowermost point of caudal-fin base. Abdomen covered with 17–20 (19) and 7–9 (8) scutes from isthmus to pelvic scute, and pelvic scute to anus, respectively. Abdomen scutes hard, sharp, and projected backwards. Pectoral-fin insertion slightly anterior to posterior margin of opercle and lower than lower margin of eye; pectoral fin triangular, 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. Single elongated axillary scale located just above pectoral fin. Pelvic-fin insertion anterior to dorsal-fin origin; posterior tip of depressed fin not reaching to vertical through dorsal-fin origin and to anus; anterior-most fin ray unbranched, other rays branched; outer profiles of fin nearly straight. Single triangular axillary scale located just above pelvic fin. 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 10th to 13th dorsal-fin ray origin (just below origin of 12th dorsal-fin ray); initial three or four (four) rays unbranched, other rays branched; contour of fin lowering from fin origin to last unbranched fin ray, thereafter parallel to fin base. Elongated sheath scales on bases of dorsal and anal fins. Caudal fin forked and bifurcate, but not lunate; both lobes

without extended tips; outer profile of each lobe nearly straight; posterior tips of both lobes pointed. Small scales densely present on caudal fin. Anus just anterior to anal-fin origin. Lower jaw projecting anteriorly than maxilla tip. Single rows of conical teeth on premaxilla, maxilla, palatine, and anterior margin of lower jaw, but not on hypomaxilla. Band of fine teeth present on pterygoid. Small conical teeth sparsely present on 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; only few grooves on scales on lateral surface of body; posteriormost one crossing scale vertically; other grooves not meeting or overlapping at center of scale, posterior margin not denticulated (Figure 2). Swimbladder shape variable; of the 18 specimens whose swimbladder shape was observed in this study, eight specimens have swimbladder without extension, five specimens have swimbladder with short posterior extensions on both sides, four have short posterior extension only on right side, and only one specimen has short posterior extension only on right side (Figure 3).

Table 1. Counts of specimens of *Ilisha motilus*.

	Neotype	Non-Types	Modes
	CAS-SU 35625	<i>n</i> = 41	
Standard length (mm)	71.7	60.8–77.0	
Unbranched dorsal-fin rays	3	3–4	3
Branched dorsal-fin rays	13	12–13	12
Total dorsal-fin rays	16	15–17	16
Unbranched anal-fin rays	4	3–4	4
Branched anal-fin rays	37	34–39	37
Total anal-fin rays	41	36–43	41
Unbranched pectoral-fin rays	1	1	1
Branched pectoral-fin rays	13	12–14	13
Total pectoral-fin rays	14	13–15	14
Unbranched pelvic-fin rays	1	1	1
Branched pelvic-fin rays	6	6	6
Total pelvic-fin rays	7	7	7
Gill rakers on 1st gill arch (upper)	12	10–13	11
Gill rakers on 1st gill arch (lower)	25	23–26	25
Gill rakers on 1st gill arch (total)	37	34–37	36
Gill rakers on 2nd gill arch (upper)	9	8–9	9
Gill rakers on 2nd gill arch (lower)	22	21–23	22
Gill rakers on 2nd gill arch (total)	31	29–32	31
Gill rakers on 3rd gill arch (upper)	7	6–9	7
Gill rakers on 3rd gill arch (lower)	15	13–16	14
Gill rakers on 3rd gill arch (total)	22	20–24	22
Gill rakers on 4th gill arch (upper)	5	5–6	6
Gill rakers on 4th gill arch (lower)	10	10–12	11
Gill rakers on 4th gill arch (total)	15	16–18	17
Gill rakers on posterior surface of 3rd fill arch	3	2–4	3

Table 1. Cont.

	Neotype	Non-Types	
Prepelvic scutes	19	17–20	19
Postpelvic scutes	8	7–9	8
Total pelvic scutes	27	24–28	27
Scales rows in longitudinal series	38	37–40	38
Transverse scales	12	11–13	12
Pseudobranchial filaments	15	13–17	13
Number of dorsal-fin rays before anal-fin origin	12	10–13	11
Pectoral-fin rays with melanophores	0	0–1	0

Table 2. Morphometrics of specimens of *Ilisha motius*.

	Neotype	Non-Types	
	CAS-SU 35625	<i>n</i> = 41	
Standard length (mm; SL)	71.7	60.8–77.0	Means
As % of SL			
Head length	25.9	24.5–27.1	25.4
Body depth	30.8	27.0–31.5	29.4
Pre-dorsal-fin length	50.8	47.7–51.3	49.9
Snout tip to pectoral-fin insertion	26.4	24.6–29.1	26.1
Snout tip to pelvic-fin insertion	46.1	43.7–47.8	45.9
Snout tip to anal-fin origin	63.0	60.6–64.8	62.8
Dorsal-fin base length	11.1	10.1–11.3	10.7
Anal-fin base length	34.4	32.1–35.4	34.1
Caudal-peduncle length	9.4	8.5–10.1	9.3
Caudal-peduncle depth	8.8	8.1–9.7	8.9
D–P1	38.5	35.6–38.6	37.3
D–P2	30.0	27.5–31.9	29.7
D–A	30.0	27.0–30.8	29.0
P1–P2	21.4	19.2–22.2	20.5
P2–A	18.9	16.5–19.9	18.6
Pectoral-fin length	18.9	18.1–19.8	18.8
Pelvic-fin length	8.1	7.6–8.5	8.1
Maxilla length	12.0	11.3–13.1	12.2
Mandibular length	13.8	12.8–14.1	13.5
Postorbital length	10.2	9.3–10.9	9.9

Coloration of preserved specimens. Body light uniformly brown, ventral surface silver in some specimens. Silver longitudinal band narrower than eye diameter running from cleithrum to caudal-fin base. Cheek and opercle silver. Snout and both jaws semi-transparent. Melanophores sparsely scattered on dorsum to upper part of lateral surface of body, just reaching to level of upper margin of eye. Double pigmented lines dorsally posterior to dorsal fin. Few melanophores scattered on lower-jaw tip and snout. A pair of distinct dark patches on parietal region. Melanophores scattered along fin rays of dorsal and caudal fins, but not on pelvic and anal fins. Pectoral fin without melanophores or only scattered on uppermost fin ray (no melanophores in neotype). Melanophores scattered on gill arch, inner surface of hyoid arch, and inner surface of opercle above pseudobranch, and not on gill rakers and gill filaments. Lower-jaw tip black. No melanophores on mouth roof, tongue, and mouth floor. Swimbladder uniformly whitish silver. Dorsal surface of eyes brown. Iris silver, pupil black. Fresh coloration unknown. According to Hamilton (1822) [11], the original description, fresh coloration of the species generally

silver; longitudinal stripe on lateral surface of body much brighter than other regions; caudal fin yellow with black posterior margin.

Table 3. Frequency distribution of total ventral scutes, total dorsal-fin rays, total pectoral-fin rays, total anal-fin rays, scale rows in longitudinal series, and vertebrae in *Ilisha motius*, *Ilisha megaloptera*, and *Ilisha russellii*.

		Total Ventral Scutes																	
		24	25	26	27	28	29	30	31	32	33	34							
<i>Ilisha motius</i>	<i>n</i> = 42	2	7	13	18	2													
<i>Ilisha megaloptera</i>	<i>n</i> = 19							6	6	4	1	2							
<i>Ilisha russellii</i>	<i>n</i> = 66					1	3	29	25	4	3	1							
		Total dorsal-fin rays																	
		15		16		17		18		19									
<i>Ilisha motius</i>	<i>n</i> = 42	18		22		2													
<i>Ilisha megaloptera</i>	<i>n</i> = 19			2		13		4											
<i>Ilisha russellii</i>	<i>n</i> = 66			2		33		25		6									
		Total pectoral-fin rays																	
		13		14		15	16	17	18		19								
<i>Ilisha motius</i>	<i>n</i> = 42	10		29		3													
<i>Ilisha megaloptera</i>	<i>n</i> = 18					2	6	6	4										
<i>Ilisha russellii</i>	<i>n</i> = 67						20	38	8		1								
		Total anal-fin rays																	
		36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	
<i>Ilisha motius</i>	<i>n</i> = 41	3	3	5	4	6	13	4	3										
<i>Ilisha megaloptera</i>	<i>n</i> = 19								1	2	4	4	1	3	1	2		1	
<i>Ilisha russellii</i>	<i>n</i> = 66			2	8	8	16	18	12	2									
		Scale rows in longitudinal series																	
		37	38	39	40	41	42	43	44	45	46	47	48						
<i>Ilisha motius</i>	<i>n</i> = 42	2	23	14	3														
<i>Ilisha megaloptera</i>	<i>n</i> = 18									1	6	4	5		2				
<i>Ilisha russellii</i>	<i>n</i> = 63		4	13	10	26	10												
		Vertebrae																	
		44		45		46		47		48		49		50					
<i>Ilisha megaloptera</i>	<i>n</i> = 14							7		2		3		2					
<i>Ilisha russellii</i>	<i>n</i> = 11	3		7		1													

Distribution and biological information. Currently known from Ganges Basin including Brahmaputra River (Hamilton, 1822 [11]; this study). Moreover, the species is also distributed in Odisha and Assam, India (Day 1875 [15], 1889 [16]) (Figure 4). According to Day (1875) [15], it is a freshwater species, “descending as low as the coast.” Day (1875) [15] gave its size as not much over 4 inches, i.e., approx. 10 cm SL. Ovarian eggs (round shape, ca. 0.3 mm diameter) were found in several present specimens in this study (CAS 251386), indicating that the species is mature at <73 mm SL. This also aligns well with Day’s (1875) [15] description.

