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Hypergastromyzon revisited, with descriptions of a new genus and two new species (Teleostei: Gastromyzontidae)

Tan Heok Hui

Abstract. The genus *Hypergastromyzon* is revised based on fresh topotypic specimens and two other locations in Borneo. *Hypergastromyzon humilis* is redescribed, along with descriptions of *H. abditus*, new species, from upper Katingan basin; and *H. sambas*, new species, from upper Sambas basin. A new genus, *Engkaria*, is erected to accommodate *H. eubranchus*. *Engkaria* differs from *Hypergastromyzon* in having very distinct sexual characters where males have heavy tuberculation over the opercle and modified pectoral-fin rays, the pelvic fins are not completely fused, and other characters. *Engkaria eubranchus* is redescribed based on a series of fresh specimens. An artificial key is provided for all species of *Hypergastromyzon*.

Key words. Southeast Asia, biodiversity, freshwaters, riparian, hillstream loach

INTRODUCTION

The riparian habitats of Borneo include numerous hill streams and tributaries with swift flowing waters over rocky substratum. There is a whole community of distantly related fishes that have adapted to riparian habitats (Inger & Chin, 1962; Lujan & Conway, 2015). For example, sisorid catfishes of the genus *Glyptothorax* have enlarged pectoral fins and a thoracic adhesive apparatus along the ventral surface of the body (Ng & Kottelat, 2016). Cyprinid fishes (e.g., *Ceratogarra*, *Garra*, *Lobocheilos*, *Paracrossocheilus*, and *Schismatorhynchos*) have inferior mouths equipped with a gular disc, large down-turned pectoral and pelvic fins, and strongly forked caudal fins (Kottelat et al., 1993). Kottelat (2020) provided a new genus name for two such rheophilic cyprinids and suggested a standardised anatomical terminology for the parts of the gular disc. Balitorid and gastromyzontid loaches have developed inferior mouths with enlarged pectoral and pelvic fins to form suctorial organs, and can simultaneously respire, feed, and cling to the substrate in swift currents (Tan, 2006; De Meyer & Geerinckx, 2014). For providing more friction on substratum in fast-flowing waters, rheophilic otophysan fishes possess unculi (plural), a term introduced by Roberts (1982) for unicellular keratinous structures. Unculi are particularly abundant on the ventral surface of the body, especially on the surface of putative adhesive structures of rheophilic taxa (Roberts, 1982)—including the thickened skin along the ventral surface of the anteriormost paired-fin rays in many cypriniforms and siluriforms; oral structures including the gular disc of some cyprinids or barbels of sisorids; and the so-called thoracic adhesive apparatus of sisorid catfishes (Saxena, 1961; Roberts, 1982; Conway et al., 2012; Ng, 2015).

The gastromyzontid loaches are unique amongst the cypriniform fishes in having the largest number of pectoral- and pelvic-fin rays (up to 29 and 25 respectively). In some species, the greatly expanded pelvic fin of the right and left side of the body are fused across the midline to form a suctorial organ in combination with the expanded pectoral fins and anterior margin of the head (Tan, 2006; De Meyer & Geerinckx, 2014). Regarding the genera endemic to Borneo, *Gastromyzon* and *Neogastromyzon* were revised by Tan (2006), which included the descriptions of 19 new species (15 *Gastromyzon* and four *Neogastromyzon*). Tan (2006) also included *Hypergastromyzon*, but due to lack of fresh specimens, no further work was conducted. Of all endemic Bornean gastromyzontid genera, *Hypergastromyzon* is the least represented in museum collections. *Hypergastromyzon humilis* is known from only two specimens (MZB 3480 [holotype], CAS 49333), and *H. eubranchus* from four (BMNH 1984.11.15:1 [holotype], BMNH 1984.11.15:2, BMNH 1984.11.15:3, CAS 55889) (Roberts, 1989, 1991).

The genus *Hypergastromyzon* was established by Roberts (1989) based on only two specimens he collected from the Kapuas River basin in 1976. Roberts (1989) described *Hypergastromyzon humilis* noting the unusually large number of pectoral- and pelvic-fin rays (shared with *Gastromyzon* and *Neogastromyzon*), greatly (dorso-ventrally) flattened body, and a narrow and simple mouth (unlike *Gastromyzon* and *Neogastromyzon*, which have a wide mouth and specialised

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oral parts; see Tan, 2006). Roberts noted the similarity of *H. humilis* with the Chinese loach genus *Beaufortia*, but listed differences in pectoral fin placement. Roberts also likened the simple mouthparts of *H. humilis* to that of *Homaloptera* (now placed in Balitoridae).

In 1991, Roberts described *Hypergastromyzon eubranchus* based on four specimens collected in 1982 by Joan Cramphorn in her inland fisheries survey at Batang Ai in Sarawak. Roberts (1991) noted the main differences to *H. humilis* as incomplete fusion of pelvic fins, larger opercular opening, and presence of tuberculation on two male specimens of *H. eubranchus*. He also reported the difference in body colour pattern between the juvenile specimen and adult specimens (see accounts later). He thus modified the definition of the genus *Hypergastromyzon* to accommodate the new character states of *H. eubranchus*.

In Tan's (2006) treatment of *Gastromyzon*, *Neogastromyzon*, and *Hypergastromyzon*, he suggested that the two species of *Hypergastromyzon* may not be congeneric, but did not provide any concrete results due to lack of fresh material. In recent years of field sampling and accessibility of commercial specimens from the ornamental fish trade, larger series of *Hypergastromyzon* are now available. Several series of *Hypergastromyzon* were obtained from Upper Katingan in Kalimantan Tengah in 2007, from the ornamental fish trade from 2006 to 2011, and from Central Sarawak in 2018. With this additional material, it is now possible to revise *Hypergastromyzon* with the descriptions of two new species, and to place *H. eubranchus* into a new genus.

MATERIAL AND METHODS

Measurements were made point to point with dial calipers and data were recorded with an accuracy of 0.1 mm. Counts and measurements were made on the left side of specimens whenever possible. Subunits of the head are presented as percentage proportions of head length (% HL). Head length and measurements between landmarks on the body are given as percentage proportions of standard length (% SL). Measurements and meristic information follow Tan (2006).

Fish specimens were obtained from the field through collecting by hand, with cast nets, push nets, scoop nets, hand nets and with electro-fishing gear (Bretschneider Spezialelektronik EFGI 650). Some lots were obtained from the ornamental fish trade and collected from the wild. Fish specimens were euthanised (in accordance to NUS Institutional Animal Care and Use Committee RCULA: F018/09), fixed in formalin solution and subsequently stored in 75% ethanol. Photographs of live individuals were obtained using a DSLR camera with a macro lens in a narrow tank. Colouration of preserved material was documented in the laboratory using a copy stand and associated camera gear (see Tan, 2014).

Specimens examined are deposited at the California Academy of Sciences (CAS), Golden Gate Park, San Francisco, USA; Collection of Maurice Kottelat (CMK), Delémont, Switzerland; Research and Development Centre for Biology (MZB), The Indonesian Institute of Sciences (LIPI, formerly the Museum Zoologicum Bogoriense), Cibinong, Indonesia; Natural History Museum (BMNH), London, United Kingdom; and the Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.

TAXONOMY

An artificial key to species of *Hypergastromyzon*

1. Position of pectoral-fin origin directly below middle of eye (Figs. 1, 2); supra-pelvic flap bi-lobed; lower lip margin entire and smooth 2
– Position of pectoral-fin origin directly below posterior margin of eye (Fig. 12); supra-pelvic flap tri-lobed; lower lip margin with concave cleft at middle (Fig. 5C) .... *Hypergastromyzon sambas*, new species
2. Lower lip in ventral view with gently curving corners towards vent (Fig. 5A); pectoral-fin ray count 25–26 (mode 25); anal pore not visible in ventral view (blocked by fused pelvic fins); lateral scale count 57–69 (mean 62)..... ..... *Hypergastromyzon humilis*
– Lower lip in ventral view with truncate anterior profile (Fig. 5B); pectoral-fin ray count 26–28 (mode 27); anal pore visible in ventral view; lateral scale count 62–74 (mean 70)..... ..... *Hypergastromyzon abditus*, new species

Hypergastromyzon Roberts, 1989

Type species: *Hypergastromyzon humilis* Roberts, 1989.

Diagnosis. Adapted from original diagnosis provided by Roberts (1989: 91).

A gastromyzontine loach with head and body wide and strongly depressed (body depth at dorsal-fin origin 9.4–15.9% SL, body depth 8.4–10.6% SL, caudal-peduncle depth 5.2–8.0% SL); pectoral and pelvic fins greatly enlarged (pectoral-fin rays 24–28, pelvic-fin rays 17–20); pectoral-fin origin below eye; pelvic fins completely fused posteriorly; mouth small, about a third of head width, with horny jaw sheaths strongly curved; three pairs of very short barbels, two rostral and one maxillary; rostral cap fused with upper lip except around base of rostral barbels; lower lip with medial groove well developed posterolaterally but interrupted anteromedially; snout rounded in dorsal view, strongly pointed in lateral view; gill opening lunate, length about equal to eye diameter, above middle of pectoral-fin base; subopercular groove absent; base of first pectoral-fin ray separated from head by a deep groove parallel to anterior edge of fin ray on ventral side of head and continuous dorsally on head to behind base of fin ray; dorsal surface of pectoral-fin base without scales; supra-pelvic flap originating immediately behind pectoral-fin base and continuing as a free flap above anterior third of pelvic-fin base; abdomen without scales; pored lateral scale rows 57–78; very short anal-fin base (2.3–5.3% SL); first anal-fin pterygiophore not bifurcated proximally; total vertebral count 30–32. Mature

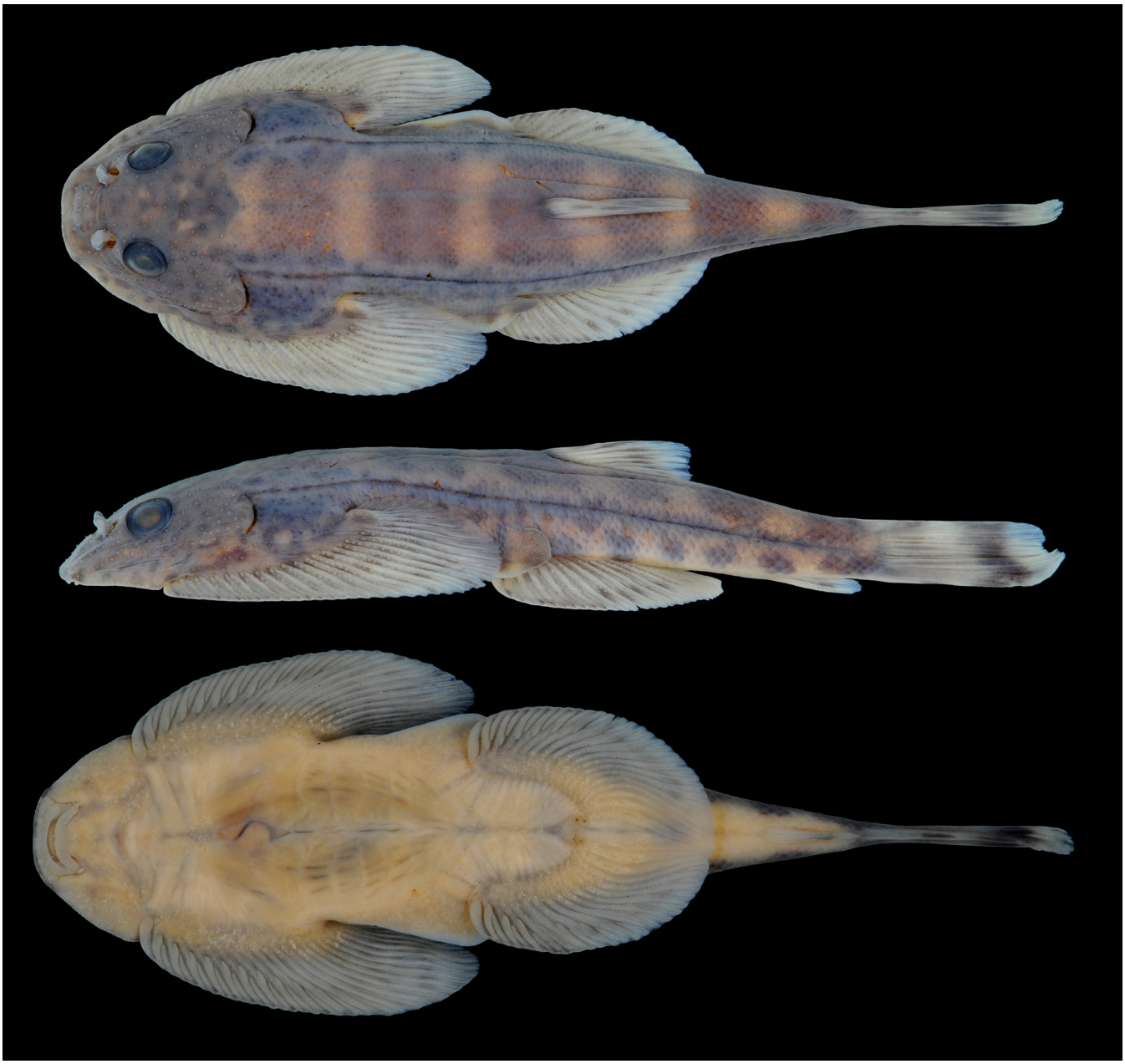

Fig. 1. *Hypergastromyzon humilis*, CMK 10574, 31.5 mm SL, male; composite of dorsal, lateral, and ventral views.

males without densely packed tubercles on pectoral-fin rays, or tuberculated ridges on opercle.

