

## THREE NEW SPECIES OF FRESHWATER HALFBEAKS (TELEOSTEI: ZENARCHOPTERIDAE: *HEMIRHAMPHODON*) FROM BORNEO

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**ABSTRACT.** — Three new species of *Hemirhamphodon* are described from Borneo island. *Hemirhamphodon sesamum*, new species, from lowland basins draining into the Makassar Strait, differs from its congeners in having unique colour markings on its dorsal fin and lower jaw; males with posterior projections on the fourth anal-fin ray, with third, fourth and eighth anal-fin rays branched, and with posterior projections on the fourth anal ray; females with third and fourth anal-fin rays branched. *Hemirhamphodon byssus*, new species, from southern Sarawak differs from the allopatric *H. kuekenthali* in having the anterior dorsal-fin ray extensions reaching to the middle of the caudal fin (vs absence or small extensions on dorsal-fin rays), black pigment on the anterior half of dorsal fin (vs middle part of dorsal fin), males with posterior projections on the fourth anal-fin ray. *Hemirhamphodon kecil*, new species, from the lower Mahakam in East Kalimantan, can be distinguished from its congeners in having few or no markings except for sparse black pigment along sub-margin of the dorsal fin and anterior dorsal margin of the caudal-fin base. It is a small species (up to 41 mm SL). Notes and a figure of the holotype of *H. phaiosoma* are provided, along with colour descriptions of fresh material. An artificial key to *Hemirhamphodon*, inclusive of the new species, is also included.

**KEY WORDS.** — *Hemirhamphodon*, Southeast Asia, biodiversity, taxonomy, allopatry

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### INTRODUCTION

The taxon *Hemirhamphodon* is one of three genera of freshwater halfbeaks in the family Zenarchopteridae that practice internal fertilisation and viviparity (the other two being *Dermogenys* and *Nomorhamphus*) with the anal fin of the males modified into an andropodium (Meisner, 2001; Collette, 2004). *Hemirhamphodon* can be further distinguished from other zenarchopterids in having the following characters: where the pleural ribs start on the 2<sup>nd</sup> vertebra (vs 3<sup>rd</sup>), and presence of anteriorly directed teeth present along the entire lower jaw (Anderson & Collette, 1991).

*Hemirhamphodon tengah* is, however, an exception. This species is oviparous (either a secondary or pleisomorphic trait), its mating behaviour documented by Dorn & Greven (2007) who observed similarities with other zenarchopterids (viz. Kottelat & Lim, 1999). Along with *H. kecil* (new species described herein), *H. tengah* is also unusual in that both male and females are approximately the same size. In all other species of *Hemirhamphodon*, males are up to 50% larger than the females (pers. obs.).

The genus *Hemirhamphodon* was revised by Anderson & Collette (1991), and included descriptions of *H. kapuasensis* and *H. tengah* by Collette, and colour images for *H. chrysopunctatus* (from central Kalimantan), *H. kapuasensis* (from West Kalimantan), and *H. pogonognathus* (from Thailand). In their guide to freshwater fishes of western Indonesia, Kottelat et al. (1993) featured all the *Hemirhamphodon* species, but only *H. chrysopunctatus* is illustrated in live colour. Roberts (1989) provided some biological notes obtained from a large series of *H. pogonognathus* from the Kapuas basin in western Borneo, showing that the main diet of this species consists of terrestrial insects, especially ants. He also collected two additional species, *H. phaiosoma* and *H. kapuasensis* (as *Hemirhamphodon* sp.) from the Kapuas.

The genus *Hemirhamphodon*, along with its congeners *Dermogenys* and *Nomorhamphus*, has been used recently in a study by de Bruyn et al. (2013) to predict evolutionary relationships correlated with paleo-geography in Southeast Asia. The main tools used were genetic data, consisting of two mitochondrial and eight nuclear genes.

In 2011, the first author made a small collection of freshwater fishes in South Kalimantan, from drainages flowing into the Makassar Strait. The ichthyofauna of this area is poorly known, and from this recent collection, a new species of *Hemirhamphodon* was identified. In writing the species description, examination of comparative material led to the discovery of two other distinct and hitherto un-named species from the same genus. These three new taxa are described in the present article.

## MATERIAL AND METHODS

Fish specimens were obtained with push nets, then fixed in formalin and stored in 75% ethanol. All measurements are taken point-to-point from the left side of body (whenever possible) with a pair of dial calipers (0.05 mm) following the methodology of Collette (1974). Standard length is measured from tip of upper jaw to caudal fin base. Scale counts were not included due to the small size, deciduous nature and possible damage to specimens. Vertebral counts were obtained from radiographs taken with a Faxitron LX60 digital system. Material examined is deposited in the Natural History Museum, London (BMNH); Collection of Maurice Kottelat, Cornol, Switzerland (CMK); Research and Development Centre for Biology, The Indonesian Institute of Sciences (MZB); National Museum of Nature and Science, Tsukuba, Japan (NSMT-P); and the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC). Abbreviations used are SL: standard length, TL: total length, HL: head length, BL: body length.

## TAXONOMY

All three new species described herein belong to the *Hemirhamphodon pogonognathus* group (sensu Anderson & Collette, 1991) consisting of *H. pogonognathus* and *H. kuekenthali*, and defined by the following characters: anal fin of male with prominent posterior projection on 4<sup>th</sup> ray, dorsal-fin rays 12–17, absence of prominent red stripe(s) on body (although some populations of *H. pogonognathus* may exhibit an incomplete or faint red stripe on body), vertebrae 37–44. All the other congeners (i.e., *H. phaiosoma*, *H. chrysopunctatus*, *H. kapuasensis*, and *H. tengah*) belong to the *Hemirhamphodon phaiosoma* group, which lack the posterior projection of the fourth anal-fin ray, but all having one or more red/brown/black stripes on their body (sensu Anderson & Collette, 1991).

Recent but yet to be published molecular research on the phylogeny of the genus *Hemirhamphodon* has indicated that the *pogonognathus* and *phaiosoma* groups (sensu Anderson & Collette, 1991) are not monophyletic (N. R. Lovejoy, pers. comm.).

## Artificial key to the genus *Hemirhamphodon* (Zenarchopteridae)

(based on external morphological characters of mature intact specimens)

1. Lower jaw elongated and curved upwards; body with 1 or more prominent stripes (live: bright pink to red, preserved: pink) .2
- 1\*. Lower jaw elongated and straight (sometimes with anterior tip bent downwards); body with distinct stripe (black or brownish), or no pattern (when preserved) ..... 3
2. Pelvic-fin origin posterior to dorsal-fin origin; mature males with 1 to 3 pink stripes on body, mature females with 1 pink stripe; 21 to 25 dorsal-fin rays; found in Biliton island, West and Central Kalimantan (Borneo) .....  
.....*H. phaiosoma* (Bleeker, 1852)
- 2\*. Pelvic-fin origin anterior to dorsal-fin origin; mature males and females with 1 pink stripe on body; 17 to 20 dorsal-fin rays; found in middle to lower Kapuas basin (West Kalimantan) ....  
.....*H. kapuasensis* Collette, in Anderson & Collette, 1991
3. Adult size  $\leq 41$  mm SL, male and female about equal size; found only in Borneo ..... 4
- 3\*. Adult size  $\geq 45$  mm SL; male up to 50% larger than female; found in Sundaland and Sundaic islands ..... 5
4. Body with single black/dark brown stripe; adult size never larger than 36 mm SL; dorsal fin melanophores continuous to base; anal fin without posterior projections; found only in peat swamps in Central Kalimantan (the only oviparous species recorded)....*H. tengah* Collette, in Anderson & Collette, 1991
- 4\*. Body without pattern, non-descript appearance; adult size not larger than 41 mm SL; dorsal fin melanophores not continuous to base, restricted to submargin; anal fin with posterior projection on fourth ray; found only from the lower Mahakam basin (East Kalimantan) .....*H. kecil*, new species
5. Dorsal fin with 2 types of melanophores, with black markings (dots or bars/streaks); body without pattern; found only in Borneo ..... 6
- 5\*. Dorsal fin with 1 type of melanophore, without any markings; body with or without stripe (when preserved); found in Sundaland and Sundaic islands ..... 8
6. Dorsal fin with black bars/streaks on anterior or middle section; adult size up to 70 mm SL; known only from western part of Borneo (Sarawak and Brunei Darussalam)..... 7
- 6\*. Dorsal fin with black spots on anterior section, anterior 6 to 7 rays elongated into free filaments (live: yellow, preserved: hyaline), reaching base of caudal fin; adult size up to 47 mm SL; found only in South Kalimantan (basins draining into the Makassar Straits) ..... *H. sesamum*, new species
7. Dorsal fin with black bars/streaks on anterior section, anterior 6 to 7 rays elongated into free filaments (live: black, preserved: black), reaching middle of caudal fin; found from southern to central Sarawak (South of Rejang basin) .....  
.....*H. byssus*, new species
- 7\*. Dorsal fin with black bars/streaks on middle section, little or no elongation of rays; found from central to northern Sarawak (North of Rejang basin) and Brunei Darussalam .....  
.....*H. kuekenthali* Steindachner, 1901
8. Anal fin of mature males with posterior projection on fourth ray; body without pattern (when preserved; live: sometimes with thin red stripe); lower jaw straight and sometimes with anterior tip bent downwards; found in Peninsular Thailand, Peninsular Malaysia, Sumatra, southern Borneo (West and Central Kalimantan), Natuna, Biliton and Banka islands.....  
.....*H. pogonognathus* (Bleeker, 1853)
- 8\*. Anal fin without posterior projections; body with distinct stripe (preserved: black, live: iridescent blue blotches along black stripe); lower jaw straight; found only in peat swamps in Central Kalimantan (Borneo).....*H. chrysopunctatus* Brembach, 1978

***Hemirhamphodon sesamum*, new species**

(Figs. 1A–D, 2A–C, 3A, B, 4, 5A–D, 6A–B)

**Material examined.** — Holotype – MZB 17209, 36.7 mm SL, male; Indonesia: South Kalimantan: Batulicin basin; stream at Simpang Alok, along road from Batulicin to Mantewe, Desa Gunung Raya (84 m asl); H. Tommy et al., 14 Sep.2011.