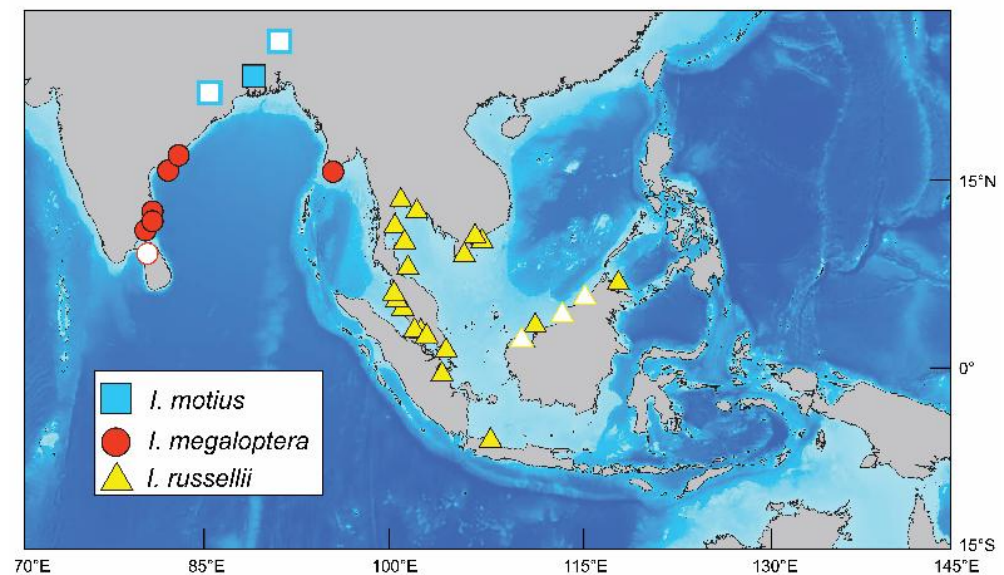


Figure 4. Distributional records of *Ilisha motius* (blue squares), *Ilisha megaloptera* (red circles), and *Ilisha russellii* (yellow triangles). Closed and open symbols indicate records based on examined specimen in this study and literature records, respectively.

Morphological comparisons. Although the shape of the swimbladder has been regarded as a major character for species identification of the genus *Ilisha*, it is observed to be quite variable in *I. motius* (see the Description section). However, *I. motius* can be diagnosed by its lower counts of ventral scutes. Following this study, the genus *Ilisha* includes 19 species (Wongratana 1983 [1]; Whitehead 1985 [2]; Kailola 1986 [3]; Randall 1994 [4]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]). *Ilisha motius* can be distinguished from all other congeners except *Ilisha kampeni* (Weber and de Beaufort, 1913) by having fewer ventral scutes (24–28) and elongated body (27.0–31.5% of SL).

Ilisha motius differs from *I. kampeni* in having a longer pectoral fin (18.1–19.8% of SL in *I. motius* vs. 15.0–16.9% in *I. kampeni*; Wongratana 1983 [1]; Whitehead 1985 [2]; Munroe et al., 1999 [5]; this study). Moreover, *I. motius* can be distinguished from *I. megaloptera* and *I. russellii*, which were previously considered to be conspecific, by having more gill rakers on first gill arch (1TGR 34–37 in *I. motius* vs. 27–32 in *I. megaloptera*; 30–34 in *I. russellii*; Figure 5A) and second gill arch (2TGR 29–32 vs. 23–29 in *I. megaloptera*; 24–29 in *I. russellii*; Figure 5B), fewer ventral scutes (24–28 vs. 30–34 in *I. megaloptera*; 28–33 in *I. russellii*; Table 3), pseudobranchial filaments (13–17 vs. 15–20 in *I. megaloptera*; 18–25 in *I. russellii*; Figure 5C), total dorsal-fin rays (15–17 vs. 16–18 in *I. megaloptera*; 16–19 in *I. russellii*; Table 3), and total pectoral-fin rays (13–15 vs. 15–18 in *I. megaloptera*; 16–19 in *I. russellii*; Table 3), slender body (body depth 27.0–31.5% of SL in *I. motius* vs. 31.7–35.1% in *I. megaloptera*; 30.1–34.9% in *I. russellii*; Figure 5D; D–P2 27.5–31.9% of SL in *I. motius* vs. 32.1–35.2% in *I. megaloptera*; 30.2–35.2% in *I. russellii*; Figure 5E; D–A 27.0–30.8% of SL in *I. motius* vs. 30.5–35.6% in *I. megaloptera*; 30.0–34.2% in *I. russellii*; Figure 5F), and shorter maxilla (11.3–13.1% of SL vs. 13.0–15.4 in *I. megaloptera*; 13.9–15.9% in *I. russellii*; Figure 5G). In addition, *I. motius* also differs from *I. megaloptera* in having anal fin with fewer fin rays (total anal-fin rays 36–43 in *I. motius* vs. 43–52 in *I. megaloptera*; Table 3) and shorter fin base (32.1–35.4% of SL vs. 37.6–40.9%; Figure 5H), longer caudal peduncle (8.5–10.1% of SL vs. 6.3–8.5%; Figure 5I), and fewer scale rows in longitudinal series (37–40 vs. 44–48; Table 3). *Ilisha motius* further differs from *I. russellii* in having shorter dorsal-fin base (10.1–11.3% of SL vs. 11.1–12.9% in *I. russellii*; Figure 5J), head (24.5–27.1% of SL vs. 26.9–27.8%; Figure 5K), postorbit area (9.3–10.9% of SL vs. 10.8–13.3%; Figure 5L), and lower jaw (12.8–14.1% of SL vs. 14.2–16.3%; Figure 5M).

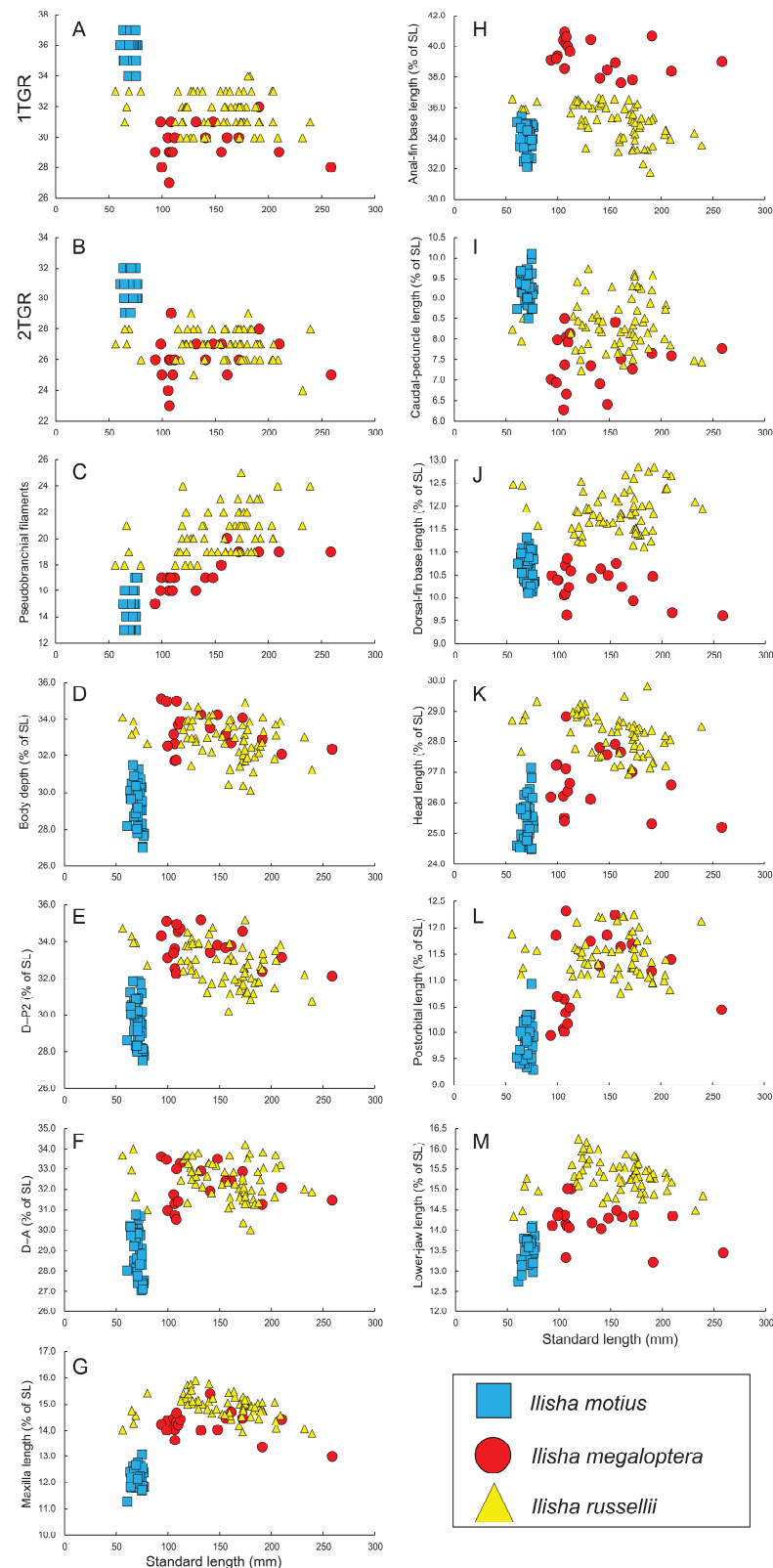


Figure 5. Relationships of (A) total gill-raker numbers on first gill arch (1TGR), (B) second arch, (C) pseudobranchial filaments, (D) body depth [% of standard length (SL)], (E) distance between dorsal-fin origin and pelvic-fin insertion (D–P2) (as % of SL), (F) distance between origins of dorsal and anal fins (D–A) (as % of SL), (G) maxilla length (as % of SL), (H) anal-fin base length (as % of SL), (I) caudal-peduncle length (as % of SL), (J) dorsal-fin base length (as % of SL), (K) head length (as % of SL), (L) postorbital length (as % of SL), and (M) lower-jaw length (as % of SL) to SL in *Ilisha motius* (blue squares), *I. megaloptera* (red circles), and *I. russellii* (yellow triangles).