Hypergastromyzon is restricted to southern Borneo, currently known only from Sambas and Kapuas River basins in West Kalimantan, and Katingan River basin in Central Kalimantan. It inhabits fast-flowing hill streams with well-oxygenated water running over rock and gravel base.

The genus, thus diagnosed, includes three taxa, of which two will be described herein as new species.

***Hypergastromyzon humilis* Roberts, 1989**
(Figs. 1–5)

Hypergastromyon humilis Roberts, 1989: 92, fig. 72; 1991: 334; Kottelat et al., 1993: 75, pl. 25; Doi, 1997: 19 (list); Tan, 2006: 201, fig. 128; Kottelat, 2013: 194.

Material examined. Holotype: MZB 3980, 34.5 mm SL; Kalimantan Barat: Kapuas basin: Sungai Tamang, small forested stream flowing into Sungai Pinoh, opposite mouth of Sungai Kelawi, 0°35′S, 111°44′E; T. R. Roberts & S. Woerjoatmodjo, 26 July 1976.

Paratypes: CAS 49333, 1 ex., 34.8 mm SL, paratype; same collection data as holotype.

Other material: CMK 10574, 4 ex., 23.6–31.8 mm SL; Borneo: Kalimantan Barat: Sungai Melawi basin; Sungai Kelawai between Nanga Pintas and about 3 km upstream, 0°36′49″S, 111°47′22″E; M. Kottelat et al., 17 September 1993. — ZRC 61394, 1 ex., 31.0 mm SL; Borneo: Kalimantan Barat: Kapuas basin, Melawi sub-basin; Sungei Elar Hulu; river along border of buffer zone with village and Bukit Raya-Bukit Baka National Park; 00°35.370′S, 112°14.354′E, 231 m asl; H. H. Tan et al., 12 August 2007.

Fig. 2. *Hypergastromyzon humilis*, CMK 10574, 31.5 mm SL, male; close-up lateral view of anterior half of body showing tubercles on head and pectoral fin.

Fig. 3. *Hypergastromyzon humilis*, ZRC 61394, 31.1 mm SL, female (?); live colouration; composite of dorsal, lateral, and ventral views.

Table 1. Meristics and morphometric data for *Hypergastromyzon humilis*; *H. abditus*, new species; *H. sambas*, new species; and *Engkaria eubranchus*. Data in brackets refer to (modal count), data in square parentheses refer to [mean ± standard deviation]; * refers to total fin-ray count, ** refers to principal fin-ray count only.

	Hypergastromyzon humilis	***Hypergastromyzon abditus*, new species**		***Hypergastromyzon sambas*, new species**		***Engkaria eubranchus***
River basin	West Kalimantan: Kapuas (Melawi)	Central Kalimantan: Katingan		West Kalimantan: Sambas		Sarawak: Lupar (Engkari)
Catalogue numbers	CMK10574, ZRC61394	MZB17233 holotype	ZRC61397, ZRC61400, MZB17234 paratypes	MZB17235 holotype	ZRC61380, ZRC61390 paratypes	ZRC60418, ZRC60468
Sample size	5	1	8 (+ holotype)	1	20 (+ holotype)	20
Standard length (mm)	23.8–31.8	37.2	31.1–40.3	32.4	28.0–33.1	34.1–41.1
Meristics						
Dorsal-fin rays*	8	8	8	8	8	7–9 (8 or 9)
Anal-fin rays*	5–6 (5)	5	7	6	5–6 (6)	7
Pelvic-fin rays*	19	19	19–20 (19)	18	17–19 (18)	19–23 (20, 21 or 22)
Pectoral-fin rays*	25–26 (25)	28	26–28 (27)	24	24–25 (24 or 25)	21–25 (22 or 23)
Caudal-fin rays**	7–8 + 7–8 (7 + 7)	8 + 9	8 + 9	8 + 7	8 + 7–8 (8 + 7)	8–9 + 8–9 (8 + 8)
Lateral scales	57–69 (69) [62.4]	62	62–74 (73) [70.8]	67	58–78 [70.8]	50–75 [67.3]
Predorsal scales	30–32 (32)	35	33–38 (35)	28	28–40 (34)	26–35 (34)
Transverse scales	7–9.1.7–9	8.1.9	8–9.1.7–9 (8.1.9)	8.1.8	7–8.1.8–9 (8.1.9)	10.1.10–11 (10.1.10)
Caudal peduncle scales	5–7.1.5–6	5.1.5	5–6.1.5 (5.1.5)	5.1.6	5–6.1.5–6 (5.1.5)	6.1.6
Scale rows below dorsal-fin origin to lateral line	10–12 (11)	11	10–12 (11)	9	9–12 (11)	9–10 (10)
Vertebral count	30–31 (30)		31–32 (31)		30–31 (30)	27–28 (28)
% Standard length						
Total length	122.9–126.0 [124.4 ± 1.20]	123.7	120.6–126.0 [122.2 ± 1.81]	121.6	120.4–125.0 [122.7 ± 1.32]	122.7–125.8 [123.9 ± 0.91]
Trunk length	72.0–78.1 [75.4 ± 2.17]	78.8	76.9–80.3 [78.5 ± 1.30]	77.5	73.7–79.3 [76.3 ± 1.39]	72.5–78.9 [75.2 ± 1.62]
Predorsal length	54.2–60.4 [57.9 ± 2.42]	58.1	56.4–60.0 [58.3 ± 1.33]	57.1	55.1–61.1 [58.0 ± 1.64]	55.7–59.7 [57.8 ± 1.20]

	Hypergastromyzon humilis	*Hypergastromyzon abditus*, new species		*Hypergastromyzon sambas*, new species		*Engkaria eubranchus*
River basin	West Kalimantan: Kapuas (Melawi)	Central Kalimantan: Katingan		West Kalimantan: Sambas		Sarawak: Lupar (Engkari)
Catalogue numbers	CMK10574, ZRC61394	MZB17233 holotype	ZRC61397, ZRC61400, MZB17234 paratypes	MZB17235 holotype	ZRC61380, ZRC61390 paratypes	ZRC60418, ZRC60468
Preanal length	83.5–88.4 [85.5 ± 1.79]	87.6	84.4–89.9 [86.5 ± 1.74]	85.5	85.1–88.5 [86.3 ± 0.78]	80.6–85.0 [82.6-1.22]
Prepelvic length	44.9–51.6 [49.6 ± 2.76]	50.0	47.5–50.0 [48.4 ± 0.98]	49.4	47.4–52.9 [49.8 ± 1.21]	48.8–53.1 [50.4 ± 1.18]
Head length	25.5–28.4 [26.6 ± 1.82]	26.3	22.7–26.3 [24.8 ± 1.33]	24.1	23.2–27.4 [24.7 ± 1.05]	26.2–30.1 [28.2 ± 1.08]
Body depth at dorsal-fin origin	10.6–15.9 [13.2 ± 1.98]	12.6	11.1–13.1 [12.5 ± 0.66]	10.2	9.4–13.6 [11.6 ± 1.16]	14.1–16.2 [15.2 ± 0.57]
Body depth at anus	8.4–10.6 [9.8 ± 0.92]	9.4	8.6–10.3 [9.4 ± 0.50]	8.6	8.6–10.4 [9.6 ± 0.56]	11.2–13.1 [12.0 ± 0.52]
Caudal-peduncle depth	5.2–6.8 [6.3 ± 0.67]	6.2	5.8–7.4 [6.6 ± 0.52]	6.2	6.2–8.0 [7.1 ± 0.45]	7.3–8.5 [7.9 ± 0.28]
Caudal-peduncle length	6.2–8.1 [7.0 ± 0.68]	7.3	4.3–7.4 [5.9 ± 1.25]	4.3	3.2–6.4 [4.8 ± 0.80]	5.9–10.3 [7.8 ± 1.23]
Dorsal-fin base length	12.0–15.2 [13.7 ± 1.38]	11.3	10.6–14.4 [12.2 ± 1.28]	11.1	10.4–13.6 [12.1 ± 0.86]	10.5–14.4 [12.9 ± 1.04]
Anal-fin base length	2.3–5.3 [3.7 ± 1.14]	4.3	3.5–5.1 [4.3 ± 0.57]	3.4	2.4–4.8 [3.5 ± 0.57]	3.6–6.6 [5.1 ± 0.82]
Pelvic-fin length	31.4–36.3 [33.8 ± 1.92]	30.6	29.2–34.3 [30.9 ± 1.64]	30.9	30.9–34.0 [32.1 ± 1.01]	27.4–31.8 [29.8 ± 1.08]
Pectoral-fin length	40.3–42.5 [41.2 ± 0.86]	39.0	37.2–40.9 [38.5 ± 1.14]	38.3	36.7–42.4 [39.1 ± 1.52]	33.4–38.3 [35.8 ± 1.16]
Head depth	8.5–9.6 [8.9 ± 0.54]	8.6	8.0–9.7 [8.8 ± 0.57]	9.3	8.4–10.2 [9.4 ± 0.45]	9.0–11.3 [10.5 ± 0.63]
Head width	20.6–24.6 [22.9 ± 1.71]	22.0	19.7–23.8 [21.8 ± 1.20]	23.1	20.6–24.3 [22.6 ± 0.96]	20.4–25.3 [22.5 ± 1.23]
Snout length	8.8–10.6 [9.8 ± 0.70]	10.8	9.4–11.1 [10.2 ± 0.64]	9.9	7.9–11.2 [9.9 ± 0.85]	9.9–13.1 [10.9 ± 0.84]

	Hypergastromyzon humilis	*Hypergastromyzon abditus*, new species		*Hypergastromyzon sambas*, new species		*Engkaria eubranchus*
River basin	West Kalimantan: Kapuas (Melawi)	Central Kalimantan: Katingan		West Kalimantan: Sambas		Sarawak: Lupar (Engkari)
Catalogue numbers	CMK10574, ZRC61394	MZB17233 holotype	ZRC61397, ZRC61400, MZB17234 paratypes	MZB17235 holotype	ZRC61380, ZRC61390 paratypes	ZRC60418, ZRC60468
Eye diameter	4.8–5.9 [5.4 ± 0.39]	4.8	3.6–5.3 [4.5 ± 0.67]	4.6	3.4–5.6 [4.6 ± 0.64]	2.9–4.4 [3.8 ± 0.40]
Interorbital width	6.5–7.9 [7.2 ± 0.25]	6.7	6.1–6.9 [6.5 ± 0.29]	6.2	6.1–7.9 [6.9 ± 0.47]	6.5–8.1 [7.4 ± 0.40]
% Head length						
Head depth	29.9–36.6 [33.6 ± 2.58]	32.7	30.8–38.6 [35.4 ± 2.72]	38.5	32.9–40.8 [38.0 ± 1.89]	31.8–43.1 [37.3 ± 3.05]
Head width	81.0–93.2 [86.0 ± 4.53]	83.7	83.7–96.4 [88.2 ± 4.41]	96.2	83.3–101.4 [91.5 ± 5.34]	72.5–91.5 [79.9 ± 4.74]
Snout length	34.1–40.5 [36.9 ± 2.31]	40.8	39.2–43.5 [41.1 ± 1.38]	41.0	33.8–46.8 [40.0 ± 3.31]	34.8–48.0 [38.7 ± 3.56]
Eye diameter	19.0–20.9 [20.2 ± 0.75]	18.4	15.7–20.7 [18.1 ± 1.90]	19.2	14.3–23.4 [18.5 ± 2.84]	10.2–16.3 [13.7 ± 1.47]
Interorbital width	25.4–28.4 [27.2 ± 1.16]	25.5	24.2–28.0 [26.4 ± 1.42]	25.6	24.4–32.9 [27.9 ± 1.96]	23.3–29.1 [26.3 ± 1.76]