Paratypes – MZB 17210, 7 ex., 19.2–44.4 mm SL; same locality as holotype. – ZRC 54009, 37 ex., 18.2–46.4 mm SL; Indonesia: South Kalimantan: Cantung basin; north of Batulicin, Sei Kupang area, amidst limestone hills (24 m asl, pH 8.0); H. Tommy et al., 12 Sep.2011. – ZRC 54010, 10 ex., 13.4–44.6 mm SL; Indonesia: South Kalimantan: Batulicin basin; hill stream at foothills of Gunung Kukusan on northeast side (52 m asl); H. Tommy et al., 12 Sep.2011. – ZRC 54013, 2 ex., 41.4–47.4 mm SL; Indonesia: South Kalimantan: north of Batulicin; T. Idei, 2004. CMK 16796, 4 ex., 34.5–46.4 mm SL; Indonesia: South Kalimantan: 25 km south of Damar Datar, Koto to Batulian; T. Idei, 12 Oct.2000.

**Diagnosis.** — *Hemirhamphodon sesamum* differs from all congeners in having the following suite of characters: 1) Dorsal fin with melanophores in two distinct sizes – for males in life (Figs. 2A, 4), first 6 to 7 rays distal one-third to half with yellow suffused throughout the rays and interradial membrane, with iridescent red margin; intense black pigments on the mid-section of interradial membrane between first 3 rays; red pigments on the mid-section of interradial membrane between 6 to 11 rays; rest of fin hyaline. For males in preservative (Fig. 2B, C), colour pattern as above, but the iridescent red margin is absent. For females in life (Fig. 3A), first 6 to 7 rays suffused with pale yellow, with iridescent red margin; small patches of black pigments on the middle section of the interradial membrane of first 6 to 7 rays; rest of fin hyaline. For females in preservative (Fig. 3B), colour pattern as above, but the iridescent red margin is absent. Black patches on anterior portion of dorsal fin present in specimens 20 mm SL or larger. 2) Unique dorsal fin morphology in the males (Fig. 4) – distal portions of first 6 to 7 rays elongated, free of interradial membrane, projected into filaments up to

twice the depth of the dorsal fin; adpressed fin rays reaching caudal-fin base and beyond. 3) Unique colouration on lower jaw; for males in life (Fig. 5A), upper jaw with corresponding portion of lower jaw yellow; dorsal surface of exposed lower jaw bluish, dermal flange below middle section of lower jaw bright red with blue lower margin, tip of lower jaw to region below upper jaw red; dermal flange of lower jaw with distinct black ventral margin from tip to region directly below eye. Males in preservative (Fig. 5B) exhibit similar colour pattern but colours are subdued or faded. Females in life (Fig. 5C) have similar colour pattern as male but colours are comparatively less intense. For females in preservative (Fig. 5D), the red band on the dermal flange of the lower jaw is replaced by yellow. 4) Males with the fourth anal-fin ray distinctly enlarged (Figs. 1A, B, 2A–C, 6A), and third, fourth and eighth anal-fin rays branched; females with third and fourth anal-fin rays branched (Figs. 1C, D, 3A, B, 6B). 5) Pelvic-fin origin anterior to dorsal-fin origin. 6) Dorsal-fin rays 13 or 14 (mode 13).

**Description.** — See Figs. 1–5 for general appearance and Table 1 for morphometric data.

Head short (head length 24.3–28.7% SL) and body slender and long (body depth 8.6–11.9% SL, caudal peduncle depth 4.7–5.7% SL, body length 70.5–75.3% SL). Lower jaw about half of body length (48.0–63.8% BL), about 1.2–1.7 times head length; usually straight, tip bent downwards in a few specimens; dermal flange of lower jaw on male deeper than that on female. Dorsal-fin origin anterior to anal-fin origin, posterior to pelvic-fin origin, situated nearer to caudal fin

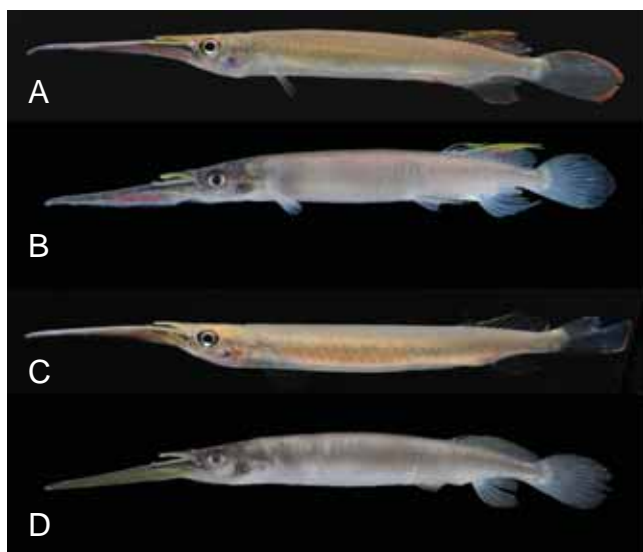


Fig. 1. Live and preserved colouration of *H. sesamum*: A, MZB 17209, 36.7 mm SL, live male holotype; B, ZRC 54009, 47.0 mm SL, preserved male; C, MZB 17210, 44.4 mm SL, live female; D, ZRC 54009, 44.3 mm SL, preserved female (not to scale).

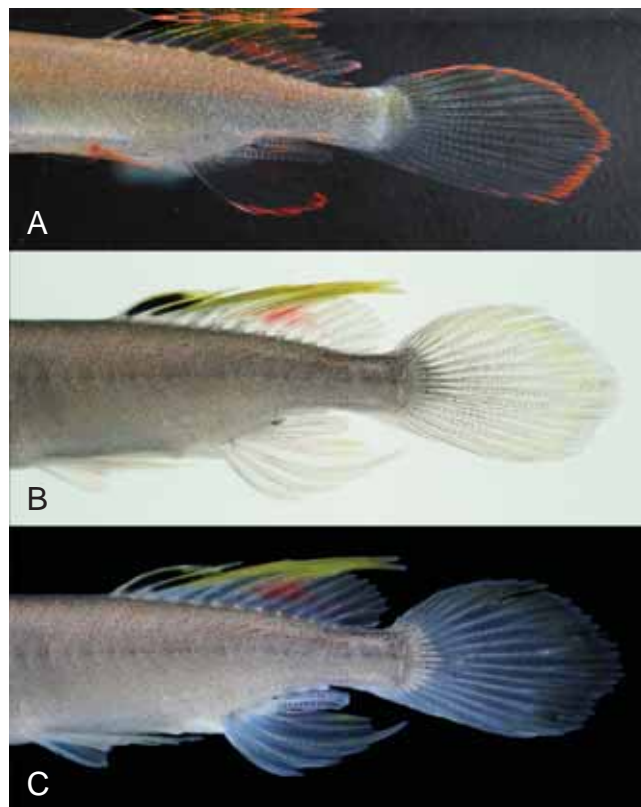


Fig. 2. Dorsal fin and anal fin colouration of male *H. sesamum*: A, live holotype, MZB 17209, 36.7 mm SL; B, ZRC 54009, 47.0 mm SL (white background); C, ZRC 54009, 47.0 mm SL (black background).

Table 1. Morphometric data of *Hemirhamphodon sesamum*, *H. byssus*, and *H. kecil*.

