Revision of the Cyprinid Genus Crossocheilus (Tribe Labeonini) with Description of a New Species

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The Southeast Asian cyprinid genus Crossocheilus was briefly described by Kuhl and van Hasselt in 1823 and, despite the short description, has remained a valid genus. However, the genus and its species are frequently misidentified in institutional collections, likely due to the absence of a detailed diagnosis and description, as well as the superficial morphological similarity with other cyprinid genera in the region. Crossocheilus and its constituent species are herein revised based on an examination of morphology and pigmentation. Eleven species are recognized, including a new species described from Indonesia. Crossocheilus pseudobagroides is a junior synonym of C. langei. Crossocheilus ichangii is removed from synonymy with C. reticulatus and is a senior synonym of C. stigmaeus. Phylogenetic relationships among species of Crossocheilus based on sequences from the nuclear encoded recombination activating gene 1 are reconstructed. The resultant phylogeny is the most taxonomically comprehensive estimation of relationships among Crossocheilus to date and resolves C. atrilimes and C. oblongus, previously hypothesized to be sister species, not to be most closely related to one another.

The Southeast Asian cyprinid genus Crossocheilus was described by Kuhl and van Hasselt in 1823, with the type species being C. oblongus. In the original publication, the name Crossocheilus appears prior to Crossocheilus, which was the spelling used in the actual description of the genus by Kuhl and van Hasselt (van Hasselt, 1823). Kottelat (1987) served as the first reviser and retained the name Crossocheilus. As noted by Roberts (1989), the original description only mentions one character in diagnosing and describing the genus and species: “mouth opening directed downwards in the form of a parallelogram” (van Hasselt, 1823; translated in Alfred, 1961). More detailed descriptions of C. oblongus and the genus Crossocheilus were later provided by Valenciennes (Cuvier and Valenciennes, 1842) and Bleeker (1854), respectively. Despite the vague initial description, Roberts (1989) accepted the name Crossocheilus as valid in maintaining nomenclatural stability. Species of Crossocheilus are frequently confused with each other and with other cyprinid genera in museum collections, likely as a result of these limited descriptions and similarities with other genera from the region.

Previous molecular phylogenetic studies have resolved species historically placed in Crossocheilus as polyphyletic with two strongly supported clades: a South Asian clade (containing species distributed from the Salween River in Thailand and Myanmar, west to Iran) closely related to the genus Garra Hamilton, 1822, and a Southeast Asian clade (containing species distributed east of the Salween River in Indochina and Indonesia) nested in a clade with labeonin species endemic to that region (Yang et al., 2012; Zheng et al., 2012). Yang et al. (2012) proposed the name Gonorynchus McClelland, 1838 for the South Asian clade and retained the name Crossocheilus for the Southeast Asian clade as it contained the type species of the genus, C. oblongus. However, Kottelat (2016) declared the name Gonorynchus to be invalid for this group, arguing the name proposed by McClelland refers to the name Gonorynchus Cuvier, 1816, a junior objective synonym of Gonorynchus Scopoli, 1777 of the marine family Gonorynchidae. Kottelat (2016) declared the name Tariqilabeo Mizra and Saboohi, 1990 to be the valid genus name for these South Asian species formerly placed in Crossocheilus and in Gonorynchus by Yang et al. (2012) and Ciccotto and Page (2016). Ciccotto and Page (2016) revised Tariqilabeo (therein still recognized as Gonorynchus), containing seven species, differentiating the genus from Crossocheilus based on oromandibular structures and counts of vertebrae and lateral-line scales.

Species of Crossocheilus are distributed throughout the Mekong, Chao Phraya, Mae Khlong, and several smaller basins draining to the Gulf of Thailand and Malacca Strait in mainland Southeast Asia, as well as the islands of Borneo, Java, and Sumatra. Species inhabit a variety of freshwater habitats, ranging in size from headwater streams to large rivers, and occasionally swamps and other lentic habitats. The diets of species of Crossocheilus consist of periphyton and phytoplankton (Rainboth, 1996). The consumption of algae scraped off of firm substrates has led to the popularity of several species of Crossocheilus in the aquarium trade.

The goals of this paper are to 1) provide a revised diagnosis of the genus Crossocheilus, 2) examine morphological variation in species of Crossocheilus to diagnose species, and 3) reconstruct phylogenetic relationships using available nuclear gene sequence data. Eleven species are recognized in Crossocheilus, including one new species described herein.

MATERIALS AND METHODS

Molecular.—Phylogenetic relationships of species of Crossocheilus were reconstructed using the nuclear recombination activating gene 1 (RAG1) for species in which material could be obtained. Available sequences of Epalzeorhynchos Bleeker, 1855 were also included in the phylogenetic analysis, and Barbichthys laevis (Valenciennes, in Cuvier and Valenciennes, 1842) was included as the outgroup. Total genomic DNA was extracted from tissues preserved in 95% ethanol using a DNeasy Blood & Tissue Kit (Qiagen, Valencia, CA). RAG1 was amplified and sequenced using the primers R1 2533F: 5’–TGAGCCTCCATGAACTTCTGAAGRTAYTT–3’ and R1 4078R: 5’–TGAGCCCTCCATGAATTCTGAGRTAYTT–3’ (López et al., 2004; Yang and Mayden, 2010). Each sample for the

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polymerase chain reaction (PCR) consisted of a 25 µl reaction containing 16.5 µl of sterile water, 2 µl of genomic DNA, 4 µl of MyTaq Reaction Buffer (BioLine, Boston, MA), 0.5 µl of MyTaq DNA Polymerase (BioLine, Boston, MA), and 1 µl of each primer. The PCR cycling parameters followed Yang and Mayden (2010). PCR cleaning with ExoSAP-IT (Affymetrix, USA) and subsequent bidirectional sequencing was conducted at the Interdisciplinary Center for Biotechnology Research at the University of Florida. Geneious version 8.1.5 (Kearse et al., 2012) was used to assemble consensus sequences. Available sequences on GenBank from Yang et al. (2012) were downloaded. Sequences were aligned in ClustalW (Thompson et al., 1994). GenBank accession numbers for all sequences are presented in Table 1.

The aligned RAG1 sequences were partitioned by each codon region prior to phylogenetic analysis. The optimal molecular evolutionary model for each of the partitions was identified using the Akaike information criterion implemented in the program PartitionFinder (Lanfear et al., 2012). The GTR+I, HKY, and HKY+G models were implemented for codon positions one, two, and three, respectively. A Bayesian phylogenetic analysis partitioned by codon position was conducted in MrBayes version 3.2.1 (Ronquist et al., 2012). Two Markov chain Monte Carlo (MCMC) analyses with four simultaneous chains were run for 5 million generations sampling every 1,000 generations. The standard deviation for split frequencies was less than 0.005, and the average potential scale reduction factor for all parameters was approximately 1.0, indicating convergence of the two runs. The first 25% of the sampled generations were discarded as burn-in, and the resulting phylogenies were summarized in a 50% majority-rule consensus tree.

**Morphological.—**Measurements and counts follow Kottelat (2001). The width between the rostral barbels is the distance between the insertions of the barbels on the snout, anterior to the mouth (Ciccotto and Page, 2016). Maxillary barbels are useful in species identification and described as tiny and hidden in the corner of the mouth; small and barely exposed at the corner of the mouth; or large, approximately ½ to ⅓ of the eye diameter, and clearly exposed. Lengths were measured to the nearest 0.1 mm on the left side, when possible, using digital calipers. Body measurements were recorded as proportions of standard length (SL) and head measurements were recorded as proportions of head length (HL). Institutional codes follow Sabaj Pérez (2014).

**RESULTS**

The 50% majority-rule consensus tree with Bayesian Posterior Probability (BPP) support values is presented in Fig. 1. *Crossocheilus* was resolved as monophyletic (BPP = 1). All species incorporated in the phylogenetic analysis with two or more specimens, including *C. atrilimes* Kottelat, 2000, *C. oblongus* Kuhl and van Hasselt, in van Hasselt, 1823, *C. obscurus* Tan and Kottelat, 2009, *C. tchangi* Fowler, 1934, and *C. tchangi* Fowler, 1935, were recovered as reciprocally monophyletic with BPP = 1. *Crossocheilus nigriloba* Popta, 1904 was resolved as sister to all other species of *Crossocheilus* included with strong support (BPP = 1). *Crossocheilus oblongus* and *C. obscurus* were resolved as sister species (BPP = 1) sister to a clade containing *C. atrilimes*, *C. reticulatus*, and *C. tchangi*, but with weak support (BPP = 0.71). *Crossocheilus atrilimes* was resolved as sister to a clade containing *C. reticulatus* and *C. tchangi* with strong support (BPP = 1). *Crossocheilus reticulatus* and *C. tchangi* were resolved as sister species (BPP = 1).

**Crossocheilus Kuhl and van Hasselt, in van Hasselt, 1823**

Figures 2, 3, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15

*Crossocheilus* Kuhl and van Hasselt, 1823:132. Type-species: *Crossocheilus oblongus* Kuhl and van Hasselt, in van Hasselt,
**Fig. 1.** Phylogeny of *Crossocheilus* based on Bayesian analysis of RAG1, with posterior probability values at nodes.

**Fig. 2.** Ventral views of heads of (A) *Crossocheilus atrilimes*, UF 185188, 79.9 mm SL, and (B) *C. microstoma*, new species, BMNH 1982.3.29.1, 80.7 mm SL. Abbreviations: l, length of lower lip; LL, lower lip; MB, maxillary barbel; RB, rostral barbel; RC, rostral cap; RL, rostral lobe; UL, upper lip; w, width of lower lip. Images not to scale.

*Crossocheilus* Bleeker, 1854:525. Unjustified emendation of *Crossocheilus* Kuhl and van Hasselt, in van Hasselt, 1823.


*Crossochilus* Günther, 1868:71. Unjustified emendation of *Crossocheilus* Kuhl and van Hasselt, in van Hasselt, 1823.


**Diagnosis.**—A member of the cyprinid tribe Labeonini based on the incised border on the first anal-fin pterygiophore, the ventrally expanded rostral fold, and the presence of a superficial posterior labial fold (Stiassny and Getahun, 2007). The diagnostic characters of Labeonini reported by Reid (1982), including the presence of a vomero-palatine organ, a terete process on the basioccipital, and the direct contact between the neural complex of the Weberian apparatus and the supraoccipital region, could not be examined in specimens on loan to us, but were reported present in *C. atrilimes* by Stiassny and Getahun (2007). Several molecular phylogenies place *Crossocheilus* within Labeonini (Wang et al., 2007; Yang et al., 2012; Zheng et al., 2012).

*Crossocheilus* is distinguished from all other genera in the tribe based on the following combination of characters: 1) inferior mouth; 2) fimbriated rostral cap covering upper lip and jaw; 3) upper lip not visibly separated from snout by groove; 4) upper lip of generally uniform width, not substantially widening at corner of mouth, and attached to lower lip; 5) lower lip free only on anterior and lateral edges, posterior edge connected to underside of head (not developed into mental disc), central region equally thick as lateral edges, anterior edge with papillae; 6) sublachrymal groove expanding anteriorly, containing immovable lateral lobes dorsal to rostral barbels; and 7) 8½ branched dorsal rays.

