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Esomus helioscopus, a new species of flying barb from Laos with putative dual aquatic and aerial vision (Teleostei: Cyprinidae)

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Abstract. *Esomus helioscopus*, a new species of flying barb, is described from the Mekong drainage in Laos. It is distinguished from all other species of *Esomus* by the flat dorsal surface of its head, level from tip of snout to nape, with the eyes situated dorsally on the head, so that the upper part of the eye is visible in dorsal view, while other modifications of the eye itself are potentially associated with aerial vision. It co-occurs with *Esomus metallicus*, from which it is further distinguished by a plain grayish body without a bold mid-lateral stripe. It usually inhabits shallow, turbid, hypoxic swamps with high organic load, high temperature and without vegetation cover. An overview of the tentatively valid species of the genus is presented. *Esomus malayensis* Ahl, 1924, *E. caudiocellatus* Ahl, 1924, and *E. ahli* Hora & Mukerji, 1928 are junior synonyms of *E. malayensis* (Matte & Reichelt, 1908).

Key words. *Esomus*, Laos, swamps, eyes, Nakai Plateau

INTRODUCTION

The flying barb genus *Esomus* includes about seven valid, named species confined to South and Southeast Asia, from the Indus drainage in the west to coastal streams of Vietnam in the east, and Peninsular Malaysia in the south. One species (identified as *E. metallicus*) has been introduced at least to Sumatra (Arbsuwan et al., 2012), Singapore (Lim & Ng, 1990: 33; Ng et al., 1993: 20; Tan et al., 2020: 160), the Pahang drainage in Malaysia (Khan et al., 1996: 32), and Sabah (Kottelat & Whitten, 1996: 2). It is also present in northern Laos in the Nam Neun drainage (CMK 15288) (= Song Ca in Vietnam) and the Nam Ma drainage (CMK 25690) (= Song Ma in Vietnam), two rivers flowing eastwards to the Gulf of Tonkin (Vinh Bac Bo). Among Danioninae, the genus *Esomus* can be easily recognized by its pair of very long mandibular barbels, which are ossified and reach at least the pelvic-fin base, by the shape of the paired rostral barbels with ventral and dorsal flanges along most of their length, by the posterior position of the dorsal fin above the anal fin, and, in most species, by an incomplete lateral line.

To date, two nominal species of *Esomus* have been recorded from the Mekong drainage, *E. longimanus* and *E. metallicus* (Kottelat, 2001, 2013; Vidthayanon, 2008; Rainboth et al., 2012; So et al., 2018). We describe here an additional species found in extremely shallow, muddy habitats in Laos.

MATERIAL AND METHODS

Measurements and counts follow Kottelat (2001) and Kottelat & Freyhof (2007). Clearing and double staining follows Taylor & Van Dyke (1985). One paratype of *E. helioscopus* (MTD 40212, 39.8 mm SL) and one specimen of *Esomus metallicus* (MTD 40214, 42.2 mm SL) were scanned with a Zeiss Context µCT scanner at 4.05 µ, 0 kV, 6W, 1.8 sec exposure, 3 frames per exposure, filter LE1 and 4501 projections. Rendering and imaging was performed in the software Dragonfly.

The last dorsal and anal-fin ray articulating on the same pterygiophore as the preceding ray is noted as "½". Pectoral- and pelvic-fin ray counts include all rays, branched and unbranched. Eye diameter is measured parallel to the axis of the body. Body depth is measured at pelvic-fin origin. The lengths of the dorsal and anal fins are measured from origin to tip of last unbranched ray. The mid-lateral scales include the row with the lateral line pored scales and the scales of the row continuing it until the base of the caudal fin + the scales on the caudal fin. Toponymy is mainly as obtained in the field; some names are from the 1:100,000 topographic map of Laos (Service Géographique d'État, 1985, sheets E 48–66, 78, 79, 91, 1986, sheet E 48–67); names or spellings differing from the map are noted in square brackets, except Nakai, which is spelled Nakay on maps; nevertheless, most names on maps are no longer useful since the sites on

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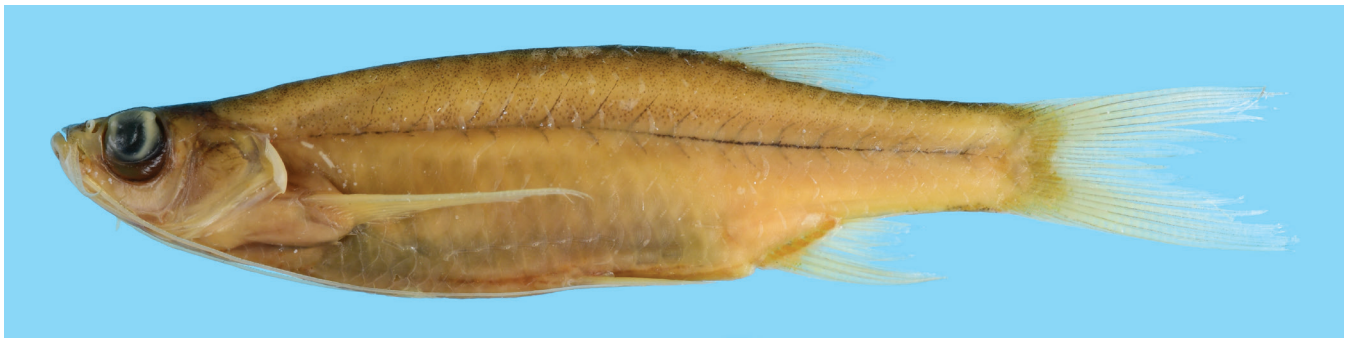

Fig. 1. *Esomus helioscopus*, MHNG 2815.033, holotype, 43.6 mm SL; Laos: Khammouan Province: Nakai Plateau.

Fig. 2. *Esomus helioscopus*; **a,** CMK 19763, paratype, 39.3 mm SL; Laos: Khammouan Province: Nakai Plateau; **b,** CMK 15219, 38.7 mm SL; Laos: Xiangkhouang: Nam Ngum on Plain of Jars.

Nakai Plateau are flooded by Nakai Reservoir (Nam Theun 2 Reservoir) and villages have been moved and renamed. Abbreviations used: ANSP, Academy of Natural Sciences, Philadelphia, U.S.A.; CMK, collection of the author; DZ, Department of Molecular Biology and Biotechnology, Peradeniya, Sri Lanka; MHNG, Muséum d'Histoire Naturelle, Genève, Switzerland; MTD, Senckenberg Naturhistorische Sammlungen Dresden, Museum für Zoologie, Dresden, Germany; and ZRC, Lee Kong Chian Natural History Museum, Singapore; c&s, cleared and stained.

Esomus helioscopus, new species

(Figs. 1, 2)

Holotype. MHNG 2815.033, 43.6 mm SL; Laos: Khammouan Province: Nong Lepui, a shallow 'lake' on Nakai Plateau; 17°44′22″N 105°11′57″E; M. Kottelat et al., 20 March 2007.

Paratypes. CMK 19763, 116, 29.2–43.3 mm SL; ZRC 70245, 20, 32.6–39.1 mm SL; MTD 40212, 15, 31.3–40.5 mm SL; MTD 40213, 5, c&s, 37.3–38.8 mm SL; same data as holotype.