Remarks. *Ilisha motius* was first described by Hamilton (1822) [11] as *Clupanodon motius*, based on a specimen collected from Brahmaputra River, a branch of the Ganges, India. Subsequently, his unpublished illustration of *C. motius* was published by Gray (1834 [12]: pl. 91, figures 3, 4 and 6) (Kottelat 2013 [21]; Fricke et al., 2026 [22]). According to Hamilton (1822) [11] and the illustration (Figure 6), the species has pectoral fins with 14 or 15 rays, anal fin with 43 rays originated as below posterior part of dorsal-fin base, and dorsal fin with 15 rays, therefore the species is considered to belong to *I. motius* as determined and defined in this study. Following Gray (1834) [12], Swainson (1839) [13] described his new species, *Clupea (Platygaster) parva*, based on the illustration of *C. motius* in Gray (1834) [12]. Since *Clupanodon motius* and *Clupea parva* were described based on the same specimen (or the illustration based on the specimen), they are the same species. Subsequently, the species has been reported from several rivers flowing into the northern part of the Bay of Bengal. Valenciennes (1847) [23] reported a single specimen (MNHN 5387) collected from Ganges estuary as *Pellona motius*, which was reidentified as *Ilisha filigera* (Valenciennes, 1847) by Whitehead (1967) [24]. Günther 1868 [14] regarded *C. motius* as a senior synonym of *I. megaloptera*. However, the taxonomic status of the nominal species was unstable. Although Whitehead (1967) [24] described the nominal species as having “doubtful status”, Whitehead (1972) [25] and Venkateswarlu and Menon (1979) [20] indicated *C. motius* was a junior synonym of *Ilisha melastoma* (Bloch and Schneider, 1801) [*Ilisha motius* can easily be distinguished from *I. melastoma* by having narrower body (27.0–31.5% of SL in *I. motius* vs. 36.2–43.1% in *I. melastoma*) and grooves on striae on body scales not meeting at center (vs. meeting or overlapping at center of scales) (Hata et al., 2025 [6]; this study)]. Whitehead (1985) [2] referred to *C. motius* as a *nomen dubium*, and while he speculated that the nominal species might be an older synonym of *Ilisha megaloptera*, he did not consider *C. motius* as a valid name. In addition, Kottelat (2013) [21] suggested that *C. motius* should be declared as a *nomen oblitus*, but he did not conduct a detailed examination. Because this nominal species has been used as a valid species in several publications such as in Norman (1923) [17], Velappan Nair 1953 [18], and Misra 1976 [19] (see the synonym list), it cannot be declared as a *nomen oblitus*. Furthermore, because the specimen used by Hamilton (1822; also basis of the description of *C. parva* Swainson, 1839) [11] to describe *C. motius* has not been preserved (Kottelat 2013 [21]; Fricke et al., 2026 [22]), a specimen collected from Pulta, West Bengal, India (CAS-SU 35635, 71.7 mm SL; Figure 1A–C and Figure 2) is herein designated as the neotype of *C. motius* and *C. parva*. Therefore, *C. parva* is now reassigned as a junior objective synonym of *C. motius*.

The existence of *I. motius* has been completely overlooked for a long period. In the comprehensive taxonomic revision of the genus by Whitehead (1985) [2], the species appeared to be confused with *I. megaloptera* and *I. russellii*. Although biological information on *I. motius* is almost entirely lacking, the fact that the specimens of *I. motius* examined in this study were collected from the Hooghly River near Kolkata, India, suggests that this species inhabits freshwater environments [also, see statements by Day (1875 [15], 1889 [16])]. Most species of *Ilisha* inhabit coastal waters, and although some species enter estuaries, only two freshwater species are known: *Ilisha amazonica* (Miranda Ribeiro, 1920) distributed in the Amazon River Basin and *I. novacula* occurring in the Irrawady River Basin (Whithead 1985 [2]). Whitehead’s (1985) [2] description of the habitat and biology of *I. megaloptera* clearly conflates those of three species, *I. motius*, *I. megaloptera*, and *I. russellii*.

The biology of *I. motius*, a small freshwater species (<8 cm SL), is thought to differ significantly from that of the other two medium-sized marine species (>20 cm SL). The biology of *I. russellii* is summarized in detail in Blaber et al. (1998) [26].

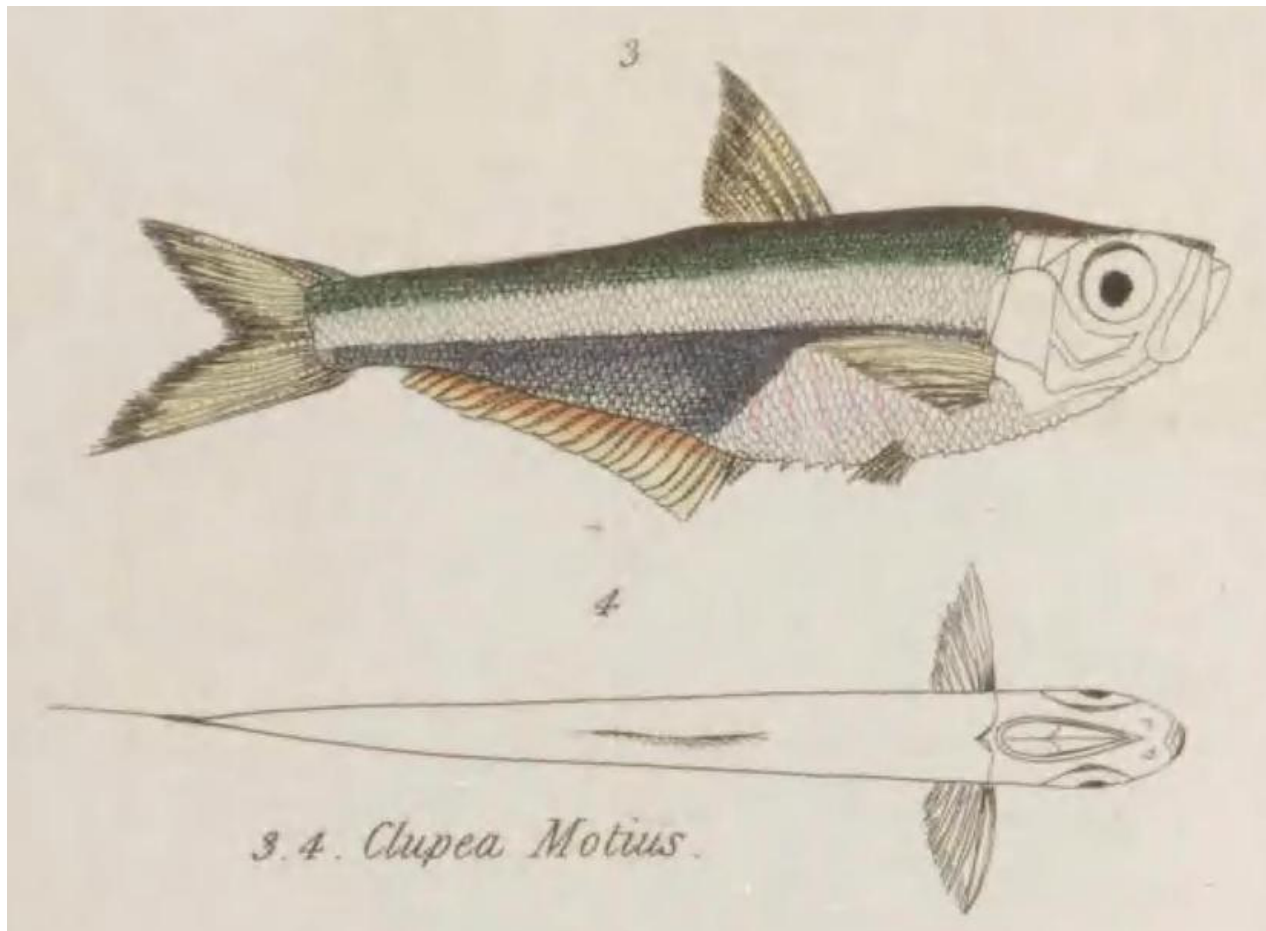


Figure 6. Illustration of a specimen of *Clupea motius* shown in Gray (1834 [12] *Clupea motius* on figures 3–4 in pl. 91 based on the Hamilton's unpublished drawing of *Clupanodon motius*, also the basis of *Clupea parva* Swainson, 1839; source: Biodiversity Heritage Library).

The high degree of variation in the shape of the swimbladder of *I. motius* is unique among pristigasterids and is found only in this species and *Ilisha sirishae* Seshagiri Rao, 1975 (Munroe et al., 1999 [5]). Lavoué et al. (2018) [27] examined the evolution of the swimbladder shape in Pristigasteridae, and they showed that a swimbladder without posterior extension represents the ancestral condition and a swimbladder with one or two posterior extensions represent derived conditions. Unfortunately, genetic information on *I. motius* and *I. sirishae* are unavailable and the phylogenetic positions of these species are unresolved [Lavoué et al.'s (2018) [27] *I. sirishae* was indicated as a misidentification of *Pellona dayi* by Hata et al. (2026b) [28]]. The presence of specimens with either one or two swimbladder posterior extensions in *I. motius* suggests a possible evolutionary mechanism where several swimbladder conditions may have coexisted in ancestral species before fixation. Lavoué et al. (2018) [27] suggested that posterior extensions on right or both sides of swimbladder are diagnostic characters of the genus *Ilisha*. However, as pointed out by Lavoué et al. (2018) [27], classification of the Pristigasteridae, including the genus *Ilisha*, is still unresolved and needs to be extensively revised. In this study, *I. motius* is tentatively included in the genus *Ilisha* following the genus definition shown in Whitehead (1985) [2] (see the Introduction).

3.2. *Ilisha megaloptera* (Swainson, 1839)

[English name: Bigeye Ilisha]

(Figures 7–9; Tables 3–5)



Figure 7. (A) Neotype of *Clupea (Platygaster) megaloptera* (MNHN 3708, also lectotype of *Pellona dussumieri*, 258.9 mm SL, Coromandel, India) and (B) neotype of *Ilisha macrophthalmia* (BMNH 1972.5.12.25, 140.9 mm SL, Visakhapatnam, Andhra Pradesh, India).

Table 4. Counts of specimens of *Ilisha megaloptera*.

	Neotype of <i>Clupea</i> <i>megalopterus</i>	Neotype of <i>Platygaster</i> <i>macrophthalmia</i>	Non-Types	
	MNHN 3708	BMNH 1972.5.12.25,	<i>n</i> = 17	
Standard length (mm)	258.9	140.9	93.7–210.1	Modes
Unbranched dorsal-fin rays	3	3	3–4	3
Branched dorsal-fin rays	14	14	13–14	14
Total dorsal-fin rays	17	17	16–18	17
Unbranched anal-fin rays	4	5	4	4
Branched anal-fin rays	41	40	42	N/A
Total anal-fin rays	45	45	43–52	45
Unbranched pectoral-fin rays	1	1	1	1
Branched pectoral-fin rays	15	14	14–17	15
Total pectoral-fin rays	16	15	15–18	16
Unbranched pelvic-fin rays	1	1	1	1
Branched pelvic-fin rays	6	6	6	6
Total pelvic-fin rays	7	7	7	7
Gill rakers on 1st gill arch (upper)	9	11	9–11	10
Gill rakers on 1st gill arch (lower)	19	19	18–21	20
Gill rakers on 1st gill arch (total)	28	30	27–32	29
Gill rakers on 2nd gill arch (upper)	6	7	6–8	7
Gill rakers on 2nd gill arch (lower)	19	19	17–21	19
Gill rakers on 2nd gill arch (total)	25	26	23–29	26
Gill rakers on 3rd gill arch (upper)	6	7	5–8	7
Gill rakers on 3rd gill arch (lower)	13	13	12–15	14
Gill rakers on 3rd gill arch (total)	19	20	17–23	20
Gill rakers on 4th gill arch (upper)	6	6	3–7	6
Gill rakers on 4th gill arch (lower)	11	11	9–13	11

Table 4. Cont.