	<i>H. sesamum</i>	<i>H. byssus</i>	<i>H. kecil</i>
	ZRC 54009, ZRC 54010	ZRC 37832, ZRC 39508	ZRC 45682
SL (mm)	34.8–46.9	45.6–70.3	31.0–40.8
Sample size	20	10	10
% SL			
Total length	117.7–123.1	118.5–123.0	114.2–123.8
Body length	70.5–75.3	68.9–72.2	71.4–74.9
Predorsal-fin length	71.7–76.9	70.6–75.5	70.6–74.9
Preanal-fin length	80.0–83.2	77.0–82.7	75.8–82.0
Prepelvic-fin length	63.5–68.1	62.0–65.5	59.4–64.9
Head length	24.3–28.7	27.3–29.4	25.1–28.1
Body depth at anus	8.6–11.9	9.0–13.1	9.3–11.1
Caudal peduncle depth	4.7–5.7	4.8–6.3	4.4–5.8
Caudal peduncle length	9.8–13.1	11.1–13.7	10.0–11.7
Dorsal-fin base length	18.9–24.5	20.8–24.3	21.5–24.9
Anal-fin base length	5.8–9.2	6.0–7.7	6.4–8.4
Lower jaw length	35.7–45.7	39.1–47.6	32.1–42.9
Orbital diameter	5.3–6.8	5.7–6.9	5.7–6.8
Interorbital width	6.7–8.0	7.2–8.1	6.4–7.2
% HL			
Lower jaw length	124.4–169.2	135.3–170.6	118.4–156.0
Orbital diameter	20.2–26.0	19.9–23.8	20.7–25.6
Interorbital width	24.4–29.1	25.9–29.1	23.8–27.9

(predorsal length 71.7–76.9% SL), dorsal-fin base short (dorsal-fin base length 18.9–24.5% SL); dorsal-fin rays 13 or 14 (mode 13); male with first 6 to 7 dorsal-fin rays elongated into filaments, adpressed rays reaching caudal-fin base and beyond. Caudal fin elongate, rounded, caudal-fin rays 26. Anal-fin rays 8 (last ray split to base), with short base (5.8–9.2% SL), male with distinct posterior projection on base of fourth fin ray, adpressed elongated anal-fin ray reaching caudal-fin base, with branched ray on rays 3, 4 and 8, andropodium developed on ray 5 to 8, rays 5 and 8 thickened throughout (Fig. 5A); female with branched ray on rays 3 and 4 (Fig. 5B). Pelvic-fin rays 6–7, fins are adpressed to body, male with longer inner rays, adpressed rays reaching anal-fin origin; female with shorter rays, adpressed rays not reaching anus. Pectoral-fin rays 8, rounded. Precaudal vertebrae 23–26, caudal vertebrae 14–16; total vertebrae 38–41 (mode 40, n = 20). First gill arch with up to 13 gill rakers. Maximum size 47.4 mm SL.

**Colouration in life.** — See Figs. 1A, 1C, 2A, 3A, 5A, 5C. Adult male – Head brown on dorsum and sides, ventrum cream. Upper jaw yellow with corresponding portion of lower jaw also yellow; dorsal surface of exposed lower jaw bluish, middle section of dermal flange on lower jaw red with blue lower margin, red section from tip to region below upper jaw; ventrum of lower jaw flange with distinct black margin from tip to region directly below eye. Eye with upper half of iris pale reddish. Operculum with scattering of melanophores, and pinkish on posterior part. Body with brown dorsal stripe, dorsum pinkish and sides yellowish brown, ventrum cream with thin reddish ventral stripe. Dorsal fin with first 6 to 7 rays distal one-third to half with yellow suffused throughout the rays and interradiation membrane; intense black pigments

on the mid-section of interradiation membrane between first 3 rays; red pigments on the mid-section of interradiation membrane between 6 to 11 rays; rest of fin hyaline. Caudal, anal and pelvic fins with bright red margin; anal fin with bright red blotch on middle of andropodium. Pectoral fins hyaline. Adult female: colouration similar, but less intense. Dorsal fin with first 6 to 7 rays suffused with pale yellow, with iridescent red margin; small patches of black pigments on the middle section of the interradiation membrane of first 6 to 7 rays; rest of fin hyaline.

**Colouration in preservative.** — See Figs. 1B, D, 2B, C, 3B, 5B, D.



Fig. 3. Dorsal fin and anal fin colouration of female *H. sesamum*: A, live paratype, MZB 17210 (with damaged dorsal and caudal fins), 44.4 mm SL; B, ZRC 54009, 44.3 mm SL.

Adult male – Head brown on dorsum and sides, ventrum cream. Upper jaw yellow with corresponding portion of lower jaw also yellow; dorsal surface of exposed lower jaw bluish, middle section of dermal flange on lower jaw red with blue lower margin, red section from tip to region below upper jaw; ventrum of lower jaw flange with distinct black margin from tip to region directly below eye. Eye with upper half of iris pale reddish. Operculum with scattered melanophores, pinkish on posterior part. Body with brown dorsal stripe, dorsum pinkish and sides yellowish brown, ventrum cream with thin reddish ventral stripe (may be faint on specimens preserved for a long time). Dorsal fin with first 6 to 7 rays and distal one-third to half suffused with yellow throughout the rays and interradiation membrane; intense black pigments on the mid-section of interradiation membrane between first 3 rays; red pigments on the mid-section of interradiation membrane between 6 to 11 rays; rest of fin hyaline. Caudal, anal, pelvic and pectoral fins hyaline.



Fig. 4. Dorsal fin morphology of freshly preserved *H. sesamum* male, ZRC 54009, 47.0 mm SL.

Adult female – colouration as for male, but subdued. All fins hyaline. Black patches on anterior portion of dorsal fin in specimens larger than or equal to 20 mm SL.

**Distribution.** — *Hemirhamphodon sesamum* is currently known only from South Kalimantan, Indonesian Borneo, in lowland drainages of the Batulicin and Cantung basins that drain eastwards into the Makassar Strait (Fig. 7).

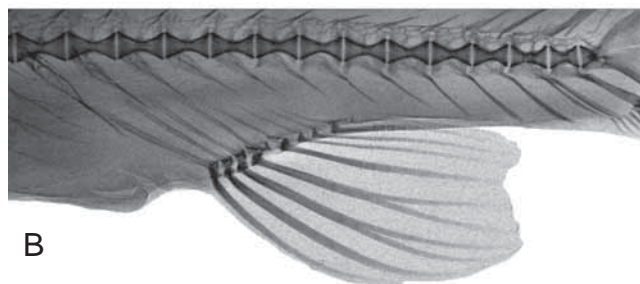
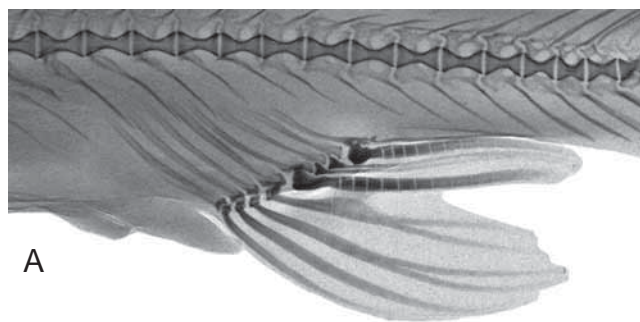


Fig. 6. Radiographs of anal fin of *H. sesamum*: A, MZB 17209, holotype, 36.7 mm SL male; B, MZB 17210, paratype, 44.4 mm SL female.

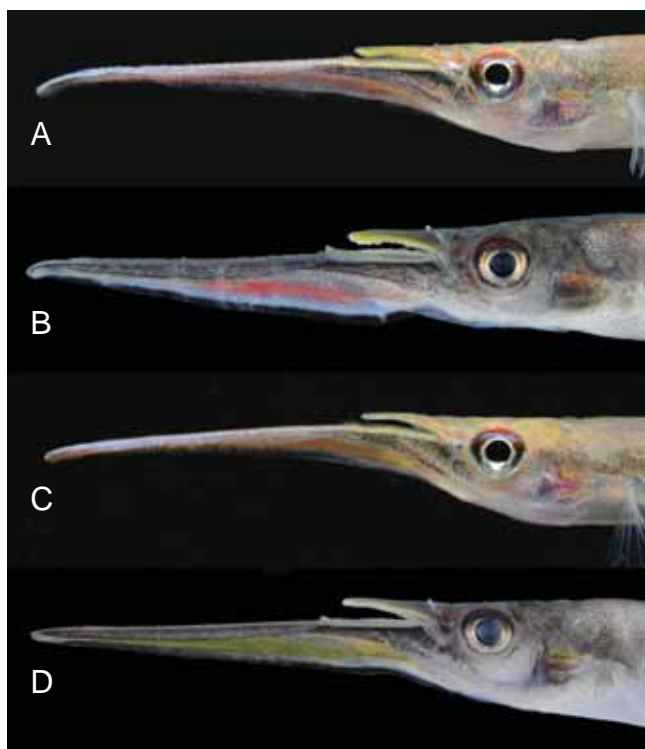


Fig. 5. Lower jaw colouration of *H. sesamum*: A, MZB 17209, 36.7 mm SL, live male holotype; B, ZRC 54009, 47.0 mm SL, preserved male; C, MZB 17210, 44.4 mm SL, live female; D, ZRC 54009, 44.3 mm SL, preserved female.

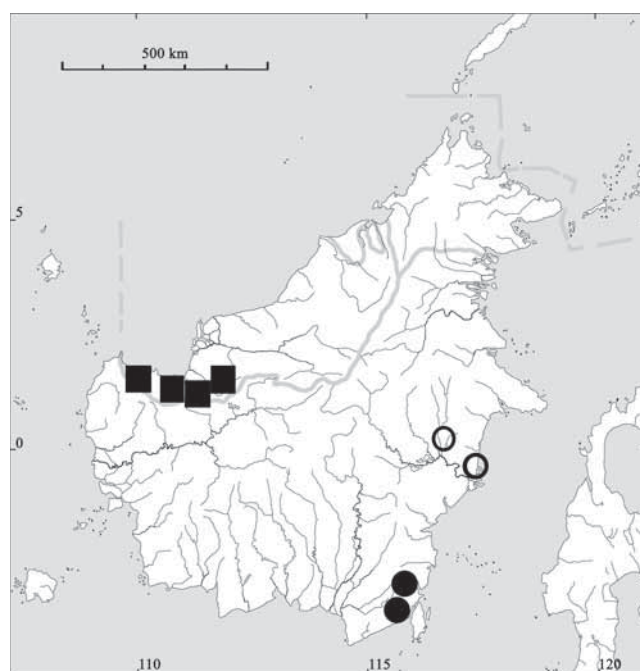


Fig. 7. Distribution of *H. sesamum* (solid circle), *H. byssus* (solid square) and *H. kecil* (hollow circle) in Borneo.