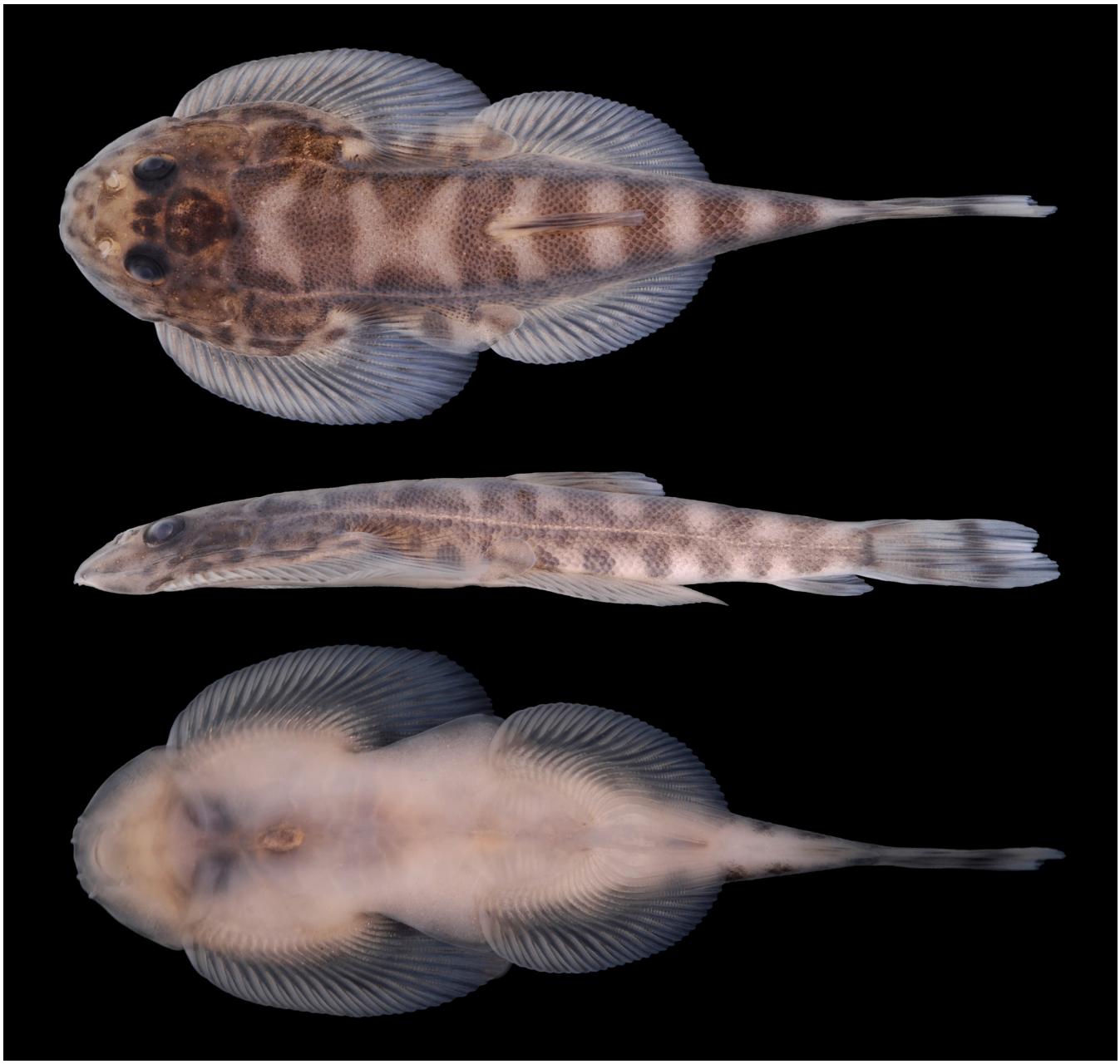

Fig. 4. *Hypergastromyzon humilis*, ZRC 61394, 31.1 mm SL, female (?); composite of dorsal, lateral, and ventral views.

Diagnosis. *Hypergastromyzon humilis* can be distinguished from its congeners in having the unique combination of characters: lowest number of lateral scales (57–69, mean 62; vs. 62–74 [mean 71] in *H. abditus* and 58–78 [mean 71] in *H. sambas*); fewer pectoral-fin rays than *H. abditus* (25–26, mode 25; vs. 26–28, mode 27); most slender caudal-peduncle depth (5.2–6.8% [mean 6.3] SL, vs. 5.8–7.4 [mean 6.6] in *H. abditus*, and 6.2–8.0 [mean 7.1] in *H. sambas*); longest caudal-peduncle length (6.2–8.1% [mean 7.0] SL, vs. 4.3–7.4 [mean 5.9] in *H. abditus*, and 3.2–6.4 [mean 4.8] in *H. sambas*); longest dorsal-fin base length (12.0–15.2% [mean 13.7] SL, vs. 10.6–14.4 [mean 12.2] in *H. abditus*, and 10.4–13.6 [mean 12.1] in *H. sambas*); longest pectoral-fin length (40.3–42.5% [mean 41.2] SL, vs. 37.2–40.9 [mean 38.5] in *H. abditus*, and 36.7–42.4 [mean 39.1] in *H. sambas*); largest eye diameter (4.8–5.9% [mean 5.4] SL, vs. 3.6–5.3 [mean 4.5] in *H. abditus*, and 3.4–5.6 [mean 4.6] in *H. sambas*); lower lip in ventral view with gently curving corners towards vent (vs. truncate in *H. abditus* and notched in *H. sambas*).

Description. See Figs. 1–4 for general appearance, and Table 1 for meristics and morphometric data.

Body greatly depressed, widest and deepest at posterior edge of pectoral-fin base, narrowest at caudal peduncle. Lateral line distinct and complete, running along median of body to caudal-fin base. Head depressed, rounded in dorsal profile, inferior mouth. Mouth simple with entire lower and upper lips, without modifications or specialised organs, lower lip in ventral view with gently curving corners towards vent, mouth width about ⅓ of head width, two pairs of distinct but short rostral barbels, one pair of relatively longer maxillary barbels, margin of both upper and lower jaws entire; shallow

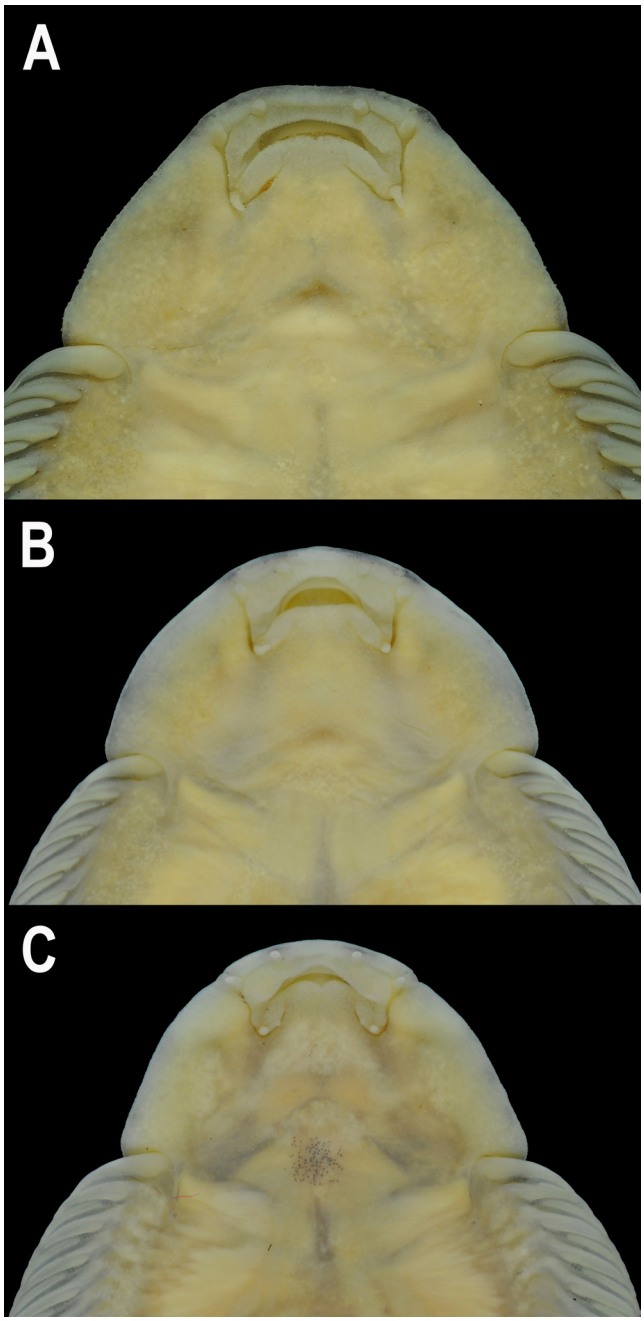

Fig. 5. Oral views. A, *Hypergastromyzon humilis*, CMK 10574, 31.5 mm SL; B, *Hypergastromyzon abditus*, MZB 17233, 37.2 mm SL; C, *Hypergastromyzon sambas*, MZB 17235, 32.4 mm SL.

pocket on both sides of mouth, lower lip with many tiny raised bumps, continuous to throat without discrete structures (Fig. 5). Naris large, ca. ⅓ eye diameter, anterior to eye. Eye situated dorsally, middle of eye located above pectoral-fin origin, eye diameter less than opercle opening. Opercle opening lunate, located above pectoral-fin rays 6–7. Tubercles present and evenly distributed over head and anterior-dorsal part of body and extending to supra-pectoral region (Fig. 2). Pectoral fins enlarged, forming a fan-like shape, total fin-ray count 25–26, posterior edge just overlapping with pelvic-fin origin. Pelvic fins enlarged and completely fused at the posterior edge, forming a U-shape, total fin-ray count 19 on each half. Belly naked. Anal pore situated nearer to pelvic-fin base than to anal-fin origin, not visible from ventral view. Both pectoral- and pelvic-fin anterior rays dorsal surface with tubercles, evenly distributed along fin ray, roughly half of ray length. Supra-pelvic flap present, bi-lobed, covering up to base of pelvic-fin rays 6–7. Anal fin small and triangular, adpressed just reaching caudal-fin base. Caudal fin truncate. Dorsal fin small, triangular; origin posterior to pelvic-fin origin. Largest examined specimen 34.8 mm SL (CAS 49333).

Total vertebral count: 30–31 (mode 30, n = 5).

Colouration in life. See Fig. 3. Head light brown with many dark brown blotches. Eye with gold iris. Opercle with iridescent gold. Dorsum of body light brown or yellowish-brown, with many scattered darker brown bars and blotches. Dorsum with up to eight dark brown saddle-like bars, extending to mid-body. Middle of body with dark brown indistinct reticulated pattern, partly extending below lateral line, lateral line cream. Venter cream. Dorsal fin with one faint dark brown bar, interradial membrane hyaline. Caudal-fin base black or dark brown, two distinct black or dark brown bars, at anterior half and median of fin, margin clear, interradial membranes hyaline. Anal fin with one dark brown bar, interradial membrane hyaline. Both pectoral and pelvic fins golden-brown with 2–3 dark brown whorls. Pectoral-fin base with continuous or interrupted dark brown outline. Supra-pelvic flap with two dark brown blotches, first at anterior half, second at posterior margin.

Colouration in preservative. See Figs. 1, 4. Colouration as above, except bright colours are absent. Lateral line dark brown or cream, potentially due to different locality populations or artefact of preservation.

Sexual characters. Genital papillae indistinguishable between sexes. Males with enlarged tubercles on pectoral- and pelvic-fin rays, tubercles along proximal ⅔ to ¾ of each fin ray, largest tubercles nearest to body, decreasing in size towards distal-fin margin.

Distribution. *Hypergastromyzon humilis* appears to be endemic to the Melawi sub-basin, which drains northwesterly from the Schwaner Range into the Kapuas River at Sintang (Fig. 6).

Field notes. *Hypergastromyzon humilis* occurs in fast-flowing hill streams with clear, well-oxygenated water, running over rock and gravel bottom. Syntopic fish species observed together with *H. humilis* (ZRC 61394) include the following: Cyprinidae—*Garra borneensis*, *Paracrossochilus acerus*, and *Tor* sp.; Gastromyzontidae—*Gastromyzon praestans* and *G. ridens*; Sisoridae—*Glyptothorax major*; and Mastacembelidae—*Mastacembelus unicolor*.

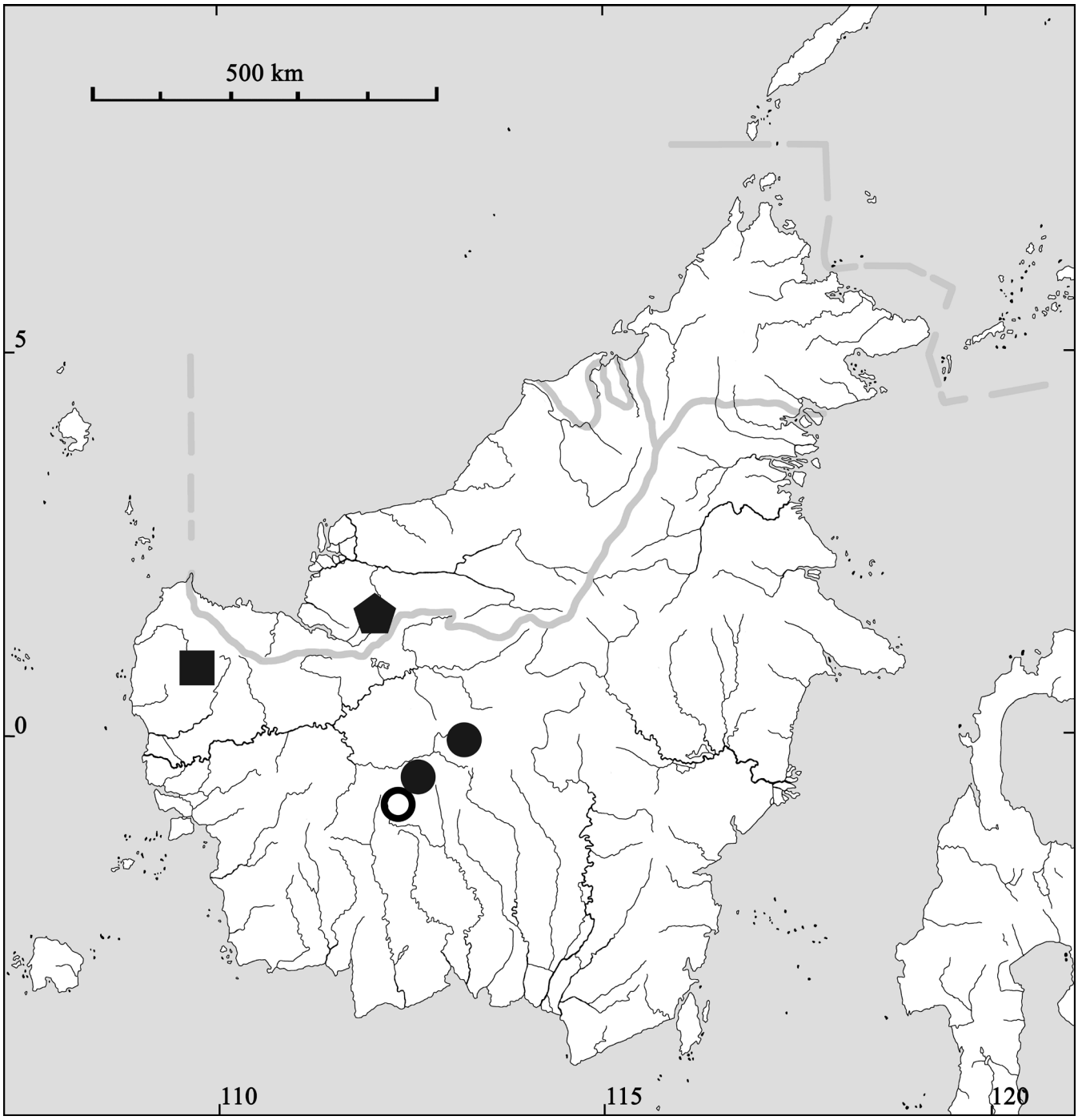

Fig. 6. Map of Borneo showing distribution of *H. humilis* (black circle), *H. sambas* (black square), *H. abditus* (white circle), and *E. eubranchus* (black pentagon). Each symbol may represent more than one location.