**Description.**—Mouth inferior. Upper lip well-developed, edge smooth or with projections (Fig. 2), attached to lower lip at corner of mouth. Lower lip free on anterior and lateral edges, but firmly attached to lower jaw; equal thickness centrally and laterally; rectangular (width greater than length) or square (length and width approximately equal) in shape (Fig. 2); distal edge with papillae. Rostral cap well-developed, covering upper lip and jaw with papilllose fimbriae. Sublachrymal groove expanded anteriorly; immovable, triangular lobe present within the expansion (Fig. 2). Rostral barbels present; maxillary barbels present or absent.

Dorsal profile slightly arched, deepest at dorsal-fin insertion; ventral profile flat to slightly concave. Head short, longer than wide; snout conical, rounded at end; eyes dorsolateral. Dorsal-fin origin anterior of pelvic-fin origin. Pectoral fins positioned ventrally, reaching approximately ½ to ¾ from origin to pelvic-fin origin. Pelvic fins reaching to anus or slightly beyond anus. Anal fin not reaching base of caudal fin. Axillary pelvic lobes well-developed. Dorsal and anal fins slightly concave to falcate; pectoral and pelvic fins triangular. Caudal fin deep forked with pointed lobes, approximately equal in length.

Dorsal fin with 3 simple and 8½ branched rays; anal fin with 3 simple and 5½ branched rays; pelvic fin with 1 simple and 8 branched rays; pectoral fin with 1 simple and 13–16 branched rays; caudal fin with 10–9 principal rays, 9–8 branched. Body entirely scaled; scales well-developed. Lateral-line scales and pored scales on caudal fin 29–32; predorsal scales 8–12, scale rows above lateral line 4½–5½, scale rows below lateral line 3½–4½, 3½–4 scale rows between lateral line and pelvic-fin origin, 1–3½ scales between anus and anal-fin origin; 16 circumpeduncular scales.

**Comparisons.**—Ciccotto and Page (2016) distinguished *Crossocheilus* from *Tariqilabeo* based on the presence of immovable rostral lobes (vs. absent in *Tariqilabeo*), a well-developed upper lip that does not widen at the corner of the mouth (vs. upper lip thin or absent; if present, widening substantially at the corner of the mouth in *Tariqilabeo*), and fewer lateral-line scales and vertebrae. Among Southeast Asian labeonins, *Crossocheilus* is most similar to *Garra* and *Epalzeorhynchos*, both of which also possess a large, fimbriated rostral cap covering the upper lip, which is not visibly separated from the snout by a groove. *Garra* possesses a mental disc, which is absent in *Crossocheilus*. *Epalzeorhynchos* possesses movable rostral lobes within the anteriorly expanded sublachrymal grooves, just dorsal to the rostral barbels; the rostral lobes are firmly attached to the side of the snout in *Crossocheilus* (Fig. 2). The distal tips of the rostral lobes in *Epalzeorhynchos* also possesses a tubercle, which is absent in *Crossocheilus*.

**Remarks.**—A number of trade names are used for *Crossocheilus* in the aquarium trade, with the most common ones being “Siamese Algae Eater” and “Siamese Flying Fox.” These names refer to multiple species in a number of superficially similar genera and families. We propose the common name...
“Fringe Barb,” in reference to the fringed edge of the rostral cap.

**Crossocheilus atrilimes** Kottelat, 2000

Siamese Fringe Barb

Figure 3

*Crossocheilus atrilimes* Kottelat, 2000:39, fig. 2. Type locality: Laos, Vientiane Province, Nam Mang at Keng Nam Mang (rapids) about 6 km upstream of Ban Hatkhai, 18.4425N, 103.1756E. Holotype: ZRC 45298.

**Diagnosis.**—Member of *Crossocheilus* as described above. Distinguished from all other species in the genus (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; well-defined, black midlateral stripe from snout to distal edge of middle two caudal-fin rays with 1–2 rows of spots below stripe in larger specimens; 1–1½ scales between anus and anal-fin insertion (rarely 2); head depth 67.4–75.8% HL; least caudal-peduncle depth 11.2–13.1% SL.

**Comparisons.**—*Crossocheilus atrilimes* is similar to *C. langeri* but differs in having a deeper head (67.4–75.8 vs. 56.7–65.0%), 1–1½ (vs. 2–3½) scales between the anus and the anal fin, and the black midlateral stripe extending to the distal edge of the middle caudal-fin rays vs. midlateral stripe extending onto middle 2 and 2–3 most dorsal rays of lower caudal-fin lobe, never reaching distal edge of fin.

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present in 17 of 22 specimens examined, tiny, hidden in corner of mouth. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 30–32 + 1–3, predorsal scales 9–12, scale rows above lateral line 5½, scale rows below lateral line 3½–4½, 3½–4 scale rows between lateral line and pelvic-fin origin, 1–2 scales between anus and anal-fin origin. Maximum length = 79.9 mm SL.

Dorsum of head and body brown, darker in larger specimens; dark brown border between head and body. Dark brown spots or crescents at anterior base of scales on dorsum; dark midline on body in smaller specimens. Dorsal half of side of head brown; ventral half cream to yellow; cheeks and ventral ¾ of opercula silver. Black midlateral stripe extending from tip of snout to distal tips of middle caudal-fin rays, sharply contrasted from body coloration on dorsal and ventral edges; 1 or 2 rows of spots below stripe in larger specimens. Scales above midlateral stripe with dark crescent-shaped spots superimposed on brown background; scales below stripe cream to yellow and immaculate, exclusive of rows of dark spots in some specimens. Venter cream to yellow; breast silvery. Dorsal fin with clusters of scattered melanophores forming faint blotches on middle portion on interradial membranes; pectoral, pelvic, and anal fins generally clear with isolated melanophores in some specimens, particularly at leading edge of pectoral fins; dorsal and ventral edges of caudal-fin rays with dark pigment, remainder of fin clear except for extension of black stripe on middle rays. Upper lip immaculate.

**Distribution.**—*Crossocheilus atrilimes* is distributed throughout the Mekong basin in Cambodia, Laos, and Thailand (Fig. 4), as well as the Areng River in southwestern Cambodia. Bănescu (1986) reported two specimens from the Chao Phraya basin in northern Thailand (USNM 107855) and noted the species to be present on the Malay Peninsula, although the whereabouts of specimens from the Malay Peninsula are unknown. Recent collections throughout Thailand have failed to document *C. atrilimes* in the Chao Phraya or on the Malay Peninsula.

**Material examined.**—(Identified, but not measured if no SL given) Cambodia: Gulf of Thailand basins: UMMZ 243787, 2, 116.0–123.5 mm SL, Koh Kong Province, Areng River, Cardemom Mountains; UMMZ 243810, 1, 107.2 mm SL, Koh Kong Province, Cardemom Mountains. Laos: Mekong basin: UMMZ 240668, 4, 40.3–55.1 mm SL, Vientiane Province, Nam Mang at Nam Tok Nam Man (rapids), about 6 km upstream of Ban Hatkhai, 18.4425N, 103.1756E; ZRC 45298, 1 (holotype), 63.8 mm SL, Vientiane Province, Nam Mang at Nam Tok Nam Man (rapids), about 6 km upstream of Ban Hatkhai, 18.4425N, 103.1756E; ZRC 45299, 5 (paratypes), 39.9–59.1 mm SL, same as ZRC 45299. Thailand: Mekong basin: UF 170101, 5, Ubon Ratchathani Province, Mun River, Warinchumraj, 15.1786N, 104.7067E; UF 173139, 3 (2 ex.), 45.2–62.8 mm SL, Ubon Ratchathani Province, Rim Mun market from Mun River, 14.7833N, 102.2E; UF 185188, 1, 79.9 mm SL; Ubon Ratchathani Province, Sae Hua Maew, Tung Lung River, 15.3372N, 105.4004E; UMMZ 195183, 1, 55.4 mm SL, Chiang Rai Province, Payao Swamp, south shore, near Muang Payao, Huai Mae Tham drainage, 19.1523N, 99.8834E; UMMZ 233756, 7 (3 ex.), 69.2–75.1 mm SL, Ubon Ratchathani Province, Huay Kwang, Khong Chiam District, 1.5 km upstream from Mun River. Chao Phraya basin: USNM 107855, 2, Mechem River, tributary of Meping.

**Crossocheilus cobitis** (Bleeker, 1854)

Loach-like Fringe Barb

Figure 5

*Lobocheilos cobitis* Bleeker, 1854:523. Type locality: Indonesia, Sumatra, Padang and Java, Batavia [=Jakarta]. Syntypes (Fricke, 1991): BMNH 1866.5.2.54 (1), part of RMNH 7006 (1), RMNH 10490 (27), SMNS 10589 (1).


**Diagnosis.**—Member of *Crossocheilus* as described above. Distinguished from all other species in the genus (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels long, clearly exposed (approximately ½ to ¾ of eye diameter); black midlateral stripe from tip of snout to caudal-fin origin, terminating in distinct black spot at base of caudal fin; relatively short caudal peduncle (caudal-peduncle length = 14.2–17.2% SL); mouth width large (21.1–27.9% of HL).

**Comparisons.**—*Crossocheilus cobitis* differs from all other species of *Crossocheilus* except *C. elegans* and *C. microstoma* in having long, exposed (approximately ½ to ¾ of eye diameter) maxillary barbels (vs. short, often hidden barbels). It differs from *C. elegans* in having a black spot on the caudal-fin base (vs. no black spot and a pale yellowish stripe above the black midlateral stripe) and a shorter caudal peduncle (14.2–17.2 vs. 18.5–20.8% SL). It differs from *C. microstoma*
Fig. 4. Distributions of georeferenced specimens examined of: (A) Crossocheilus atrilimes, (B) C. cobitis and C. microstoma, (C) C. elegans and C. nigriloba, and (D) C. gnathopogon and C. langei. Syntypes of C. cobitis plotted at Padang, Sumatra (0.9471S, 100.4172E) and Jakarta, Java (6.2088S, 106.8456E). Syntypes of C. nigriloba plotted on the Bo River in East Kalimantan, Borneo (1.1817N, 115.1156E). Lectotype of C. gnathopogon plotted at Bukittinggi, Sumatra (0.3039S, 100.3835E). Holotype of C. langei plotted at Palembang, Sumatra (2.9761S, 104.7754E).
in having a smooth edge on the upper lip (vs. having projections on the edge of the upper lip), the lower lip rectangular in shape with the width greater than the length (vs. square in shape with the width approximately equal to the length), and a wider mouth (21.1–27.9 vs. 18.3–20.0% SL).

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present, clearly exposed, approximately ½ to ⅓ of eye diameter. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 29–32 + 2–3, predorsal scales 8–9½, scale rows above lateral line 4½, scale rows below lateral line 3½–4½, 3½ scale rows between lateral line and pelvic-fin origin, 2–3 scales between anus and anal-fin origin. Maximum length = 52 mm SL (Kottelat and Tan, 2011).

Dorsum of head and body brown; dark brown spots or crescents at anterior base of scales on dorsum. Dorsal half of side of head brown; ventral half cream; silver patches on cheeks and opercula in some specimens. Dark brown midlateral stripe, extending from tip of snout to caudal-peduncle base, terminating in distinct black spot at caudal-peduncle base; middle caudal-fin rays occasionally faint brown, but never forming obvious continuation of midlateral stripe. Scales above midlateral stripe with dark crescent-shaped spots superimposed on brown or olive background; scales below stripe cream, generally immaculate but scattered melanophores on scale row below midlateral stripe in some specimens. Venter cream colored. In smaller specimens, faint dark blotch between anus and anal-fin origin present; spots on dorsal and ventral margins at base of caudal peduncle. Pelvic fins with dark leading edge; other fins generally clear, occasionally with scattered melanophores, never forming distinct blotches or bands. Upper lip immaculate.