	Neotype of <i>Clupea</i> <i>megalopterus</i>	Neotype of <i>Platygaster</i> <i>macrothalma</i>	Non-Types	
Gill rakers on 4h gill arch (total)	17	17	13–19	17
Gill rakers on posterior surface of 3rd fill arch	4	3	2–5	3
Prepelvic scutes	21	21	21–23	21
Postpelvic scutes	9	9	8–11	9
Total pelvic scutes	30	30	30–34	30
Scales rows in longitudinal series	47	48	44–48	45
Transverse scales	14	13	12–14	14
Pseudobranchial filaments	19	17	15–20	17
Vertebrae		47	47–50	47
Number of dorsal-fin rays before anal-fin origin	14	9	7–14	11
Pectoral-fin rays with melanophores	7	damaged	0–11	0

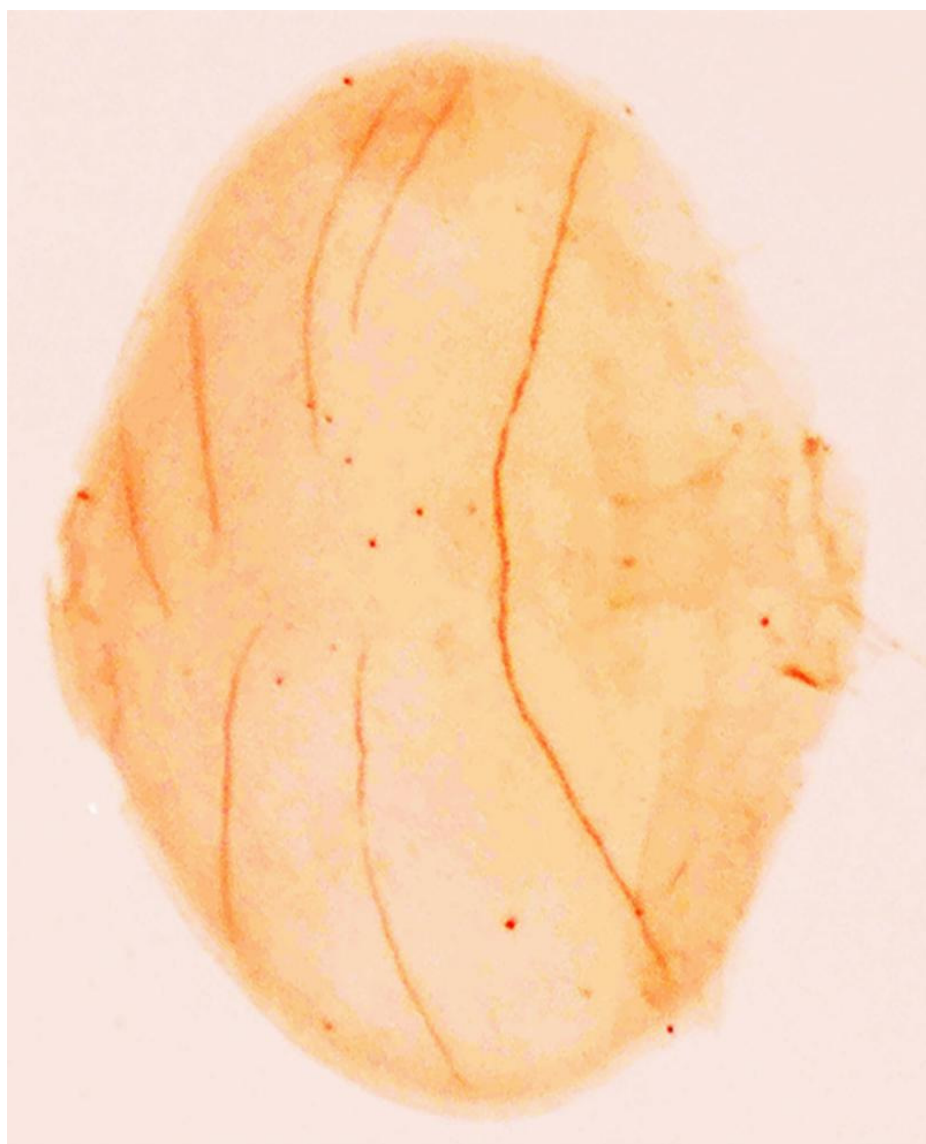


Figure 8. Stained scale removed from right side of midbody (below dorsal fin) of *Ilisha megaloptera*, USNM 276412, 105.7 mm SL, Kakinada, Andhra Pradesh, India (left-right inverted).



Figure 9. Form of swimbladder of preserved specimen of *Ilisha megalopectera*: (A) left (without posterior extension) and (B) right (extending posteriorly) sides of *I. megalopectera*, USNM 283220, 132.0 mm SL, Thirumullaivasal, Tamil Nadu, India (red triangle indicating posterior tip of swimbladder).

Table 5. Morphometrics of specimens of *Ilisha megalopectera*.

	Neotype of <i>Clupea</i> <i>megalopecterus</i>	Neotype of <i>Platygaster</i> <i>macrothalma</i>	Non-Types	
	MNHN 3708	BMNH 1972.5.12.25,	<i>n</i> = 17	
Standard length (mm; SL)	258.9	140.9	93.7–210.1	Means
As % of SL				
Head length	25.2	27.8	25.3–28.8	26.7
Body depth	32.4	33.5	31.7–35.1	33.4
Pre-dorsal-fin length	51.2	51.5	49.8–54.6	52.2
Snout tip to pectoral-fin insertion	25.3	28.3	25.3–28.6	26.9
Snout tip to pelvic-fin insertion	46.2	47.8	43.3–47.9	46.1
Snout tip to anal-fin origin	62.6	61.7	59.6–63.9	61.7
Dorsal-fin base length	9.6	10.6	9.6–10.9	10.3
Anal-fin base length	39.0	38.0	37.6–40.9	39.3
Caudal-peduncle length	7.8	6.9	6.3–8.5	7.5
Caudal-peduncle depth	9.7	9.1	7.9–9.6	8.8
D–P1	36.8	36.6	35.8–38.7	37.4
D–P2	32.1	33.4	32.3–35.2	33.7
D–A	31.5	31.9	30.5–33.6	32.1
P1–P2	20.6	19.7	17.8–21.4	19.9
P2–A	17.9	15.9	15.0–19.9	17.3
Pectoral-fin length	damaged	damaged	20.2–20.8	20.5
Pelvic-fin length	damaged	damaged	6.4–6.8	6.6
Maxilla length	13.0	15.4	13.4–14.7	14.2
Mandibular length	13.5	14.0	13.2–15.0	14.2
Postorbital length	10.4	11.3	9.9–12.3	11.1

Platygaster macrophthalma Swainson, 1838 [29]: 278 [original locality: Vizagapatnam (currently Visakhapatnam), Andhra Pradesh, India, based on pl. CXCI (figure of “Jangarloo”) of Russell (1803) [30]; type locality: Coromandel coast, India, based on the neotype designated by Seshagiri Rao (1977) [31]].

Clupea (Platygaster) megalopterus Swainson, 1839 [13]: 294 [original locality: Vizagapatnam (currently Visakhapatnam), Andhra Pradesh, India, based on pl. CXCI (figure of “Jangarloo”) of Russell (1803) [30]; type locality: Visakhapatnam, Andhra Pradesh, India, based on the neotype designated by Kottelat (2013) [21]].

Pellona dussumieri Valenciennes, 1847 [23]: 316 (type locality: Coromandel coast, India).

Pellona megaloptera: Day 1875 [15]: 645, figure 2 in pl. CLXV (Indian coast); Day 1889 [16]: 384 (Indian coast).

Ilisha melastoma (not of Bloch and Schneider): Velappan Nair 1953 [18]: 124 (India); Misra 1976 [19]: 80 (in part: India).

Ilisha megaloptera: Norman 1923 [17]: 10 (in part: India); Whitehead 1967 [32]: 247, figure 25 (in part: India); Dutt 1967 [33]: 210 (Visakhapatnam, Andhra Pradesh, India); Seshagiri Rao 1972 [34]: 882, left illustration on figure 1 (Visakhapatnam, Andhra Pradesh, India); Whitehead 1972 [25]: 213, figure 38 [in part: India and Ceylon (Sri Lanka)]; Seshagiri Rao 1973 [35]: 736, figure 1a, right individual of figure 3 (Visakhapatnam, Andhra Pradesh, India); Ramaiyan and Whitehead 1975 [36]: 191 [in part: Tamil Nadu (Thirumullaivasal, Porto Novo and Madras), Pondicherry, and West Bengal (Calcutta), India; and Jaffna, Ceylon (Sri Lanka)]; Seshagiri Rao 1977 [31]: 73, figure 1 (designation of the neotype of *Platygaster macrophthalma*; Visakhapatnam, Andhra Pradesh, India); Jayaram 1981 [37]: 45 (in part: India and Sri Lanka, Bangladesh, and Burma); Talwar and Kacker 1984 [38]: 154, figure 57 (in part: eastern coast of India); Whitehead 1985 [2]: 270 (in part: Indian coast); De Bruin et al., 1994 [39]: 296 (Sri Lanka); Munroe et al., 1999 [5]: 1763 (in part: Indian coast); Psomadakis et al., 2019 [40]: 303 (Myanmar); Anderson 2022 [41]: 162 (in part: Bay of Bengal and Andaman Sea); Hata et al., 2024 [42]: 20, figure 31 (in part: northern part of Andaman Sea, Myanmar).

Neotype. MNHN 3708, also lectotype of *Pellona dussumieri* Valenciennes, 1847, 258.9 mm SL, Coromandel, India, 1830.

Other materials examined. 18 specimens, 93.7–210.1 mm SL. **MYANMAR:** PMBC 6744, 191.2 mm SL, northern Andaman Sea, 30–40 m depth, otter trawl; USNM 345431, 4 specimens, 98.8–148.0 mm SL, approx. 25 km south of Ayeyarwady River, Myanmar (15°32' N, 94°53' E), 16–29 m depth. **INDIA:** AMS B 7663, 210.1 mm SL, Madras (currently Chennai), Tamil Nadu; BMNH 1972.5.12.25, neotype of *Ilisha macrophthalma* Swainson, 1838, 140.9 mm SL, Visakhapatnam, Andhra Pradesh; USNM 276412, 6 specimens, 93.7–109.9 mm SL, Yanam, Kakinada, Andhra Pradesh; USNM 276413, 2 specimens, 161.2–172.3 mm SL, Kakinada, Andhra Pradesh; USNM 283220, 2 specimens, 106.7–132.0 mm SL, Thirumullaivasal, Tamil Nadu; USNM 283221, 155.8 mm SL, approx. 5 km east of Parangipettai, Tamil Nadu (11°30' N, 79°50' E).