***Hypergastromyzon abditus*, new species**
(Figs. 5, 7–10)

Material examined. Holotype: MZB17233, 37.2 mm SL; Kalimantan Tengah: Katingan basin, Mendawai sub-basin; stream at km 57 logging road at buffer zone of Bukit Raya-Bukit Baka National Park; at deep pool (ca. 2–3 m depth) at first cascade series, about 15 m high, about 800 m upstream, 00°45.011′S, 112°17.183′E, 211 m asl; H. H. Tan et al., 11 August 2007.

Paratypes: MZB17234, 1 ex., ZRC 61397, 2 ex., 31.1–35.9 mm SL; same locality data as holotype. — ZRC 61400, 4 ex., 36.0–40.3 mm SL; Kalimantan Tengah: Katingan basin, Mendawai sub-basin; Sungei Baha'e, km 64 logging road at buffer zone of Bukit Raya-Bukit Baka National Park, 00°47.593′S, 112°19.220′E, 218 m asl; H. H. Tan et al., 12–13 August 2007.

Diagnosis. *Hypergastromyzon abditus* can be distinguished from its congeners in having the unique combination of characters: large number of lateral scales (62–74 [mean 71]); highest number of pectoral-fin rays (26–28, mode 27, vs. 24–25 for other two species); slender caudal-peduncle depth (5.8–7.4% [mean 6.6] SL); short caudal-peduncle length (4.3–7.4% [mean 5.9] SL); short dorsal-fin base length

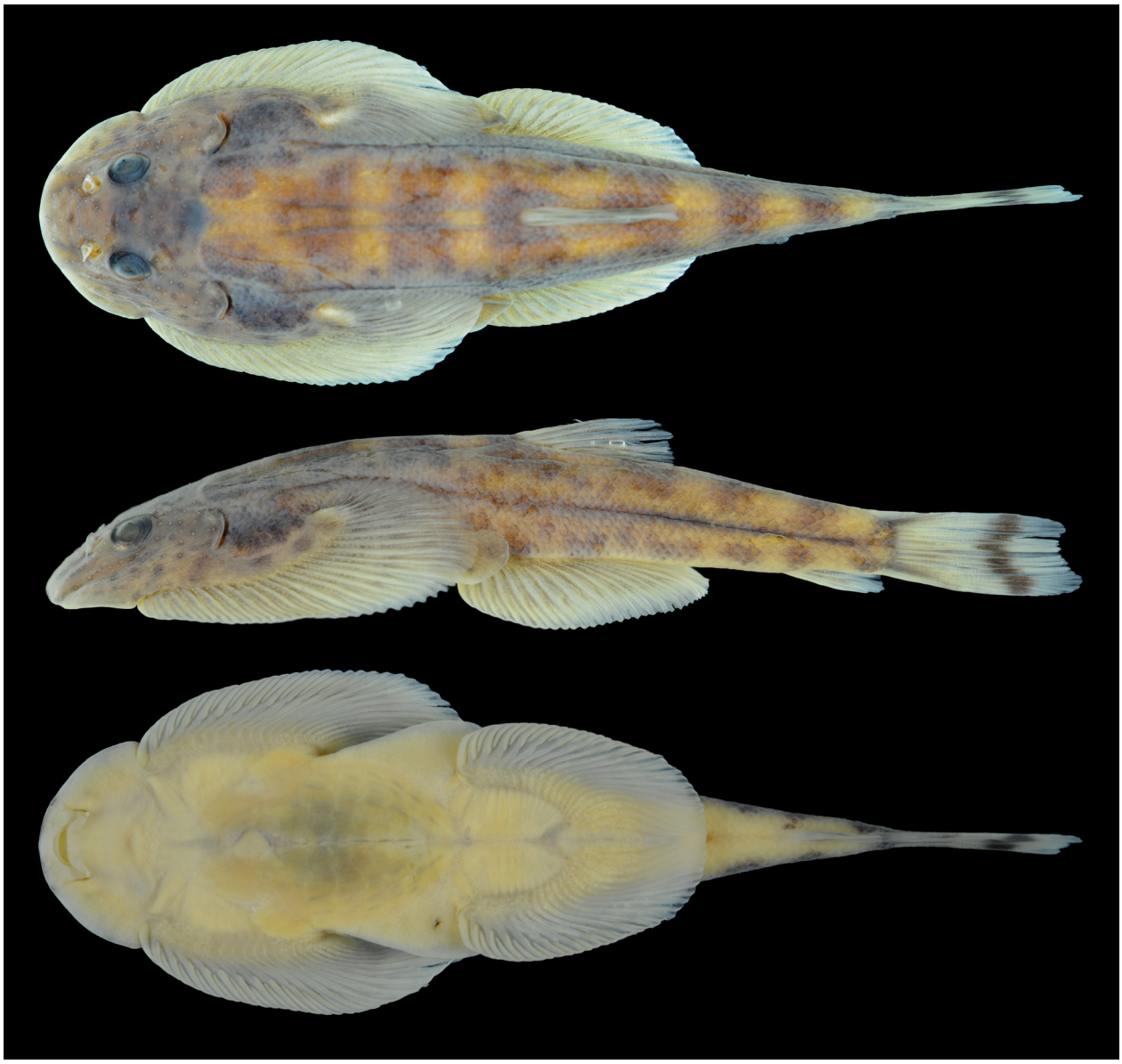

Fig. 7. *Hypergastromyzon abditus*, MZB 17233, 37.2 mm SL, holotype, male; composite of dorsal, lateral, and ventral views.

Fig. 8. *Hypergastromyzon abditus*, ZRC 61400, 40.3 mm SL, paratype, male; close-up of lateral view of anterior half of body showing tubercles on head, body, and pectoral fin.

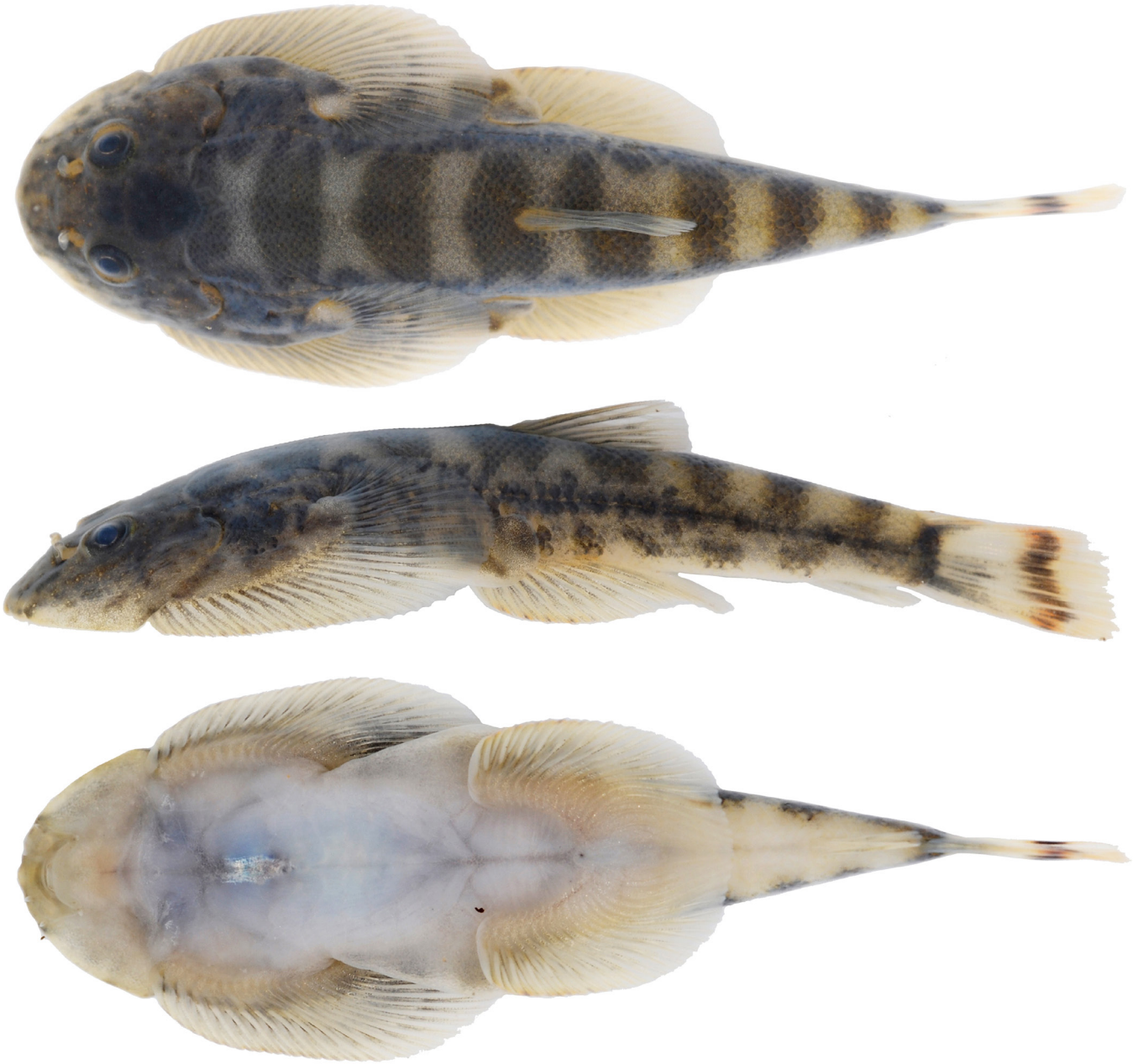

Fig. 9. *Hypergastromyzon abditus*, ZRC 61397, ca. 38 mm SL, female; freshly preserved colouration; composite of dorsal, lateral, and ventral views.

(10.6–14.4% [mean 12.2] SL); shortest pectoral-fin length (37.2–40.9% [mean 38.5] SL, vs. 40.3–42.5 [mean 41.2] in *H. humilis*, and 36.7–42.4 [mean 39.1] in *H. sambas*); smallest eye diameter (3.6–5.3% [mean 4.5] SL, vs. 4.8–5.9 [mean 5.4] in *H. humilis*, and 3.4–5.6 [mean 4.6] in *H. sambas*); lower lip with truncate anterior margin (vs. gently curved in *H. humilis* and bilobed with median cleft in *H. sambas*).

Description. See Figs. 7–10 for general appearance, and Table 1 for meristic and morphometric information.