Additional material (non-types)**.** All from Laos: Nam Theun watershed: CMK 19409, 3, 25.7–28.2 mm SL; Khammouan Prov.: Nakai Plateau, Nong [lake] Bo Cho, near Ban Boua Kham, 17°48′01″N 105°05′07″E; M. Kottelat & T. M. Leong, 8 May 2006. — CMK 19795, 218, 35.1–46.1 mm SL; Khammouan Prov.: Nong Khonken (a shallow lake) near old Ban Khonken (abandoned), Nakai Plateau, 17°39′17″N 105°18′17″E; M. Kottelat et al., 22 Mar 2007. — CMK 19825, 26, 30.5–46.1 mm SL; Khammouan Prov.: Nong Huam (a shallow lake) on Nakai Plateau, 17°48′41″N 105°03′44″E; M. Kottelat et al., 23 Mar 2007. — CMK 19950, 97, 25.7–47.7 mm SL; Khammouan Prov.: Nong Manao, a shallow lake on Nakai Plateau, 17°45′49″N 105°07′39″E; M. Kottelat et al., 30 March 2007. — CMK 19958, 82, 28.3–44.6 mm SL; Khammouan Prov.: Nong Ken, a shallow lake on Nakai Plateau, 17°48′12″N 105°08′33″E; M. Kottelat et al., 30 March 2007. — CMK 20075, 34, 30.7–45.4 mm SL; Bolikhamxai Prov.: Khamkheut Distr.: Nam Houai Keo Toi near Ban Kuapan, northeast of Laksao; mud pool in dry stream bed; standing water, 18°17′57″N 105°00′13″E; M. Kottelat et al., 9 April 2007. — CMK 28813, 85, 31.1–49.3 mm SL; CMK 28814, 120, 32.3–49.1 mm SL; Bolikhamxai

Table 1. *Esomus helioscopus*, morphometric data of holotype and 9 paratypes. Range and mean include holotype data.

	Holotype	Range	Mean
Standard length (mm)	43.6	37.9–43.6	
Total length (mm)	54.2	50.3–54.2	
In % of standard length			
Total length	124.4	124.4–134.3	130.0
Head length	24.9	21.9–26.0	24.6
Predorsal length	65.1	65.1–69.1	67.3
Prepelvic length	53.9	53.6–57.8	55.9
Preanal length	73.3	72.3–73.9	73.3
Head depth at nape	15.5	14.9–16.3	15.5
Head width	12.2	12.0–13.7	12.8
Body depth at pelvic-fin origin	24.2	22.7–24.9	24.1
Depth of caudal peduncle	11.0	11.0–12.3	11.6
Length of caudal peduncle	18.5	18.5–21.9	20.3
Eye diameter (horizontal)	6.5	6.5–7.7	7.0
Snout length	5.3	4.5–6.0	5.5
Interorbital distance	6.3	5.1–6.4	5.8
Length of dorsal fin	19.4	18.0–21.2	19.8
Length of upper caudal-fin lobe	26.8	26.8–30.6	29.0
Length of median caudal-fin rays	15.1	14.9–16.9	15.7
Length of lower caudal-fin lobe	29.6	28.6–32.3	30.7
Length of anal fin	18.9	18.9–21.8	20.2
Length of pelvic fin	15.5	14.1–16.5	15.1
Length of pectoral fin	29.6	29.6–33.8	31.4
In % of head length			
Snout length	21	19–26	22.2
Eye diameter (horizontal)	26	25–32	28.3
Interorbital distance	25	22–25	23.8
Head width	49	49–57	52.2

Prov.: Khamkheut Distr.: Nam Houai Hin at Ban Phonsy; mud pan and adjacent creek, 18°04′33″N 105°02′37″E; M. Kottelat et al., 9 April 2007.

Diagnosis. *Esomus helioscopus* can be readily distinguished from all congeners by its dorsally positioned eye which, in lateral view, is flush with the dorsal profile of the head (Fig. 3). The eye shows a conspicuous angle at its outer dorsal margin, with the lateral part vertical and convex and the dorsal part almost horizontal and flat. The cornea has an outer translucent, whitish layer that is especially well-developed in the dorsal part of the eye; the pupil is vertically elongated to an oval opening, and constricted by the whitish opaque layer of the cornea in its upper third. The constriction is caused by a narrowing in the sclera, which lacks the dorsal part of the cartilaginous scleral ring. The interorbital distance is only 1.0–1.4 times in the eye diameter. In lateral view, the dorsal profile of the head is straight and level from the tip of snout to the nape. Additional diagnostic characters (but not unique to the species) are: the maxillary barbel reaching at least to the base of the pelvic fin; the lateral line reaching between the pelvic and anal fins, with 13–19 pored scales; the body pale yellow, with the axial streak from gill opening to the end of the caudal peduncle, clearly distinct from below the dorsal-fin origin backwards.

Description. See Figs. 1, 2 for overall appearance, and Table 1 for morphometric data of holotype and 9 paratypes.

Body slender. Dorsal profile of head and body about straight from tip of snout to dorsal-fin origin, sometimes with a shallow concavity at nape, straight or slightly concave along dorsal-fin base, then straight to caudal-fin base. Body compressed, almost forming a keel between pectoral and pelvic fins. Body depth increasing until about pelvic-fin origin, then decreasing to about posterior extremity of anal-fin base, then depth about constant to caudal-fin base. Ventral profile convex from chin to pelvic-fin base. Depth of caudal peduncle 1.5–1.9 times in its length.

Mouth slightly superior. Maxilla not reaching backwards to level of anterior naris. Rostral barbel short, reaching backwards until posterior margin of eye, with a dorsal and ventral flange along most of its length, ventral flange more developed (Figs. 3, 4b). Maxillary barbel reaching at least to base of pelvic fin, in some specimens as far as anal-fin origin.

Dorsal fin with 2 unbranched and 6½ branched rays; origin above lateral line scales 16–18; distal edge straight to slightly convex. Pectoral fin with 12 (1), 13 (8) or 14 (1*) rays; falcate; reaching slightly beyond pelvic-fin base; anterior