**Field notes.** — *Hemirhamphodon sesamum* inhabits clear flowing waters of small streams, about 2–5 m wide and up to 2 m deep, with sand and gravel bottoms (see Fig. 8). It tends to form small groups of 3 to 5 individuals at the surface, preferring quiet pools near or under overhanging bank vegetation. Syntopic ichthyofauna includes: *Hampala macrolepidota*, *Osteochilus* cf. *waandersii*, *Rasbora dies*, *R. elegans*, *R. lacrimula*, *Systemus anchisporus*, *S. banksi* (Cyprinidae), *Balitoropsis stephensoni*, *Homalopteroides nebulosus* (Balitoridae), *Nemacheilus* cf. *spiniferus* (Nemacheilidae), *Betta edithae* (Osphronemidae), *Channa lucius* (Channidae), and *Macrogathus maculatus* (Mastacembelidae).

**Etymology.** — The species name refers to the minute oily seeds of the *Sesamum* plant (Pedaliaceae); in allusion to the small black spots/dashes on the dorsal fin with which resemble black sesame seeds. Used as a noun in apposition.

**Comparisons with congeners.** — *Hemirhamphodon sesamum* shares with *H. pogonognathus*, *H. kuekenthali*, *H. byssus*, and *H. kecil* a posterior projection on the fourth anal-fin ray, a similar range of dorsal-fin rays (12–17) and a similar number of vertebrae (37–44). *Hemirhamphodon sesamum* further shares with *H. kuekenthali* and *H. byssus* two types of melanophore on the dorsal fin.



Fig. 8. Habitat of *H. sesamum*, South Kalimantan: Batulicin basin (2011).

*Hemirhamphodon sesamum* seems to be most closely related to *H. kuekenthali* in terms of external morphology. The current distribution of *H. kuekenthali* within Borneo (Kottelat & Lim, 1995; pers. obs.) is from central to northern Sarawak and Brunei Darussalam. While *H. sesamum* is currently known only from the southernmost tip of Borneo. It seems to represent a vicariant distribution. The ichthyofauna of the short coastal basins in South Kalimantan draining into the Makassar Straits is poorly known. As evident from other parts of Southeast Asia where short coastal basins are present, such as the western coast of Sumatra (Lumbantobing, 2010), the rate of endemism is expected to be relatively high.

### *Hemirhamphodon byssus*, new species

(Figs. 9A–E, 10A, 11A, B)

*Dermogenys* species undetermined – Doi et al., 2001: 16, Fig. 2  
*Hemirhamphodon kuekenthali* (non-Steindachner) – Anderson & Collette, 1991 (part); Kottelat & Lim, 1995 (part); Doi et al., 2001; Jongkar & Lim, 2004

*Hemirhamphodon pogonognathus* (non-Bleeker) – Roberts, 1989 (part)

**Material examined.** — Holotype: ZRC 54067, 1 ex., 70.5 mm SL; Sarawak: Matang Wildlife Centre, Sungai Rayu; M. Kottelat et al., 5 May 1994.

Paratypes: ZRC 37832, 6 ex., 24.7–53.0 mm SL; CMK 10861, 4 ex., 12.0–60.4 mm SL; same locality as holotype. – ZRC 26042, 7 ex., 28.0–58.2 mm SL; CMK 8413, 10 ex., 20.2–51.2 mm SL; Sarawak: 42 km before Lundu from Kuching, after Sungai Stinggang; M. Kottelat & P. K. L. Ng, 3 Jul.1992. – ZRC 39361, 5 ex., 31.2–54.0 mm SL; Sarawak: Sungai Stinggang, along Bau-Lundu road; H. H. Tan et al., 6 Sep.1995. – ZRC 37873, 15 ex., 26.8–58.5 mm SL; Sarawak: Lundu-Bau road, 27 km before Bau; M. Kottelat et al., 8 May 1994. – ZRC 39500, 16 ex., 25.5–58.7 mm SL; Sarawak: Sungai Stom Muda, 71 km before Sematan towards Bau; H. H. Tan et al., 6 Sep.1995. – ZRC 39376, 9 ex., 39.5–58.5 mm SL; Sarawak: Sungai Stom Muda, 71 km before Sematan towards Bau; H. H. Tan et al., 7 Sep.1995. – ZRC 39508, 12 ex., 20.2–64.4 mm SL; Sarawak: 12 km before turnoff to Sungai Cinta Matang; H. H. Tan et al., 4 Sep.1995. – NSMT-P 0111739, 2 ex., 40.6–68.2 mm SL; Sarawak: Rayu basin, Sendok stream down stream (0065); A. Doi, 14 Aug.1998. – NSMT-P 0111740, 5 ex., 45.0–69.3 mm SL; Sarawak: Rayu basin, Sendok stream upstream (221); A. Doi, 18 Sep.1998. – NSMT-P 0111741, 3 ex., 45.1–71.3 mm SL; Sarawak: Rayu basin, Buluh stream (380); A. Doi, 11 Sep.1998. – NSMT-P 0111742, 1 ex., 61.8 mm SL; Sarawak: Rayu basin, Ijyo stream (505); A. Doi, 11 Sep.1998. – ZRC 39405, 20 ex., 33.4–55.0 mm SL; Sarawak: Serian, Sungai Kuhas, before Kampung Lanchang along Tebelu Tebakang turnoff; H. H. Tan et al., 5 Sep.1995. – ZRC 41206, 6 ex., 39.5–57.3 mm SL; Sarawak: Serian, tributary of Sungei Kuhas, before Kampung Lanchang along Tebelu Tebakang turnoff; H. H. Tan et al., 19 Feb.1997.

Non-type material: ZRC 43642, 5 ex., 35.5–57.4 mm SL; Sarawak: Lundu, Sungai Sebiris, 9 km to Sematan on Lundu-Sematan road; H. H. Tan & P. Yap, 2 Oct.1998. – ZRC 37766, 2 ex., 49.0–63.3 mm SL; Sarawak: Bako, Sungai Senait at goldmine; N. Sivasothi et al., 30 Jun.1994. – ZRC 39459, 8 ex., 27.6–41.8 mm SL; Sarawak: Sungai Noren, 11 km to Bau from Serikin; H. H. Tan et al., 7 Sep.1995. – ZRC 25927, 4 ex., 33.5–58.4 mm SL; Sarawak: Sungai Jaguh, 99 km from Kuching, after Balai Ringin; M. Kottelat & K. K. P. Lim, 2 Jul.1992. – ZRC 39872, 8 ex., 13.6–46.5 mm SL; Sarawak: Gedong peat swamps, along Serian-Sri Aman road; H. H. Tan et al., 16 Jan.1996. – ZRC 37893, 4 ex., 39.1–62.9 mm

SL; Sarawak: blackwater ditch along Sri Aman-Sibu road, ca. 1 km south of junction with Lubok Antu road; M. Kottelat et al., 10 May 1994. – ZRC 37864, 8 ex., 11.5–60.7 mm SL; Sarawak: Sungai Nibung, ca. 1 km north of Durin ferry on Sri Aman-Sibu road; M. Kottelat et al., 15 May 1994.

**Diagnosis.** — *Hemirhamphodon byssus* differs from its congeners in having the following suite of characters: 1) Dorsal fin with melanophores in two sizes (Fig. 10A) – on both male and female examples above 30 mm SL, interradiial membranes on the anterior half of the dorsal fin with large and intense melanophores throughout fin depth, appearing as thin black streaks. 2) Unique dorsal fin morphology on large males above 50 mm SL (Figs. 9A, 9C–D, 10A) – distal portions of first 6 to 7 rays elongated, free of interradiial membrane, projected into filaments up to four times the depth of the dorsal fin; adpressed fin rays reaching half of caudal-fin. 3) Males with an enlarged posterior projection on the fourth anal-fin ray (Fig. 9A, 11A), with third, fourth and eighth anal-fin rays branched; females with third, fourth and eighth anal-fin rays branched (Fig. 11B). 4) Pelvic-fin origin anterior to dorsal-fin origin. 5) Dorsal-fin rays 13 to 14 (mode 14).