Diagnosis. A species of *Ilisha* with the following combination of characters: body somewhat deep, 31.7–35.1% of SL, distance between dorsal-fin origin and pelvic-fin insertion 32.1–35.2% of SL, distance between origins of dorsal and anal fins 30.5–33.6% of SL; abdomen covered with 21–23 + 8–11 = 30–34 scutes; anal fin with 43–52 fin rays, its base long, 37.6–40.9% of SL; scales rows in longitudinal series 44–48; vertebrae 47–50; pelvic fin short, 6.4–6.8% of SL, its posterior tip posteriorly not reaching to vertical through dorsal-fin origin when depressed; grooves on body scales not overlapping at center; 1UGR 9–11, 1LGR 18–21, 1TGR 27–32; 2UGR 6–8, 2LGR 17–21, 2TGR 23–29; swimbladder with single tube passing posteriorly into muscles on right side of haemal spines; head somewhat long, 25.2–28.8% of SL; dorsal-fin base short, 9.6–10.9% of SL; maxilla long, 13.0–15.4% of SL,

without distinct lobe; lower jaw somewhat short, 13.2–15.0% of SL; caudal peduncle short, 6.3–8.5% of SL; maximum standard length approx. 26 cm.

Description. Counts and measurements (expressed as percentages of SL) are shown in Tables 4 and 5. Data for neotype of *Clupea megalopterus* given in parentheses (if different). Body strongly compressed, somewhat deep, deepest at dorsal-fin origin. Dorsal contour of body gradually elevated from snout tip to dorsal-fin origin, thereafter gently decreased to uppermost point of caudal-fin base. Ventral profile of body lowering from lower-jaw tip to point just below dorsal-fin origin and subsequently rising to lowermost point of caudal-fin base. Abdomen covered with 21–23 (21) and 8–11 (9) scutes from isthmus to pelvic scute, and pelvic scute to anus, respectively. Abdomen scutes hard, sharp, and projected backwards. Pectoral-fin insertion slightly anterior to posterior margin of opercle and lower than lower margin of eye; pectoral fin fragile (broken in most examined specimens including neotype); 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. Single elongated axillary scale located just above pectoral fin. Pelvic-fin insertion anterior to dorsal-fin origin; posterior tip of depressed fin not reaching to vertical through dorsal-fin origin and to anus; anterior-most fin ray unbranched, other rays branched; outer profiles of fin nearly straight. Single triangular axillary scale located just above pelvic fin. 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 7th to 14th dorsal-fin ray origin (just below origin of 14th dorsal-fin ray); initial four or five (four) rays unbranched, other rays branched; contour of fin lowering from fin origin to last unbranched fin ray, thereafter parallel to fin base. Elongated sheath scales on bases of dorsal and anal fins. Caudal fin forked and bifurcate, but not lunate; both lobes without extended tips; outer profile of each lobe nearly straight; posterior tips of both lobes pointed. Small scales densely present on caudal fin. 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 present 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; many grooves on scales on lateral surface of body; posteriormost one crossing scale vertically; other grooves not meeting or overlapping at center of scale, posterior margin not denticulated (Figure 8). Swimbladder asymmetrical; posterior portion extending beyond body cavity and posterior to first haemal spine only on right side, while left side not extending posteriorly into body cavity (Figure 9).

Coloration of preserved specimens. Body uniformly pale, light ivory, or silver (silver in neotype). Dorsum brown. Melanophores densely scattered on dorsum to lateral surface of body, reaching to level of center of eye, sometimes beyond level of pectoral-fin insertion (scattered melanophores difficult to see in specimens where guanine remains including neotype); scales on dorsum posteriorly margined black. Melanophores scattered along fin rays of dorsal and caudal fins and outer margin of anal fin but not on pelvic-fin. Pectoral fin with scattered melanophores on first to eleventh fin rays (from uppermost) in some specimens larger than 100 mm SL (first to seventh in neotype). Melanophores scattered on

gill rakers, gill arches, gill filaments on anterior part, and inner surfaces of hyoid arch and opercle but not on mouth roof, tongue and mouth floor. Swimbladder uniformly whitish silver. Iris silver, pupil black.

Distribution and biological information. *Ilisha megalopectera* is distributed in the Bay of Bengal from the eastern coast of India to the northern part of the Andaman Sea (Figure 4). *Ilisha megalopectera* and related nominal species were taxonomically confused and *I. megalopectera* has been frequently misidentified. As stated in Hata et al. (2025) [6], *I. megalopectera* has often been confused with *I. melastoma*. For example, a color photograph of a pristigasterid individual collected from Phuket, Thailand, identified as “*I. megalopectera*” in Rainboth (2012: figure 236) [43] is *I. melastoma*; one specimen identified as “*I. megalopectera*” (KAUM-I. 67304, collected from Ha Long Bay, Vietnam) in Kimura (2018 [44]; photo shown in the middle of p. 47) is also reidentified as *I. melastoma*. A second specimen identified as “*I. megalopectera*” in Kimura (2018 [44]; photo in the bottom on p. 47) is, however, *I. russellii*. Although Gosh and Vase (2022) [45] researched the biology of *I. megalopectera* in the northeastern Arabian Sea, the photographed individual shown in figure 1 is *I. melastoma* because of its deep body as pointed out by Hata et al. (2025) [6]. Hata et al. (2025) [6] also pointed out that biological data on “*I. megalopectera*” shown in Gosh and Vase (2022) [45] is not based on *I. melastoma* but on *I. megalopectera*. However, no specimen identified as *I. megalopectera* was observed from the Arabian Sea in this study, and the species whose ecology was reported by Gosh and Vase (2022) [45] is probably different from *I. megalopectera*. Bampouri et al. (2024) [46] examined minerals and trace elements contained in various body parts of *I. megalopectera* obtained from the northern part of the Gulf of Oman. Hata et al. (2025) [6] already pointed out that the pristigasterid individual shown in figure 1 in Bampouri et al. (2024) [46] is probably *I. melastoma* because of its deep body. Hata et al. (2024) [42] reported two specimens (PMBC 3576, 6744) of *I. megalopectera* collected from the Andaman Sea deposited in the Phuket Marine Biological Center (PMBC): whereas PMBC 6744 was correctly identified, PMBC 3576 is herein reidentified as *I. sirishae*. Satapoomin (2011) [47] reported *I. megalopectera* from the Andaman Sea based on the same two PMBC specimens, therefore his record probably includes *I. sirishae* along with the true *I. megalopectera*.

Morphological comparisons. In the genus *Ilisha*, six species [e.g., *Ilisha elongata* (Anonymous [Bennett], 1830), *I. filigera*, *Ilisha macrogaster* Bleeker, 1866, *I. megalopectera*, *Ilisha pristigasteroides* (Bleeker, 1852), *I. russellii*] are known to have an asymmetric swimbladder with a single tube passing posteriorly into muscles on the right side of haemal spines (Wongratana 1983 [1]; Whitehead 1985 [2]; Kailola 1986 [3]; Randall 1994 [4]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]; this study). Among these species, *I. megalopectera* can be distinguished from all other species, except for *I. russellii*, by having 34 or less ventral scutes. Furthermore, *I. megalopectera* differs from *I. elongata* in having a deeper body (body depth 31.7–35.1% of SL in *I. megalopectera* vs. 27–31% in *I. elongata*) and anal-fin origin located below origin of 7th to 14th dorsal-fin ray origin (vs. posterior to dorsal-fin base end). In addition, counts of 1LGR of *Ilisha megalopectera* (18–21) separate the species from *I. macrogaster* (23–25) and *I. pristigasteroides* (17) (Wongratana 1983 [1]; Whitehead 1985 [2]; Kailola 1986 [3]; Randall 1994 [4]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]; this study). Detailed comparisons of *I. megalopectera* and *I. russellii* are given under “Morphological comparisons” for the latter.

Remarks. The oldest name considered to be a synonym of *I. megalopectera* is *Platygaster macrophthalmus* Swainson, 1838, described based on an illustration of a pristigasterid fish given in Russell (1803 [30]: pl. 191: Figure 10). According to Russell (1803 [30]: p. 73), the fish was collected at Visakhapatnam, Andhra Pradesh, India, where it was locally known as “Jangarloo”. Meristics and morphological traits in Russell’s (1803) [30] description and illustration generally match *I. megalopectera*, as recognized in this study. Subsequently,

Seshagiri Rao (1977) [31] showed that *P. macrophthalma* was a synonym of *I. megaloptera*, and he designated a specimen BMNH 1972.5.12.25 collected from Visakhapatnam, Andhra Pradesh, India (Figure 7B), as the neotype of *P. macrophthalma*. Thereafter, *Clupea megalopterus* was described by Swainson (1839: 294) [13] again based on Russell's (1803) [30] pl. 191; the same figure was used for the description of *Platygaster macrophthalmus*. Whitehead (1967) [24] recognized that *P. macrophthalmus* is a senior synonym of *C. megalopterus* and suggested that *P. macrophthalmus* should be regarded as a *nomen oblitum*. Although Whitehead (1967) [24] stated that an application for suppression would be made in due course, this was never done. As pointed out by Whitehead (1967) [24], *P. macrophthalmus* has never been used as a valid name since 1838 (original description) whereas *I. megaloptera* has been used as a valid name in more than 25 publications between 2017 and 2026: Satapathy and Panda (2017) [48]; Hadiuzzaman et al. (2017) [49]; Wijayanti et al. (2017) [50]; Saher et al. (2018) [51]; Kimura (2018) [44]; Lavoué et al. (2018) [27]; Jamshidi et al. (2018) [52]; Psomadakis et al. (2019) [40]; Bhakta et al. (2019) [53]; Ibadah and Saptarini (2020) [54]; Jafarpour and Ataei (2020) [55]; Ray et al. (2021) [56]; Krishnan and Talwar (2021) [57]; Anderson (2022) [41]; Hata et al. (2022a) [58]; Gosh and Vase (2022) [45]; Manna et al. (2022) [59]; Kamaludeen et al. (2023) [60]; Afrand et al. (2024) [61]; Hata et al. (2024) [42]; Yamen et al. (2024) [62]; Bampouri et al. (2024) [46]; Bhakta et al. (2025) [63]; Lin and Keh (2025) [64]; Hata et al. (2025) [6]; Haghpourast et al. (2025) [65]; Hata et al. (2026a) [66]. Therefore, the prevailing usage of *I. megaloptera* must be maintained, following ICZN (1999 [67]: article 23.9)—“Reversal of precedence”. Valenciennes (1847) [23] described *Pellona dussumieri* based on specimens collected from India and Whitehead (1967) [24] designated MNHN 3708 as the lectotype. Because the lectotype was also designated as the neotype of *C. megalopterus* by Kottelat (2013 [21]: p. 50), *P. dussumieri* is considered a junior objective synonym of *C. megalopterus*. Therefore, *Ilisha megaloptera*, the oldest available name, is applied for the Indian Ocean species. In addition, Ray et al. (2021) [56] reported mature stage and number of eggs of a single individual of pristigasterid fish collected from Fraserganj, West Bengal, India, as *I. megaloptera*. Although their report provides little morphological information on the specimen, making accurate species identification difficult, the specimen is significantly larger than the specimens defined as *I. megaloptera* in this study (maximum 239.3 mm SL) at 48.4 cm SL and 54.8 cm in total length. Moreover, proportions of head length and body depth of the specimen do not match those of *I. megaloptera* shown in this study. Therefore, their specimen appears not to be *I. megaloptera*.