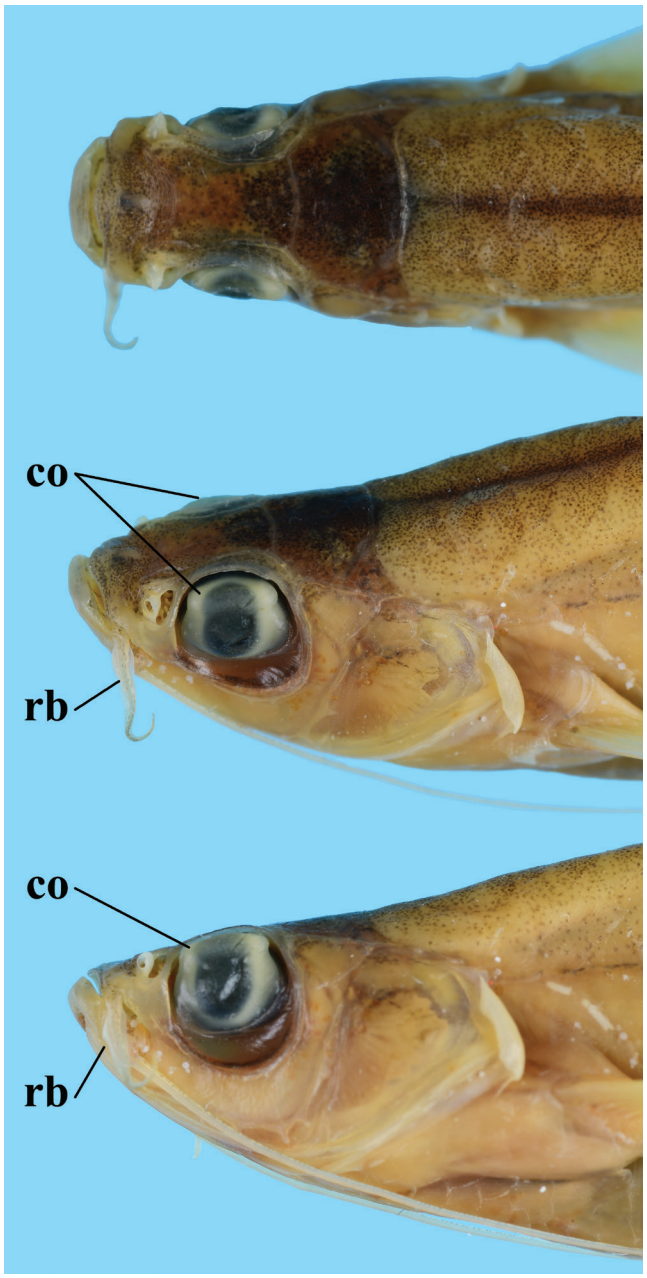

Fig. 3. *Esomus helioscopus*, MHNG 2815.033, holotype, 43.6 mm SL. **co,** opaque part of cornea on dorsal part of eye; **rb,** rostral barbel with flanges.

ray elongated. Band of tubercles arranged in single series along posterior margin of pectoral-fin rays 1–4 present in males only (Fig. 5). Pelvic fin with 8 rays (total); slightly falcate, posterior edge straight, almost reaching anus; no modified axillary scales. Anal fin with 3 unbranched and 5½ branched rays; origin below base of branched dorsal-fin rays 4–5; distal edge concave. Caudal fin deeply forked, with 8+8 (4) or 9+8 (6*) branched rays, length of upper lobe 1.8–2.0 times length of middle rays.

Top of head flat from snout to occiput. Interorbital distance 1.0–1.4 times in horizontal eye diameter (Fig. 3). Eye vertically elongate, extending dorsally on side to top of head (Figs. 3, 6). Surface of lateral part convex, surface of dorsal part almost flat and level with dorsal surface of head, resulting in almost a right angle between the two parts; sclera constricted at angle, and cornea with opaque outer layer on dorsal part and thus covering dorsal-most corner of pupil. Pupil vertically elongated into oval opening; iris narrow (Fig. 7). Some of these features, such as the opaque corneal layer and the degree of constriction of the sclera may have been caused by fixation; the degree of constriction is about uniform within individual populations, but shows some differences between populations. However, this may be because different tissues react differently to the fixation (formalin and ethanol). Also, the effect of the chemistry of the water used to dilute formalin is not known. Rock-salt deposits (and salt licks) exist on the plateau (MK, pers. obs.), the presence of mercury deposits has been reported (e.g., Roberts, 1996: 19, 2004: 20, based on unpublished reports and communications), organic load in some swamps is very high, urine concentration in the swamp and buffalo wallows is unavoidably very high; and finally, the Nakai Plateau was heavily bombed during the Vietnam War, leaving numerous large craters (forming pools), unstudied chemical pollutants, and unexploded ordnance (MK, pers. obs.).

Lateral line incomplete, perforating 13 (2), 14 (2), 15 (2), 17 (1), 18 (2) or 19 (1*) scales (anteriormost ones difficult to discern). 29+2 (1), 30+2 (2), 31+ 2 (6*) or 32+2 (1) scales in midlateral row. 16 (4*) or 17 (6) predorsal scales. 6 (8*) or 7 (2) scale rows between dorsal-fin origin and lateral line; 8 scale rows between dorsal-fin origin and anal-fin origin; 2½ scale rows between lateral line and mid-ventral line (counted about 2–3 scales in front of pelvic-fin base); 1 or 1½ scales between lateral line and pelvic-fin origin, 14 scale rows around caudal peduncle.

Colouration. In formalin, about one year after fixation. Body and head pale yellowish, with a mid-dorsal band of small melanophores. Axial streak extending from gill opening to end of caudal peduncle, clearly distinct from below dorsal-fin origin backwards, only faintly visible forwards. A band of sparsely distributed melanophores on scale row above axial streak. Top of head dark gray. Rest of body without visible pigments. All fins hyaline.

Colour and pigmentation in life was not recorded. The fish were all caught in murky water, were uniformly grey, and mostly coated in mud.

Distribution. *Esomus helioscopus* was found on the Nakai Plateau and downstream in the Nam Theun watershed, and on the Plain of Jars in the Nam Ngum watershed (Fig. 2b). We have seen material of *E. helioscopus* (or a species with the same ocular and head modifications) from the area of Ratanakiri in Cambodia (MHNG 2152.087), that we are not able to distinguish from the material from Nakai Plateau.

Field observations. On the Nakai Plateau, in 2006 and 2007, *Esomus helioscopus* was only observed in standing water, very shallow (sometimes drying marshes, in only a few millimetres of water), murky, turbid, warm, often with high organic load (dry decayed vegetation, buffalo excrement, etc.), and without tree cover (Fig. 8). It was never observed in moving, deep or cool water, or in riparian shade. This