**Description.** — See Figs. 9A–E for general appearance and Table 1 for morphometric data.

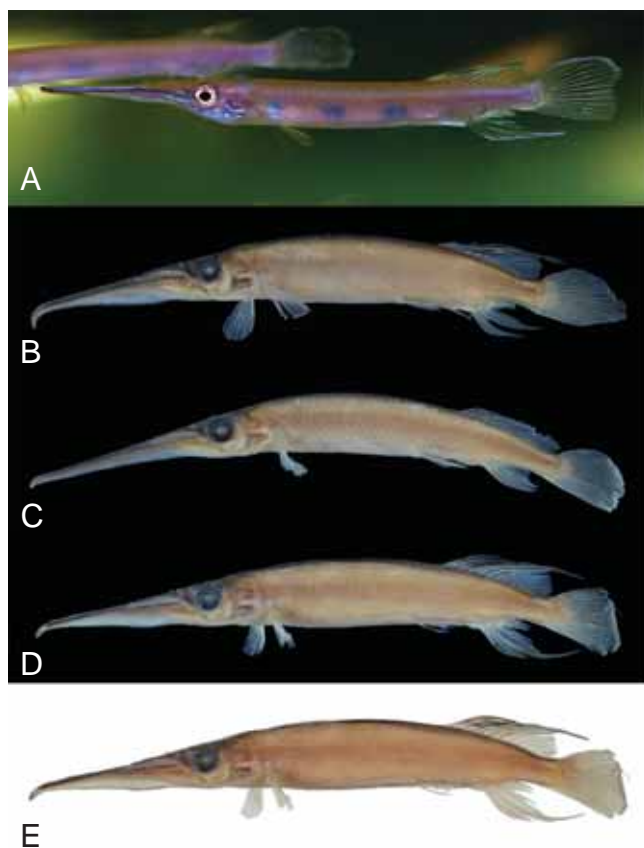


Fig. 9. Live and preserved colouration of *H. byssus*: A, live male from Sematan, Sarawak, not preserved (photograph right side reversed, by Daron Tan); B, ZRC 37832, 70.5 mm SL, male holotype; C, ZRC 37832, 47.1 mm SL, female paratype; D, E, ZRC 43642, 57.3 mm SL, male paratype from Sematan (black and white background respectively; not to scale).

Head short (head length 27.3–29.4% SL) and body slender and long (body depth 9.0–13.1% SL; caudal peduncle depth 4.8–6.3% SL; body length 68.9–72.2% SL). Lower jaw more than half of body length (54.8–66.7% BL), about 1.4–1.7 times head length; usually straight, tip bent downwards in a few specimens; dermal flange of lower jaw on male deeper than that on female. Dorsal-fin origin anterior to anal-fin origin, posterior to pelvic-fin origin, situated nearer to caudal fin (predorsal length 70.6–75.5% SL), dorsal-fin base short (dorsal-fin base length 20.8–24.3% SL); dorsal-fin rays 13–14 (mode 14); male with first 6 to 7 dorsal-fin rays elongated into filaments, adpressed rays reaching midway of caudal fin. Caudal fin elongate, rounded, caudal-fin rays 25. Anal-fin rays 8 (last ray split to base), with short base (6.0–7.7% SL), male with distinct posterior projection on base of fourth fin ray, adpressed elongated anal-fin ray reaching up to midway of caudal fin, with branched ray on rays 3, 4 and 8, andropodium developed on ray 5 to 7, rays 5 and 7 thickened throughout (Fig. 10A); female with rays 3, 4 and 8 branched (Fig. 10B). Pelvic-fin rays 8, fins adpressed to body, male with longer inner rays, adpressed rays reaching anal-fin origin; female with shorter rays, adpressed rays not reaching anus. Pectoral-fin rays 8, rounded. Precaudal vertebrae 24–25, caudal vertebrae 14–16; total vertebrae 39–40 (mode 40, n = 10). First gill arch with up to 16 gill rakers. Maximum size 71.3 mm SL.

**Colouration in life.** — See Fig. 9E.

Adult male – Head yellowish-brown on dorsum and sides, ventrum cream. Upper jaw brownish with corresponding portion of lower jaw with 2 blue iridescent stripes with reddish band in between; dorsal surface of exposed lower jaw iridescent blue, middle section of dermal flange on lower jaw reddish with cream sub-margin; ventrum of lower jaw flange with thin black margin from tip to region directly below upper jaw. Eye with upper half of iris pale pinkish. Operculum flushed bluish with 2 to 3 iridescent blue stripes alternating with pink on posterior half of opercle. Body with reddish dorsal stripe, dorsum pinkish and sides yellowish brown with pinkish flush, ventrum cream. Dorsal fin with first 6 to 7 rays distal one-third to half with dark brown to black pigments suffused throughout the rays and interradiial



Fig. 10. Dorsal fin morphology: A, *H. byssus* male, ZRC 43642, 57.3 mm SL, Sarawak: Sematan; B, *H. kuekenthali* male, ZRC 37991, 61.5 mm SL, Sarawak: Baram.

membrane; rest of fin hyaline. Caudal, anal and pelvic fins with bright blue margin. Pectoral fins hyaline. Adult female: not recorded.

**Colouration in preservative.** — See Fig. 9A–D.

Adult male — Head brown on dorsum and sides, ventrum cream. Upper jaw dark brown, dorsal surface of exposed lower jaw black, middle section of dermal flange on lower jaw brownish and cream, ventrum of lower jaw flange with distinct thin black margin from tip to region directly below eye. Operculum with scattering of melanophores, dark brown flush on posterior part. Body with brown dorsal stripe, dorsum dark brown and sides light brown, ventrum cream; no discernable markings on body. First 6 to 7 rays on dorsal fin with intense melanophores on interradial membrane, resulting in black streaks; distal tips of anterior half of dorsal fin extended to form black filaments, reaching up to middle of caudal fin; rest of fin hyaline. Caudal, anal, pelvic and pectoral fins hyaline.

Adult female — colouration as for male, but subdued. Anterior half of dorsal fin with black streaks, as in male. All other fins hyaline. Black streaks on anterior portion of dorsal fin present in specimens larger than or equal to 30 mm SL.

**Distribution.** — *Hemirhamphodon byssus* is known from the lowland stream systems in southern Sarawak that include Sematan, Lundu, Bau, Batu Kawa, Matang, Bako, Serian, Balai Ringin, Gedong and Sri Aman (Fig. 7). From Sibul northwards (including Bintulu and Baram areas, and Brunei Darussalam), it is replaced by *H. kuekenthali* with which it is apparently allopatric. This distribution pattern is shared with the following allopatric species pairs (in south–north orientation): *Rasbora kalochroma*/*R. kottelati* (Lim, 1995), *Betta ibanorum*/*B. akarensis* (Tan & Ng, 2004, 2005).

**Field notes.** — *Hemirhamphodon byssus* occurs in streams of lowland forest and peat swamps. In streams with clear water, the body is lighter in colour; while in tannin stained waters, the body tends to be darker coloured, at times appearing black.

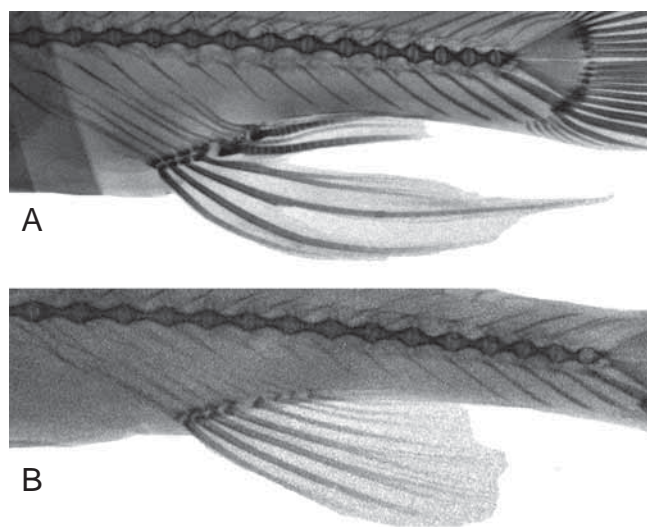


Fig. 11. Radiographs of anal fin of *H. byssus*: A, ZRC 37832, 70.5 mm SL male holotype (note: missing branch of ray 2); B, ZRC 37832, 47.1 mm SL female paratype.

**Etymology.** — From the Latin *byssus*, meaning fine thread, in allusion to the distinct filamentous dorsal-fin rays of large males. Used as a noun in apposition.

**Comparisons with congeners.** — *Hemirhamphodon byssus* can be distinguished from its closest congener, *H. kuekenthali*, by the following characters: anterior half of dorsal fin with black streaks on the interradial membrane (vs black streaks in the middle, Fig. 10B); anterior half of dorsal fin with filamentous fin rays reaching up to middle of caudal fin (vs small extensions or none); up to 16 gill rakers on the first gill arch (vs 18). The filamentous dorsal-fin rays of *H. byssus* are distinct and pronounced in large male specimens from the southern parts of Sarawak (Sematan, Lundu, Bau, Batu Kawa, Matang, Rayu, Bako, Serian, Balai Ringin and Gedong). From Sri Aman northwards to region south of Sibul, the filamentous fin rays are not as pronounced; but the diagnostic black streaks on the dorsal fin are present.

**Remarks.** — *Hemirhamphodon kuekenthali* was described by Steindachner (1901) based on specimens obtained from the Baram River in northern Sarawak. It was regarded as a synonym of *H. pogonognathus* until it was revalidated by Anderson & Collette (1991). They designated a lectotype for *H. kuekenthali* and diagnosed it as the only species with two types of melanophores on the dorsal fin. As they did not have access to fresh specimens from southern Sarawak, they were not able to discern differences between the populations in the northern and southern parts of Sarawak. Subsequent workers identified halfbeaks from all over Sarawak as *H. kuekenthali* (e.g., Kottelat & Lim, 1995; Jongkar & Lim, 2004). Doi et al. (2001) did observe the dorsal fin extensions in only three specimens among their more than 1,600 specimens from the Rayu basin of western Sarawak but listed these as ‘*Dermogenys* species undetermined’. Without access to large series of *Hemirhamphodon* from various parts of Sarawak for comparison, it would not have been likely for *H. byssus* to be recognised as distinct from *H. kuekenthali*.

