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REVISION OF THE *BETTA WASERI* SPECIES GROUP (TELEOSTEI: BELONTIIDAE)

Peter K. L. Ng and **Maurice Kottelat**

ABSTRACT. - A revision of the newly defined *Betta waseri* species group is presented. The identity of *Betta waseri* Krummenacher, 1986 (Teleostei: Belontiidae) is clarified on the basis of fresh material from and near the type locality in the state of Pahang, Peninsular Malaysia. Specimens from peat swamps in the states of Selangor and Perak are referred to a new species, *B. hipposideros*. A second new species, *B. tomi*, is described from freshwater swamps in Johor; this species apparently also inhabited Singapore waters in the past but is now extinct on the island. A third new species, *B. spilotogena*, is also described from freshwater swamps in Pulau Bintan in the Riau Archipelago, Indonesia.

INTRODUCTION

Eight native species of fighting fishes of the genus *Betta* are known at present from Peninsular Malaysia: *Betta pugnax* (Cantor, 1850), *B. bellica* Sauvage, 1884, *B. imbellis* Ladiges, 1975, *B. coccina* Vierke, 1979, *B. tussyae* Schaller, 1985, *B. waseri* Krummenacher, 1986, *B. persephone* Schaller, 1987, and *B. livida* Ng & Kottelat, 1992.

Recent surveys of blackwater fishes in the blackwater peat swamps of northern Selangor (Fig. 1) obtained a large *Betta* initially referred to *Betta* aff. *waseri* (Ng, 1993a; Ng *et al.*, 1992). Direct comparisons with the type as well as fresh material of *B. waseri* obtained from the type locality (near Kuantan, Pahang) revealed distinct differences between the Selangor and Pahang populations. The specimens from northern Selangor are here recognised as a new species, *B. hipposideros*. Another population of *B. waseri*-like specimens from Johor is referred to a second new species, *B. tomi*. A third new species, *B. spilotogena*, is also described from recent material collected from Pulau Bintan, Riau Archipelago, Indonesia.

Witte & Schmidt (1992) recognised several species in what they called the *B. anabatoides* group. *Betta waseri* and the three new species described here however, should be separated

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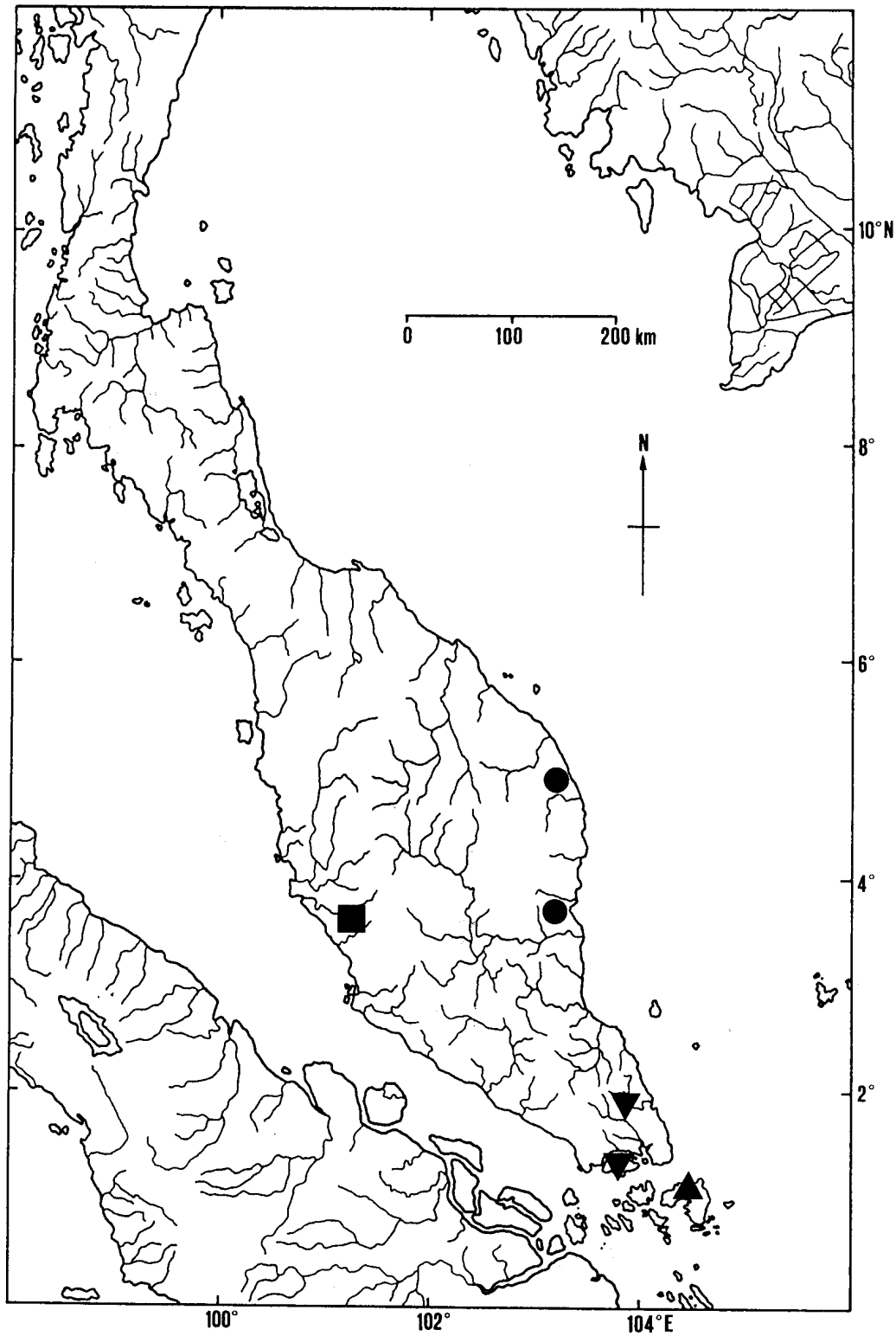