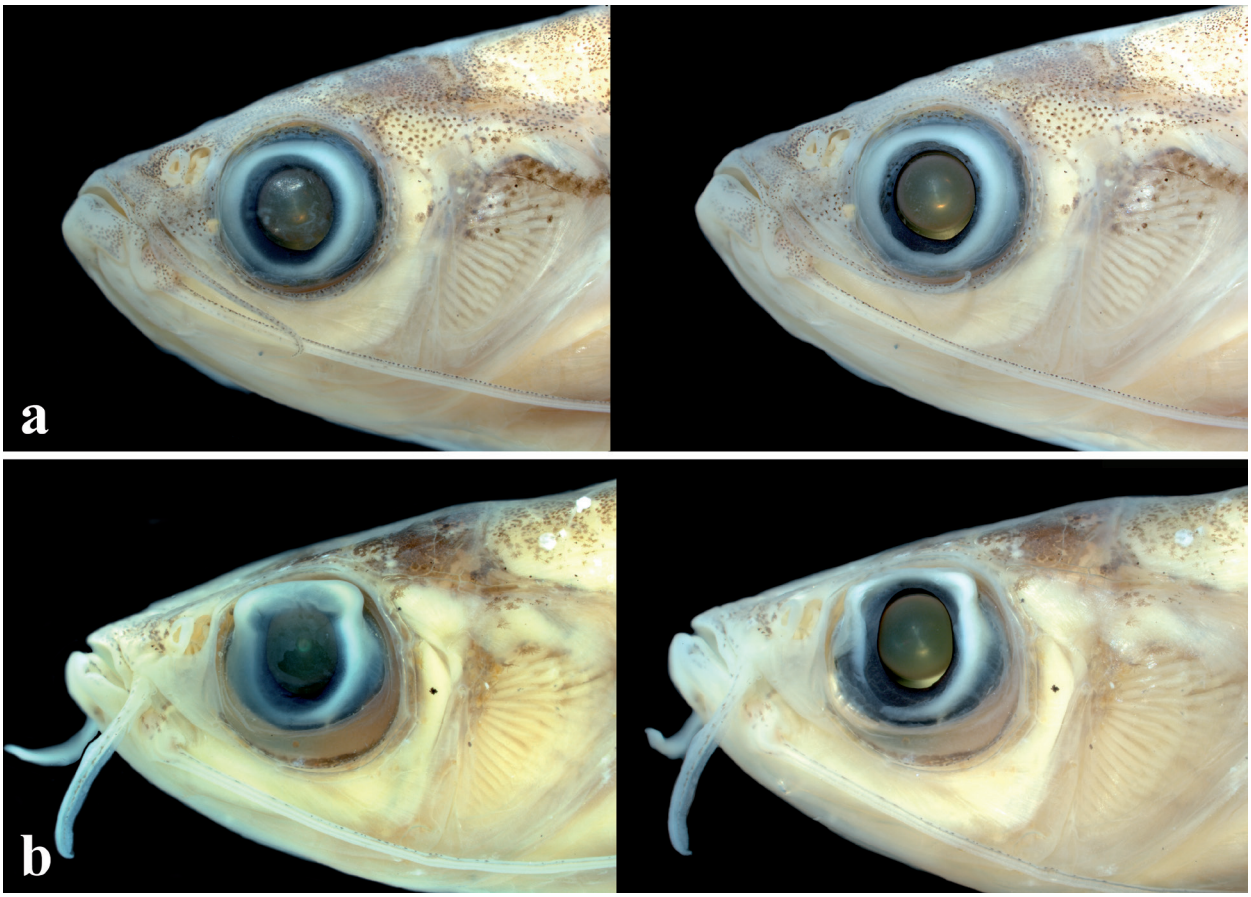

Fig. 4. Lateral view of head region of *Esomus* species, showing differences in eye position: **a,** *E. metallicus*, MTD 40214, 41.0 mm SL; and **b,** *E. helioscopus*, MTD 40212, 33.1 mm SL. Note scleral constriction and vertically elongated, oval pupil in *E. helioscopus*. Cornea removed in specimens on the right to expose margin of pupil and shape of lens.

is based on observations made between March and May; no surveys have been conducted in other seasons. At that time, females over about 40 mm SL had eggs. Stomach content of the examined material could not be identified. Before creation of the Nakai Reservoir, at the peak of the dry season, the plateau was almost totally dry, except for a few small deep lakes and ephemeral ponds. The Nam Theun (river) was flowing restricted to its minor bed. In the rainy season, the Nam Theun would flood almost the whole plateau (Kottelat, 1998, 2016).

Other fish species collected with *E. helioscopus* include *Microcobitis stilaspi* and *Oryzias* cf. *songkramensis* at most sites; *Lepidocephalichthys hasselti*, *Oryzias* sp. 2, *Clarias* cf. *batrachus*, *Trichopsis schalleri*, and *Puntius brevis* were also present in several of the sites (Kottelat, 2016, 2025).

Etymology. The species name is derived from the Greek words for the sun, ἥλῐος (helios), and watcher or gazer, σκοπός (skopos), alluding to the dorsally situated eye with its numerous morphological modifications, potentially associated with aerial vision in its sun-exposed habitat. A noun in apposition, indeclinable.

Fig. 5. *Esomus helioscopus*, CMK 19958, pectoral fin, dorsal side. **a,** female, 43.4 mm SL; **b,** male, 37.9 mm SL, with rows of tubercles on anterior rays 1–3.

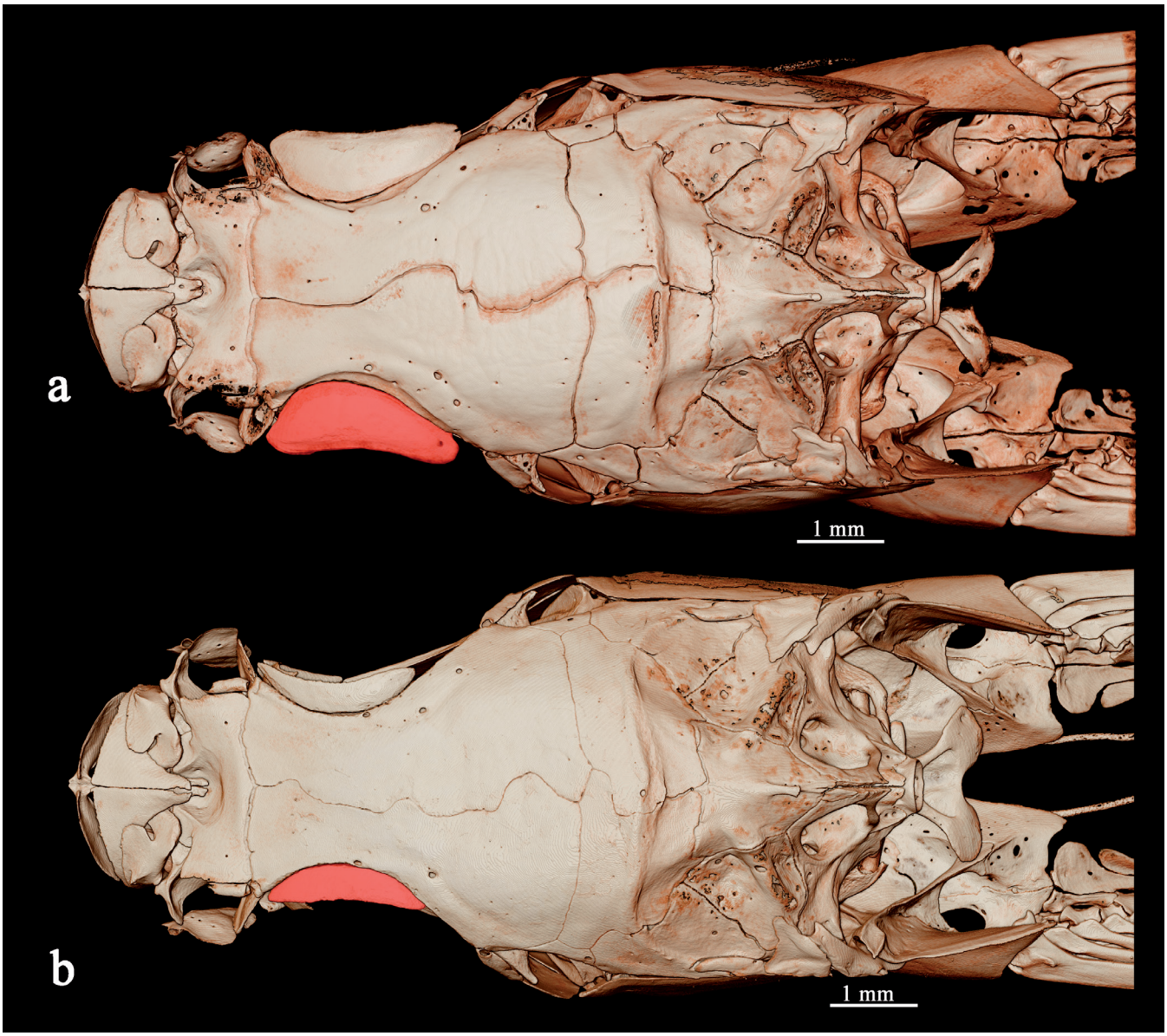

Fig. 6. µ-CT image of skull in dorsal view of: **a,** *Esomus metallicus*, MTD 40214, 42.2 mm SL; and **b,** *E. helioscopus*, MTD 40212, 39.8 mm SL. Note differences in shape and size of supraorbital (highlighted in red).