**Distribution.**—*Crossocheilus cobitis* is native to the islands of Borneo (Mahakam, Barito, and Kinabatangan drainages), Java, and Sumatra (Batang Hari and Musi drainages). The syntypes are reported from Padang in western Sumatra and Jakarta in Java; we are unaware of recent collections from Java, however. The species is rare in Indochina, with only a few specimens sporadically collected from the Mekong and Chao Phraya basins in Thailand, as well as Peninsular Malaysia (Fig. 4).

**Remarks.**—In their description of *C. elegans* from the headwaters of the Kinabatangan basin in northern Borneo, Kottelat and Tan (2011) discussed the tentative status of *C. cobitis* in the lower reaches of the same basin. Three small (<23 mm SL) specimens of *Crossocheilus* from the lower Kinabatangan River (FMNH 44786, n = 2; FMNH 44787, n = 1) were examined. Along the lateral midline in two of these specimens, there are scattered melanophores forming what appears to be a stripe, extending onto the snout on one specimen, and there is no lateral pale yellow stripe indicative of *C. elegans* (see species account below). These specimens are herein identified as *C. cobitis* based on this dark midlateral stripe, the presence of long maxillary barbels, a rectangular-shaped lower lip, the absence of projections on the upper lip, and shorter caudal-peduncle length (13.0–15.6% SL). The locality information for both of these lots indicates the collections were made at lakes near Lamag and Bukit Garam, likely indicating oxbow lakes of the Kinabatangan River.

Roberts (1989) reported *C. cobitis* from the Kapuas basin in western Borneo and noted the presence of “large marginal papillae” on the upper lip. This character runs counter to the smooth upper lip of *C. cobitis* discussed by Bleeker (1860), as well as specimens of *C. cobitis* examined here from other localities throughout Southeast Asia. Four lots of the
specimens included in Roberts (1989) were confirmed to possess projections on the upper lip, as well as a unique lower lip shape, and are herein described as *C. microstoma*.

The holotype and only specimen of *Epalzeorhynchos kalliurus* (USNM 109764) described by Smith (1945) from the Mekong basin at Chiang Saen in northern Thailand was identified as *C. cobitis* by Bănărescu (1986) based on the presence of immovable rostral lobes (placing it in *Crossocheilus*), maxillary barbels, and an estimated 30–31 lateral-line scales. The original description and accompanying illustration of *E. kalliurus* note the presence of a dark lateral stripe on the posterior half of the body and a black spot at the base of the caudal peduncle. *Crossocheilus atrilimes*, *C. cobitis*, *C. oblongus*, and *C. reticulatus* are known from the Mekong basin. However, only *C. cobitis* has both a dark midlateral stripe and a black spot at the base of the caudal peduncle, and we follow Bănărescu (1986) in considering *E. kalliurus* to be a junior synonym of *C. cobitis*.

**Material examined.**—(Identified, but not measured if no SL given) Malaysia: East Malaysia: FMNH 44786, 2, Sabah, East Coast Residency, Kinabatangan District, Lake Bukit Garam; FMNH 44787, 1, Sabah, East Coast Residency, Kinabatangan District, Lamang, Lake Duadan, 5.4924N, 117.8373E. Penin-

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**Fig. 7.** *Crossocheilus gnathopogon*, ZMA 113745, lectotype, 91.6 mm SL. Photo by R. de Ruiter (RMNH).

**Fig. 8.** *Crossocheilus langei*. (A) BMNH 1866.5.2.106, holotype, 59.3 mm SL, (B) ZRC 44175, 98.7 mm SL. Photo A by J. Maclaine (BMNH); photo B by H. H. Tan (LKCNHM).
sular Malaysia: ZRC 13781, 1, 24.9 mm SL, Pahang, Kuala Lipis, 4.1843N, 102.0542E; ZRC 14522, 1, Selangor, North Selangor Peat Swamp forest, 3.5342N, 101.2814E. Indonesia: Borneo: BMNH 2000.10.25.736, 1, 31.8 mm SL, Central Kalimantan, Barito River, sand bars and rocks of Sungai Busang; BMNH 2000.25.699–706, 8, 24.3–31.8 mm SL, Central Kalimantan, Barito River, market at Puruk Cahu and Sungai Barito, 0.6159S, 114.5729E; BMNH 2001.1.15.2824-2827, 4, 23.8–26.5 mm SL, Central Kalimantan, Sungai Barito, approximately 2 km below Muara Luang; ZRC 38874, 1, 37.5 mm SL, Central Kalimantan, Sungai Barito between Muara Jan and Muara Untu, 0.6298S, 114.6472E. Java or Sumatra: BMNH 1866.5.2.54, 1 (syntype), Padang, Sumatra or Jakarta, Java, Sumatra: UMMZ 243854, 1, 34.6 mm SL, Jambi, Pasar Angso Duo (fish market); ZRC 39060, 3, Jambi, Bengkwan of Batang Kuantan (Indragiri), 4 hours downstream of Rengat; ZRC 42352, 2, 29.9–32.0 mm SL, Jambi, Perlingat, along main confluence of Batang Hari; ZRC 42376, 18 (3 ex.), 36.4–38.7 mm SL, Jambi, Desa Louderang, Batang Hari confluence, 1.58S, 103.6108E. Thailand: Mekong basin: UMMZ 217645, 1, 41.7 mm SL, Ubon Ratchathani Province, Huay Thom-loe at Ban Bung Rhee-lek, 7 km E of Khemerat, 1 km from Mekong River, 15.9909N, 105.3688E; USNM 109764, 1 (holotype of *Epalzeorhynchus kalliurus*), Mekong at Chiang Sen Kao. Chao Phraya basin: USNM 108012, 1, 39.1 mm SL, Bung Borapet, 15.7061N, 100.2322E.

**Crossocheilus elegans Kottelat and Tan, 2011**
Elegant Fringe Barb

![Image of C. elegans](image)

**Fig. 6**


*Crossocheilus cobitis* (non Bleeker, 1854).—Martin-Smith and Tan, 1998:580.

*Crossocheilus elegans* Kottelat and Tan, 2011:195, fig. 1. Type locality: Malaysia, Borneo, Sabah, Danum Valley, Kinaba-

![Image of C. elegans](image)
tangan drainage, stream at km 111 on main line west after turnoff to Borneo Rainforest Lodge, 5.0183N, 117.544E. Holotype: ZRC 51184.

**Diagnosis.**—Member of *Crossocheilus* as described above. Distinguished from all other species in the genus (Table 2) by the combination of the following characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels long, clearly exposed (approximately ½ to ⅔ of eye diameter); black midlateral stripe beginning just posterior of operculum, terminating at middle of caudal-fin base, separated from dark brown dorsum by pale yellowish stripe; relatively long caudal peduncle (caudal-peduncle length = 18.5–20.8% SL).

**Comparisons.**—*Crossocheilus elegans* differs from all other species of *Crossocheilus* except *C. cobitis* and *C. microstoma* in having long, exposed (approximately ½ to ⅔ of eye diameter) maxillary barbels (vs. short, often hidden barbels). It differs from *C. cobitis* in having no black spot (vs. a black spot) on the caudal-fin base, a pale yellowish stripe (vs. no stripe) above the black midlateral stripe, and a longer caudal peduncle (18.5–20.8 vs. 14.2–17.2% SL). It differs from *C. microstoma* in having a smooth edge on the upper lip (vs. having projections on the edge of the upper lip) and the lower lip rectangular in shape with the width greater than the length (vs. square in shape with the width approximately equal to the length).

**Description.**—Morphometrics and meristics presented in Table 3 (also see Kottelat and Tan, 2011). Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present, clearly exposed, approximately ½ to ⅔ of eye diameter. Pectoral fin with 14 branched rays. Lateral-line scales and pored scales on caudal fin 30–32 + 1–2, predorsal scales 8–8½, scale rows above lateral line 4½, scale rows below lateral line 4½, 3½ scale rows between lateral line and pelvic-fin origin, 2½–3½ scales between anus and anal-fin origin. Maximum length = 106.3 mm SL (Kottelat and Tan, 2011).

Dorsum of head brown to gray, body brown; dark brown border between head and body. Dark brown spots or crescents at anterior base of scales on dorsum; dark midline present in larger specimens. Dorsal ⅔ to ⅔ of side of head brown to gray; ventral portion cream to yellow. Black midlateral stripe, sharply contrasted from body coloration on dorsal and ventral edges, extending from posterior of operculum to base of caudal peduncle. Row of scales above midlateral stripe cream to yellow, scale rows above this row brown; scales below stripe cream to yellow, with brown outline on posterior edges. Venter cream to yellow. All fins

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**Table 2.** Characteristics distinguishing species of *Crossocheilus.*

<table>
<thead>
<tr>
<th></th>
<th><em>C. atrilimes</em></th>
<th><em>C. cobitis</em></th>
<th><em>C. elegans</em></th>
<th><em>C. gnathopogon</em></th>
<th><em>C. langei</em></th>
<th><em>C. microstoma</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Edge of upper lip</strong></td>
<td>Smooth Rectangular; width &gt; length 1–1½ (rarely 2)</td>
<td>Smooth Rectangular; width &gt; length 2–3</td>
<td>Smooth Rectangular; width &gt; length 2½–3½</td>
<td>??</td>
<td>Smooth Rectangular; width &gt; length 2–3½</td>
<td>With projections Square; length = width 2½–3</td>
</tr>
<tr>
<td><strong>No. scales between anus and anal fin</strong></td>
<td>Tiny, hidden in corner of mouth</td>
<td>Long, exposed (¼–½ eye diameter)</td>
<td>Long, exposed (¼–½ eye diameter)</td>
<td>Tiny, hidden in corner of mouth</td>
<td>Small, barely exposed</td>
<td>Long, exposed (¼–½ eye diameter)</td>
</tr>
<tr>
<td><strong>Maxillary barbels (when present)</strong></td>
<td>Ca. ½ eye diameter Black midlateral stripe from snout to distal edge of middle caudal-fin rays; 1–2 rows of spots below stripe</td>
<td>Ca. ½ eye diameter Black midlateral stripe from snout to caudal-fin insertion; black spot at base of caudal fin</td>
<td>Ca. ½ eye diameter Pale yellowish stripe above black midlateral stripe from operculum to caudal-fin base</td>
<td>No dark midlateral stripe or spot on flank or caudal peduncle</td>
<td>Brown to black midlateral stripe from snout to blotch in upper half of lower lobe of caudal fin</td>
<td>Black midlateral stripe from snout to caudal fin ending in black spot at caudal-fin base</td>
</tr>
<tr>
<td><strong>Pigment on side of body</strong></td>
<td>Black midlateral stripe from snout to distal edge of middle caudal-fin rays; 1–2 rows of spots below stripe</td>
<td>Black midlateral stripe from snout to caudal-fin insertion; black spot at base of caudal fin</td>
<td>Pale yellowish stripe above black midlateral stripe from operculum to caudal-fin base</td>
<td>No dark midlateral stripe or spot on flank or caudal peduncle</td>
<td>No dark midlateral stripe or spot on flank or caudal peduncle</td>
<td>No dark midlateral stripe or spot on flank or caudal peduncle</td>
</tr>
</tbody>
</table>

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**Fig. 11.** *Crossocheilus oblomus*, UF 173140, 80.9 mm SL. Photo by Z. Randall (FLMNH).
clear with occasional melanophores, particularly on edges of pectoral and caudal fin. Upper lip immaculate.