### *Hemirhamphodon kecil*, new species

(Figs. 12A–E, 13A, B)

*Hemirhamphodon pogonognathus* (non-Bleeker) – Anderson & Collette, 1991 (part); Christenson, 1992; Kottelat et al., 1993 (part); Kottelat, 1994.

**Material examined.** — Holotype: MZB 17211, 37.4 mm SL; Kalimantan Timur: Mahakam basin; downstream of Taman Wisata Air Terjun at Tanah Merah; H. H. Tan & D. Wowor, 2 Dec. 1999. Paratypes: MZB 17212, 3 ex., 30.4–33.4 mm SL; ZRC 45684, 30 ex., 17.0–40.8 mm SL; same locality as holotype. — MZB 6002, 20 ex., 20.4–44.7 mm SL; CMK 21765, 19 ex., 19.4–46.0 mm SL; Kalimantan Timur: Mahakam drainage, Belayan system, REA plantations, Sungai Nyiur, PT SYB (Sasany Yudha Bhakti) Tepian Estate, 0°10'45"N 116°16'04"E; R. K. Hadiaty & M. Kottelat, 19 Nov. 2009. — MZB 6003, 8 ex., 28.0–40.0 mm SL; CMK 21871, 8 ex., 32.2–40.6 mm SL; Kalimantan Timur: Mahakam drainage, Belayan system, REA plantations, Long (=Sungai) Buluh, Damai estate, 0°14'29"N 116°19'14"E; R. K. Hadiaty & M. Kottelat, 22 Nov. 2009.



**Diagnosis.** — *Hemirhamphodon kecil* differs from its congeners in having the following suite of characters: 1) Absence of discernable markings on body and fins, except dorsal part of caudal fin base with sparse black pigments on both male and female; and submargin of dorsal fin suffused with black pigments (Fig. 12D, E). 2) Small adult size, up to 41 mm SL (only *H. tengah* is smaller). 3) Adult sizes for male and female similar (as with *H. tengah*), other congeners with males up to 50% larger than females. 4) Males with an enlarged posterior projection on the fourth anal-fin ray (Fig. 13A), with third, fourth, sixth and eighth anal-fin rays branched; females with third, fourth and eighth anal-fin rays branched (Fig. 13B). 5) Pelvic-fin origin anterior to dorsal-fin origin. 6) Dorsal-fin rays 14 to 15 (mode 14).

**Description.** — See Fig. 12A–E for general appearance and Table 1 for morphometric data.

Head short (head length 25.1–28.1% SL) and body slender and long (body depth 9.3–11.1% SL; caudal peduncle depth 4.4–5.8% SL; body length 71.4–74.9% SL). Lower jaw about half of body length (44.0–59.9% BL), about 1.2–1.6 times head length; usually straight, tip bent downwards in a few specimens; dermal flange of lower jaw on male deeper than on female. Dorsal-fin origin anterior to anal-fin origin, posterior to pelvic-fin origin, situated nearer to caudal fin (predorsal length 70.6–74.9% SL), dorsal-fin base short (dorsal-fin base length 21.5–24.9% SL); dorsal-fin rays 14–15 (mode 14); male without dorsal-fin ray extensions; dorsal fin of male about twice deeper than that of female. Caudal fin elongate, rounded, caudal-fin rays 25. Anal-fin rays 8 (last ray split to base), with short base (6.4–8.4% SL), male with distinct

posterior projection on base of fourth fin ray, adpressed elongated anal-fin ray reaching caudal-fin base, with branched ray on rays 3, 4, 6 and 8, andropodium developed on ray 5 to 7, rays 5 and 7 thickened throughout (Fig. 13A); female with anal rays 3, 4 and 8 branched (Fig. 13B). Pelvic-fin with 6 rays, fins adpressed to body, male with longer inner rays, adpressed rays reaching anal-fin origin; female with shorter rays, adpressed rays not reaching anus. Pectoral-fin rounded, with 9 rays. Precaudal vertebrae 24–25, caudal vertebrae 14–16; total vertebrae 39–41 (mode 39, n = 10). First gill arch with up to 16 gill rakers. Maximum size 41 mm SL.

**Colouration in preservative.** — See Figs. 12A–E.

Adult male – Head brown on dorsum, sides and ventrum cream. Upper rim of lower jaw below upper jaw with black stripe, ventrum of dermal flange on lower jaw with distinct black margin from tip to region directly below eye. Operculum with scattering of melanophores, appearing dusky on posterior part. Body with brown dorsal stripe, dorsum brownish and sides cream with diffused pale brown longitudinal stripe, ventrum cream. Dorsal fin with submargin suffused with black pigments. Dorsal region of anterior part of caudal-fin base with sparse black pigments. Rest of fins hyaline.

Adult female – colouration as for male. All fins hyaline.

**Distribution.** — *Hemirhamphodon kecil* is currently known only from East Kalimantan, Indonesian Borneo, in the waterways of the lower Mahakam basin that drain eastwards into the Makassar Strait (Fig. 7).

**Field notes.** — *Hemirhamphodon kecil* occurs in streams with submerged bank vegetation and clear water of pH 7.0 flowing over rocky, sand and silt substratum. It tends to school in small

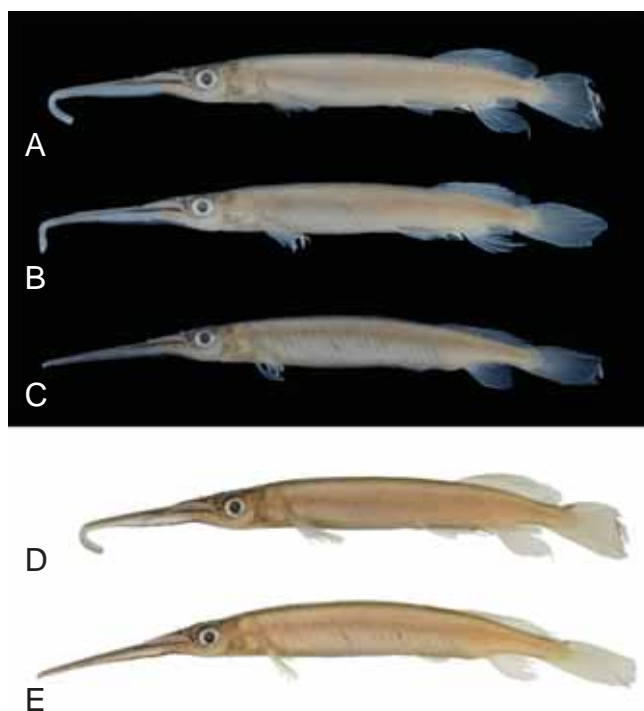


Fig. 12. Preserved colouration of *H. kecil*: A, ZRC 54684, 37.4 mm SL, male paratype; B, MZB 17211, 34.6 mm SL, male holotype; C, ZRC 54684, 38.6 mm SL, female paratype; D, ZRC 54684, 37.4 mm SL male paratype (white background); E, ZRC 54684, 38.6 mm SL, female paratype (white background; not to scale).

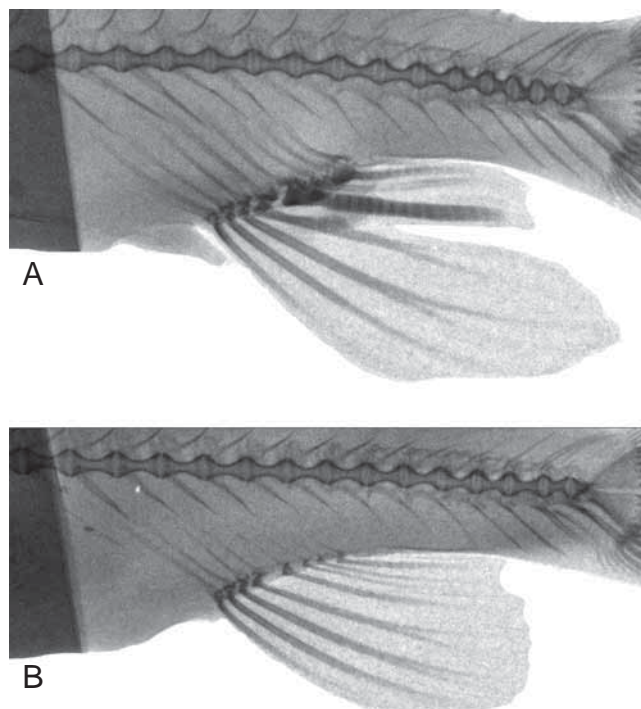


Fig. 13. Radiographs of anal fin of *H. kecil*: A, MZB 17211, 37.4 mm SL male holotype; B, ZRC 54684, 38.6 mm SL female paratype.

groups of about 3 to 5 individuals at the surface, preferring quiet pools and dwelling near or under overhanging bank vegetation. Syntopic ichthyofauna consists of *Osteochilus vittatus*, *Rasbora elegans*, *Systemus binotatus* (Cyprinidae), *Betta patoti*, *Trichopodus trichopterus* (Osphronemidae), and *Channa lucius* (Channidae).

**Etymology.** — From the Bahasa Indonesian word ‘kecil’, meaning small, in reference to the diminutive size of this species. Used as a noun in apposition.

**Comparisons with congeners.** — *Hemirhamphodon kecil* can be distinguished from its closest congener, *H. pogonognathus*, by the following characters: smaller adult size (41 vs. 58 mm SL); longer body (71.4–74.9 vs 68.7–71.8% SL); shorter head (25.1–28.1 vs 28.4–30.5 mm SL); shorter dorsal-fin base (21.5–24.9 vs 24.0–26.5% SL).