DISCUSSION

Anatomical modifications in the eye of *Esomus helioscopus*. The modifications of the eye, which we described above as potentially related to aerial vision, are less dramatic than in the few other fishes that have adapted to vision above the water surface. The most modified and most studied among them is *Anableps*, in which the pupil is separated into a dorsal and ventral half by a horizontal septum originating from the iris (Klinckowström, 1894; Schneider-v.Orelli, 1907). The lens is also modified and is egg or pear shaped instead of the usual spherical shape (Klinckowström, 1894; Schneider-v.Orelli, 1907; Schwassmann & Krüger, 1965) to account for the differences in refraction above and below water. Another taxon with ocular adaptations to vision above the water level is the blenny *Dialommus fuscus*. Here, the eye including its lens is not greatly modified, but there is a nearly vertical pigment band on the cornea, which separates the pupil into anterior and posterior halves (Breder & Gresser, 1943). A third group with ocular modifications which may be related to changing levels of brightness

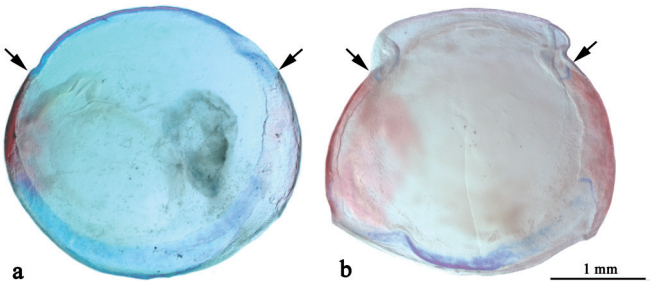

Fig. 7. Cleared and stained eye, lateral view, left side, of: **a,** *Esomus metallicus*, MTD 40215, 38.6 mm SL; and **b,** *E. helioscopus*, MTD 40213, 39.4 mm SL. Note presence of dorsal scleral cartilage (ends marked by arrows) connecting anterior and posterior sclerotic bones in *E. metallicus*, but its absence in *E. helioscopus*. Instead, the sclera in *E. helioscopus* above the sclerotic bones (dorsal margin marked by arrows) is constricted and thickened dorsally.

Fig. 8. Laos: Nakai Plateau, habitat of *Esomus helioscopus*; **a,** type locality, 20 March 2007; **b,** habitat of CMK 20075, 9 April 2007.

when swimming at the water surface are the osteoglossoids (Schwartz, 1971; Haedrich et al., 1973). In *Osteoglossum*, *Scleropages*, *Heterotis*, *Arapaima*, and *Pantodon*, a septum inside the eye separates the retina into dorsal and ventral halves. The eye modification that we describe for *Esomus helioscopus*, however, is quite different. Here, the pupil is pear-shaped with an additional open space extending further dorsally, potentially allowing light to enter the eye from above. This dorsally enlarged part of the pupil is covered by an opaque area of the cornea, which may function as a protective layer against direct sunlight, given the habitat in which *E. helioscopus* was caught. Further studies are necessary to better understand the modifications we described and establish their precise function. Interestingly, the more dorsal position of the eye in *E. helioscopus* is also correlated with modifications of the skull, especially its supraorbital bone, which is smaller and narrower than in the sympatric *E. metallicus*. Among the taxa mentioned above, it seems only *Anableps* has skeletal modifications associated with its modified eye (Perez et al., 2017).

***Esomus helioscopus* and *E. metallicus* sympatric but not syntopic.** The flat dorsal surface of the head of *E. helioscopus*, the dorsally positioned eyes with the upper part level with the dorsal surface of the head, the upturned mouth, and the paired rostral barbels held forward in life with their flanges forming a kind of 'funnel' in front of the mouth when the fish is swimming are likely adaptations to life in the uppermost few millimeters of the water column, immediately below the surface. Here, *E. helioscopus* potentially utilise the higher oxygen content of this water layer closest to atmospheric air, where they can feed on prey at the surface film, and detect potential surface and aerial predators. The opaque dorsal part of the cornea has possibly a function to protect the eye from intense direct sunlight.

The 2006 and 2007 surveys were a pre-impoundment survey (before closure of the Nakai Dam); the species was not seen in a survey conducted in 2012, after flooding of the reservoir (2008), but these surveys were targeting other species and habitats and no conclusion should be derived except with further investigation.

There is no information on the habitat during the wet season (May–October) and the beginning of the dry season. One may guess that with the onset of rains in May, before flooding of the Nakai Reservoir, the water level would be increasing, resulting in the inter-connection of swamps and the fish would be able to move laterally, possibly reaching some specific habitat to spawn. However, no fry were observed among the available material. The situation after closure of the dam (2008) and flooding of the reservoir is not known, but the reservoir has an extensive annual drawdown in the dry season (November–May) and most of the plateau becomes exposed.

Esomus metallicus (Fig. 9b) too is present on the Nakai Plateau and is easily distinguished by the position and shape of the eyes, the convex top of the head, and the presence of a midlateral stripe, usually conspicuous. In the dry season, prior to the flooding of the plateau, it was observed in slow-flowing creeks, ponds and small lakes deeper than those in which *E. helioscopus* was encountered. The habitats of *E. metallicus* usually have clear water (at least in the dry season). In one case it was found in a pond with relatively turbid but slowly flowing (spring-fed) water; the specimens were discolored but the midlateral stripe was still distinct and the eyes in lateral position (CMK 19975; Figs. 10, 11b) excluding possible confusion with *E. helioscopus*. In 2012, after flooding of the reservoir, *E. metallicus* was observed in swampy areas, but *E. helioscopus* was not encountered.

We entertained the possibility that the eye and head modifications could be an individual adaptation of some *E. metallicus* occupying the peculiar habitat of shallow swamps. We ruled out this hypothesis because the modifications seem too extreme to develop individually in the few weeks between the moment the swamps become isolated (December–January) and the time when the water depth was drastically reduced to a few centimeters at the time of collecting (March–April). Molecular techniques were not routinely available at the time of sampling and no suitable material was preserved for DNA analysis.

We have a single sample in which both *E. helioscopus* and *E. metallicus* are present, but it is not very informative because the habitat was made of a pool and a small creek with clear water a few meters away; unfortunately, the material from the two habitats were not preserved separately. The sample includes 205 specimens unambiguously identifiable as *E. helioscopus* (CMK 28813, 28814, 31.1–49.3 mm SL; Fig. 9a) and 63 specimens unambiguously identified as *E. metallicus* (CMK 20068, 28812, 29.5–45.9 mm SL; Fig. 9b). There was no specimen with an intermediate morphology. From this, we conclude that *E. helioscopus* cannot be an

Fig. 9. The two species of *Esomus* in the Nam Theun watershed, collected at same site. **a,** *E. helioscopus*, from turbid water, mud pool, CMK 28813, 46.0 mm SL; **b,** *E. metallicus*, from clear water, creek, CMK 20068, 45.3 mm SL.

Fig. 10. *Esomus metallicus* with faint melanophore markings; CMK 19975, 55.2 mm SL; Laos: Nakai Plateau.