**Distribution.**—*Crossochilus elegans* is native to the Segama and Kinabatangan basins in Sabah, Borneo (Fig. 4).

**Material examined.**—East Malaysia: FMNH 68501, 3, 48.8–70.5 mm SL, Sabah, East Coast Residency, Kinabatangan District, Deramakot Camp, hill stream, below waterfall, Sta. 6; FMNH 68502, 3, 51.1–65.6 mm SL, Sabah, East Coast Residency, Kinabatangan District, Deramakot Camp, hill stream, pool, Sta. 7, 5.2833N, 117.55E; ZRC 51184, 1 (holotype), 78.6 mm SL, Sabah, Danum Valley, Kinabatangan drainage, stream at km 111 on main line west after turnoff to Borneo Rainforest Lodge, 5.0183N, 117.544E.

*Crossochilus gnathopogon* Weber and de Beaufort, 1916

**Sumatran Fringe Barb**

Figure 7


**Diagnosis.**—Member of *Crossochilus* as described above. *Crossochilus gnathopogon* is distinguished from all other species of *Crossochilus* (Table 2) by the following combination of characters: rostral barbels minute, maxillary barbels short, barely exposed out of corner of mouth; no dark middlateral stripe or spot on the flank, caudal peduncle, or lower lobe of the caudal fin. As discussed by Tan and Kottelat (2009), *C. gnathopogon* was originally diagnosed from all other species in the genus by the absence of rostral barbels, but examination of the lectotype revealed the presence of tiny rostral barbels that are much shorter than those in all other species of *Crossochilus*. The dorsal ¼ of the flank of *C. gnathopogon* is light brown, while the ventral ¼ are silvery and devoid of melanin, as noted in the original description (Weber and de Beaufort, 1916).

**Distribution.**—*Crossochilus gnathopogon* is only known from Bukittinggi (formerly Fort de Kock), Sumatra (Fig. 4). As noted by Tan and Kottelat (2009), there are no data indicating the type specimens were collected from Lake Mannindjan in Bukittinggi as reported by Bânego (1986). Streams from this area all drain into the Indian Ocean.

**Material examined.**—Indonesia: Sumatra: ZMA 113745, 1, 91.6 mm SL (lectotype), Bukittinggi.

*Crossochilus langei* Bleeker, 1860

**Lange’s Fringe Barb**

Figure 8

*Crossochilus langei* Bleeker, 1860:127. Type locality: Indonesia, Sumatra, Palembang. Holotype: BMNH 1866.5.2.106.

**Diagnosis.**—Member of *Crossochilus* as described above. *Crossochilus langei* is distinguished from all other species of *Crossochilus* (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, short, barely exposed out of corner of mouth; dark brown to black middlateral stripe from snout to blotch in upper half of lower lobe of caudal fin, not reaching to distal

<table>
<thead>
<tr>
<th><strong>Table 2.</strong> Extended.</th>
<th><strong>C. nigriloba</strong></th>
<th><strong>C. oblongus</strong></th>
<th><strong>C. obscurus</strong></th>
<th><strong>C. reticulatus</strong></th>
<th><strong>C. tchangi</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Smooth</strong></td>
<td>With projections</td>
<td>With projections</td>
<td>Smooth</td>
<td>Smooth</td>
<td>Smooth</td>
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<tr>
<td><strong>Rectangular; width &gt; length</strong></td>
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<td>Rectangular; width &gt; length</td>
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<td><strong>3½–4</strong></td>
<td>2–3½</td>
<td>2–3½</td>
<td>1½–3</td>
<td>1½–3</td>
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<tr>
<td>Tiny, hidden in corner of mouth</td>
<td>Tiny, hidden in corner of mouth</td>
<td>Tiny, hidden in corner of mouth</td>
<td>Small, barely exposed</td>
<td>Tiny, hidden in corner of mouth</td>
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<tr>
<td>Ca. ½ eye diameter</td>
<td>Ca. ½ eye diameter</td>
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<tr>
<td>Black middlateral stripe connected to black blotch on anterior ¾ of lower caudal-fin lobe</td>
<td>Black middlateral stripe from snout to distal edge of median caudal-fin rays</td>
<td>Black middlateral stripe (edges obscure) from tip of snout to distal edge of median caudal-fin rays</td>
<td>No dark middlateral stripe; large black oval blotch on caudal-peduncle base; dark reticulated pattern on flank</td>
<td>Black middlateral stripe on posterior ¼ of body, not on caudal-fin rays; black spot on caudal peduncle</td>
<td></td>
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</tbody>
</table>

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**Ca.**

3

Black midlateral Tiny, hidden in discussed by Tan and Kottelat (2009). The species is morphometric and meristic data, has been previously

pl. 7), although the status of this species, including published photographs of the same (Tan and Kottelat (2009: fig. 24) and one other specimen (Kottelat et al., 1993: pl. 7), although the status of this species, including morphometric and meristic data, has been previously discussed by Tan and Kottelat (2009). The species is distinguished from all other species in *Crossochilus* based on the minute rostral barbels and the absence of a distinct dark middlateral stripe or spot on the flank, caudal peduncle, or lower lobe of the caudal fin. As discussed by Tan and Kottelat (2009), *C. gnathopogon* was originally diagnosed from all other species in the genus by the absence of rostral barbels, but examination of the lectotype revealed the presence of tiny rostral barbels that are much shorter than those in all other species of *Crossochilus*. The dorsal ¼ of the flank of *C. gnathopogon* is light brown, while the ventral ¼ are silvery and devoid of melanin, as noted in the original description (Weber and de Beaufort, 1916).

**Distribution.**—*Crossochilus gnathopogon* is only known from Bukittinggi (formerly Fort de Kock), Sumatra (Fig. 4). As noted by Tan and Kottelat (2009), there are no data indicating the type specimens were collected from Lake Mannindjan in Bukittinggi as reported by Bânego (1986). Streams from this area all drain into the Indian Ocean.

**Material examined.**—Indonesia: Sumatra: ZMA 113745, 1, 91.6 mm SL (lectotype), Bukittinggi.

**Crossochilus langei** Bleeker, 1860

**Lange’s Fringe Barb**

Figure 8

*Crossochilus langei* Bleeker, 1860:127. Type locality: Indonesia, Sumatra, Palembang. Holotype: BMNH 1866.5.2.106.

**Diagnosis.**—Member of *Crossochilus* as described above. *Crossochilus langei* is distinguished from all other species of *Crossochilus* (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, short, barely exposed out of corner of mouth; dark brown to black middlateral stripe from snout to blotch in upper half of lower lobe of caudal fin, not reaching to distal
Table 3. Morphometric and meristic values of Crossocheilus atrilimes, C. elegans, C. obscurus, C. nigripinnis, and C. tchangi.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>Range 1</th>
<th>Range 2</th>
<th>Mean</th>
<th>Range 1</th>
<th>Range 2</th>
<th>Mean</th>
<th>Range 1</th>
<th>Range 2</th>
<th>Mean</th>
<th>Range 1</th>
<th>Range 2</th>
<th>Mean</th>
<th>Range 1</th>
<th>Range 2</th>
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<tbody>
<tr>
<td>C. atrilimes</td>
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<td>C. obscurus</td>
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<td>C. nigripinnis</td>
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<td>C. tchangi</td>
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</table>

- **Standard length (mm)**
  - Mean: 280.12 mm
  - Range: 38.1–79.9 mm
- **% Standard length**
  - Mean: 50.5%
  - Range: 50.1–50.8%
- **Preanal length**
  - Mean: 76.5 mm
  - Range: 74.6–80.3 mm
- **Prepelvic length**
  - Mean: 51.9 mm
  - Range: 48.2–55.0 mm
- **Head length**
  - Mean: 23.1 mm
  - Range: 20.2–25.6 mm
- **Dorsal-fin base length**
  - Mean: 15.7 mm
  - Range: 14.2–17.6 mm
- **Head depth**
  - Mean: 70.9 mm
  - Range: 67.4–75.8 mm
- **Interorbital width**
  - Mean: 40.9 mm
  - Range: 35.1–48.5 mm
- **Pectoral-fin rays**
  - Mean: 13.2 mm
  - Range: 12.4–14.3 mm
- **Scales between pelvic-fin origin and lateral line**
  - Mean: 3.2 mm
  - Range: 3.0–3.4 mm
- **Etymology**
  - Korean: Gyeong-Fi, a short fish

**MERISTICS**

- Pectoral-fin rays
  - Mean: 13.15
  - Range: 13–15
- Lateral-line scales
  - Mean: 33
  - Range: 30–35
- Pored scales posterior to bitalial line
  - Mean: 33
  - Range: 30–35
- Predorsal scales
  - Mean: 33
  - Range: 30–35

**Scale lengths**

- Scales between anal-fin origin and lateral line
  - Mean: 3.2 mm
  - Range: 3.0–3.4 mm
- Scales between anal-fin origin and pelvic-fin origin
  - Mean: 3.2 mm
  - Range: 3.0–3.4 mm

**Etymology**

- Korean: Gyeong-Fi, a short fish
edge of rays; 2–3½ scales between anus and anal-fin origin; head depth 56.7–65.0% HL.

**Comparisons.** *Crossocheilus langei* is most similar to *C. atrilimes* but differs in having a shallower head (56.7–65.0 vs. 67.4–75.8%), 2–3½ (vs. 1–1½) scales between the anus and the anal fin, and the midlateral stripe extending onto middle 2 and 2–3 most dorsal rays of lower caudal-fin lobe, never reaching distal edge of fin vs. extending to the distal edge of the middle caudal-fin rays.

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present in 6 of 14 specimens examined, generally short, only barely exposed at corner of mouth. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 30–34 1–3, predorsal scales 8–9, scale rows above lateral line 4½, scale rows below lateral line 4½, 3½ scale rows between lateral line and pelvic-fin origin, 2–3½ scales between anus and anal-fin origin. Maximum length = 98.7 mm SL.

Dorsum of head and body brown; dark brown border between head and body. Dark brown spots or crescents at anterior base of scales on dorsum. Dorsal half of side of head brown; ventral half creamy yellow; cheeks and ventral ½ of operculum silver. Black midlateral stripe, sharply contrasted from body coloration on dorsal and ventral edges, extending from tip of snout to blotch in upper half of lower lobe of caudal fin, not reaching distal edge of caudal rays. Row of scales above midlateral stripe yellow, scale rows above this row brown; scales below stripe cream, usually immaculate although some specimens with row of spots below stripe on anterior half of flank. Venter creamy yellow; breast silvery. Small brown or black spots, typically forming single blotch, between anus and anal-fin origin. All fins clear, occasionally with scattered melanophores. Upper lip immaculate.

**Remarks.**—Alfred (1971) first considered *C. pseudobagroides* Duncker, 1904 as a junior synonym of *C. langei* based on overall similarities between the type specimens. Tan and Kottelat (2009) treated *C. pseudobagroides* as a valid species, differentiating the two species based on the presence of up to 4 spots on the dorsal midline of *C. pseudobagroides* (vs. spots absent in *C. langei*) and the midlateral stripe ending in a blotch on the upper half of the lower lobe of the caudal fin in *C. pseudobagroides* (vs. extending to tip of middle caudal-fin rays in *C. langei*). In the illustration of *C. langei* from the original description (Bleeker, 1860), the midlateral stripe does not extend to the distal portion of the middle caudal-fin rays. An examination of the holotype of *C. langei* further showed the presence of a blotch on the caudal-fin rays that does not extend to the distal edge of the fin and extends ventrally onto the lower caudal-fin lobe (Fig. 8). Additionally, as noted by Tan and Kottelat (2009), the spots on the dorsal midline of *C. pseudobagroides* can be poorly contrasted and difficult to see. In light of these similarities in pigmentation, as well as other characters discussed herein, we consider *C. pseudobagroides* a junior synonym of *C. langei*. The presence of spots on the dorsal midline is a polymorphic character in *C. langei*.