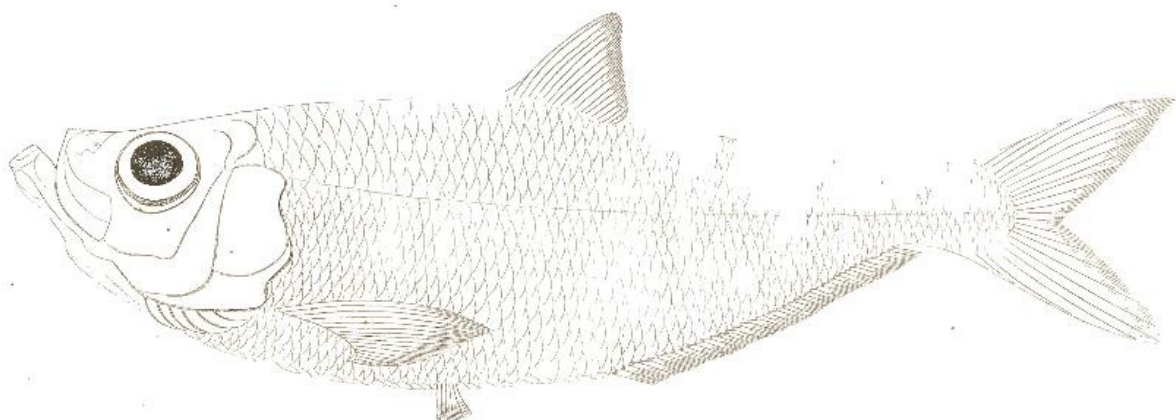


Figure 10. Illustration of a specimen shown in Russell (1803 “Jangalroo” on pl. CXCI, the basis of *Platygaster macrophthalma* Swainson, 1838 and *Clupea megaloptera* Swainson, 1839; source: Biodiversity Heritage Library).

3.3. *Ilisha russellii* (Bleeker, 1852)

[New English name: Pacific Bigeye Ilisha]

(Figures 11–13; Tables 3, 6 and 7)

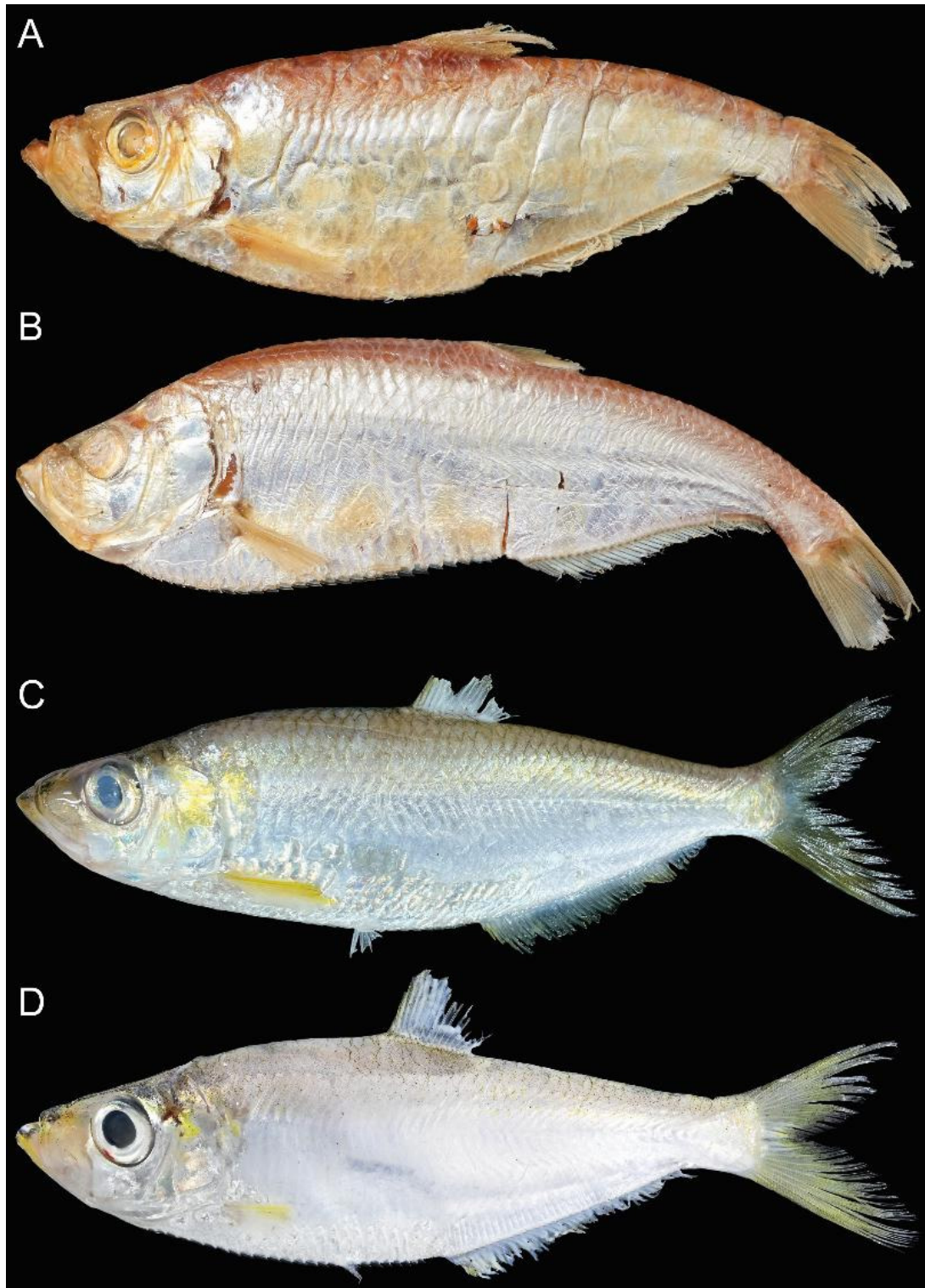


Figure 11. (A) Lectotype of *Pellona russellii* (BMNH 1867.11.28.13, 170.0 mm SL, Java, Indonesia), (B) holotype of *Ilisha bleekeri* (BMNH 1867.11.28.19, 176.0 mm SL, Java, Indonesia) and (C,D) non-type specimens of *Ilisha russellii* in fresh condition ((C), USMFC (92) 00015 (specimen code BM24-13), 239.3 mm SL, Batu Maung, Penang, Malaysia; (D), USMFC (92) 00026 (specimen code BM25-36b), 123.8 mm SL, Batu Maung, Penang, Malaysia).



Figure 12. Stained scale removed from right side of midbody (above anal fin) of *Ilisha russellii*, OCF-URM-P 44370, 127.2 mm SL, Tanjung Sepat, Selangor, Malaysia (left-right inverted).

Pellona russellii Bleeker, 1852 [68]: 23 [original localities: Batavia (currently Jakarta), Samarang (Semarang), Surabaya (Surabaya), Pasuruan, Kammal (Kamal), Tandjong, and Madura Islands, Java, Indonesia; type locality: Java, Indonesia, based on the lectotype designated by Whitehead et al. (1966) [69]].

Pellona motius (not of Hamilton); Günther 1868 [14]: 456 (in part: East Indies).

Ilisha novacula (not of Valenciennes); Bleeker 1870 [70]: figure 4 in pl. CCLXIX [Batavia (currently Jakarta), Java, Indonesia]; Bleeker 1872 [71]: 120 [Batavia (Jakarta), Java, Indonesia].

Ilisha megaloptera (not of Swainson): Norman 1923 [17]: 10 (in part: Malay Peninsula); Whitehead 1967 [32]: 247, figure 25 (in part: Singapore and Indonesia); Ramaiyan and Whitehead 1975 [36]: 191 [in part: Singapore; Sarawak, Borneo, Malaysia; Cochinchina (southern Vietnam)]; Whitehead 1985 [2]: 270, unnumbered fig. (in part: Malacca Strait to South China Sea); Blaber et al., 1998 [26]: 500 (Sarawak, Borneo, Malaysia); Munroe et al., 1999 [5]: 1763, unnumbered fig. (in part: Malacca Strait to South China Sea); Randall and Lim 2000 [72]: 587 (South China Sea); Kimura 2015 [73]: 13, unnumbered figs. (Johor Strait and Port Dickson, Malaysia); Kimura 2018 [44]: 47, bottom fig. (in part: Johor Strait,

Malaysia); Anderson 2022 [41]: 162, unnumbered fig. (in part: Bay of Bengal and Andaman Sea); Hata et al., 2022a [58]: 25 (Sarawak, Borneo, Malaysia); Hata et al., 2025 [6]: 526, Table 3 (Sekinchan, Selangor, Malaysia).



Figure 13. Form of swimbladder of fresh specimens of *Ilisha russellii*: (A) left (without posterior extension; USMFC (92) 00017 (specimen code BM25-06), 139.9 mm SL, Batu Maung, Penang, Malaysia) and (B) right (extending posteriorly; USMFC (92) 00017 (specimen code BM25-07), 143.3 mm SL, Batu Maung, Penang, Malaysia) sides of *I. megaloptera* (red triangles indicating posterior tip of swimbladder).