Fig. 1. Map of Peninsular Malaysia, Singapore and Pulau Bintan to indicate known distribution of *Betta waseri* (●), *B. hipposideros* (■), *B. tomi* (▼) and *B. spilotogena* (▲).

into another group. The *Betta waseri* group may be characterised as follows: large, stout-bodied, mouth-brooding *Betta*, adult 60-90 mm SL; vertebral formula 2, 8-9, 21-22 (total 31-33); operculum without iridescent scales; lower lip always black, throat with two oval black marks of varying shape and size which may coalesce with black lower lip marking; body brown, with submedian brown or black stripe which runs from just behind eye to mid-basal caudal spot, with broken, narrow brown or black stripe just above anal fin sheath scales; flanks of males with scattered or patches of iridescent golden scales on anterior half; scale counts: lateral 31-32$^1/_2$, transverse 8$^1/_2$-10$^1/_2$.

MATERIAL AND METHODS

The meristic and morphometric measurements used here essentially follow that proposed by Witte & Schmidt (1992); see Ng (1993b) for minor modifications. Specimens are deposited in: California Academy of Sciences, San Francisco (CAS), U.S.A.; Museum Zoologicum Bogoriense, Bogor (MZB), Indonesia; Zoologisches Museum der Universität, Zurich (ZMZ), Switzerland; Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore; and the collections of the second author (CMK) and Kai Erik-Witte (KEW).

SYSTEMATICS

Betta waseri Krummenacher, 1986
(Figs. 2A; 3A, B; 4A, B; 5)

Betta waseri Krummenacher, 1986: 177.
Betta macrophthalma: Schmidt, 1988: 341; Linke, 1990: 37 (nec Regan, 1910).

Material examined. - Holotype - ZMZ 129201, male, 90.8 mm SL; PENINSULAR MALAYSIA: PAHANG, Kuantan, 22.5 km from Kuantan; coll. W. Schar, viii.1985.

Other material - PENINSULAR MALAYSIA: PAHANG: KEW 5.12, female, 48.5 mm SL; same locality as holotype, no other data. — ZRC 35402, male, 80.7 mm SL; 16 km stone, Johor Bahru to Kuantan road, shallow blackwater stream, pH 4.0; coll. P.K.L. Ng *et al.*, 9.iii.1992. — ZRC 35403-35408, 6 ex., 80.3, 50.8, 46.3, 43.7, 42.4, 39.6 mm SL; ca. 100 m south of 68 km stone, on road from Johor Bahru to Kuantan, near Pekan, well shaded peat swamp forest stream, blackwaters, pH 3.4; coll. P.K.L. Ng *et al.*, 19.x.1992. — CMK 8057, 4 ex., 20.6-44.0 mm SL; same locality; coll. M. Kottelat *et al.*, 9.iii.1992. — ZRC 18617-18620, 4 ex., 20.5-33.2 mm SL; about 200 m north of 16 km stone, on road from Johor Bahru to Kuantan; coll. P.K.L. Ng *et al.*, 20.x.1991. — ZRC 25907, 1 ex., 56.6 mm SL, CMK 8074, 2 ex.; stream at 16 km stone, on road from Mersing to Kuantan; coll. P.K.L. Ng *et al.*, 9.iii.1992. — ZRC 25210, 25211, 2 ex., 21.9, 32.0 mm SL; stream at 16 km stone, on road from Mersing to Kuantan; coll. P.K.L. Ng *et al.*, 9.iii.1992. – CMK 3189, 1 ex., 31.1 mm SL; Kuantan, Sungai Soi; coll. P. Nagy, v.1981. TERENGGANU: ZRC 24370, 1 ex., 19.7 mm SL; near Rantau Abang, 56 km stone, on road from Kuantan to Kuala Terengganu; coll. P.K.L. Ng *et al.*, 18.iii.1992.