**Distribution.**—*Crossocheilus langei* is distributed in the Kapuas River basin in Borneo, the Batang Hari, Tulangbawang, and Musi basins in Sumatra, and streams in Peninsular Malaysia (Fig. 4).

**Material Examined.**—(Identified, but not measured if no SL given) Indonesia: Borneo: CAS 49193, 2, 41.8–43.3 mm SL, West Kalimantan, Kapuas River Basin, Sungai Seriang forested tributary of Sungai Palin, 37 km W of Putussibau, 3–5 km up from Kapuas mainstream, 0.8583N, 112.6E. Sumatra: BMNH 1866.5.2.106, 1, 59.3 mm (holotype), Palembang; UMMZ 243319, 1, 77.8 mm SL, West Sumatra, Market at Kiliranjo, Batang Hari drainage; UF 166340, 4, 50.3–80.3 mm SL, South Sumatra, Air Rambang, 3.5505S, 104.2639E; UF 166342, 1, 57.3, South Sumatra, Air Kikim Timur, 3.67685, 103.3640E; USNM 389867, 1, West Sumatra, Batang Tangkung River, 0.9028S, 101.3936E; ZRC 51614, 4, 53.9–68.5 mm SL, Sumatra, Jambi, aquarium trade; ZRC 51615, 1, 42.5 mm SL, same as ZRC 51614. Malaysia: ZMH 373, 1 (holotype of *Crossocheilus pseudobagroides*), Muar River near Tubing Tingii; ZRC 1783, 1, Johor; ZRC 1788, 1, Johor, Mawai Dist., 1.8416N, 103.9574E; ZRC 44175, 1, 98.7 mm SL, Johor, Sungai Kahang, 2.2446N, 103.585E.

**Crossocheilus microstoma** Ciccotto and Page, new species

urn:lsid:zoobank.org:act:B1EB3349-73A6-47F6-B47E-480218D1884F

Smallmouth Fringe Barb

**Figure 9**

**Crossocheilus cobitis** (non Bleeker, 1854).—Roberts, 1989:32.

**Holotype.**—USNM 230159, 74.9 mm SL, Indonesia, Borneo, West Kalimantan, Kapuas River drainage, rocky channel in mainstream of Sungai Pinoh at Nanga Salian, 45 km S of Nangapinoh, 0.72S, 111.642E, T. R. Roberts and S. Woerjroatmodjo, 22–26 July 1976.

**Paratypes.**—Indonesia, Borneo, West Kalimantan, Kapuas River drainage: BMNH 1982.3.29.1, 1, 80.7 mm SL, rocky channel in mainstream of Sungai Pinoh, 37 km south of Nangapinoh, 0.5333S, 111.658E, T. R. Roberts, 24 July 1976; CAS 49191, 2, 65.7–91.0 mm SL, Sungai Pinoh mainstream, 20–60 km upstream from Nangapinoh, 0.4583S, 111.65E, T. R. Roberts and S. Woerjroatmodjo, 22–26 July 1976; USNM 230160, 1, 43.3 mm SL, bar in mouth of Sungai Melawi at Sintang, 0.08S, 111.48E, T. R. Roberts, 29 July 1976.

**Diagnosis.**—Member of *Crossocheilus* as described above. *Crossocheilus microstoma* is distinguished from all other species of *Crossocheilus* (Table 2) by the following combination of characters: edge of upper lip with projections; lower lip square in shape, width approximately equal to length; maxillary barbels long, clearly exposed (approximately ½ to ⅙ of eye diameter); black midlateral stripe from tip of snout to caudal-fin base, terminating in distinct black spot at base of caudal fin; mouth width small (18.3–20.0% HL).

**Comparisons.**—*Crossocheilus microstoma* differs from all other species of *Crossocheilus* in having the lower lip square in shape with the width approximately equal to the length (vs. lower lip rectangular in shape with the width greater than the length). It further differs from all species except *C. cobitis* and *C. elegans* in having long, exposed (approximately ½ to ⅙ of eye diameter) maxillary barbels (vs. short, often hidden barbels). It differs from *C. cobitis* and *C. elegans* in having projections on the edge of the upper lip (vs. smooth edge on lip), from *C. elegans* in having a black spot at the caudal-fin base, and from *C.
**Description.**—Morphometrics and meristics presented in Table 4. Edge of upper lip with projections; lower lip square in shape, width approximately equal to length. Rostral barbels present, clearly exposed, approximately ¼ to ½ of eye diameter. Pectoral with 14–15 branched rays. Lateral-line scales 31, scale rows below lateral line 4, scale rows between dorsal-fin origin and lateral line 4, scale rows between anal-fin origin and lateral line 4, scale rows between pelvic-fin origin and lateral line 3, scale rows between anus and anal-fin origin 2. Maximum length = 91.0 mm SL.

Dorsum of head light brown, body brown; dark brown spots or crescents at anterior base of scales on dorsum. Dorsal half of side of head brown; ventral half lighter brown. Dark brown midlateral stripe, extending from tip of snout to caudal-peduncle base, terminating in distinct spot at caudal peduncle. Scales above midlateral stripe with dark crescent-shaped spots superimposed on brown background; scales below stripe cream with dusky edges. Venter cream. Membranes on all fins clear, rays with melanin between segments; pelvic fins with dark leading edge. Upper lip immaculate.

**Etymology.**—The specific name *microstoma*, from the Greek *mikrō*, meaning small, and *stōma*, meaning mouth, in reference to the small mouth width of the species.

**Distribution.**—*Crossocheilus microstoma* is found in the Kapuas basin of West Kalimantan, Borneo (Fig. 4).

**Crossocheilus nigriloba Popta, 1904**
Black-lobed Fringe Barb

**Figure 10**

*Crossochilus oblongus* var. *nigriloba* Popta, 1904:200 (also in Popta, 1906:120, pl. 8, fig. 27). Type locality: Indonesia, Borneo, Kalimantan Timur, Bo River. Syntypes: RMNH 7589 (3).

**Diagnosis.**—Member of *Crossocheilus* as described above. *Crossocheilus nigriloba* is distinguished from all other species of *Crossocheilus* (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, tiny, hidden in corner of mouth; black midlateral stripe connected to black blotch on anterior ¾ of lower caudal-fin lobe.

**Comparisons.**—*Crossocheilus nigriloba* differs from all other species of *Crossocheilus* in having a black blotch on the lower lobe of the caudal fin.

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present in 5 of 18.3–20.0 vs. 21.1–27.9% SL).

**Table 4.** Morphometric and meristic values of holotype (H) and four paratypes of *Crossocheilus microstoma*.

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<thead>
<tr>
<th></th>
<th>USNM 230159 (H)</th>
<th>USNM 230160</th>
<th>BMNH 1982.3.29.1</th>
<th>CAS 49191</th>
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<tr>
<td><strong>MORPHOMETRICS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Standard length (mm)</td>
<td>74.9</td>
<td>43.3</td>
<td>80.7</td>
<td>91.0</td>
</tr>
<tr>
<td>% Head length</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head depth</td>
<td>70.9</td>
<td>73.9</td>
<td>73.4</td>
<td>76.1</td>
</tr>
<tr>
<td>Head width</td>
<td>62.7</td>
<td>64.6</td>
<td>64.5</td>
<td>68.5</td>
</tr>
<tr>
<td>Snout length</td>
<td>44.8</td>
<td>36.2</td>
<td>47.8</td>
<td>47.5</td>
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<tr>
<td>Orbit diameter</td>
<td>23.2</td>
<td>25.4</td>
<td>25.6</td>
<td>23.6</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>42.0</td>
<td>39.7</td>
<td>41.0</td>
<td>42.5</td>
</tr>
<tr>
<td>Mouth width</td>
<td>19.7</td>
<td>20.0</td>
<td>19.2</td>
<td>18.9</td>
</tr>
<tr>
<td>Width between rostral barbels</td>
<td>12.6</td>
<td></td>
<td>11.0</td>
<td>12.1</td>
</tr>
<tr>
<td><strong>MERISTICS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Branched pectoral-fin rays</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>Lateral-line scales</td>
<td>31</td>
<td>30</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Pored scales posterior to lateral line</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Predorsal scales</td>
<td>8½</td>
<td>8½</td>
<td>8</td>
<td>8½</td>
</tr>
<tr>
<td>Scales between dorsal-fin origin and lateral line</td>
<td>4½</td>
<td>4½</td>
<td>4½</td>
<td>4½</td>
</tr>
<tr>
<td>Scales between anal-fin origin and lateral line</td>
<td>4½</td>
<td>4½</td>
<td>4½</td>
<td>4½</td>
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<tr>
<td>Scales between pelvic-fin origin and lateral line</td>
<td>3½</td>
<td>3½</td>
<td>3½</td>
<td>3½</td>
</tr>
<tr>
<td>Scales between anus and anal-fin origin</td>
<td>2½</td>
<td>2½</td>
<td>2½</td>
<td>2½</td>
</tr>
</tbody>
</table>
6 specimens examined, tiny, hidden in corner of mouth. Pectoral fin with 14–16 branched rays. Lateral-line scales and pored scales on caudal fin 30–31 + 2–3, predorsal scales 8–10, scale rows above lateral line 4½–5½, scale rows below lateral line 4½, 3½ scale rows between lateral line and pelvic-fin origin, 3½–4 scales between anus and anal-fin origin. Maximum length = 73.6 mm SL.

Dorsum of head and body brown, darker in larger specimens. Dark brown spots or crescents at anterior base of scales on dorsum. Dorsal half of side of head brown; ventral half cream to yellow. Black midlateral stripe extending from tip of snout to distal tips of middle caudal-fin rays; sharply contrasted from body coloration on dorsal and ventral edges. Anterior ¼ of lower caudal-fin lobe black. Scales above midlateral stripe brown; scales below stripe yellow and immaculate. Venter cream to yellow. Pelvic fins with dark leading edge; lower lobe of caudal fin with dark blotch; other fins generally clear, occasionally with scattered melanophores. Upper lip immaculate.

**Distribution.**—*Crossocheilus nigriloba* is native to the Mahakam River basin in East Kalimantan, Borneo (Fig. 4).

**Material examined.**—(Identified, but not measured if no SL given) Indonesia: Borneo: CAS 94551, 2, 63.1–71.3 mm SL, East Kalimantan, Mahakam basin, Sungai Belayan from mouth of Sungai Sentekan southwards for about 6 km at all spots with overhanging branches, 0.2504N, 116.2541E; CAS 94577, 2, 55.5–73.6 mm SL, Mahakam basin, just upstream of Muyub Ilir from a stretch of river about 1 km long on both sides of river, 0.0476S, 115.72E; CAS 96123, 4 (2 ex.), 45.0–58.1 mm SL, East Kalimantan, Mahakam basin, just downstream from Muyub Ilir, 0.0833S, 115.75E; CAS 226167, 9, East Kalimantan, Middle Mahakam; RMNH 7589 (3, syntypes), East Kalimantan, Bo River.

**Crossocheilus oblongus** Kuhl and van Hasselt, in van Hasselt, 1823

Oblong Fringe Barb

Figure 11


*Epalzeorhynchus siamensis* Smith, 1931:20, fig. 9. Type locality: Thailand, Nakhon Sritamarat Province, upper part of Tadi stream. Holotype: USNM 90302.