Body depressed, widest and deepest at posterior margin of pectoral-fin base, narrowest at caudal peduncle. Lateral line distinct and complete, running along median of body to caudal-fin base. Head depressed, rounded in dorsal profile, inferior mouth. Mouth simple, lower lip in ventral view with truncate anterior profile, mouth width about ¼ of head width, two pairs of distinct but short rostral barbels, one pair of relatively longer maxillary barbels, margin of both upper and lower lips entire; shallow pocket on both sides of mouth, lower lip without tiny raised bumps, continuous to throat without discrete structures. Naris large, ca. ⅓ eye diameter, anterior to eye. Eye situated dorsally, middle of eye located above pectoral-fin origin, eye diameter less than opercle opening. Opercle opening lunate, located above pectoral-fin rays 6–7. Tubercles present and evenly distributed over head and anterior-dorsal part of body and extending to supra-pectoral region. Pectoral fins enlarged, forming a fan-like shape, total fin-ray count 26–28, posterior edge just overlapping with pelvic-fin origin. Pelvic fins enlarged and completely fused at the posterior edge, forming a U-shape, total fin-ray count 19–20 on each half. Belly naked. Anal pore situated nearer to pelvic-fin base than to anal-fin origin, just visible from ventral view. Both pectoral- and pelvic-fin

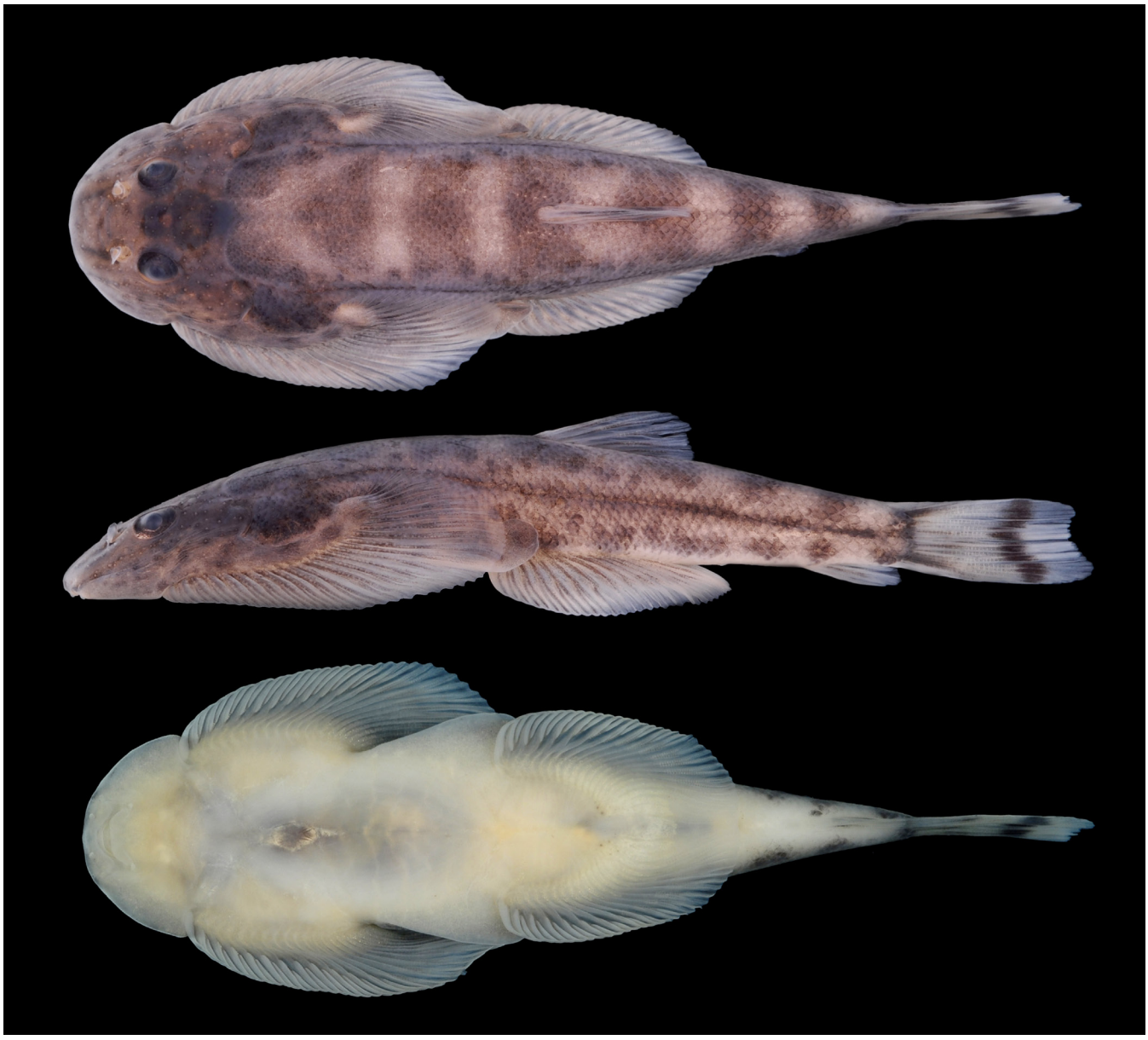

Fig. 10. *Hypergastromyzon abditus*, ZRC 61397, 38.0 mm SL, female; composite of dorsal, lateral, and ventral views.

anterior rays dorsal surface with tubercles, evenly distributed along fin ray, roughly half of ray length. Supra-pelvic flap present, bi-lobed, covering up to base of pelvic-fin ray 6. Anal fin small and triangular, adpressed extending past caudal-fin base. Caudal fin truncate. Dorsal fin small, triangular; origin posterior to pelvic-fin origin. Largest examined specimen 40.3 mm SL (ZRC 61400).

Total vertebral count: 31–32 (mode 31, n = 8).

Colouration in life. See Fig. 9. Head light brown with many dark brown blotches. Pupil of eye with gold ring. Opercle with iridescent gold. Dorsum of body light brown or yellowish-brown, with many scattered darker brown bars and blotches. Dorsum with up to eight dark brown saddle-like bars edged with black, extending to mid-body, maybe extended downwards but not to venter. Middle of body with clear patternless border dorsal and ventral to lateral line, lateral line black. Venter cream. Dorsal fin with one faint black bar, interradial membrane hyaline. Caudal-fin base black, one distinct thick black bar, at median of fin, border clear, interradial membranes hyaline. Anal fin with one black bar, interradial membrane hyaline. Both pectoral and pelvic fins anterior ⅔ dark brown with yellowish-brown margin. Pectoral-fin base light brown with irregular dark brown blotches. Supra-pelvic flap with three black blotches, first at anterior portion, second at middle and third at posterior margin.

Colouration in preservative. See Figs. 7, 8, 10. Colouration as above, except bright colours are absent. Lateral line dark brown.

Sexual characters. Genital papillae indistinguishable between sexes. Males with enlarged tubercles on pectoral- and pelvic-fin rays, tubercles along whole fin ray, largest

Fig. 11. *Hypergastromyzon sambas*, ZRC 61381, ca. 30 mm SL, male (?); live colouration; composite of dorsal, lateral, and ventral views.

tubercles nearest to body, decreasing in size towards fin margin. Large male (ZRC 61400, 40.3 mm SL) with tubercles on venter of caudal peduncle.

Distribution. *Hypergastromyzon abditus* appears to be endemic to the upper Katingan basin, which drains southeasterly from the Schwaner Range (Fig. 6). The current known distribution of *H. abditus* is directly adjacent to that of *H. humilis*, which is northwards in the Melawi sub-basin.

Field notes. See Tan (2009) for a list of syntopic species. From the locality of the type series above a small cascade, only the following syntopic fish species were observed: Cyprinidae—*Paracrossochilus acerus* and *Tor* sp.; and Gastromyzontidae—*Gastromyzon* cf. *psiloetron*. Downstream of the cascade, the following fish species were observed: Cyprinidae—*Barbodes sealei*; Balitoridae—*Pseudohomaloptera batek*; and Channidae—*Channa limbata*.

Etymology. From the Latin *abditus*, meaning hidden, concealed. This is in reference to its cryptic colouration and ability to blend into its environs. Used as a noun in apposition.

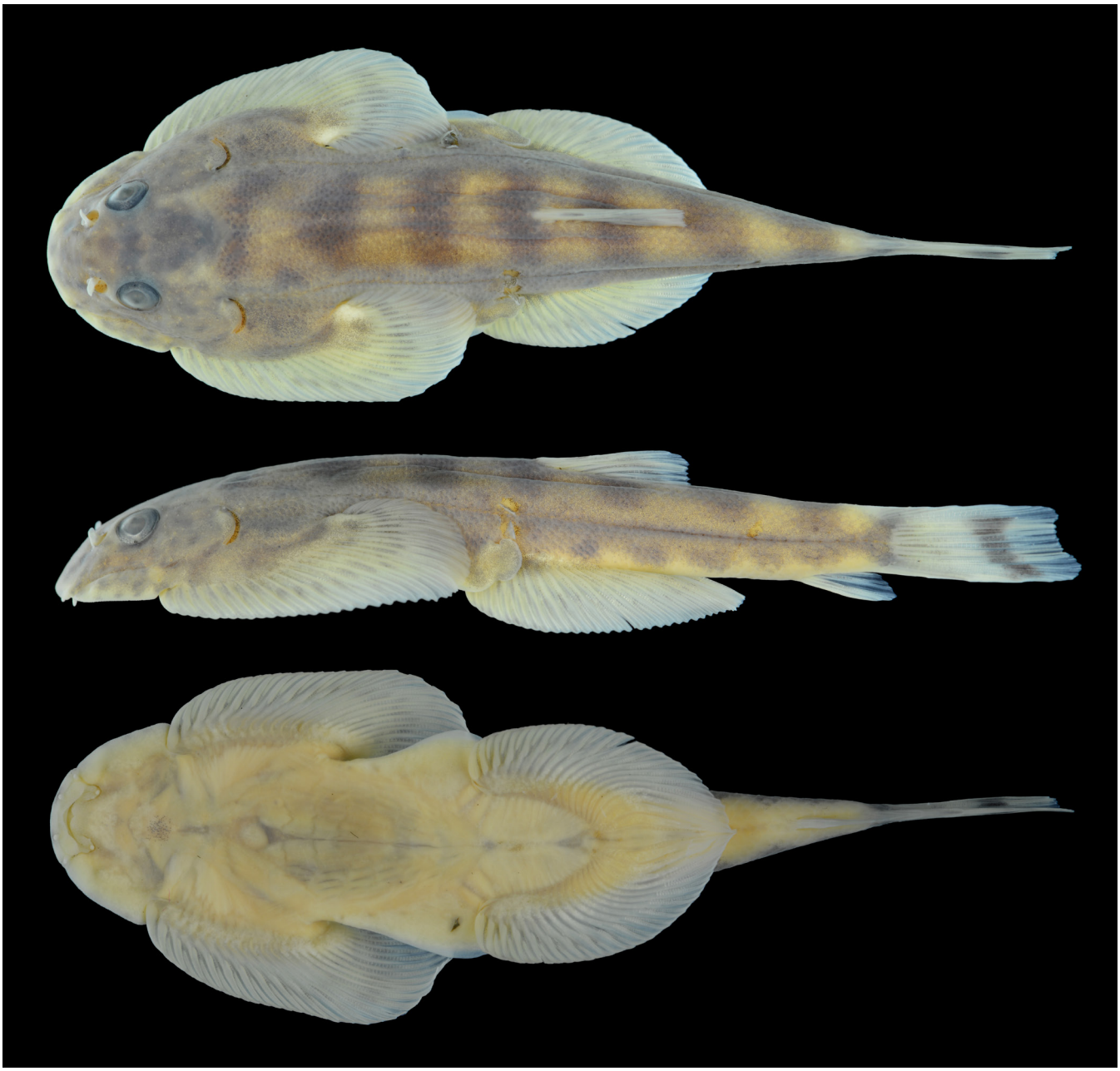

Fig. 12. *Hypergastromyzon sambas*, MZB 17235, 32.4 mm SL, holotype, female (?); composite of dorsal, lateral, and ventral views.

***Hypergastromyzon sambas*, new species**
(Figs. 5, 11–13)

Material examined. Holotype: MZB17235, 1 ex., 32.4 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 24 August 2011.

Paratypes: MZB17236, 5 ex., ZRC 61380, 48 ex., 23.6–32.4 mm SL; same locality data as holotype. — ZRC 61383, 18 ex., 22.6–30.8 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 9 February 2007. — ZRC 61384, 16 ex., 23.1–33.9 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 18 November 2008. — CMK 28828, 7 ex., ZRC 61390, 10 ex., 21.6–33.1 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 17 October 2008. — ZRC 61381, 7 ex., 24.5–32.2 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 8 September 2008.

Other material: ZRC 61382, 14 ex., 24.6–30.8 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 26 March 2010. — ZRC 61386, 3 ex., 23.1–27.5 mm SL; Borneo: Kalimantan Barat: Sambas basin, Bengkayang area; aquarium trade; don. Sunbeam Aquarium, 28 October 2008.

Diagnosis. *Hypergastromyzon sambas* can be distinguished from its congeners in having the unique combination of characters: lateral scales 58–78 [mean 71]; least slender caudal-peduncle depth (6.2–8.0% [mean 7.1] SL, vs. 5.2–6.8 [mean 6.3] in *H. humilis*, and 5.8–7.4 [mean 6.6] in *H.*

Fig. 13. *Hypergastromyzon sambas*. Top and middle: ZRC 61383, 28.0 mm SL, 31.6 mm SL; lateral views showing numerous tiny black spots. Bottom: ZRC 61381, 31.0 mm SL; ventral view of female showing ripe ova (estimated at 2 mm diameter).

abditus); shortest caudal-peduncle length (3.2–6.4% [mean 4.8] SL, vs. 6.2–8.1 [mean 7.0] in *H. humilis*, and 4.3–7.4 [mean 5.9] in *H. abditus*); shorter dorsal-fin base length than *H. humilis* (10.4–13.6% [mean 12.1] SL, vs. 12.0–15.2 [mean 13.7] in *H. humilis*); shorter pectoral-fin length than *H. humilis* (36.7–42.4% [mean 39.1] SL, vs. 40.3–42.5 [mean 41.2] in *H. humilis*); smaller eye diameter than *H. humilis* (3.4–5.6% [mean 4.6] SL, vs. 4.8–5.9 [mean 5.4] in *H. humilis*); lower lip in ventral view with a median notch (vs. truncate of *H. abditus* and gentle downturned curve of *H. humilis*).

Description. See Figs. 11–13 for general appearance, and Table 1 for meristics and morphometric data.