Diagnosis. - The differences between *B. waseri* and the three new species in their throat markings, markings on the dorsal, anal and caudal fin membranes, number of transverse scales, lateral scales above beginning of anal fin, lateral scales below beginning of dorsal fin, subdorsal scales, postdorsal scales, dorsal fin rays, and proportions of the head, body

depth, and distance from edge of operculum to base of first dorsal fin ray or spine, are summarised in Table 1.

Description. - Body relatively long, stout, body depth 23.1-27.6% SL; HL 28.6-33.3% SL; vertebral formula 2, 9, 22 (total 33); head short, stout (Fig. 3A, B); lower margin of operculum black, operculum with several short, black streaks, without iridescent green scales; throat with two tear-drop shaped black marks below but not connected to black lower lip (Fig. 2A); body brown, with broad, submedian brown stripe which runs from just behind eye to caudal peduncle, with broken, narrow brown stripe just above anal fin sheath scales; flanks of males with 9-15 scattered golden scales on anterior half; distal part of pelvic rays iridescent yellow. Scale counts: lateral $31^1/_2$-$32^1/_2$ (mode 32), transverse $9^1/_2$-10 (mode $9^1/_2$), dorsal fin begins at lateral scale 17-18 (mode 17), anal fin begins at lateral scale 8-9 (mode 8), predorsal $23^1/_2$-24 (mode 24), subdorsal 6-$6^1/_2$ (mode 6) (Fig. 4A, B), postdorsal $10^1/_2$-12 (mode 11). Fin ray counts: dorsal I, 8-9 (total 9-10, mode 9), caudal ii,6+7,i, anal II, 26-29 (total 28-31, mode 30), pelvic I,1,4, pectoral 13-15 (mode 14) (see Table 2).

Remarks. - *Betta waseri* was described from aquarium specimens, and only one large male (the holotype) was preserved (Krummenacher, 1986). Schmidt (1988) suggested that *B. waseri* was synonymous with *B. macrophthalma* Regan, 1910 (type locality Singapore), a classification followed by Linke (1990). The two species however, differ significantly in body form and meristics, and *B. macrophthalma* belongs to the *B. pugnax* group. Witte & Schmidt (1992) regarded *B. macrophthalma* as a subjective synonym of *B. pugnax*, and noted that *B. waseri* was a distinct species belonging to a group they referred to as the *B. anabatoides* complex.

The main species character of *B. waseri*, as depicted by Witte & Schmidt (1992: 320 Fig. 8o) and Kottelat & Whitten (1993: Fig. 317d), is the distinctive throat marking; the lower lip being black, with two black, tear drop-like spots on the throat (Fig. 2A). The pattern of the throat markings in *B. waseri* is very constant in the series of specimens obtained, and is evident even in juveniles. As a species character, it seems to be reliable (see General Remarks).

Krummenacher (1986) reported the SL of the holotype as 97.5 mm. The specimen actually is 90.8 mm SL. The length of 97.5 mm corresponds to the length from the tip of the chin to the posterior edge of last scale on caudal fin.

Sexual dimorphism. - The head of adult males, especially the snout, is generally sharper and more tapering than in adult females which appear blunter. The colour patterns of both sexes differ, with the dark stripes and markings on the head, operculum and flanks more pronounced in females. Only males apparently possess scattered gold scales on the anterior half of the flanks.

Colour notes. - In juveniles of this species, the distal half of the anal fin is pale red whilst the proximal half is a pale dull green. These colours are not obvious in large individuals. None of the specimens examined has the vertical black bars on the dorsal or caudal fin membranes so distinct in *B. hipposideros*.

Ecological notes. - Sampling around the now very disturbed type locality of *B. waseri* (around Kuantan) obtained only few specimens, most of which were juveniles. Nevertheless, most of the juveniles possessed the very distinctive throat markings which characterise the species. At a site some 30 kilometres from Kuantan, on the Kuantan to Pekan road, large specimens were found, suggesting that the primary habitat of the species seems to be well shaded peat forest blackwater streams with dense leaf litter beds, mud substrates and dense growths of roots. The waters in this stream were shallow, flowing blackwaters with a pH between 4 and 5. The habitats near Kuantan were also blackwater habitats, albeit very disturbed by human activities. Belontiids occuring sympatrically with *B. waseri* were *Betta bellica*, *B. tussyae*, *Parosphromenus nagyi*, *Sphaerichthys osphromenoides*, *Trichogaster trichopterus* and *Belontia hasselti*.