## DISCUSSION

All the nine species of *Hemirhamphodon* (including the three described here) presently known occur on Borneo. Seven of these appear to have very restricted distribution and are endemic to Borneo, suggesting that this large island could be the centre of speciation for this genus (de Bruyn et al., 2013; present study).

The seven species with restricted ranges are as follows:

1. *Hemirhamphodon byssus* – hill stream, swamp forest and peat swamp habitats in southern Sarawak (south of the Rejang and Tatau basins).
2. *Hemirhamphodon kuekenthali* – swamp forest, heath forest and peat swamp habitats from central Sarawak (Rejang and Tatau basins northwards) to Brunei Darussalam.
3. *Hemirhamphodon kapuasensis* – swamp forest streams and peat swamps in the middle and lower Kapuas basin.
4. *Hemirhamphodon chrysopunctatus* – lowland peat swamp habitats in Central Kalimantan.
5. *Hemirhamphodon tengah* – lowland peat swamp habitats in Central Kalimantan.
6. *Hemirhamphodon sesamum* – eastward flowing lowland coastal basins of South Kalimantan that drain into the Makassar Straits.
7. *Hemirhamphodon kecil* – lower Mahakam basin in East Kalimantan, only from low lying hill streams.

The remaining two species are more widely distributed, and are also found outside Borneo.

8. *Hemirhamphodon pogonognathus* – southern Thailand to Peninsular Malaysia, Singapore, western Borneo, Natuna, Banka and Biliton islands, Java and Sumatra (Anderson & Collette, 1991; Kottelat et al., 1993; Tan & Lim, 2004).
9. *Hemirhamphodon phaiosoma* – Biliton and Banka islands and western part of Kalimantan Borneo (Roberts, 1989; Anderson & Collette, 1991; present study).

In some locations, more than one species of *Hemirhamphodon* are present in the same habitat. As all are surface feeders, they may be segregated by niche or diet, but this requires further

investigation. Examples of such syntopy are as follows: 1) In the coastal Anjungan basin of West Kalimantan, *H. kapuasensis* and *H. pogonognathus* are found together in a blackwater stream. 2) In Central Kalimantan, *H. tengah* and *H. chrysopunctatus* are almost always found together in the lowland peat swamp habitats. *Hemirhamphodon chrysopunctatus* seems to prefer the faster flowing sections while *H. tengah*, areas with more sluggish water. Anderson & Collette (1991) recorded *H. phaiosoma* occurring syntopically with *H. tengah* and *H. chrysopunctatus* in some habitats in Central Kalimantan.

The distribution of *H. pogonognathus*, *H. byssus* and *H. kuekenthali* provides an example of allopatric speciation of closely related or sister species separated by large river basins or mountain ranges. *Hemirhamphodon pogonognathus* occurs in West Kalimantan. In southern Sarawak to the north, it is replaced by *H. byssus*. Further north in central and northern Sarawak and Brunei Darussalam, *H. kuekenthali* takes over (Roberts, 1989; Kottelat & Lim, 1995; present study). A similar pattern is seen on the sister pairs of the cyprinids *Rasbora kalochroma* and *R. kottelati* (Lim, 1995), and the osphronemids *Betta ibanorum* and *B. akarensis* (Tan & Ng, 2004, 2005). *Rasbora kalochroma* and *Betta ibanorum* are restricted to southern Sarawak, while *R. kottelati* and *B. akarensis* occur in central and northern Sarawak and Brunei. *Hemirhamphodon kecil* and *H. sesamum* appear to form another allopatric pair where *H. kecil* occupies East Kalimantan and *H. sesamum*, South Kalimantan, in more or less adjacent river basins (present study).

## NOTES ON HEMIRHAMPHODON PHAIOSOMA

*Hemirhamphodon phaiosoma* (Bleeker, 1852) appears to be the least known species of the genus (pers. obs.), as very little of its biology or colouration is documented.

Bleeker (1852) described *H. phaiosoma* based on material from Biliton and Banka islands. The holotype from Biliton (BMNH 1866.5.2.21) is in a poor state, with broken fins and having lost its lower jaw, scales and markings (Fig. 14). *Hemirhamphodon phaiosoma* was illustrated in a colour lithograph (Bleeker, 1866–1872: Scombres VIII, Fig. 2), showing a drab coloured halfbeak. Weber & de Beaufort (1922: 140) listed the colouration of preserved material of *H. phaiosoma* being brownish. Thus far, no colouration of live *H. phaiosoma* has been depicted. In the present article, a live male specimen from Biliton Island, the type locality of this species is illustrated (Fig. 15A), along with another



Fig. 14. Holotype of *H. phaiosoma* – BMNH 1866.5.2.21, 40.9 mm SL, Biliton.

male from the Anjungan area in West Kalimantan (Fig. 15B). *Hemirhamphodon phaiosoma* is known from West Kalimantan and Central Kalimantan (Anderson & Collette, 1991). The Biliton specimen was obtained from a lowland stream with water slightly stained with tannin (H. Ishizu, pers. comm.). The Anjungan specimens were from a stream at the base of a hill surrounded by peat swamps. The stream had clear water flowing over a rocky substratum (pers. obs.). In Central Kalimantan, the first author has collected specimens from a flowing creek in a peat swamp where the water was dark from high concentration of tannins. As observed by de Beaufort (1939), this species exhibits sexual dichromatism in which the male has two or more red stripes on the body and the female with a single red stripe (Fig. 16).

**Colouration of *H. phaiosoma* in life.** — Adult male from Biliton (Fig. 15A) – Head yellowish-brown on dorsal and lateral aspects, ventrum cream. Upper jaw yellowish-brown with corresponding portion of lower jaw also yellowish-brown; dorsal surface of exposed lower jaw pale greenish-blue, middle section of dermal flange on lower jaw pale blue with iridescent blue lower margin; ventrum of lower jaw flange with distinct black margin from tip to region directly below upper jaw. Eye with upper half of iris golden. Operculum with scattering of melanophores, and with pink flush on posterior part. Body with brown dorsal stripe, dorsum and sides yellowish brown, ventrum cream; sides with two distinct reddish-brown stripes from post-opercle to caudal-fin base. Dorsal fin yellowish. Caudal fin with reddish margin. Anal, pelvic and pectoral fins hyaline.

Adult male from Anjungan (Fig. 15B) – Head brownish on dorsal and lateral aspects, ventrum cream. Upper jaw brownish with corresponding portion of lower jaw bluish; dorsal surface of exposed lower jaw pale yellowish-brown, middle section of dermal flange on lower jaw bright red with black upper margin and iridescent blue lower sub-margin; lower jaw flange below upper jaw bright red; ventrum of lower jaw flange with distinct black margin from tip to region directly below eye. Eye with upper half of iris blue, with red on both sides. Operculum with scattering of melanophores, and with pink flush on posterior part. Body with brown dorsal stripe, dorsum and sides bluish with pink flush, ventrum cream; sides with two distinct red stripes from post-operculum to caudal-fin base, upper stripe more distinct. Dorsal fin yellowish with red margin. Caudal and anal fin with red margins. Pelvic and pectoral fins hyaline.



Fig. 15. Live material of *H. phaiosoma*: A, live male from Biliton, not preserved (photograph by H. Ishizu); B, ZRC 54048, live male from Anjungan, Kalimantan Barat.

**Colouration of *H. phaiosoma* in preservative.** — Adult male from Biliton (Fig. 16A) – Head dark brown on dorsum, pale brown on sides, ventrum cream. Upper jaw dark brown with corresponding portion of lower jaw pale brown; dorsal surface of exposed lower jaw pale brown, middle section of dermal flange on lower jaw with distinct blue and red markings; ventrum of lower jaw flange with distinct black margin from tip to region directly below upper jaw. Eye with upper half of iris pale red. Operculum with scattering of melanophores, and pinkish on posterior part. Body with brown dorsal stripe, dorsum and sides pale brown, ventrum cream; sides with two distinct reddish-pink stripes from post-opercle to caudal-fin base, a faint third pinkish stripe below the two stripes. Dorsal fin hyaline. Caudal, anal, pelvic and pectoral fins hyaline.

Adult female from Biliton (Fig. 16B) – colouration as for male, but subdued. Sides of body with single distinct reddish-pink stripe. All fins hyaline.