Body depressed, widest and deepest at posterior edge of pectoral-fin base, most narrow at caudal peduncle. Lateral line distinct and complete, running along median of body to caudal-fin base. Head depressed, rounded in dorsal profile, inferior mouth. Mouth simple, a gentle downturned curve, mouth width about ⅓ of head width, two pairs of distinct but short rostral barbels, one pair of relatively longer maxillary barbels, margin of both upper and lower jaws entire; shallow

pocket on both sides of mouth, lower lip with notch at median, without tiny raised bumps, continuous to throat without discrete structures. Naris large, ca. ⅓ eye diameter, anterior to eye. Eye situated dorsally, posterior edge of eye located above pectoral-fin origin, eye diameter less than opercle opening. Opercle opening lunate, located above pectoral-fin rays 6–7. Tubercles present and evenly distributed over head and anterior-dorsal part of body and extending to supra-pectoral region. Pectoral fins enlarged, forming a fan-like shape, total fin-ray count 24–25, posterior edge not overlapping with pelvic-fin origin. Pelvic fins enlarged and completely fused at the posterior edge, forming a U-shape, total fin-ray count 17–19 on each half. Belly naked. Anal pore situated nearer to pelvic-fin base than to anal-fin origin, not visible from ventral view (blocked by pelvic fins). Both pectoral- and pelvic-fin anterior rays dorsal surface with tubercles, evenly distributed along fin ray, roughly half of ray length. Supra-pelvic flap present, weakly tri-lobed, covering up to base of pelvic-fin ray 6. Anal fin small and triangular, adpressed extending past caudal-fin base. Caudal fin truncate. Dorsal fin small, triangular; origin posterior to pelvic-fin origin. Largest examined specimen 33.9 mm SL (ZRC 61384).

Total vertebral count: 30–31 (mode 30, n = 20).

Colouration in life. See Figs. 11, 13. Head very light brown with many dark brown blotches. Pupil of eye with gold ring. Opercle with iridescent gold. Dorsum of body light brown or yellowish-brown, with many scattered darker brown bars and blotches. Dorsum with up to eight dark brown thin bars, extending to mid-body. Middle of body with dark brown indistinct reticulated pattern, partly extending below lateral line, lateral line cream. Venter cream. Dorsal fin with one brown bar, interradial membrane hyaline. Caudal-fin base black, two distinct thick dark brown bars, at anterior half and median of fin, margin clear, interradial membranes hyaline. Anal fin with one brown bar, interradial membrane hyaline. Both pectoral and pelvic fins very light brown with one faint brown whorl. Pectoral-fin base with dark brown blotches. Supra-pelvic flap with faint dark brown blotches.

Some specimens covered with tiny black dots all over body and head (see Fig. 13).

Colouration in preservative. See Fig. 12. Colouration as above, except bright colours are absent. Lateral line dark brown to black.

Sexual characters. Genital papillae indistinguishable between sexes. Males with enlarged tubercles on pectoral- and pelvic-fin rays, tubercles along proximal ⅔ to ¾ of fin ray, largest tubercles nearest to body, decreasing in size towards fin margin. Gravid females with ripe ova visible through belly (see Fig. 13); ovum estimated to be around 2 mm in diameter.

Distribution. *Hypergastromyzon sambas* appears to be endemic to the upper Sambas basin, which is a short coastal drainage flowing easterly from the Pueh Range into the South China Sea (Fig. 6).

Field notes. *Hypergastromyzon sambas* was encountered as a contaminant in shipments of *Gastromyzon* imported from Indonesia from 2006 to 2011. From trusted sources, these fish were obtained from the upper Sambas drainage system. The main target for the trade is *Gastromyzon*, and this consists of *G. stellatus*, *G. ctenocephalus*, *G.* cf. *viriosus*, and occasionally *G. ocellatus*.

Etymology. Named for the Sambas River basin, where the fish inhabits in the upstream tributaries. Used as a noun in apposition.

REMARKS

Specimens of *Hypergastromyzon* have always been uncommon in collections or rarely reported upon. Part of that stems from inadequate surveys in headwater streams, in extremely fast-flowing habitats, and possibly mis-identification in the field as juveniles due to their smaller size. The increase in fresh collections stemmed from access to previously poorly surveyed habitats and use of appropriate collecting tools (e.g., electro-fishing).

Engkaria, new genus

Diagnosis. A gastromyzontine loach with head and body relatively wide and depressed (body depth at dorsal-fin origin 14.1–16.2% SL, body depth 11.2–13.1% SL, caudal-peduncle depth 7.3–8.5% SL); pectoral and pelvic fins greatly enlarged (pectoral-fin rays 21–25, pelvic-fin rays 19–23); pectoral-fin origin below posterior margin of eye; pelvic fins not completely fused, posterior third not fused; mouth small, about half of head width, with horny jaw sheaths strongly curved towards vent; four pairs of very short barbels, two rostral and two maxillary; rostral cap fused with upper jaw except around base of rostral barbels; lower lip with medial groove well developed posterolaterally but interrupted anteromedially; snout rounded in dorsal view, strongly acuminate from lateral view; gill opening angular and large, above middle of pectoral-fin base to anterior of pectoral-fin origin; subopercular groove absent; base of first pectoral-fin ray separated from head by a deep groove parallel to anterior edge of fin ray on ventral side of head and continuous dorsally to gill opening, dorsal surface of pectoral-fin base without scales; supra-pelvic flap originating immediately behind pectoral-fin base and continuing as a free flap above anterior third of pelvic-fin base; abdomen without scales except for area where the pelvic fins are not fused; pored lateral scale rows 50–75; very short anal-fin base (3.6–6.6% SL); first anal-fin pterygiophore bifurcated; total vertebral count 27–28. Mature male with densely packed tubercles on anterior 5–6 pectoral-fin rays, and many tubercle ridges on opercle submargin. For *Engkaria*, the opercular tubercles appear as ridges of tubercles along the opercle submargin (Fig. 19), and some ridges form a continuous line of up to 30 tubercles, a character unique to this genus.

Engkaria eubranchus can be differentiated from other Bornean gastromyzontines in having the unique combination of characters: small mouth width (around ⅓ to ¼ of head width), shared with *Hypergastromyzon* and *Parhomaloptera*; other genera *Gastromyzon*, *Glaniopsis*, *Katibasia*, *Neogastromyzon*, and *Protomyzon* having a wider mouth (½ to ¾ head width). Incomplete fusion of pelvic fins with posterior portion free, vs. complete fusion in *Gastromyzon*, *Hypergastromyzon*, and *Neogastromyzon*; separate pelvic fins in *Glaniopsis*, *Katibasia*, *Parhomaloptera*, and *Protomyzon*. Greatly enlarged pectoral and pelvic fins which overlap to form a suction structure with the belly, shared with *Gastromyzon*, *Hypergastromyzon*, and *Neogastromyzon*. *Engkaria* can be differentiated from *Hypergastromyzon* by the following characters: large angular opercular opening with anterior edge at pectoral-fin origin, vs. small lunate opening above pectoral-fin ray 6–7; fewer vertebrae (27–28, vs. 30–32); longer rostral barbels than maxillary barbels (vs. short rostral barbels and more elongate maxillary barbels); more pectoral-fin rays (19–23, vs. 17–19); more transverse scales (10.1.10–11, vs. 7–9.1.7–9); less vertebrae (27–28, vs. 30–32); more thickset body (body depth at anus 11.2–13.1% SL, vs. 8.4–10.6; caudal-peduncle depth 7.8–8.5% SL, vs. 5.2–8.0); smaller pectoral-fin length (33.4–38.3% SL, vs. 36.7–42.5); smaller eye (2.9–4.4% SL, vs. 3.4–5.9).

This genus is restricted to western Borneo, currently known only from the upstream area (Engkari branch) of Lupar River basin in Central Sarawak. It inhabits fast-flowing hill streams with well-oxygenated water running over rock and gravel base. As currently recognised, the genus is monotypic.

Etymology. Named for the Engkari River (Lupar River basin), a riparian stream system within the Lanjak Entimau Wildlife Sanctuary, which drains into the Batang Ai reservoir; and currently known only from Engkari River. Latinised and gender feminine.

Type species. *Hypergastromyzon eubranchus* Roberts, 1991.

Engkaria eubranchus (Roberts, 1991)

(Figs. 14–20)

Gastromyzontinae sp. nov. – Cramphorn, 1982: 26, 38 (list).
Hypergastromyzon eubranchus Roberts, 1991: 334, fig. 1; Kottelat et al., 1993: 75, pl. 25; Kottelat & Lim, 1995: 236; Doi, 1997: 19 (list); Tan, 2006: 203, figs. 129, 130; Kottelat, 2013: 194.

Material examined. Holotype: BMNH 1984.11.15:1, 30.7 mm SL; Sarawak: Batang Ai, Lupar basin, near Wang Mepai; J. Cramphorn, 1982.

Paratypes: BMNH 1984.11.15:2, 35.6 mm SL; Sarawak: Batang Ai, Lupar basin, below confluence with Batang Enkori; J. Cramphorn, 1982. — BMNH 1984.11.15:3, 16.8 mm SL; Sarawak: Batang Ai, Lupar basin, Sungei Delek, Wong Nanga Jeliak; J. Cramphorn, 2–5 July 1982. — CAS 55889, 1 ex., 30.9 mm SL; Sarawak: Batang Ai, Lupar basin, confluence of Sungai Delok; J. Cramphorn, 1982.

Other material: ZRC 37806, 3 ex., 36.0–41.0 mm SL; CMK 10833, 2 ex., 32.1–35.1 mm SL; Sarawak: Batang Lupar basin, Sungai Engkari; R. Stuebing, 14 August 1993. — ZRC 37802, 1 ex., 31.9 mm SL; Sarawak: Batang Lupar basin, Sungai Engkari; R. Stuebing, 7 August 1993. — CMK 10846, 1 ex., 37.4 mm SL; Sarawak: Sarikei district, Sungai Sekarang; R. Stuebing, 8 October 1993. — ZRC 60479, 5 ex., 37.9–39.3 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Engkari mainstream, adjacent to Nanga Segerak Field Station, 01°24.813′N, 112°00.253′E, 318 m asl; H. H. Tan et al., 20 September 2018. — ZRC 60390, 1 ex., 36.9 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Segerak, feeder stream to Sungei Engkari, 01°24.813′N, 112°00.253′E, 318 m asl; H. H. Tan et al., 21 September 2018. — ZRC 60401, 8 ex., 30.6–35.8 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Kaup, tributary of Sungei Engkari, 01°24.084′N, 111°59.494′E, 246 m asl; H. H. Tan et al., 26 September 2018. — ZRC 60468, 31 ex., 31.0–41.1 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Engkari mainstream, ca. 500 m–1 km upstream of Nanga Segerak Field Station, just past Sungei Tapayang (source of freshwater for field station), 01°24.875′N, 112°00.379′E, 289 m asl; H. H. Tan et al., 22 September 2018. — ZRC 60418, 20 ex., 29.7–38.8 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Engkari mainstream, ca. 500 m–1 km downstream of Nanga Segerak Field Station; 01°24.881′N, 111°59.960′E, 388 m asl (start), 01°24.845′N, 112°00.060′E, 305 m asl (lunch stop); H. H. Tan et al., 23 September 2018. — ZRC 60354, 17 ex., 29.5–37.1 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Segerak, feeder stream to Sungei Engkari; ca. 500 m upstream of THH18-31 (01°24.813′N, 112°00.253′E, 318 m asl); H. H. Tan et al., 24 September 2018. — ZRC 60337, 11 ex., 31.2–38.0 mm SL; Sarawak: Sri Aman Div: Lupar basin; Sungei Engkari mainstream, ca. 200–400 m downstream of Nanga Segerak Field Station, before first series of cascades; including a small feeder stream; H. H. Tan et al., 25 September 2018.

Diagnosis. See generic diagnosis.

Description. See Figs. 14–20 for general appearance, and Table 1 for meristics and morphometric data.

Body depressed, widest and deepest at area anterior to dorsal-fin origin, most narrow at caudal peduncle. Lateral line distinct and complete, running along median of body to caudal-fin base. Head depressed, bluntly wedge-shaped in dorsal profile, inferior mouth. Mouth simple, a gentle downturned curve, mouth width about ¼ of head width, two pairs of distinct slender rostral barbels, 1 pair of short maxillary barbels, margin of both upper and lower jaws entire; relatively deep pocket on both sides of mouth, lower lip with cleft at median, continuous to throat without discrete structures. Naris large, ca. ⅓ eye diameter, anterior to eye. Eye situated dorsally, anterior to pectoral-fin origin, eye diameter less than half of opercle opening. Opercle opening angular, originating above pectoral-fin ray 5. Tubercles present and evenly distributed over head and anterior-dorsal part of body and extending to supra-pectoral region. Pectoral fins enlarged, forming a fan-like shape, total fin-ray count

Fig. 14. *Engkaria eubranchus*, ZRC 60479, ca. 38 mm SL, male; live colouration; composite of dorsal, lateral, and ventral views.

Fig. 15. *Engkaria eubranchus*, ZRC 60479, ca. 40 mm SL, female; live colouration; composite of dorsal, lateral, and ventral views.