**Diagnosis.**—Member of *Crossocheilus* as described above. *Crossocheilus oblongus* is distinguished from all other species of *Crossocheilus* (Table 2) by the following combination of characters: edge of upper lip with projections; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, tiny, hidden in corner of mouth; well-defined, black midlateral stripe from snout to distal edge of middle two caudal-fin rays; 2–3½ scales between anus and anal-fin origin; least caudal-peduncle depth 9.3–11.6% SL.

**Comparisons.**—*Crossocheilus oblongus* is similar to *C. obscurus* in having projections on the edge of the upper lip, but differs in having a well-defined black midlateral stripe from the tip of the snout to the distal edge of the median caudal-fin rays, vs. having a stripe with poorly defined edges grading into the lateral pigmentation. The only other species of *Crossocheilus* with projections on the edge of the upper lip is *C. microstoma*, from which *C. oblongus* differs in having the lower lip rectangular in shape with the width greater than the length (vs. square with the width approximately equal to the length), the black midlateral stripe extending to the distal edge of the caudal-fin rays (vs. the black midlateral stripe ending at a black spot on the caudal peduncle), and tiny barbels, if present, hidden in the corner of the mouth (vs. long, exposed maxillary barbels).

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip with projections; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ¼ eye diameter. Maxillary barbels present in 15 of 43 specimens examined, tiny, hidden in corner of mouth. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 30–32 + 1–3, predorsal scales 8–9, scale rows above lateral line 4½–5½, scale rows below lateral line 3–4½, 3½–4 scale rows between lateral line and pellic-fin origin, 2–3½ scales between anus and anal-fin origin. Maximum length = 142 mm SL (Tan and Kottelat, 2009).

Dorsum of head and body brown, darker in larger specimens; dark brown border between head and body. Dark brown spots or crescents at anterior base of scales on dorsum; faint midline on body in some specimens. Dorsal half of side of head brown; ventral half cream to yellow; cheeks and ventral ¾ of opercula silver. Black midlateral stripe extending from tip of snout to distal tips of middle caudal-fin rays, sharply contrasted from body coloration on dorsal and ventral edges. In smaller specimens, a distinctly darker spot is present at the base of the caudal peduncle and the middle caudal-fin rays are faint brown. Scales above midlateral stripe with dark crescent-shaped spots superimposed on brown background; scales below band cream to yellow and immaculate. Venter cream to yellow; breast silvery. Scattered melanophores between anus and anal-fin origin in some specimens (see Remarks). Dorsal fin with clusters of scattered melanophores forming faint blotches on middle portion on interradial membranes; pectoral, pelvic, and anal fins generally clear with isolated melanophores in some specimens, particularly at leading edge of pectoral fins; dorsal and ventral edges of caudal-fin rays with dark pigment, remainder of fin clear except for extension of black stripe on middle rays. Upper lip immaculate.

**Remarks.**—The presence of black pigment between the anus and the anal-fin origin has long been used to differentiate *C. oblongus* (pigment absent) and *C. langei* (pigment present; Alfred, 1971; Tan and Kottelat, 2009). As noted in the descriptions of *C. langei* and *C. oblongus* above, the two species differ in upper lip structure and pigmentation on the middle portion of the caudal fin. Scattered melanophores were observed between the anus and anal-fin origin in specimens from four lots: CAS 66252 (2 of 3 specimens; Peninsular Malaysia), ZRC 7196 (1 specimen; Peninsular Malaysia), ZRC 38885 (7 specimens; Borneo, Central Kalimantan), and ZRC 54643 (Singapore). In all of these specimens in question, there were projections on the upper
lip and the midlateral stripe extended to the distal edge of the middle two caudal-fin rays (although faint in ZRC 7196), as is observed in all other specimens of *C. oblongus*, rather than *C. langei*, examined here. Furthermore, pigment between the anus and anal-fin origin was also observed in some, but not all, specimens of *C. cobitis* and *C. obscurus* (see species accounts). Based on the apparent variation in this character within species, pigmentation between the anus and anal-fin origin may not have significant value in taxonomic identities of *Crossoscheilus*. These specimens are thus identified as *C. oblongus* in light of the upper lip structure and pigmentation on the middle caudal-fin rays and the absence of any diagnostable characters between specimens with melanophores between the anus and anal-fin origin and those without them.

**Distribution.**—In Indonesia, *Crossoscheilus oblongus* is native to West Java, the Kapuas and Barito basins in Borneo, and the Batang Hari, Tulongbawang, and Musi basins in Sumatra. In Indochina, the species is found in the Mae Khlong basin in Thailand, the Mekong basin in Cambodia, Laos, and Thailand, and several smaller basins on the Malay Peninsula (Fig. 12). A single specimen was collected from the Punggol Reservoir in Singapore, a likely aquarium introduction (H. H. Tan, pers. comm.).

**Material examined.**—(Identified, but not measured if no SL given) Indonesia: Borneo: Barito basin: BMNH 2000.10.25.696, 1, 72.4 mm SL, Central Kalimantan, in sand bar between Sungai Busang and Barito; BMNH 2001.1.15.1398–1400, 3, 41.9–76.5 mm SL, Central Kalimantan, Desa Rahaden on Sungai Lahe; ZRC 38885, 7, 72.0–100.6 mm SL, Central Kalimantan, Sungai Merawing at confluence with Sungai Muio. Kapuas basin: CAS 49192, 2, 41.0–43.5 mm SL, West Kalimantan, Kapuas mainstream and mouth of Sungai Sekayam at Sanggau, 0.1167N, 110.5833E; USNM 230161, 3, 29.8–38.4 mm SL, West Kalimantan, Kapuas mainstream at Selimbau, 92 km NE of Sintang, 0.6083N, 112.12E; ZRC 38828, 3, 36.4–42.3 mm SL, West Kalimantan, Sungai Lanjak in Lanjak and Sungai Lanjak Deras 1 km east of Lanjak, 0.8878N, 112.2029E. Java: RMNH D.1755, 1 (lectotype), unknown locality; UMMZ 155652, 2, 86.8–109.7 mm SL, (Tjisokan) Lab Binnenvisscherij, 6.9049S, 107.634E; ZRC 13533, 1, 89.7 mm SL, Bogor, Cisadane River, 6.5974S, 106.784E. Malaysia: Peninsular Malaysia: CAS 241772, 2, 102.0–106.9 mm SL, Attapeu morning market, 14.7833N, 106.8E. Singapore: ZRC 54643, 1, Punggol Reservoir, 1.3897N, 103.9162E. Sumatra: UF 166338, 1, 48.7 mm SL, Lampung, Way Sungkai, 4.60TS3I, 104.9642E; UF 166905, 1, 65.3 mm SL, South Sumatra, Air Enim, 3.7729S, 103.7975E; ZRC 41550, 2, West Sumatra, Sungai Dareh Pulau, Pijung market, 0.9698S, 101.5062E; ZRC 43106, 1, 68.9 mm SL, Jambi, Angso Duo market, 1.4869S, 102.1138E; ZRC 44141, 2, 72.3–74.3 mm SL, same as ZRC 43106. Thailand: Peninsular Thailand: ANSP 179984, 1, 55.5 mm SL, Surat Thani Province, trib. Mae Nam Tapi (Gulf of Thailand Dr.), ca. 25 km NNW of town of Phra Saeng; USNM 90302, 1 (holotype of *Epalzeorhynchus siamensis*), Nakhon Sritamrat Province, upper part of Tadi stream. Mae Khlong basin: UF 173140, 1, 80.9 mm SL, Kanchanaburi Province, Huay Lin Tin at km 95 on Rt. 323, near Sai Yoke, 14.4167N, 98.85E. Mekong basin: CAS 63035, 1, 55.2 mm SL, Loei Province, Mekong R. at Chiang Khan, 17.9016N, 101.6712E; UMMZ 195670, 2, 64.3–72.8 mm SL, Ubon Ratthathani Province, Market at Ubol; UMMZ 195705, 1, 62.5 mm SL, Mun River about 5 km downstream from Ubol, 15.2265N, 104.9231E; UMMZ 233750, 1, 74.3 mm SL, Ubon Ratthathani Province, Huay Hin Taek, just across Mun River from Ban Dan, 1.5 km up Huay Hin Taek from Mun River; UMMZ 233756, 7 (4 ex.), 73.1–78.0 mm SL, Ubon Ratthathani Province, Khong Chiam District, Huay Kwang, 1.5 km upstream from Mun River.

*Crossoscheilus obscurus* Tan and Kottelat, 2009

**Dusky Fringe Barb**

Figure 13

*Crossocheilus obscurus* Tan and Kottelat, 2009:28, fig. 19. Type locality: Indonesia, Sumatra, Sumatra Barat, market at Kiliiran Jao, a village along road from Sungai Dareth to Solok. Holotype: MZB 10706.

**Diagnosis.**—Member of *Crossoscheilus* as described above. *Crossoscheilus obscurus* is distinguished from all other species of *Crossoscheilus* (Table 2) by the following combination of characters: edge of upper lip with projections; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, tiny, hidden in corner of mouth; midlateral stripe from tip of snout to distal portion of median caudal-fin rays (sometimes faint on caudal-fin rays); edges of stripe leaching dorsally and ventrally, not sharply contrasted from background; 2–3½ scales between anus and anal-fin origin.

**Comparisons.**—*Crossoscheilus obscurus* is similar to *C. oblongus* in having projections on the edge of the upper lip, but differs in having a diffuse midlateral stripe with poorly defined edges (vs. having a well-defined midlateral stripe) extending from the tip of the snout to the distal edge of the median caudal-fin rays. The only other species of *Crossoscheilus* with projections on the edge of the upper lip is *C. microstoma*, from which *C. obscurus* differs in having the lower lip rectangular in shape with the width greater than the length (vs. square with the width approximately equal to...
Fig. 12. Distributions of georeferenced specimens examined of: (A) *Crossocheilus oblongus*, (B) *C. obscurus*, (C) *C. reticulatus*, and (D) *C. tchangi*. Lectotype of *C. oblongus* plotted in Java (6.5972S, 106.806E). Holotype of *C. reticulatus* plotted at Bua Yai District, Thailand (15.5702N, 102.3922E).
the length), the black midlateral stripe extending to the distal edge of the caudal-fin rays (vs. the black midlateral stripe ending at a black spot on the caudal peduncle), and tiny barbels, if present, hidden in the corner of the mouth (vs. long, exposed maxillary barbels).

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip with projections; lower lip rectangular in shape, width greater than length. Rostral barbels approximately \( \frac{1}{2} \) eye diameter. Maxillary barbels present in 19 of 41 specimens examined, tiny, hidden in corner of mouth. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 30–31 + 1–3, predorsal scales 8–9, scale rows above lateral line 4\( \frac{3}{5} \)–5\( \frac{1}{5} \), scale rows below lateral line 3–4\( \frac{1}{2} \), 3\( \frac{3}{5} \)–4\( \frac{1}{2} \) scale rows between lateral line and pelvic-fin origin, 2–3\( \frac{1}{2} \) scales between anus and anal-fin origin. Maximum length = 142 mm SL (Tan and Kottelat, 2009).