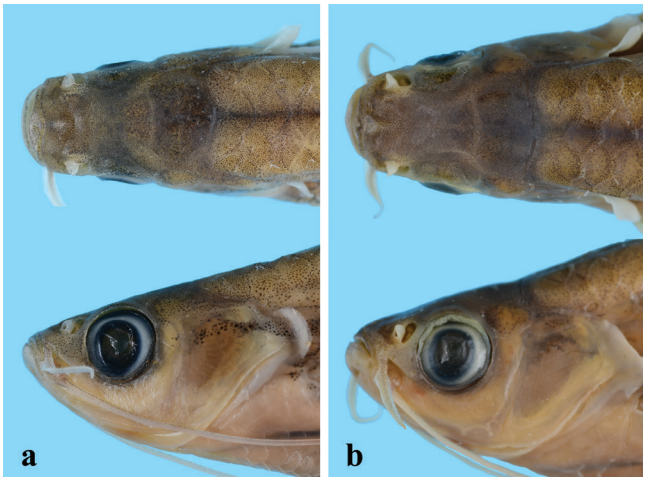

Fig. 11. *Esomus metallicus*, Laos: Nakai Plateau; **a,** CMK 20068, 45.3 mm SL, from clear water (specimen on Fig. 9b); **b,** CMK 19975, 55.2 mm SL, from turbid water (specimen on Fig. 10).

individual variation and adaptation of *E. metallicus* to the extreme habitat.

If the morphology of *E. helioscopus* were merely an adaptation of some individual *E. metallicus* to this extreme habitat, then it should be observed at other localities where *E. metallicus* is present in similar extreme environments. While *E. metallicus* is frequently observed in the floodplain of the Mekong drainage, including shallow, muddy swamps, *E. helioscopus* was not observed. Outside the Nakai Plateau, we have seen *E. helioscopus* (or a species with similar orbital and ocular modifications of the head) only on the Plain of Jars in Nam Ngum watershed (CMK 15219; Fig. 2b), where no *E. metallicus* was observed. We have seen one specimen from Ratanakiri in Cambodia (MHNG 2152.087) that we are not able to distinguish from our material of *E. helioscopus* from Nakai Plateau. It remains to be determined whether

Fig. 12. *Esomus danrica*; **a,** CMK 10769, 31.1 mm SL; India: West Bengal (right side, reversed); **b,** CMK 24183, 37.8 mm SL; Myanmar: Irrawaddy drainage: Lake Indawgyi basin.

all are conspecific. We have not seen *E. helioscopus* among the available *Esomus* samples from Thailand.

The species of *Esomus*. As mentioned in the Diagnosis, *E. helioscopus* differs from all species of the genus, among other characters, by the position and morphological structure of the eye. In all the other species, the eye is circular and positioned laterally.

The genus *Esomus* was last reviewed by Hora & Mukerji (1928) who recognised five valid species. Since, additional species have been recognised, synonyms have been revalidated and some nominal species have been treated as synonyms. As presently understood, the genus *Esomus* includes about seven valid species (Kottelat, 2013, updated).

Esomus danrica (Hamilton, 1822) (Fig. 12), type species of the genus and oldest species recognised as valid, is reported from the Indus to the Brahmaputra drainages. Several nominal species have been described from India that have at some time been treated as synonyms of *E. danrica* (e.g., Hora & Mukerji, 1928; Kottelat, 2013: 102) but this should be revisited. *Esomus* populations from the Irrawaddy drainage in Myanmar had been identified as *E. danrica*. Populations reported as *E. danrica* from the Salween drainage in Thailand are identified, for the time being, as *E. metallicus* (pers. obs.).

After Hora & Mukerji's (1928) revision, some nominal species were described but soon came to be treated as synonyms of *E. danrica*. *Esomus danrica jabalpurensis* Visweswara Rao & Sharma, 1973 is considered a synonym of *E. danrica* by Talwar & Jhingran (1991: 377) and Menon (1999: 48). *Esomus manipurensis* Tilak & Jain, 1990 is considered a synonym of *E. danrica* by Talwar & Jhingran (1991: 377) but as valid by Menon (1999: 48); this species is not mentioned in Vishwanath's (2021) review of fishes of northeastern India. *Esomus bengalensis* Bhakat & Sinha, 2020 is based on two specimens, very poorly preserved, very poorly photographed, and from which no identification can be derived and which, frankly, are useless for any purpose.

In addition, the name *E. nimasowi* was created for a fish from Assam (Abujam et al., 2021), and would possibly have been a synonym of *E. danrica*. However, the name is not available for zoological nomenclature because it does not satisfy the criteria of availability set forth by Article 8.5 (amended 2012) of the International Code of Zoological Nomenclature (ICZN, 1999, 2012). It was created in a publication that exists only as PDF and the authors or editor did not care to have it registered in Zoobank, as required by the Code. Further, the reported supposedly diagnostic characters do not distinguish the species; they seem to be merely variable features, based on poorly fixed or damaged specimens of *E. danrica*. The localities of all these nominal species are surrounded by the range of the widely distributed, eurytopic *E. danrica*. In the absence of a critical study, based on good sampling of numerous localities and numerous well-preserved specimens, it does not seem to serve any purpose to comment further.

Esomus altus (Blyth, 1860) (Fig. 13) is a large-sized species (up to at least 87 mm SL) known from the Irrawaddy, Sittaung and lower Salween drainages and distinguished, among other characters, by its complete lateral line, a black spot above the base of the pectoral fin, and the absence of any other colour pattern on body and fins (Hora & Mukerji, 1928; pers. obs.).

Fig. 13. *Esomus altus*, CMK 28245, 71.7 mm SL; Myanmar: Sittaung drainage: Shwegyin.

Fig. 14. *Esomus thermoicos*, Sri Lanka: Attanagalu; **a,** DZ 3819, 56.2 mm SL; **b,** not preserved, about 50 mm SL. Photographs by H. Sudasinghe.

Esomus thermoicos (Valenciennes, in Cuvier & Valenciennes, 1842: 238, pl. 472) (Fig. 14) is known from Sri Lanka and southern India (Sudasinghe et al., 2019). *Esomus barbatus* (Jerdon, 1849), *E. malabaricus* (Day, 1867), *E. maderaspatensis* (Day, 1867), and *E. danrica brevibarbata* Deraniyagala, 1958 are synonyms.

Esomus malayensis (Matte & Reichelt, 1908) (Fig. 15) was originally used (as *Nuria danrica* var. *malayensis* for fishes from "Hinterindien" ['Farther India']) in a booklet that served as catalogue of an aquarium-fish farm in Germany. The text, although minimal, includes enough information to identify it as a species of *Esomus* and make the name available for nomenclatural purposes, but it provides no information other than the presence of a black spot on the caudal peduncle. The text also mentions "this Malayan subspecies". An almost identical text is repeated by Matte & Kuhnt (1908: 10), but this time accompanied by a figure. Mandée (1909: 11) repeated this information and republished the figure. "Hinterindien" corresponds to today's Mainland Southeast Asia; its western limit is the divide between Brahmaputra and Irrawaddy drainages; its eastern limit is the divide between the Mekong and Red River drainages (Anonym, 1876: 936–938).

Ahl (1924: 43) also described an *E. malayensis* based on material from "Malay peninsula or Archipelago?" provided by Paul Stieler and likely imported to Germany as aquarium fishes (Paepke, 1995: 90). Ahl (1924) made no reference to Matte & Reichelt (1908), Matte & Kuhnt (1908), and Mandée (1909) and thus *E. malayensis* Ahl (1924) is a distinct nominal species and it has its own type series. But, at the

Fig. 15. *Esomus malayensis*, CMK 24116, 32.9 mm SL; Myanmar: Irrawaddy drainage: Lake Indawgyi basin.

Fig. 16. *Esomus metallicus*, CMK 24414, 35.1 mm SL; Laos: Nam Mang watershed (reversed).

same time, *E. malayensis* Ahl (1924) also is a secondary junior homonym of *Nuria danrica* var. *malayensis* Matte & Reichelt (1908) and therefore permanently invalid. The two nominal species share the presence of a black spot at the posterior extremity of the caudal peduncle, the only useful information included in Matte & Reichelt (1908) and Matte & Kuhnt (1908).