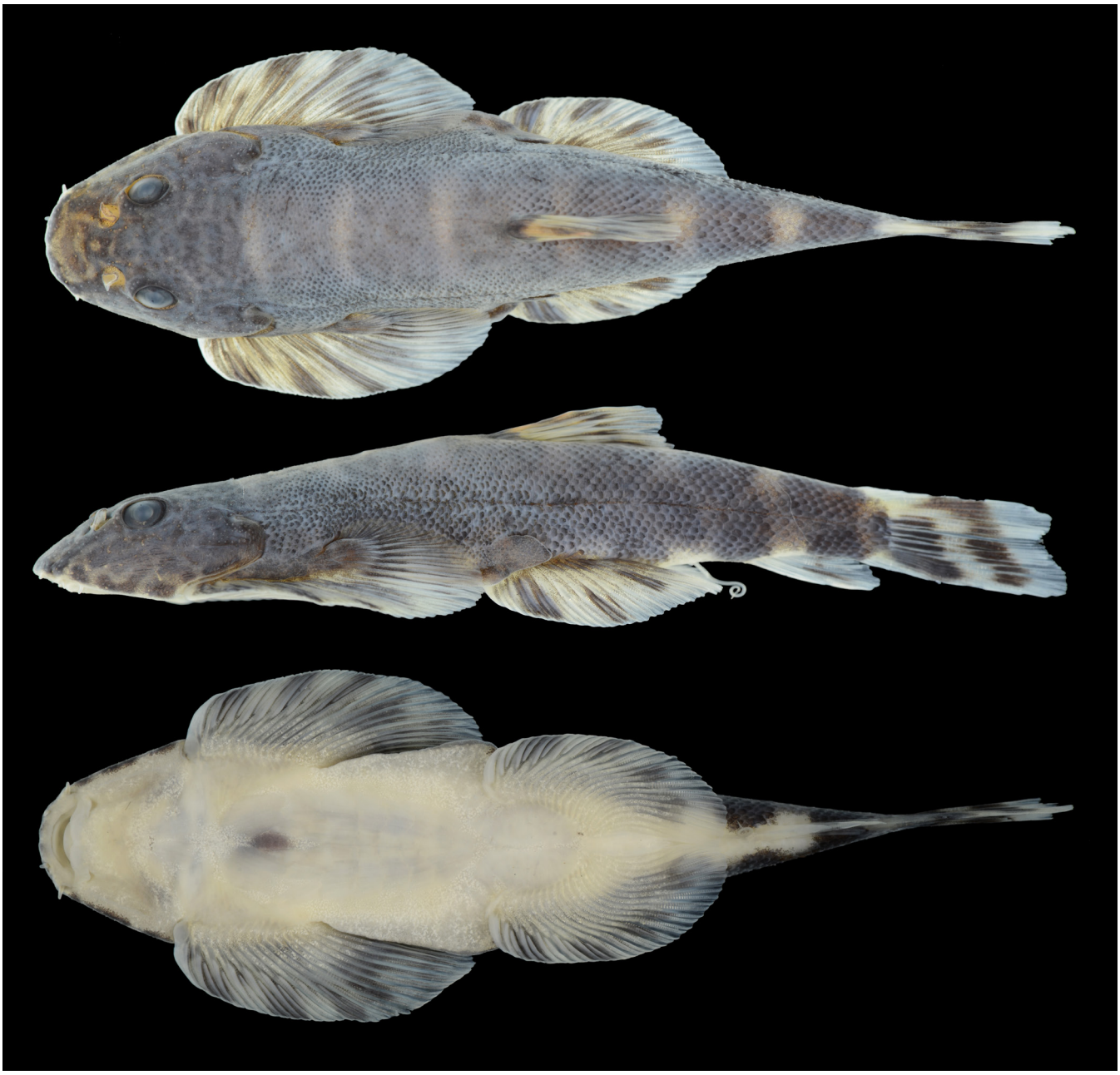

Fig. 16. *Engkaria eubranchus*, ZRC 60479, 41.1 mm SL, male; composite of dorsal, lateral, and ventral views.

21–25, posterior edge just overlapping with pelvic-fin origin. Pelvic fins enlarged with incomplete fusion leaving posterior ½–⅔ margin free, forming a U-shape, total fin-ray count 17–19 on each half. Belly anterior portion naked, scaled at area bordered where pelvic fin is fused to body. Anal pore situated nearer to pelvic-fin base than to anal-fin origin, not visible from ventral view (blocked by pelvic fins). Pectoral fin with densely packed tiny tubercles on the anterior 5th to 6th rays; rest of tubercles are larger and single file along posterior rays. Pelvic fin with anterior ⅔ covered with larger tubercles along proximal part of rays. Supra-pelvic flap present, bi-lobed, covering up to base of pelvic-fin ray 8. Anal fin small and triangular, adpressed extending past caudal-fin base. Caudal fin broadly emarginate. Dorsal fin small, triangular; origin posterior to pelvic-fin origin. Largest examined specimen 41.1 mm SL (ZRC 60468).

Total vertebral count: 27–28 (mode 28, n = 20).

Colouration in life. See Figs. 14, 15. Head light brown with many dark brown blotches and reticulated pattern. Pupil of eye with gold ring. Dorsum of body light brown with 6–7 large saddle-like dark brown bars or rounded blotches, extending to mid-body. Middle of body with many gold tiny spots, lateral line with gold dots. Lower half of body with many small dark brown blotches. Venter cream, shimmery gold over belly area. Caudal peduncle usually with two dark brown blotches continuous to venter. Dorsal fin with two black bars, interradial membrane hyaline. Caudal-fin base median black with top and bottom white wedges, two distinct thick dark brown bars with red edges, at anterior half and median of fin, margin clear, interradial membranes hyaline. Anal fin with one brown bar near distal edge, interradial membrane hyaline. Both pectoral and pelvic fins light brown with 3–4

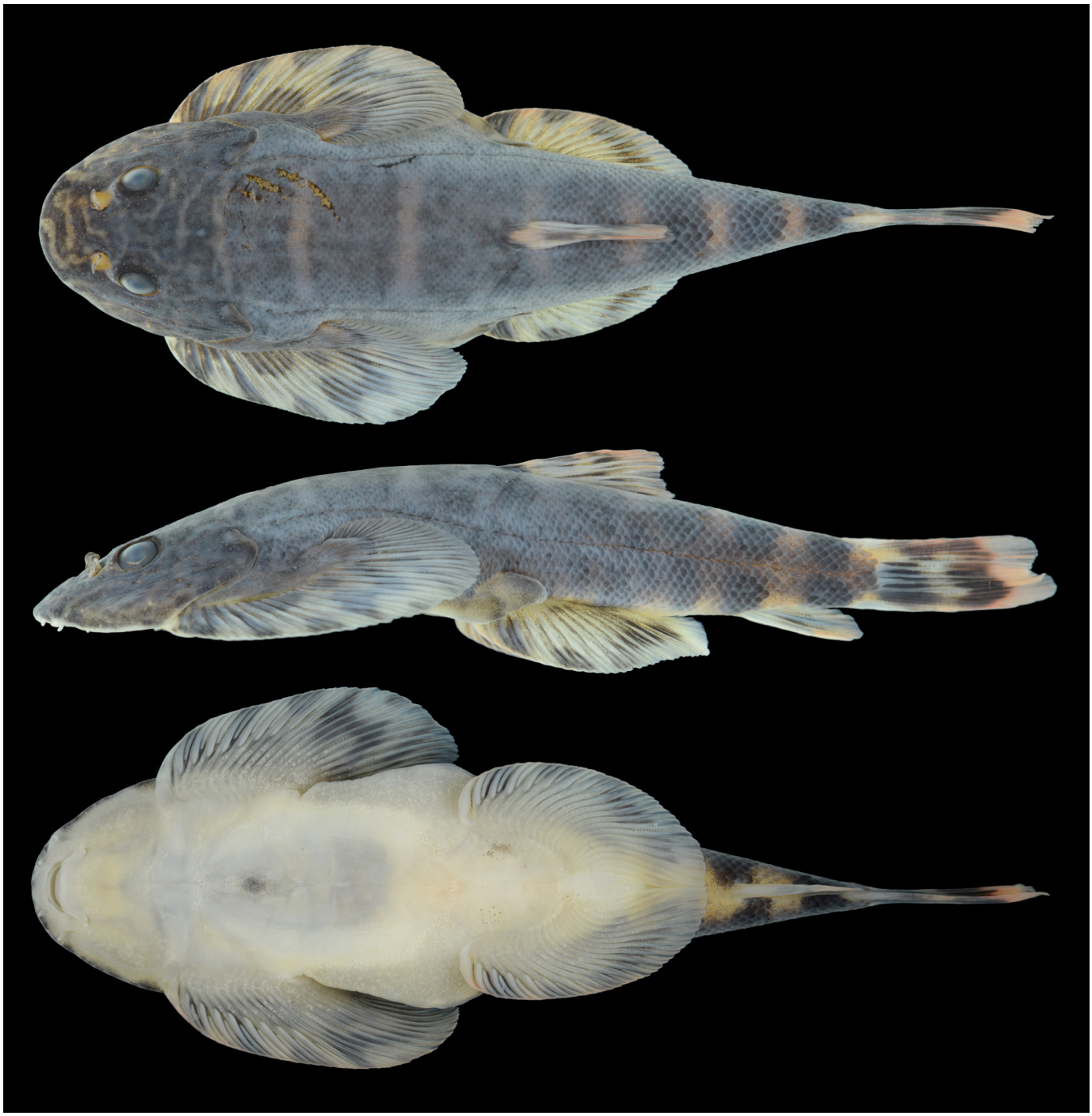

Fig. 17. *Engkaria eubranchus*, ZRC 60468, 40.1 mm SL, female; composite of dorsal, lateral, and ventral views. Note abrasion marks on dorsal surface due to artefact from collection.

large dark brown blotches, evenly spaced. Pectoral-fin base light brown with corresponding dark brown blotches to those on fin. Supra-pelvic flap with two dark brown blotches, one at anterior and other at distal half.

Colouration in preservative. See Figs. 16, 20. Colouration as above, except bright colours are absent. Well-demarcated dark brown blotches faded and muted to grey.

Roberts (1991) mentioned the juvenile pattern being different from that of adults (based on a 16.8 mm SL specimen, BMNH 1984.11.15:3); however, he did not provide any illustrations. The Natural History Museum (London) has provided an online resource for its zoological collection, and the data resource (including image and radiograph) of the juvenile specimen is available (https://data.nhm.ac.uk/object/efbf1c6d-d51e-4903-8c21-70dd1fbc4038/1620259200000).

The juvenile lacks the defined blotches on the bodies of adults and exhibits a dark brown longitudinal swath from behind the eye to caudal-fin base; with lighter brown dorsum and cream venter. The only fin pattern discernible is two distinct dark brown bars on the caudal fin, with a hyaline margin. The differences between juvenile and adult colour patterns in members of *Gastromyzon* and *Neogastromyzon* have been covered in detail by Tan (2006). Juveniles of

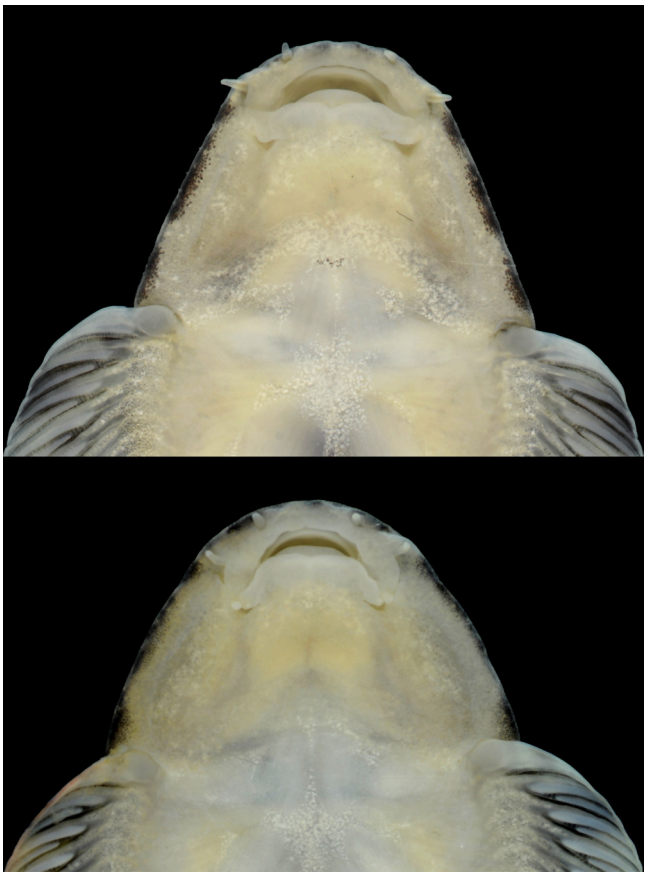

Fig. 18. Oral views of *Engkaria eubranchus*. Top: ZRC 60479, 41.1 mm SL male; bottom: ZRC 60468, 40.1 mm SL female.

Gastromyzon in general have a more reticulated pattern that matures into a more uniformly coloured pattern. Juveniles of *Neogastromyzon* have a more distinct barred pattern that matures into a more reticulated pattern.

The difference in juvenile colouration pattern can be perhaps used as part of the genus diagnosis; however, lacking fresh material or a larger series of juvenile specimens, this is left for future studies/surveys to confirm.

Sexual characters. Genital papillae indistinguishable between sexes. Males with densely packed minute tubercles on pectoral fin, tubercles along proximal ⅔ to ¾ of fin ray (Fig. 18). Larger tubercles on rest of pectoral and pelvic fins. Males also with tubercles and ridges of tubercles on sub-orbital and opercle respectively (Fig. 19). The head shape of male and female is slightly different as evident in Fig. 17. Male with a more pointed snout and female with a more rounded snout. Mature females also appear more robust (Figs. 15, 17).

Distribution. *Engkaria eubranchus* appears to be endemic to the Engkari River, which drains into Batang Ai reservoir, which is part of the Lupar basin (Fig. 6).