Dorsum of head and body brown, darker in larger specimens; dark brown border between head and body. Dark brown spots or crescents at anterior base of scales on dorsum; faint midline on body in some specimens. Dorsal 3\( \frac{1}{2} \) of side of head brown; ventral 3\( \frac{3}{4} \) cream with occasional dusky patches. Black midlateral stripe extending from tip of snout to distal tips of middle caudal-fin rays, not sharply contrasted from body coloration on dorsal and ventral edges, often appears to be leaching onto scale rows above and below. In smaller specimens, a distinctly darker spot is present at the base of the caudal peduncle and the middle caudal-fin rays are faint brown. Scales above midlateral stripe with dark crescent-shaped spots superimposed on brown background; scales below stripe with cream background overlaid with scattered melanophores, forming dusky appearance. Background of venter cream with scattered melanophores. Blotch between anus and anal-fin insertion present in most specimens. Dorsal fin dusky with scattered melanophores on membranes; pectoral, pelvic, and anal fins generally dusky; dorsal and ventral edges of caudal-fin rays with concentrations of dark pigment. Upper lip usually with dark spots.

**Remarks.**—Several specimens previously identified as *C. oblongus* from river basins flowing into the Strait of Malacca on Peninsular Malaysia possess a midlateral stripe that is not well-defined from the background coloration. These specimens are herein identified as *C. obscurus*, expanding the species’ range from Sumatra to mainland Southeast Asia.

In more recently collected specimens of *C. obscurus*, the upper lip possesses black spots. These spots are absent in *C. oblongus*. However, we did not observe spots in the paratypes of *C. obscurus* (ZRC 49879, \( n = 2 \)), although these specimens were generally devoid of any melanin-based pigmentation. We thus omitted this character from the formal diagnosis of *C. obscurus*.

**Distribution.**—*Crossocheilus obscurus* occurs in the Batang Hari, Musi, Besai, and Tulangbawang basins in Sumatra, as

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**Fig. 13.** *Crossocheilus obscurus*, UF 162186, 44.7 mm SL.

**Fig. 14.** *Crossocheilus reticulatus*, UF 185185, 61.1 mm SL.
well as the Muar and Batang Padang basins in Peninsular Malaysia (Fig. 12).

**Material examined.**—Indonesia: Sumatra: UF 162186, 9, 38.4–54.8 mm SL, Lampung, Way Rarem and tributary, 4.9221S, 104.7946E; UF 166337, 1, 55.3 mm SL, South Sumatra, Air Muara Lawai, 3.6586S, 103.7409E; UF 166339, 6, 33.1–60.0 mm SL, South Sumatra, Air Ogan, 4.1055S, 104.1384E; UF 166341, 2, 49.7–89.9 mm SL, Lampung, Way Besai, 4.7575S, 104.5554E; UF 166363, 4, 75.2–84.5 mm SL, 3.7877S, 103.5485E; UMMZ 155654, 13, 30.4–43.8 mm SL, Moeara Klingi, Moesi River, 3.1234S, 103.2202E; ZRC 42352, 1, Jambi, Perlingat, along main confluence of Batang Hari, 1.5850S, 103.6108S; ZRC 49879, 2 (paratypes), 84.8–124.6 mm SL, West Sumatra, Saturday market at Kiliran Jao, village along road from Sungai Dareh to Soloh, 0.8914S, 101.3619E.

Malaysia: Peninsular Malaysia: CAS-SU 39348, 5, 89.3–111.0 mm SL, Perak, Batang Padang R., near Tapah Fisheries, 4.1988N, 101.2595E; FMNH 40827, 1, 99.6 mm SL, Perak, Batang Padang River, Tapah Fisheries Station; USNM 101272, 1, 93.3 mm SL, Negri Sembilan, Muar River.

**Crossocheilus reticulatus** (Fowler, 1934)
Reticulated Fringe Barb

Figure 14


**Diagnosis.**—Member of Crossocheilus as described above. *Crossocheilus reticulatus* is distinguished from all other species of *Crossocheilus* (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, short, barely exposed out of corner of mouth; absence of midlateral stripe; large black oval blotch at base of caudal peduncle; brown to black spots at posterior edges of scales on dorsum and flank forming reticulated pattern.

**Comparisons.**—*Crossocheilus reticulatus* is similar to *C. tchangi* but differs in having no black midlateral stripe (vs. black stripe on posterior ¾ of body), a large black oval at the base of the caudal peduncle touching or nearly touching the dorsal and ventral edges of the caudal peduncle (vs. smaller, horizontally elongated black spot), and, if present, small but exposed maxillary barbels (vs. tiny barbels hidden in the corner of the mouth).

**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present in 20 of 22 specimens examined, short, but barely exposed out of corner of mouth. Pectoral fin with 13–15 branched rays. Lateral-line scales and pored scales on caudal fin 30–32 + 2–3, predorsal scales 8–9½, scale rows above lateral line 4½–5½, scale rows below lateral line 4½, 3–3½ scale rows between lateral line and pelvic-fin origin, 1½–3 scales between anus and anal-fin origin; 16 circumpeduncular scales. Maximum length = 90.3 mm SL.

Dorsum of head and body brown, darker in larger specimens. Dark brown spots or crescents at anterior base of scales on dorsum. Dorsal half of side of head brown; ventral half cream to yellow; cheeks and ventral ¾ of opercula silver. Dorsal ¾ of side of body brown, ventral third cream to yellow. Lateral scales outlined with dark brown pigment, thickened at anterior portions forming dark brown crescent-shaped spots. Black oval blotch on caudal peduncle from caudal-fin insertion extending anteriorly ½ way to posterior insertion of anal fin, touching or nearly touching dorsal and ventral edges of caudal peduncle. Venter cream to yellow, immaculate; breast silvery. Dorsal fin with clusters of scattered melanophores forming faint blotches on middle portion on interradial membranes, distal edges occasionally pigmented; pectoral, pelvic, and anal fins generally clear with isolated melanophores in some specimens, particularly at leading edge of pectoral fins; caudal-fin rays with scattered melanophores. Upper lip immaculate.

**Distribution.**—*Crossocheilus reticulatus* is distributed throughout the Mekong basin in Cambodia, China, Laos, Thailand, and Vietnam, and the Chao Phraya basin in Thailand (Fig. 12).

**Material examined.**—(Identified, but not measured if no SL given) Cambodia: Mekong basin: UMMZ 232561, 1, 59.8 mm SL, Stung Treng Province, Mekong River rapids 18 km downstream from Stung Treng, 13.3667N, 105.95E; UMMZ 234652, 5, Stung Treng Province, Mekong River, 2 km downstream from mouth of Tonle Sap on sandbars, 13.5167N, 105.9333E; UMMZ 235502, 8, Kandal, Tonle Sap at Dai fishery row 9, 15 km upstream from Phnom Penh, 11.7623N, 104.8281E. Laos: Mekong basin: UMMZ 238825, 1, Attapen Province, Xe Kamen River at crossing on road to Pleiku (the old Ho Chi Minh trail), Sekong drainage, 14.9N, 107.15E. Thailand: Chao Phraya: ANSP 57568, 1 (holotype of *Holotylognathus reticulatus*), Bua Yai, 200 mi. northeast of Bangkok, eastern Siam; ANSP 61335, 1 (holotype of *Crossocheilus reticulatus*), 50.1 mm SL, Khao Nam Poo; ANSP 61336, 1, 47.1 mm SL, same as ANSP 61335; ANSP 68202, 1 (holotype of *Tylognathus coatesi*), 61.7 mm SL, Bangkok; UMMZ 192988, 1, Nam Pong River; UMMZ 195236, 2, 74.4–88.3 mm SL, Sukothai, Mae Nam Yom at Kang Luang, ca. 11 km SSE Sisatchanalai, 17.3654N, 99.8124E. Mekong basin: UF 170105, 1, 41.3 mm SL, Chiang Rai Province, Kok River, 19.9696N, 99.9687E; UF 185185, 5, 43.6–68.1 mm SL, Ubon Ratchathani Province, Sae Hua Maew, Tung Lung River, 15.3372N, 105.4004E; UF 237383, 10, Chiang Rai Province, Chiang Saen, Kham Nong Bua River, trib. of Mekong River at Rt. 1016 bridge 0.3 mi west of Rt. 1290, 20.2681N, 100.0721E; UMMZ 192623, 1, 72.0 mm SL, Nam Pong River at Nong wai diversion dam at confluence with main irrigation canal, 16.7244N, 102.8011E; UMMZ 224557, 7, Ubon Ratchathani Province, Huay Hin Taek across, Mun River from Ban Dan, 1.6 km up Huay Hin Taek from Mun River; UMMZ 224564, 6 (2 ex.), Ubon Ratchathani Province, Khong Chiam District, Huay Kwang, 1.5 km upstream from Mun River; UMMZ 233795, 13, Ubon Ratchathani Province, Mun River, 3 km downstream from Ubon Ratchathani, 15.2331N, 104.9328E; UMMZ 235121, 1, Ubon Ratchathani Province, Huay Mark Tai, 1 km from Mekong River, 15.7667N, 106.1E; USNM 108013, 1, 90.3 mm SL, Pakjong; USNM 222925, 5, 41.7–82.9 mm SL, Menam Kok at Thaton, 20.0358N, 99.5074E. Vietnam: Mekong basin: UMMZ 218565, 5, Phong Dinh, Bassac River at city of Can Tho, CF-4, 10.0790N, 105.7583E.

### Crossocheilus tchangi Fowler, 1935

**Tchang’s Fringe Barb**

**Figure 15**


**Epalzeorhynchos stigmaeus** Smith, 1945:267, fig. 53. Type locality: Thailand, Mekhan [Mae Khan], tributary of Meping [Mae Ping]. Holotype: USNM 109765.

**Crossocheilus oblongus stigmaeus**.—Bănărescu, 1986:144, fig. 4.

**Crossocheilus stigmaeus**.—Kottelat, 2013:90.

**Diagnosis.**—Member of Crossocheilus as described above. *Crossocheilus tchangi* is distinguished from all other species of *Crossocheilus* (Table 2) by the following combination of characters: edge of upper lip smooth; lower lip rectangular in shape, width greater than length; maxillary barbels, if present, tiny, hidden in corner of mouth; black midlateral stripe present only on posterior ¾ of body, terminating in distinct horizontally elongated spot on caudal peduncle, not on caudal-fin rays.

**Comparisons.**—*Crossocheilus tchangi* is similar to *C. reticulatus* but differs in having a black stripe on posterior ¾ of body (vs. no black midlateral stripe), a horizontally elongated black spot (vs. large black oval touching or nearly touching dorsal and ventral edges) at the base of the caudal peduncle and, if present, tiny maxillary barbels hidden in the corner of the mouth (vs. short but exposed barbels).
**Description.**—Morphometrics and meristics presented in Table 3. Edge of upper lip smooth; lower lip rectangular in shape, width greater than length. Rostral barbels approximately ½ eye diameter. Maxillary barbels present in 10 of 12 specimens examined, usually tiny, hidden in corner of mouth. Pectoral fin with 1 simple and 14–15 branched rays. Lateral-line scales and pored scales on caudal fin 29–32 + 1–3, predorsal scales 8–10, scale rows above lateral line 4½–5½, scale rows below lateral line 4½, 3½ scale rows between lateral line and pelvic-fin origin, 1½–3 scale spaces between anus and anal-fin origin. Maximum length = 129.4 mm SL.