Adult male from Central Kalimantan (Fig. 16C) – head dark brown on dorsum, brown on sides, ventrum cream. Upper jaw yellowish brown with corresponding portion of lower jaw reddish; dorsal surface of exposed lower jaw brown, middle section of dermal flange on lower jaw with distinct pale blue and red markings; ventrum of lower jaw flange with distinct black margin from tip to region directly below upper jaw. Eye with upper half of iris pale blue. Operculum with scattering of melanophores, and pinkish on posterior part. Body with brown dorsal stripe, dorsum and sides pale brown, ventrum cream; sides with two distinct reddish-pink stripes from post-opercle to caudal-fin base, faint third and

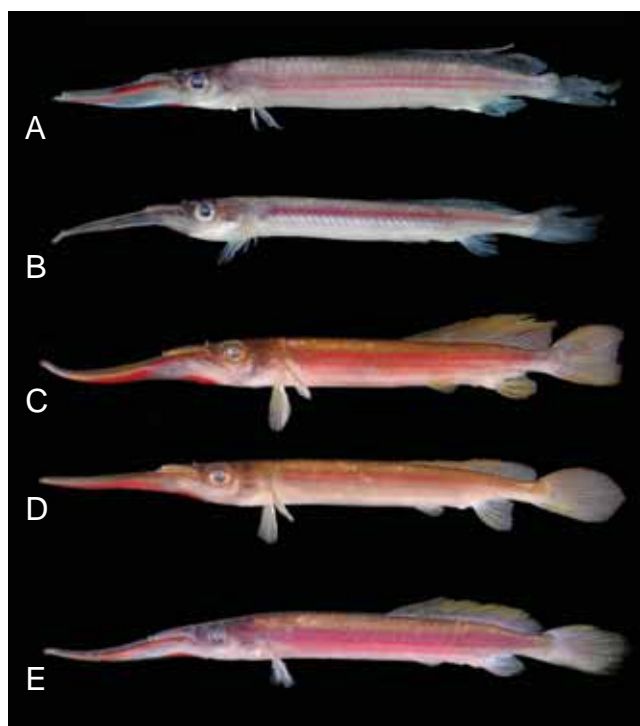


Fig. 16. Freshly preserved material of *H. phaiosoma*: A, ZRC 54012, 57.5 mm SL male, Biliton; B, ZRC 54012, 48.0 mm SL female, Biliton; C, ZRC 54049, 54.6 mm SL male, Kalimantan Tengah, Kotawaringin; D, ZRC 54049, 49.7 mm SL female, Kalimantan Tengah, Kotawaringin; E, ZRC 54048, 54.8 mm SL male, Kalimantan Barat, Anjungan.

fourth pinkish stripes below the two stripes. Dorsal fin yellowish. Caudal and anal fins with reddish margin. Pelvic fin yellowish. Pectoral fin hyaline.

Adult female from Central Kalimantan (Fig. 16D) – colouration as for male, but subdued. Sides of body with single distinct reddish-pink stripe and up to two faint pinkish stripes. All fins hyaline.

Adult male from Anjungan (Fig. 16E) – head dark brown on dorsum and sides, ventrum cream. Upper jaw yellowish brown with corresponding portion of lower jaw reddish; dorsal surface of exposed lower jaw brown, middle section of dermal flange on lower jaw with distinct pale blue and red markings; ventrum of lower jaw flange with distinct black margin from tip to region directly below upper jaw. Eye with upper half of iris pale blue. Operculum with scattering of melanophores, and pinkish on posterior part. Body with brown dorsal stripe, dorsum and sides pale brown, ventrum cream; sides with two distinct reddish-pink stripes from post-opercle to caudal-fin base, and a third faint pinkish stripe below the two stripes. Dorsal fin yellowish. Caudal fin yellowish. Anal, pelvic and pectoral fins hyaline.

From the afore-mentioned colour descriptions, *H. phaiosoma* appears to be variable in colour. Part of this can be attributed to the water conditions in the habitat. For example, in tannin-stained waters, the colours on the fish are more intense than those that occur in clear or murky waters. To ascertain if the Kalimantan populations are distinct from *H. phaiosoma* from Biliton, it would be necessary to obtain a larger series of specimens from the type locality.

**Comparative material examined.** — *Hemirhamphodon phaiosoma* – BMNH 1866.5.2:21, holotype, 40.9 mm SL; Biliton. – ZRC 54012, 2 ex., 49.4–57.5 mm SL; Biliton: Badau area; H. Zhou, Feb.2012. – ZRC 54015, 2 ex., 39.4–45.0 mm SL; ZRC 54016, 7 ex., 29.5–46.8 mm SL; Central Kalimantan: Kudangan; T. Idei, 2004. – ZRC 54049, 30 ex., 9.7–54.6 mm SL; Central Kalimantan: Pankalanbun outskirts, Pasir Panjang, Sungai Pasir Panjang; H. Tommy et al., 11 Mar.2008. – ZRC 54048, 23 ex., 25.0–54.8 mm SL; West Kalimantan: Anjungan, Sungai Belado, Bukit Kloncet base; H. H. Tan et al., 17 Aug.2007. – ZRC 49983, 57 ex., 11.3–51.4 mm SL; West Kalimantan: Anjungan, Sungai Belado, Bukit Kloncet base; H. H. Tan et al., 28 Apr.1998. *Hemirhamphodon pogonognathus* – BMNH 1866.5.2:20, syntype, 50.6 mm SL; Banka. – ZRC 54011, 4 ex., 30.7–45.6 mm SL; Banka: Sungai Baturusa area, near Sempan; H. Zhou, Feb.2012. – ZRC 30729, 7 ex., 28.5–47.7 mm SL; Sumatra: Banka, 9 km east of Muntok; M. Kottelat et al., 4 Mar.1993. – ZRC 31348, 12 ex., 15.2–47.7 mm SL; Sumatra: Banka, 3 km north of Payung; M. Kottelat et al., 5 Mar.1993. – ZRC 31185, 11 ex., 15.0–48.8 mm SL; Sumatra: Banka, 5.5 km north of Payung; M. Kottelat et al., 5 Mar.1993. – ZRC 54014, 3 ex., 43.6–47.0 mm SL; Central Kalimantan: SE Muara Teweh; T. Idei, 2004. – ZRC 54045, 8 ex., 28.7–47.6 mm SL; West Kalimantan: Sungai Sawak, road Sintang-Pontianak near Nanga Pinoh turnoff; H. H. Tan, 15 Aug.2007. – ZRC 54046, 3 ex., 34.1–41.4 mm SL; West Kalimantan: Anjungan, Ulu Sungai Kepayan, km 60 Pontianak on old road; H. H. Tan et al., 17 Aug.2007.

*Hemirhamphodon chrysopunctatus* – ZRC 54017, 2 ex., 50.2–53.0 mm SL; Central Kalimantan: Kasongan; T. Idei, 2004. – ZRC 54018, 1 ex., 36.4 mm SL; Central Kalimantan: Sampit, Plantalang Hulu; T. Idei, 2004.

*Hemirhamphodon tengah* – ZRC 54019, 1 ex., 28.2 mm SL; Central Kalimantan: Sampit, Plantalang Hulu; T. Idei, 2004. – ZRC 54020, 10 ex., 27.4–33.6 mm SL; Central Kalimantan: Sampit, Kuala Kuayan; T. Idei, 2004.

*Hemirhamphodon kuekenthali* – ZRC 42719, 4 ex., 44.0–63.8 mm SL; Brunei Darussalam: Belait District, Sungai Pelok, flowing into Sungei Ingei; H. H. Tan et al., 11 May 1996. – ZRC 42693, 3 ex., 34.3–54.0 mm SL; Brunei Darussalam: Tutong District, Sungai Meluncur east of Tasik Merimbun; H. H. Tan et al., 15 May 1996. – ZRC 37991, 13 ex., 23.5–61.5 mm SL; Sarawak: Marudi airport, Lubok Nibong road; M. Kottelat & T. Tan, 19 Jun.1994. – ZRC 54050, 10 ex., 21.4–45.2 mm SL; Sarawak: Bintulu, Ulu Kakus, Tatau River basin: Batu Rusa, swampforest at Bukit Sarang; H. H. Tan et al., 18 Aug.2005. – ZRC 54052, 8 ex., 30.5–46.1 mm SL; Sarawak: Bintulu, Ulu Kakus, Tatau River basin: Bukit Sarang Field Station, unnamed feeder stream to Sungai Sarang; H. H. Tan et al., 17 Aug.2005. – ZRC 54053, 4 ex., 26.9–40.4 mm SL; Sarawak: Bintulu, Ulu Kakus, Tatau River basin: brown water feeder stream flowing into Sungai Sarang; H. H. Tan et al., 19 Aug.2005. – ZRC 54054, 25 ex., 23.8–46.3 mm SL; Sarawak: Bintulu, Tatau River basin: Sungai Rengah, tributary of Binyo; I. Wong, 26 Sep.2005. – ZRC 54055, 8 ex., 36.0–52.4 mm SL; Sarawak: Bintulu, Tatau River basin: Sungai Pinyilan; I. Wong, 15 Aug.2005. – ZRC 37843, 6 ex., 25.1–61.4 mm SL; Sarawak: outskirts of Sibu, north of airport runway end on Jalan Teku; M. Kottelat et al., 15 May 1994. *Hemirhamphodon kapuasensis* – ZRC 38461, 48.5 mm SL, male holotype; West Kalimantan: Insiluk, 16 km WNW from Sanggau on road to Pontianak; M. Kottelat et al., 23 Apr.1990. – ZRC 54047, 2 ex., 45.0–49.5 mm SL; West Kalimantan: Anjungan, Ulu Sungai Kepayan, km 60 Pontianak on old road; H. H. Tan et al., 17 Aug.2007. – ZRC 50089, 20 ex., 11.9–48.4 mm SL; West Kalimantan: Sintang area, stream at km 442 Pontianak on Sintang-Putussibau road; H. H. Tan et al., 21 Apr.1998. – ZRC 49922, 70 ex., 13.4–46.5 mm SL; West Kalimantan: Sanggau area, stream at km 249 Pontianak on Sosok-Sanggau road; H. H. Tan et al., 26 Apr.1998. – ZRC 50044, 50 ex., 11.1–47.0 mm SL; West Kalimantan: Sintang area, stream bear Nanga Sayan along Nanga Pinoh-Nanga Sayan road; H. H. Tan et al., 24 Apr.1998.

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