Table 6. Counts of specimens of *Ilisha russellii*.

	Lectotype of <i>Pellona russellii</i>	Holotype of <i>Ilisha bleekeri</i>	Non-Types	
	BMNH 1867.11.28.13	BMNH 1867.11.28.19	<i>n</i> = 66	
Standard length (mm)	170.0	176.0	56.2–239.3	Modes
Unbranched dorsal-fin rays	3	damaged	3–4	4
Branched dorsal-fin rays	14	damaged	13–15	14
Total dorsal-fin rays	17	18	16–19	17
Unbranched anal-fin rays	damaged	damaged	4	4
Branched anal-fin rays	damaged	damaged	34–39	27
Total anal-fin rays	44	43	38–44	42
Unbranched pectoral-fin rays	1	1	1	1
Branched pectoral-fin rays	15	15	15–18	16
Total pectoral-fin rays	16	16	16–19	17
Unbranched pelvic-fin rays	1	1	1	1
Branched pelvic-fin rays	6	6	6	6
Total pelvic-fin rays	7	7	7	7
Gill rakers on 1st gill arch (upper)	10		9–12	11

Table 6. Cont.

	Lectotype of <i>Pellona russellii</i>	Holotype of <i>Ilisha bleekeri</i>	Non-Types	
Gill rakers on 1st gill arch (lower)	21		19–23	21
Gill rakers on 1st gill arch (total)	31		30–34	31
Gill rakers on 2nd gill arch (upper)	6		6–8	7
Gill rakers on 2nd gill arch (lower)	20		18–21	20
Gill rakers on 2nd gill arch (total)	26		24–29	27
Gill rakers on 3rd gill arch (upper)	6		5–7	6
Gill rakers on 3rd gill arch (lower)	14		12–15	14
Gill rakers on 3rd gill arch (total)	20		18–21	20
Gill rakers on 4th gill arch (upper)	6		4–7	5
Gill rakers on 4th gill arch (lower)	11		10–12	11
Gill rakers on 4th gill arch (total)	17		14–18	17
Gill rakers on posterior surface of 3rd fill arch	3		2–5	3
Prepelvic scutes	21	25	20–24	22
Postpelvic scutes	8	9	8–10	9
Total pelvic scutes	29	34	28–33	30
Scales rows in longitudinal series	39	41	38–42	41
Transverse scales	13		11–14	13
Pseudobranchial filaments	damaged		18–25	19
Vertebrae	45	44	44–46	45
Number of dorsal-fin rays before anal-fin origin	10	9	6–14	12
Pectoral-fin rays with melanophores	4	damaged	0–7	0

Table 7. Morphometrics of specimens of *Ilisha russellii*.

	Lectotype of <i>Pellona russellii</i>	Non-Types	
	BMNH 1867.11.28.13	<i>n</i> = 66	
Standard length (mm; SL)	170.0	56.2–239.3	Means
As % of SL			
Head length	27.3	26.9–29.8	28.2
Body depth	34.0	30.1–34.9	32.9
Pre-dorsal-fin length	50.0	49.8–53.7	51.6
Snout tip to pectoral-fin insertion	27.5	26.4–28.8	28.0
Snout tip to pelvic-fin insertion	47.4	42.7–50.7	47.6
Snout tip to anal-fin origin	62.3	58.7–67.7	63.3
Dorsal-fin base length	11.8	11.1–12.9	11.9
Anal-fin base length	34.2	31.8–36.7	35.1
Caudal-peduncle length	8.2	7.2–9.7	8.4
Caudal-peduncle depth	damaged	8.4–10.1	9.3
D–P1	35.9	34.9–37.5	36.3
D–P2	33.2	30.2–35.2	32.7
D–A	31.2	30.0–34.2	32.5
P1–P2	20.8	16.4–22.6	20.2
P2–A	16.7	15.0–20.0	17.2
Pectoral-fin length	damaged	17.0–20.6	18.8
Pelvic-fin length	damaged	6.2–7.4	6.9
Maxilla length	14.4	13.9–15.9	14.9
Mandibular length	15.2	14.2–16.3	15.3
Postorbital length	10.8	10.8–12.3	11.5

Ilisha bleekeri Bertin, 1941 [74]: 24 (type locality: Jakarta, Java, Indonesia).

Ilisha elongata (not of Bennett): Ahmad et al., 2018 [75]: 36, unnumbered fig. (South-east Asia).

Ilisha melastoma (not of Bloch and Schneider): Jaafar 2021 [76]: 26, unnumbered fig. (Kuantan, Pahang, Malaysia);

Lectotype. BMNH 1867.11.28.13, 170.0 mm SL, Java, Indonesia.

Other materials examined. 67 specimens, 56.2–239.3 mm SL. **THAILAND:** ANSP 59952, 168.8 mm SL, Bangkok; ANSP 60597, 4 specimens, 164.7–174.2 mm SL, Bangkok; CAS 59745, 2 of 8 specimens, 179.1–182.7 mm SL, approx. 5 miles (approx. 8 km) off-shore of Prachuap Khiri Khan (11°47'23.5" N, 99°48'59.8" E), 40 m depth; CAS 59746, 2 specimens, 189.5–191.9 mm SL, approx. 3–22 km offshore southwest of Goh Samae San (12°16'0"–12°33'0" N, 100°44'0"–100°54'0" E); CAS 59747, 171.5 mm SL, Gulf of Thailand, approx. 16 km east of north end of Ko Phangan, Surat Thani Province (09°48'00" N, 100°11'00" E); NSMT-P 23084, 119.7 mm SL, Songkhla; OCF-URM-P 13763, 232.0 mm SL, Samyan Market, Bangkok; UMMZ 222935, 2 specimens, 174.7–177.1 mm SL, Gulf of Thailand (obtained at fish market in Bangkok); UMMZ 223165, 2 specimens, 172.2–208.9 mm SL, Gulf of Thailand, obtained at market in Bangkok. **VIETNAM:** UMMZ 219886, 133.4 mm SL, Mekong Plume (8°58'12" N, 105°58'30" E), 19–20 m depth; UMMZ 227200, 154.9 mm SL, Mekong River Delta (9°55'00" N, 106°56'42" E), 25 m depth; UMMZ 227445, 56.2 mm SL, mouth of Bassac River, Truong Binh, Ba Xuyen Province. **MALAYSIA:** AMS I. 27630-029, 129.6 mm SL, Kuala Kurau, Perak; CAS 33829, 118.9 mm SL, Penang; CAS-SU 69044, 80.1 mm SL, Penang; KPM-NI 90599, 112.6 mm SL, Malaysia; KPM-NI 90600, 122.7 mm SL, Malaysia; NSMT-P 93963, 174.5 mm SL, Port Dickson, Negeri Sembilan; OCF-URM-P 44370, 127.2 mm SL, Tanjung Sepat, Selangor; OCF-URM-P 44413, 139.5 mm SL, obtained at Port Dickson Fish Market, Port Dickson; UMMZ 214976, 2 specimens, 204.3–204.7 mm SL, Penang; UMMZ 226376, 191.0 mm SL, Penang; USMFC (92) 00025 (specimen code ME23-19), 187.0 mm SL, Sungai Merbok, Kedah; USMFC (92) 00012, 2 specimens (ME24-03), 114.9 mm SL, (ME24-04), 121.9 mm SL, Sungai Merbok, Kedah (1 Jun 2024); USMFC (92) 00015, 3 specimens (BM24-13), 239.3 mm SL, (BM24-14), 142.4 mm SL, (BM24-15), 159.6 mm SL, Batu Maung, Pulau Pinang (3 Jun. 2024); USMFC (92) 00022 (PB25-03), 117.2 mm SL, Pasar Bichir, Merbok, Kedah (13 Feb. 2025); USMFC (92) 00017, 2 specimens (BM25-06), 139.9 mm SL, (BM25-07), 143.3 mm SL, Batu Maung, Pulau Pinang (12 February 2025); USMFC (92) 00026, 2 specimens (BM25-35b), 118.8 mm SL, (BM25-36b), 123.8 mm SL, Batu Maung, Pulau Pinang (04 Nov. 2025); USMFC (92) 00020 (BM25-41), 64.9 mm SL, Batu Maung, Pulau Pinang (14 Feb. 2025); USMFC (92) 00027 (BM25-44), 121.0 mm SL, Batu Maung, Pulau Pinang (4 November 2025); USMFC uncat., 5 specimens, 146.7–173.4 mm SL, Batu Maung, Pulau Pinang; ZRC 3138, 123.0 mm SL, Malacca; ZRC 64500, 2 specimens, 176.9–180.8 mm SL, off Sarawak, Borneo (2°46'15" N, 111°10'30" E–2°56'15" N, 111°10'30" E), 13–18 fathoms (approx. 23.8–32.9 m) depth; ZUMT 62098, 138.0 mm SL, ZUMT 62099, 158.7 mm SL, ZUMT 62100, 129.4 mm SL, Sarawak, Borneo; USNM 404601, 126.7 mm SL, Sandakan, Sabah, Borneo. **SINGAPORE:** CAS 33830, 2 specimens, 160.0–192.4 mm SL, Singapore; CAS-SU 32106, 152.4 mm SL, Singapore; NMW 82043, 203.3 mm SL, Singapore. **INDONESIA:** BMNH 1867.11.28.19, holotype of *Ilisha bleekeri*, 176.0 mm SL, Java; MZB 795, 174.9 mm SL, Indonesia; OCF-URM-P 46202, 66.7 mm SL, Kuala Tungkal, Jambi, Sumatra; USNM 72513, 68.8 mm SL, Jakarta, Java, 42–43 m depth. **SOUTH CHINA SEA** (precise locality unknown): KPM-NI 84357, 179.9 mm SL, South China Sea; KPM-NI 84358, 187.9 mm SL, South China Sea; KPM-NI 84359, 184.0 mm SL, South China Sea; KPM-NI 84360, 172.8 mm SL, South China Sea.

Diagnosis. A species of *Ilisha* with the following combination of characters: body somewhat deep, 30.1–34.9% of SL, distance between dorsal-fin origin and pelvic-fin insertion 30.2–35.2% of SL, distance between origins of dorsal and anal fins 30.0–34.2% of SL; abdomen covered with 20–25 + 8–10 = 28–34 scutes; anal fin with 38–44 fin rays, its base short, 31.8–36.7% of SL; scale rows in longitudinal series 38–42; vertebrae 44–46; pelvic fin short, 6.2–7.4% of SL, its posterior tip posteriorly not reaching to vertical through dorsal-fin origin when depressed; grooves on body scales not overlapping at center; 1UGR 9–12, 1LGR 19–23, 1TGR 30–34; 2UGR 6–8, 2LGR 18–21, 2TGR 24–29; swimbladder with single tube passing posteriorly into muscles on right side of haemal spines; no distinct lobe on maxilla; head somewhat long, 26.9–29.8% of SL; dorsal-fin base long, 11.1–12.9% of SL; maxilla long, 13.9–15.9% of SL; lower jaw somewhat long, 14.2–16.3% of SL; caudal peduncle short, 7.2–9.7% of SL; maximum standard length approx. 24 cm.