Esomus caudiocellatus Ahl (1924: 43) is described in the same article, also based on material obtained from Paul Stieler, but without known origin (Paepke, 1995: 90); it too is described as having a black spot at the end of the caudal peduncle; an additional character is the absence of the lateral line. In the absence of information to distinguish *E. caudiocellatus* Ahl, 1924 and *E. malayensis* Ahl, 1924, we treat them as simultaneous subjective synonyms and as first revisers we give precedence to *E. caudiocellatus*. This makes *E. caudiocellatus* Ahl (1924) a senior synonym of the invalid *E. malayensis* Ahl (1924). and at the same time a junior synonym of *E. malayensis* (Matte & Reichelt, 1908).

Esomus ahli Hora & Mukerji, 1928: 47, fig. 3 (type locality: Burma: Rangoon) also has a black spot at the end of the caudal peduncle and a lateral line with 4–6 pored scales. Hora & Mukerji merely mentioned the two species just described by Ahl (1924) but did not comment on them, nor did they mention the species named by Matte & Reichelt (1908).

Presently, the only *Esomus* in Southeast Asia known to have a black spot on the caudal peduncle is the species from the Irrawaddy and Sittaung drainages in Myanmar that is currently called *E. caudiocellatus*. No *Esomus* with this pattern has ever been reported from the Malay Peninsula. Panitvong (2565 [2022]: 114) recorded it from the Mekong drainage in extreme northern Thailand, but does not provide further information. For the time being, there is no apparent reason to think that more than one species with a caudal peduncle spot is involved. *Esomus malayensis* (Matte & Reichelt, 1908) is the name to be used for this species; and therefore *E. malayensis* Ahl (1924), *E. caudiocellatus* Ahl (1924) and *E. ahli* Hora & Mukerji (1928) are its junior synonyms.

Esomus metallicus Ahl, 1924 (Fig. 16), originally described from Petchaburi (Thailand), is widespread in the Chao Phraya, Mae Khlong, Bangpakong, Salween, and Mekong drainages, in Vietnam in coastal drainages northwards to Quang Tri, and in the Malay Peninsula southwards to Satun on the western slope and Terengganu on the eastern slope (Arbsuwan et al., 2012; pers. obs.). Further studies are needed to show whether they are all conspecific.

Esomus longimanus (Lunel, 1881) was originally described from an unspecified locality in Cambodia. Since then, it has been reported from Cambodia by So et al. (2018: 40) without specified locality, by Rainboth (1996: 73, pl. 4 fig. 25), who used both the drawing of *E. goddardi* of Fowler (1937) and his own photograph of a specimen from unstated locality, by Rainboth et al. (2012: 62, pl. 16 fig. 320), who used the same photograph, this time with stated locality (Odong Mean Chey,

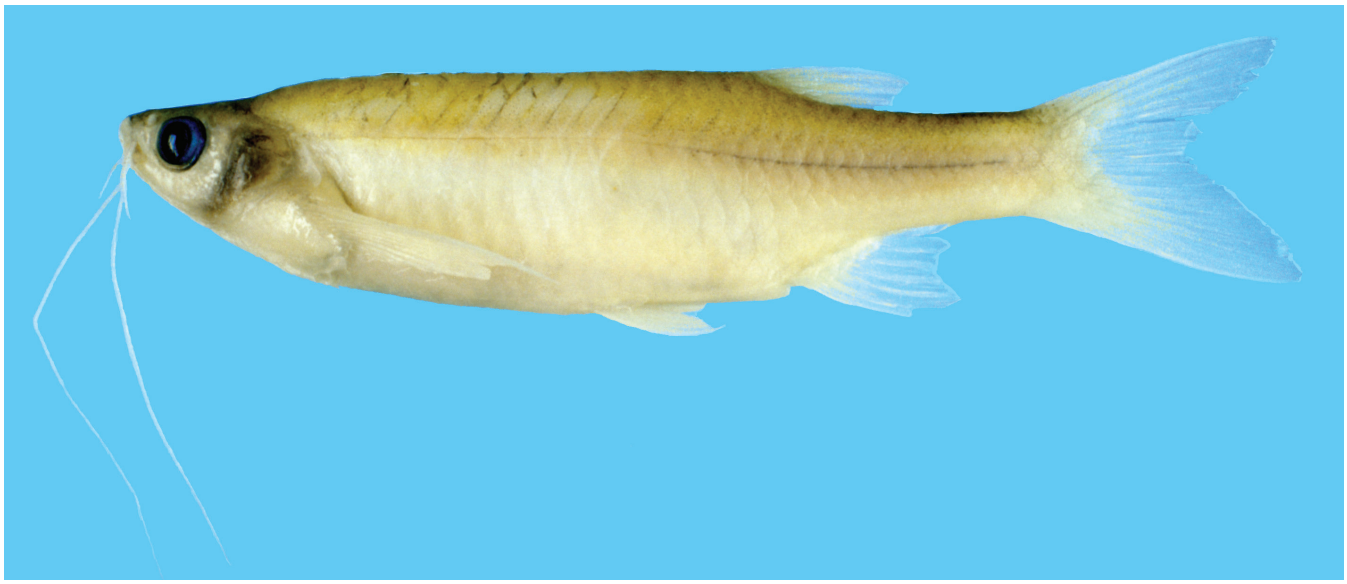

Fig. 17. *Esomus goddardi*, CMK 13812, 58.0 mm SL; Laos: Mekong: Savannakhet.

floodplain lake near Phum Kraom; caption of fig. 321 says that Odong Mean Chey is a swamp NW of Phnom Penh), and by Nagao Natural Environment Foundation (2021: 93) "from a very restricted [but unnamed] area of Cambodia". *Esomus longimanus* is diagnosed by the very long pectoral fin reaching posteriorly to about the anus and a very long maxillary barbel reaching the caudal-fin base. The original description and the accompanying figures are very detailed. The eye is circular, positioned laterally, as in *E. metallicus* and as figured by Rainboth (1996: pl. 4 fig. 25), Rainboth et al. (2012: pl. 16 fig. 320) and So et al. (2018: 40). The holotype was in Musée Cantonal de Zoologie, Lausanne, Switzerland, but is missing since at least 1882 (MK, pers. obs., 1982; Olivier Glaizot, Naturéum, Lausanne, pers. comm., 2026).

The specimen identified as *E. longimanus* from the Mekong drainage in Laos (Kottelat, 2001: 50) is from Savannakhet (CMK 13812; Fig. 17) and is re-identified as *E. goddardi*.

Esomus goddardi Fowler, 1937 was described from the Chao Phraya drainage. There is some uncertainty about the type locality. Fowler (1937: 170) reported the type locality as "Mae Poon, Siam". De Schauensee (1946: 5), who collected the material, reported it as: "Me Poon.—A small tributary of the Me Yom which enters it at lat. 17°40′N., long. 99°42′E. More properly spelled Me Phun; on one map, Me Bhun". This is the locality reported in Kottelat (1990: 207, 2013: 102). Smith (1945: 24) record the locality as "Poon (Mae Nam), Phum: stream tributary of the Mae Yom, probably that which enters the main river about 43 miles SW of Muang Phrae". But Rainboth (1989: 12) reported that "the Me Poon locality is in the Mae Nam Ping drainage, north of Chiang Mai (R. M. de Schauensee, pers. comm. through Barry Chernoff). Inspection of Thai language maps indicates that a better transliteration of the locality name is Mae Poong, and it identifies a small village 60 km NNE of Chiang Mai".