Field notes. Syntopic fishes from the main stream of Sungei Engkari include the following: Cyprinidae—*Barbodes banksi*, *Barbonymus collingwoodii*, *Hampala bimaculata*, *Lobocheilos* cf. *erinaceus*, *L. ovalis*, *Osteochilus sarawakensis*, *O. waandersii*, *Tor tambra*, *T. tambroides*; Danionidae—*Rasbora fasciata*; Cobitidae—*Pangio piperata*; Nemacheilidae—*Nemacheilus kapuasensis*; Balitoridae—*Homalopteroides weberi*; Gastromyzontidae—*Gastromyzon megalepis*, *G. stellatus*, *Neogastromyzon chini*, *Parhomaloptera microstoma*; Bagridae—*Hemibagrus bongan*, *H. fortis*, *Leiocassis poecilopterus*; Sisoridae—*Glyptothorax major*; Clariidae—*Clarias planiceps*; Mastacembelidae—*Macrognathus circumcinctus*, *Mastacembelus unicolor*; and Channidae—*Channa lucius*.

In Sungei Engkari, *Engkaria eubranchus* was obtained only in the main stream, exclusively from the riffle zone. It was absent from the slower flowing and smaller feeder streams. During the visit in September 2018, no juveniles were obtained, and the total size range of individuals collected was 29.5–41.1 mm SL. Mature males could be discerned by the presence of ridged tubercles on the opercle, but this was not readily observed in the field. As the rocky substratum was mostly dark grey or black, fishes were darkly pigmented, appearing almost black when freshly obtained.

When Cramphorn (1982) conducted her fish survey, it was from May to August 1982, from the lower Batang Ai to Sungei Ekori [= Engkari]. From her report, only three sites yielded *Engkaria* (identified as Gastromyzontinae sp. nov.)—A2, A3, and A4. She did note that certain sites had thousands of *Gastromyzon* present. Her local Iban helpers helped to catch the fish, primarily using cast nets (which is not the most efficient way to catch smaller benthic fishes).

DISCUSSION

The fusion of pelvic fins for *Engkaria*, *Gastromyzon*, *Hypergastromyzon*, and *Neogastromyzon* appears to be similar. The skin surrounding the dorsal surface of the last 5–6 pelvic-fin rays is continuous with the skin of the venter. In *Gastromyzon*, *Hypergastromyzon*, and *Neogastromyzon*, the distalmost part of the inner ray of the left and right pelvic fins are in direct contact along the ventral midline because the interradial membrane is greatly reduced between these rays. In *Engkaria*, the distal part of the outermost ray of the left and right pelvic fin ray are connected across the ventral midline by skin, yet the distalmost tip remains free, and the ray tips of the left and right side may even overlap each other (see Fig. 20). The region where the skin surrounding the pelvic-fin rays attaches to the skin of the venter appears to be larger for *Engkaria*, and is scaled, unlike in *Gastromyzon* (except *G. psiloetron* [see Tan, 2006]), *Hypergastromyzon*, and *Neogastromyzon*, in which it is naked.

The genus *Engkaria* shares with *Gastromyzon* (represented by *G. ctenocephalus*; Fig. 21) and *Neogastromyzon* (represented by *N. chini*; Fig. 22) similar characters relating to sexual dimorphism. The mature males possess heavy tuberculation on the sub-orbital area, operculum, and base of pectoral-fin rays (Figs. 18, 19); whereas *Hypergastromyzon* males only have more numerous tubercles on the opercle, base, and dorsal surface of pectoral-fin rays (Figs. 2, 8). For *Engkaria*,

Fig. 19. *Engkaria eubranchus*, ZRC 46068, 39.0 mm SL, male. Top: lateral view of head region showing tuberculation pattern on opercle; bottom: close-up of dorsal view of left pectoral fin showing tuberculation pattern (not to scale).

the opercular tubercles appear as ridges of tubercles along the opercle submargin (Fig. 19), and some ridges form a continuous line of up to 30 tubercles, a character unique to this genus.

The tuberculation on the dorsal surface of the pectoral-fin rays is worth highlighting. Mature males of *Engkaria*, *Gastromyzon*, and *Neogastromyzon* (Figs. 18, 21, 22) have densely packed tiny tubercles on the anterior 5–6 rays, making visual counts of the tubercles extremely difficult; the remaining tubercles are larger and arranged in single file along more posterior rays. In contrast, for *Hypergastromyzon*, tubercles are enlarged and in a single row along the fin rays.

In *Engkaria*, the first pterygiophore of the anal fin is bifurcated at the proximal tip (Figs. 23, 24), a condition similar to that found in *Gastromyzon* and *Neogastromyzon*, whereas in *Hypergastromyzon*, this pterygiophore is not bifurcated and has the usual straight tapering shape (Figs. 23, 24).

No molecular analysis has been conducted yet on *Hypergastromyzon* and *Engkaria*, but once available is expected to show that they are not so closely related.

Fig. 20. *Engkaria eubranchus*, ZRC 60468, 36.8 mm SL; ventral view of fused pelvic fins, showing posterior half of last rays free; with view of anal pore.

Comparative material examined (See Tan (2006) for a detailed listing).

Gastromyzon ctenocephalus — ZRC 47031, 88 ex., 22.5–39.8 mm SL; Sarawak: Penrissen area, hill stream near Kampung Benut.

Neogastromyzon chini — ZRC 59951, 61 ex., 30.4–45.7 mm SL; Sarawak: Song District: Rejang River basin: Katibas River: Ulu Katibas, Sungei Bloh branch, Sungei Joh, ca. 25 min. upriver from confluence of Sungei Bloh and Sungei Katibas (01°37.635′N, 112°17.991′E, 112 m asl).

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Fig. 21. *Gastromyzon ctenocephalus*, ZRC 47031, 39.8 mm SL, male. Top: close-up of dorsal half of body showing tuberculation on left pectoral fin and dorsum; bottom: close-up of lateral half of body showing tuberculation pattern on opercle and head.

Fig. 22. *Neogastromyzon chini*, ZRC 59951, 37.8 mm SL, male. Top: close-up of dorsal half of body showing tuberculation on left pectoral fin and dorsum; bottom: close-up of lateral half of body showing tuberculation pattern on opercle and head.

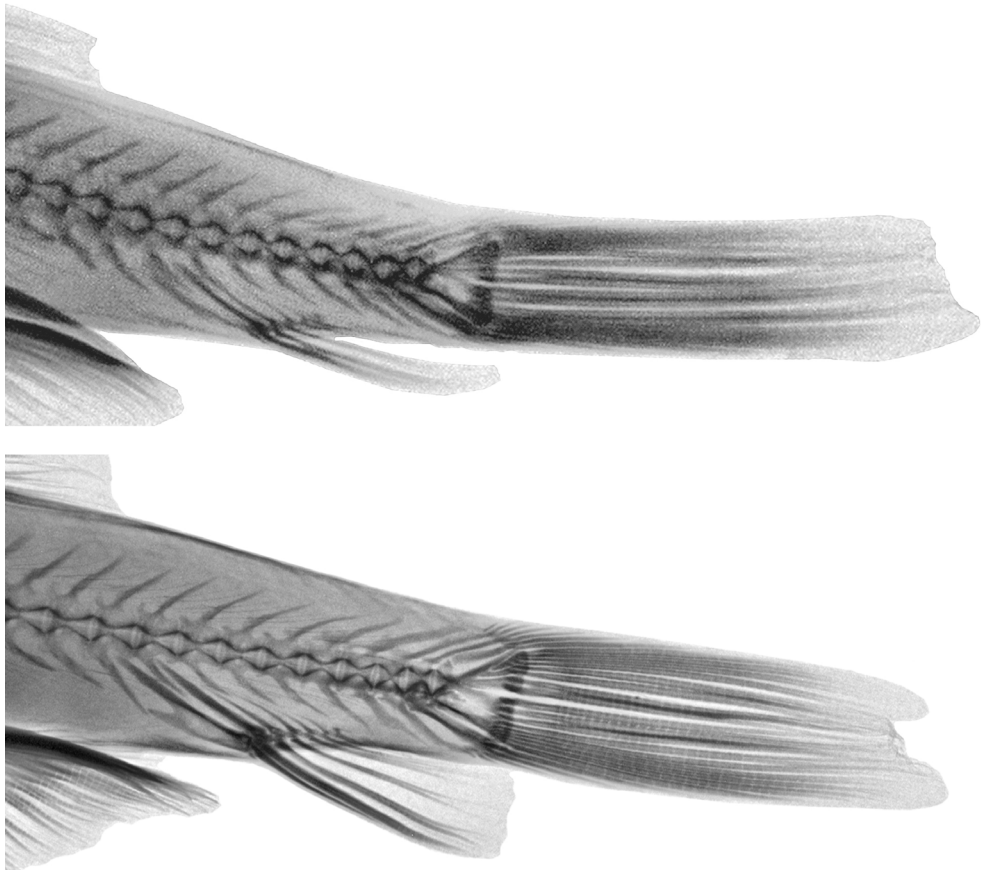

Fig. 23. X-ray images of posterior bodies, showing absence of V-shape pterygiophore of first anal fin ray vs. presence. Top: *Hypergastromyzon humilis*, CMK 10574, 31.5 mm SL; bottom: *Engakaria eubranchus*, ZRC 60468, 38.0 mm SL.

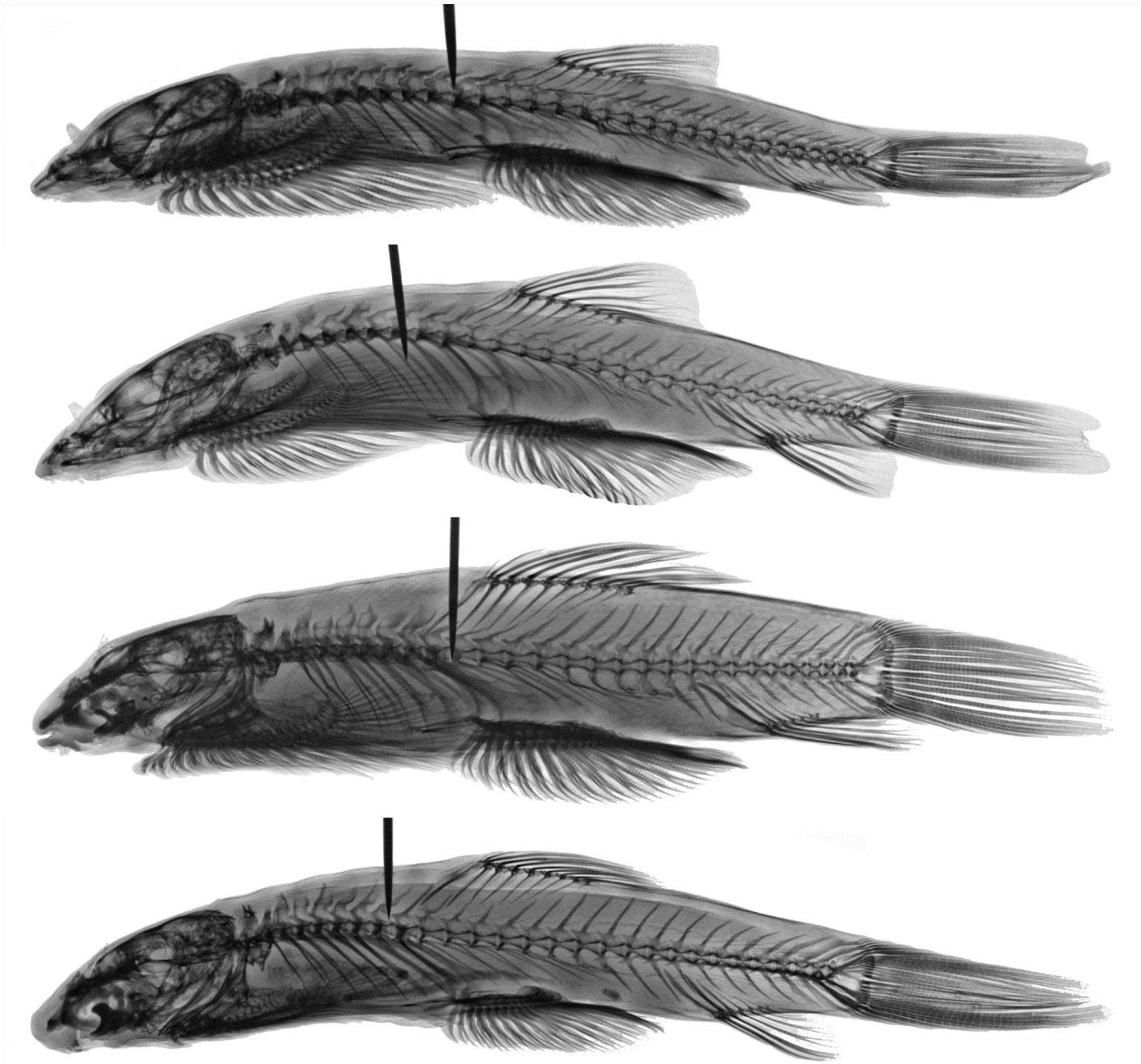

Fig. 24. X-ray images of lateral views showing presence of bifurcated first anal-fin pterygiophore in latter three species (pin used to prop specimen up). Top to bottom: *Hypergastromyzon humilis*, CMK 10574, 31.5 mm SL; *Engkaria eubranchus*, ZRC 60468, 38.0 mm SL; *Gastromyzon ctenocephalus*, ZRC 47031, 39.8 mm SL; and *Neogastromyzon chini*, ZRC 59951, 37.8 mm SL.

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