Dorsum of head and body light brown. Dark brown spots or crescents at anterior base of scales on dorsum. Side of head yellow to light brown; cheeks and ventral ⅔ of opercula silver. Dorsal ⅔ of side of body light brown, ventral ⅓ cream. Lateral scales outlined with dark brown pigment, thickened at anterior portions forming dark brown crescent-shaped spots. Oval blotch at base of caudal peduncle, extending anteriorly into lateral stripe on posterior ⅓ of body, becoming row of spots on anterior ⅔ of body; blotch on caudal peduncle not touching dorsal and ventral edges of caudal peduncle, 1–2 scale rows below edges. Lateral scales outlined with dark brown pigment, thickened at anterior portions forming dark brown crescent-shaped spots on dorsal ⅓ of flanks. Venter cream. Dorsal fin with clusters of scattered melanophores forming faint blotches on middle portion on interradial membranes, distal edges occasionally pigmented; pectoral, pelvic, and anal fins generally clear with isolated melanophores in some specimens; caudal-fin rays with scattered melanophores. Upper lip immaculate.

**Remarks.**—Subsequent to its initial description by Fowler (1935), *C. tchangi* was first reviewed by Băranescu (1986) who considered it to be a possibly valid species based on the original illustration and description. Rainboth (1996) placed the name *C. tchangi* under possible misidentifications/synonyms of *C. reticulatus*. Zhang and Chen (1997) and Su et al. (2000) treated *C. tchangi* as a junior synonym of *C. reticulatus*. Most recently, Kottelat (2013) treated *C. tchangi* as a questionable synonym of *C. reticulatus*. An examination of the holotype of *C. tchangi* (ANSP 61690) indicates it is distinct from *C. reticulatus* in possessing a narrow spot at the base of the caudal peduncle that extends anteriorly on the posterior ⅔ of the body into a narrow, punctuated stripe (vs. lateral stripe absent in *C. reticulatus*). This pattern matches that of the type series of *Crossocheilus stigmaeus* (USNM 109763, 109765). Overlap of morphometric and meristic data between the holotype of *C. tchangi*, the type series of *C. stigmaeus*, and specimens with the similar lateral patterning indicate these all represent a single species. *Crossocheilus tchangi* is thus the senior synonym of *C. stigmaeus*, and is herein revalidated.

**Distribution.**—*Crossocheilus tchangi* is distributed in the Chao Phraya, Mae Khlong, Bangpakong, Tapi, and Trang basins in Thailand (Fig. 12).

**Material examined.**—Thailand: Bangpakong basin: ANSP 179903, 1, 108.7 mm SL, Sa Kaeo Province, trib. Khlong Phra Prong at hwy 3259 bridge due west of Khlong Hat, 13.4396N, 102.1621E. Mae Khlong basin: ANSP 61690, 1 (holotype), 129.4 mm SL, Srisawat, a town in west-central Thailand on the west bank of Mae Khlong; UF 173138, 1, 71.2 mm SL, Kanchanaburi Province, Huay Lin Tin, at km 95 on Rt. 323, near Sai Yoke, 14.5623N, 98.78772E. Chao Phraya basin: USNM 107814, 2, 99.7–103.7 mm SL, Menam Nan near head waters at Muang Ngop; USNM 109763, 1, 84.7 mm SL, Mekhan, trib. of Meping River; USNM 109765, 1 (holotype of *Epalzeorhynchos stigmaeus*), 93.6 mm SL, same as USNM 109763; USNM 118435, 1, 97.3 mm SL, Doi Angka. Peninsular Thailand: ANSP 89363, 1, 48.4 mm SL, a 12.2 m fall of the Trang River at Chong, 12 mi. E of Thap Thian or Trang, 7.5514N, 99.6125E; ANSP 89364, 1, 64.1 mm SL, same as ANSP 89363; UF 236093, 1, 50.3 mm SL, Nakhon Si Thhammarat Province, Chawang, Ta Pi River, 8.5073N, 99.5087E; UF 236102, 1, 50.5 mm SL, Nakhon Si Thhammarat Province, Chawang, Ta Pi River, 8.5418N, 99.5141E.

**DISCUSSION**

*Crossocheilus* has consistently been resolved as sister to the Southeast Asian genus *Epalzeorhynchos* in molecular phylogenies of the tribe Labeonini (Yang and Mayden, 2010; Yang et al., 2012; Zheng et al., 2012). These two morphologically similar genera are distinguished by the structure of the rostral lobes, which are moveable and possess a tubercle on the tip in *Epalzeorhynchos* and are firmly attached to the snout and without a tubercle in *Crossocheilus*. Traditional morphology-based hypotheses have placed *Crossocheilus* and *Epalzeorhynchos* as closely related to *Garra* (and *Tariqilabeo*, see above) based on similarities in oromandibular structures. However, molecular phylogenies have resolved the clade containing *Crossocheilus* and *Epalzeorhynchos* as sister to a clade containing *Henicerhynchus* Smith, 1945 and *Lobocheilos* Bleeker, 1854, nested in a clade that is phylogenetically divergent from *Garra* and *Tariqilabeo* (Yang and Mayden, 2010; Yang et al., 2012; Zheng et al., 2012).

The phylogeny presented here is the most taxonomically comprehensive phylogeny of *Crossocheilus* to date, and includes six of the 11 species of the genus from across most of its geographic range. Counter to traditional morphological hypotheses (e.g., Băranescu, 1986), *C. atrilimes* and *C. oblongus*, both of which possess a midlateral stripe from the tip of the snout to the distal edge of the middle caudal-fin rays, were not resolved as sister taxa. *Crossocheilus oblongus* was instead resolved as sister to *C. obscurus*, both of which possess projections on the upper lip. *Crossocheilus atrilimes* was sister to the clade containing *C. reticulatus* and *C. tchangi*, forming a strongly supported clade of those species restricted exclusively to river basins in mainland Southeast Asia. Unlike the phylogeny presented in Yang et al. (2012), *C. nigriloba* was not resolved as sister to *C. reticulatus*, but rather sister to the clade including all other species. This discrepancy may be the result of differences in methodology and taxon sampling, although *C. nigriloba* is a geographically and morphologically unique species, being restricted to the Mahakam River basin draining to Makassar Strait in eastern Borneo and possessing distinct pigmentation on the lower caudal-fin lobe. Additional taxon sampling is clearly warranted to resolve the phylogenetic relationships of species within the genus.

The number of barbels (2 vs. 4) has long been considered an important character in differentiating species of *Crossocheilus* (Bleeker, 1860; Weber and de Beaufort, 1916; Băranescu, 1986; Roberts, 1989; Tan and Kottelat, 2009). However, most individuals of all species examined here possess four barbels (rostral and maxillary). The size of the maxillary barbels is useful in species identifications, with species possessing either tiny maxillary barbels hidden in the
corner of the mouth (C. atrilimes, C. gnathopogon, C. nigriloba, C. oblongus, C. obscurus, C. tchangi), short maxillary barbels that are barely exposed out of the corner of the mouth and less than ¼ of the eye diameter (C. langei and C. reticulatus), or large maxillary barbels that are clearly exposed and approximately ½ to ¾ of the eye diameter (C. cobitis, C. elegans, and C. microstoma). The absence of maxillary barbels in several specimens in each species, exclusive of the three species with large maxillary barbels, may reflect ontogenetic variation. In C. oblongus in particular, larger specimens tend to lack maxillary barbels. This may reflect variation in microhabitat use associated with size, but further data are needed to examine the cause of this variation in barbel presence and absence.

Limited ecological information is available for species of Crossocheilus. Most species (C. elegans, C. langei, C. microstoma, C. oblongus, C. obscurus, C. nigriloba, and C. reticulatus) inhabit fast-flowing, rocky streams (Roberts, 1989; Kottelat, 1995, 2000; Baird et al., 2003; Tan and Kottelat, 2009; Kottelat and Tan, 2011). Crossocheilus atrilimes inhabits slower habitats when it is syntopic with C. oblongus (Kottelat, 2000). The habitat preference of Crossocheilus cobitis is anomalous for the genus, in that this species inhabits slow-flowing, murky habitats with muddy substrate (including swamps and lakes) and often is found on the undersides of large structures such as logs (Kottelat and Widjanarti, 2005; Kottelat and Tan, 2011).termvichakorn and Hortle (2013) recorded the development of larvae of C. reticulatus in floodplain habitats in the Mekong basin. Baird et al. (2003) observed the seasonal upstream migration of C. reticulatus in the Mekong River to Khone Falls with other small cyprinids. The updated taxonomic and distributional data of the genus presented here should facilitate future ecological research, as well as aid in determining potential conservation issues for species of Crossocheilus.

KEY TO SPECIES OF Crossocheilus

1a. Rostral barbels tiny; no midlateral stripe or oval blotch at base of caudal peduncle; Indonesia (Sumatra) ......... C. gnathopogon

1b. Rostral barbels ½ of eye diameter; midlateral stripe or oval blotch at base of caudal peduncle present .... 2

2a. Maxillary barbels large, ½ to ¾ eye diameter, exposed ........................................ 3

2b. Maxillary barbels, if present, short, either hidden in corner of mouth or barely exposed ............... 5

3a. Edge of upper lip with projections; mouth width small (18.3–20.0% HL); lower lip square shaped with length approximately equal to width; Indonesia (Borneo). C. microstoma, new species

3b. Edge of upper lip smooth; mouth width wide (21.1–28.3% HL); lower lip rectangular shaped with length smaller than width ................................ 4

4a. Pale yellow stripe directly dorsal of brown midlateral stripe from dark dorsum present; midlateral stripe extends from posterior of operculum to base of caudal peduncle; caudal-peduncle length long (18.5–20.8% SL); Malaysia....... C. elegans

4b. Pale yellow stripe dorsal of brown midlateral stripe absent; midlateral stripe extends from tip of snout to base of caudal peduncle; caudal-peduncle length short (14.2–17.2% SL); Indonesia (Borneo, Java, Sumatra), Malaysia, and Thailand ....... C. cobitis

5a. Edge of upper lip with projections ..................... 6

5b. Edge of upper lip smooth ............................... 7

6a. Midlateral stripe sharply contrasted from background color, not leaching on ventral and dorsal edges; flank below midlateral stripe immaculate; Cambodia, Indonesia (Borneo), Java, Sumatra) Laos, Malaysia, and Thailand ..................... C. oblongus

6b. Midlateral stripe not sharply contrasted from background color, often leaching on edges; flank below midlateral stripe often with diffuse pigment, producing a dusky appearance; Indonesia (Sumatra) and Malaysia ...................... C. obscurus

7a. Anterior ½ of lower caudal-fin lobe with distinct dark blotch; Indonesia (Sumatra) .... C. nigriloba

7b. Lower caudal-fin lobe without such blotch .............. 8

8a. Midlateral stripe from tip of snout to base of caudal peduncle and onto caudal .................... 9

8b. Midlateral stripe absent or only present on posterior third of body ..................................... 10

9a. Midlateral stripe to distal edge of middle two caudal-fin rays; 1–1½ (rarely 2) scales between anus and anal-fin origin; head depth large (67.4–75.8% HL); Cambodia, Laos, and Thailand ....... C. atrilimes

9b. Midlateral stripe onto middle 2 and 2–3 most dorsal rays of lower caudal-fin lobe, never reaching distal edge of fin; 2–3½ scales between anus and anal-fin origin; head depth small (56.7–65.0% HL); Indonesia (Borneo, Sumatra) and Malaysia ........ C. langei

10a. Midlateral stripe on posterior ⅔ of flank, terminating in horizontally elongate oval spot at base of caudal peduncle; Thailand ..................... C. tchangi

10b. Midlateral stripe absent; oval blotch at base of caudal peduncle nearly touching dorsal and ventral edges of caudal peduncle; Cambodia, China, Laos, Thailand, and Vietnam ..................... C. reticulatus

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