Esomus goddardi Fowler, 1937 (Figs. 17, 18) is reported from the Chao Phraya and Mekong drainages (Taki, 1974: 93; pers. obs., CMK 5034, Nong Khai, CMK 13812, Savannakhet, Fig. 17). Kottelat (1989: 7) considered that *E. goddardi* is possibly a junior synonym of *E. longimanus* and later listed it as a synonym (Kottelat, 2013: 102). The photograph of *E. longimanus* in Kottelat (2001: 51; here Fig. 17) shows a fish with a different appearance and with the pectoral fin and maxilary barbel much smaller than those of *E. longimanus* as pictured in the original description and in the literature mentioned above, and with only a thin, inconspicuous midlateral stripe on the posterior half of the body.

Finally, Endruweit (2025: 79) created the name *E. hypothrix* for a species of the Song Ma drainage in northern Vietnam (at Trung Son, 20°36′24″N 104°51′15″E). The Nam Ma flows east of the Annamite Range; it originates in Vietnam, flows through northeastern Laos, then through Vietnam, where it is called Song Ma, and enters the Gulf of Tonkin south of the mouth of the Red River. Endruweit compared this species only with *E. metallicus*, based only on the descriptions by Ahl (1924) and Hora & Mukerji (1928) from which he distinguished *E. hypothrix* by the length of the maxillary barbel (reaching about ⅔ of length of pectoral fin, vs reaching beyond the anal-fin origin) and of the pectoral fin (not reaching pelvic-fin origin vs. reaching beyond it), the number of predorsal scales (19–20 vs 17) and possibly by the presence of an oblique cleithral mark (not distinct on his figure 67). He speculated that in the figure of *E. metallicus* in Kottelat (2001: 50, fig. 73) the maxillary barbels are missing or "lost during image editing". [In fact, the maxillary barbels of the specimen (CMK 15061, 49.9 mm SL) are present, the right one is on the right side (!), the left one is adpressed on the left cheek, then continues folded on the right side; it is not 'lost in editing' (!) but indistinct because of the grain of the printed picture.] The identity of *E. hypothrix* cannot be decided from the original description and figure. Our material of *E. metallicus* CMK 25690 (Fig. 19) from the Nam Ma watershed in Laos (about

Fig. 18. *Esomus goddardi*, ANSP 68047, holotype, about 55 mm SL; Thailand: Me Poon; right side, reversed (photograph by Kyle Luckenbill).

Fig. 19. *Esomus metallicus*, CMK 25690, 39.9 mm SL; Laos: Houaphan Prov.: Nam Ma drainage.

60 river-km upstream of the type locality of *E. hypothrix*) cannot be distinguished from our *E. metallicus* from the Mekong drainage in Laos. However, it differs from the types of *E. hypothrix* as described by Endruweit in having 16–17 predorsal scales (vs. 19–20) and a possibly slenderer body. Without access to more material from the Nam Ma drainage, a further discussion of the status of *E. hypothrix* would be of no avail.

Comparison material. *Esomus helioscopus*: CMK 15219, 7, 35.1–41.8 mm SL; Laos: Xiangkhouang Prov.: Nam Ngum watershed: rice fields near Ban Peup; 19°36′21″N 103°15′13″E; M. Kottelat et al., 30 April 1999. — MHNG 2152.087, 1, 28.9 mm SL; Cambodia: road from Ratanakiri to Boumlong; F. d'Aubenton, 22 February 1964.

Esomus metallicus: Laos: Nam Theun watershed: CMK 19797, 41, 29.9–46.6 mm SL; Khammouan Prov.: Nakai Plateau, Nong Pa Pak (pond) about 1 km north of old Ban Khonken (abandoned), on other side of Nam On; 17°39′30″N 105°19′05″E; M. Kottelat et al., 22 March 2007. — CMK 19813, 102, 38.0–47.9 mm SL; MTD 40214, 5, 42.6–46.1 mm SL; MTD 40215, 5 c&s, 39.8-47.4 mm SL; Khammouan Prov.: Nong Bocho (= Nong Bua), a shallow lake on Nakai Plateau; 17°48′11″N 105°05′19″E; M. Kottelat et al., 23 March 2007. — CMK 19961, 1, 33.6 mm SL; Kammouan Prov.: Nong Seac, a deep (up to 7 m) clear-water lake on Nakai Plateau; 17°46′46″N 105°07′51″E; M. Kottelat et al., 30 March 2007. — CMK 19975, 8, 44.3–56.9 mm SL; Khammouan Prov.: swamp immediately south of Ban Nong Boua Kham, Nakai Plateau, 17°47′23″N 105°04′54″E; M. Kottelat et al., 1 April 2007. — CMK 20068, 26, 29.5–45.9 mm SL; CMK 28812, 37, 30.5–40.9 mm SL; Bolikhamxai Prov.: Khamkheut Distr.: Nam Theun watershed: Nam Houai Hin at Ban Phonsy; mud pan and adjacent stream, 18°04′33″N 105°02′37″E; M. Kottelat et al., 9 April 2007.

Mekong drainage, other watersheds: CMK 15061, 9; Thailand: Nong Khai Prov.: Ban Tad Soem, on road Loei–Nong Khai. — CMK 24414, 16, 28.7–35.1 mm SL, Laos: Saysomboune Prov.: Nam Mang near Ban Pa La Veak. — CMK 24622, 20, 25.4–47.2 mm SL; Laos: Bolikhamsai Prov.: Nam Ngiep drainage: Nam Xao downstream of Ban Phounxong [Ban Namxon].

Outside Mekong drainage: CMK 15288, 6, 39.1-45.3 mm SL; Laos: Xiangkhouang Prov.: Nam Mat at Ban Phathang, 19°36′16″N 103°41′47″E. — CMK 25690, 2, 37.1–39.9 mm SL; Laos: Houaphan Prov.: Nam Ma drainage: Houay Heng, downstream of Ban Heng, near confluence with Nam Hao,

20°31′09″N 104°21′45″E. — CMK 20178, 16, 24.7–47.5 mm SL; Thailand: Chantaburi Prov.: heath forest, on road from Pong Nam Ron to Chantaburi. — CMK 4117, 5, 41.6–52.7 mm SL; Thailand: Chiengmai Prov.: Khan River where it intersects road from San Pa Tong to Ban Kat.

E. altus: CMK 28245, 1, 71.7 mm SL; Myanmar: Bago Region: Sittaung drainage: Son Thike chaung at northern edge of Shwegyin.

E. malayensis: CMK 24116, 15; Myanmar: Kachin State: Nam Yin Hka Chaung (stream), entering lake Indawgyi south of Lonton.

E. goddardi, ANSP 68047, holotype, about 55 mm SL; Thailand: Me Poon (photograph only). — CMK 13812, 2; Laos: Savannakhet: Mekong at Ban Donsen, about 6 km south of Savannakhet. — CMK 5034, 16; Thailand: market in Nong Khai.

E. thermoicos: CMK 9343, 2; India: Kerala: Kolapuram, on road from Chalakudy to Calicut.

E. danrica: CMK 10769, 7; India: West Bengal: aquarium-fish trade. — CMK 24183, 13; Myanmar: Kachin State: Indawgyi Lake: Nan Mon Chaung.

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