Description. Counts and measurements (expressed as percentages of SL) are shown in Tables 5 and 6. Data for lectotype of *Pellona russellii* given in parentheses (if different). Body strongly compressed, somewhat deep, deepest at dorsal-fin origin. Dorsal contour of body gradually elevated from snout tip to dorsal-fin origin, thereafter gently decreased to uppermost point of caudal-fin base. Ventral profile of body lowering from lower-jaw tip to point just below dorsal-fin origin and subsequently rising to lowermost point of caudal-fin base. Abdomen covered with 20–25 (21) and 8–10 (8) scutes from isthmus to pelvic scute, and pelvic scute to anus, respectively. Abdomen scutes hard, sharp, and projected backwards. Pectoral-fin insertion slightly anterior to posterior margin of opercle and lower than lower margin of eye; pectoral fin fragile (broken in most examined specimens including lectotype); 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. Single elongated axillary scale located just above pectoral fin. Pelvic-fin insertion anterior to dorsal-fin origin; posterior tip of depressed fin not reaching to vertical through dorsal-fin origin and to anus; anterior-most fin ray unbranched, other rays branched; outer profiles of fin nearly straight. Single triangular axillary scale located just above pelvic fin. 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 6th to 14th dorsal-fin ray origin (just below origin of 10th dorsal-fin ray); initial four rays unbranched, other rays branched; contour of fin lowering from fin origin to last unbranched fin ray, thereafter parallel to fin base. Elongated sheath scales on bases of dorsal and anal fins. Caudal fin forked and bifurcate, but not lunate; both lobes without extended tips; outer profile of each lobe nearly straight; posterior tips of both lobes pointed. Small scales densely present on caudal fin. Anus just anterior to anal-fin origin. Lower jaw projecting anteriorly beyond 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 present 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; many grooves on scales on lateral surface of body; posteriormost one crossing scale vertically; other grooves not meeting or overlapping at center of scale, posterior margin not denticulated (Figure 12). Swimbladder asymmetrical;

posterior portion extending beyond body cavity and posterior to first haemal spine only on right side, while left side not extending posteriorly into body cavity (Figure 13).

Coloration of fresh specimens. Body uniformly silver, dorsum brown, upper part of lateral surface yellowish green. Posterior margins of scales on dorsum black. Dorsal surfaces of both jaws black. Snout to interorbital area semitransparent, yellowish. Lateral surfaces of both jaws semitransparent, whitish. Opercle silver, upper part yellow. Iris silver, pupil black. Melanophores densely scattered upper margin of iris. Pectoral fin whitish, upper part light yellow. Pelvic fin whitish, semitransparent. Dorsal fin whitish, semitransparent, marginal area yellow. Anal fin white basally, yellow marginally; outer margin black. Caudal fin yellow, melanophores densely scattered on fin rays. Swimbladder uniformly white. Intestine pale white. Liver dark red. Testes pinkish white. Lateral muscle pinkish white.

Coloration of preserved specimens. Body uniformly pale, light ivory, or silver (silver in lectotype). Dorsum light brown. Melanophores densely scattered on dorsum to lateral surface of body, reaching to the level of center of eye, sometimes beyond level of pectoral-fin insertion (scattered melanophores difficult to see in specimens where guanine remains, including lectotype); scales on dorsum posteriorly margined black. Melanophores scattered along fin rays of dorsal and caudal fins and outer margin of anal fin but not on pelvic-fin. Pectoral fin with scattered melanophores on first to seventh fin rays (from uppermost) in some specimens (first to fourth in lectotype). Melanophores scattered on gill rakers, gill arches, and inner surfaces of hyoid arch and opercle, but not on gill filaments, mouth roof, tongue and mouth floor. Swimbladder uniformly whitish silver. Iris silver, pupil black.

Distribution and biological information. *Ilisha russellii* is distributed in the Malacca Strait and western Pacific from the Gulf of Thailand to Java, Indonesia (Figure 4). According to Blaber et al. (1998) [26], which reported the ecology and life history of a population of *I. megaloptera* in Sarawak, the species is found in coastal waters, and juveniles smaller than 90 mm SL are found in low salinities in the upper reaches of estuaries. It mainly feeds on fish and secondarily on crustaceans, and the majority live for about 2 years. Although *I. russellii* has traditionally been treated as *I. megaloptera* (see the synonym list), like other species of the genus *Ilisha*, it has often been confused with other congeners. Although Ahmad et al. (2018) [75] showed a color photograph of a pristigasterid fish collected from Southeast Asia as *I. elongata*, the individual is identified as *I. russellii* because of its deep body. Although Jaafar (2021) [76] showed a color photograph of a specimen collected from Kuantan, Pahang, Malaysia, as *Ilisha melastoma*, that specimen is probably *I. russellii* because of its elongated body. Although Wijayanti et al. (2017) [50] reported sexual dimorphism in *I. megaloptera* in Cilacap, Java, Indonesia, the fishes shown in figures 1–3 are not pristigasterid fish but rather fish of the genus *Thrissina* (Engraulidae).

Morphological comparisons. *Ilisha russellii* most closely resembles *I. megaloptera*, both sharing an asymmetrical swimbladder posteriorly extending only on the right side and ventral scutes fewer than 35 (Wongratana 1983 [1]; Whitehead 1985 [2]; Kailola 1986 [3]; Randall 1994 [4]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]; this study). However, *I. russellii* differs from *I. megaloptera* in having a longer dorsal-fin base (11.1–12.9% of SL in *I. russellii* vs. 9.6–10.9% in *I. megaloptera*; Figure 5J), an anal fin with fewer fin rays (total anal-fin rays 38–44 vs. 43–52; Table 3) and shorter fin base (31.8–36.7% of SL vs. 37.6–40.9%; Figure 5H), more gill rakers on first gill arch [30–33 (rarely 34) vs. 28–31 (27 or 32); Figure 5A], and fewer scale rows in longitudinal series (38–42 vs. 44–48; Table 3) and vertebrae (44–46 vs. 47–50; Table 3).

Remarks. *Ilisha russellii* was described by Bleeker (1852) [68] based on specimens collected from various localities in Java, Indonesia, as *Pellona russellii*. He regarded his species to be the same species as the “Jangarloo” in Russell (1803) [30] (also the basis for

the descriptions of *Platygaster macrophthalma* Swainson, 1838 and *Clupea megalopterus* Swainson, 1839). Subsequently, Whitehead et al. (1966) [69] designated BMNH 1867.11.28.13 (Figure 11A) as the lectotype. In addition, Bertin (1941) [74] described *Ilisha bleekeri* based on a specimen collected from Jakarta, Java, Indonesia, and reported by Bleeker (1870 [70], 1872 [71]) as *Ilisha novacula* (Valenciennes, 1847). Because the holotype of the nominal species (BMNH 1867.11.28.19; Figure 11B) is morphologically shown to be conspecific with the lectotype of *P. russellii*, *I. bleekeri* is considered a junior synonym of *I. russellii*. Additionally, *I. novacula* distinctively differs from *I. russellii* by the absence of posterior extension of tubes of swimbladder (Whitehead 1985 [2]; this study). Although *I. russellii* has been regarded as a junior synonym of *I. megaloptera* by many studies (e.g., Whitehead 1985 [2]; Kottelat 2013 [21]), its validity is confirmed in the present study.

At present, we can only provide reference COI “barcode” fragments for four specimens of *I. russellii* from Malaysia (GenBank accession numbers MH325640, MH325641, MH325638 and MH325639), as no tissue samples were available for the two other species, *I. megaloptera* and *I. motius*. However, given the difficulty of identifying species of *Ilisha* based solely on morphology, and the consequently high level of misidentification in the available COI dataset for these fishes, these reference COI sequences will certainly be useful for identification. These four sequences represent three unique haplotypes that differ from one another by one to three nucleotide substitutions, corresponding to a maximum intraspecific genetic distance of 0.45%.

4. Discussion

This study revealed that specimens previously identified as *Ilisha megaloptera* belong to at least three distinct species: *I. motius*, *I. megaloptera*, and *I. russellii*. As stated in the Morphological comparison sections for each species, these three species are easily distinguishable morphologically, and some characters, such as differences in the numbers of anal-fin soft rays and gill rakers, are frequently used to identify other pristigasterid species (Whitehead 1985 [2]; Munroe et al., 1999 [5]; Hata et al., 2025 [6]; Hata et al., 2026a [66]; Hata et al. (2026b) [28]). Because there is no genetic data yet available for *I. motius* and *I. megaloptera*, the genetic-based phylogenetic positions of these species within the family Pristigasteridae are not known. This situation prevents us from further discussing their evolution and biogeography.

Our taxonomic revision of *Ilisha megaloptera* illustrates that the species diversity of Pristigasteridae is likely to be significantly underestimated. Some currently recognized species of Pristigasteridae, widely distributed in the Indo-West Pacific region, may actually hide multiple species, each with a more limited distribution range. For example, *I. elongata* and *I. filigera*, currently thought to be widely distributed across the Indian and Pacific oceans (Whitehead 1985 [2]; Munroe et al., 1999 [5]) may represent species complexes. On the other hand, the pristigasterid *I. melastoma*, widely distributed from the Persian Gulf to Taiwan and Indonesia, does not exhibit morphological and genetic differentiation throughout its range (Hata et al., 2025 [6]). We note that *Ilisha russellii* and *I. melastoma* differ significantly in their biology; the former has a maximum lifespan of 3 years, grows to >20 cm SL, and has a reproductive lifespan of 1–2 years, while the latter has a lifespan of less than 2 years, grows to <15 cm SL, and has a reproductive lifespan of less than 100 days (Blaber et al., 1998 [26]; Hata et al., 2025 [6]; this study). These differences in reproductive ecology may have influenced their dispersal capabilities, and therefore may explain the difference in the size of the distributional ranges of the two species.

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Data Availability Statement: The specimens described in this study are available at fish-specimen collections (see the Material and Methods). COI nucleotide sequences newly determined for this study are publicly available from GenBank.

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