Distribution. - Known from the Malaysian states of Pahang and Terengganu.

Betta hipposideros, new species

(Figs. 2B; 3C, D; 4C, D; 6)

Material examined. - Holotype - ZRC 18688, male, 69.0 mm SL, PENINSULAR MALAYSIA: SELANGOR, north Selangor peat swamp forest, 39 km stone, on road from Sungai Besar to Tanjong Malim; coll. P.K.L. Ng *et al.*, 24.viii.1991.

Paratypes - PENINSULAR MALAYSIA: SELANGOR: ZRC 18689-18705, 17 ex., 33.4-71.1 mm SL, north Selangor peat swamp forest, 39 km stone, on road from Sungai Besar to Tanjong Malim; coll. P.K.L. Ng *et al.*, 24.viii.1991. — ZRC 15351, 1 ex., 32.0 mm SL, north Selangor peat swamp forest, stream at 34 km stone, on road to Tanjong Malim; coll. Zoology Honours Class, 17.vi.1991. — ZRC 15352, 1 ex., 25.9 mm SL, north Selangor peat swamp forest, stream at 50 km stone, on road to Tanjong Malim (United Plantations Estate); coll. Zoology Honours Class, 18.vi.1991. — ZRC 15353, 1 ex., 43.1 mm SL, north Selangor peat swamp forest, stream at 43 km stone, on road to Sungai Besar; coll. Zoology Honours Class, 18.vi.1991. — ZRC 15354, 15355, 2 ex., 27.5, 37.0 mm SL, north Selangor peat swamp forest, stream 700 m from 41 km stone, on road to Tanjong Malim; coll. Zoology Honours Class, 19.vi.1991. — ZRC 15356, 15357, 2 ex., 35.3, 38.7 mm SL, north Selangor peat swamp forest, 47 km stone, on road from Sungai Besar to Tanjong Malim; coll. Zoology Honours Class, 19.vi.1991. — ZRC 15358-15361, 4 ex., 25.8-39.6 mm SL, north Selangor peat swamp forest, 800 m from 45 km stone, on road to Sungai Besar; coll. Zoology Honours Class, 18.vi.1991. — ZRC 17097, 1 ex., 54.6 mm SL, north Selangor peat swamp forest, stream at 50 km stone, on road to Tanjong Malim (United Plantations Estate); coll. K.K.P. Lim, 14.ix.1991. — ZRC 18029-18034, 6 ex., 29.5-47.3 mm SL, north Selangor peat swamp forest, 500 m from 36 km stone, on road to Tanjong Malim; coll. P.K.L. Ng *et al.*, 25.viii.1991. — ZRC 27761, 1 ex., 64.0 mm SL, north Selangor peat swamp forest, 650 m from 35 km stone, on road from Sungai Besar to Tanjong Malim; coll. P.K.L. Ng *et al.*, 18.ix.1992. — ZRC 28550, 1 ex., 25.2 mm SL, north Selangor peat swamp forest, 200 m from 45 km stone, road to Sungai Besar; coll. P.K.L. Ng *et al.*, 18.ix.1992. — CMK 10037, 16 ex., 37.8-77.8 mm SL, north Selangor peat swamp forest, stream at 43 km stone on road from Tanjong Malim to Sungai Besar; coll. P.K.L. Ng *et al.*, 19.vi.1991. — CMK 10038, 10 ex., 27.9-59.6 mm SL, north Selangor peat swamp forest, stream at 0.2 km from 45 km stone on road from Tanjong Malim to Sungai Besar; coll. P.K.L. Ng *et al.*, 17.vi.1991. PERAK: ZRC 28515-28517, 69.1-77.9 mm SL, peat swamp forest, north shore of Sungai Bernam; coll. P.K.L. Ng *et al.*, 19.ix.1992.

Diagnosis. - The differences between *B. hipposideros*, *B. waseri*, *B. tomi* and *B. spilotogena* in the markings of their throats, dorsal, anal and caudal fin membranes of adult males, number of transverse scales, lateral scales above beginning of anal fin, lateral scales below beginning of dorsal fin, subdorsal scales, postdorsal scales, dorsal fin rays, and proportions of the head, body depth, and distance from edge of operculum to base of first dorsal fin ray or spine, are summarised in Table 1.

Description. - Body relatively long, stout, body depth 23.8-33.1% SL; HL 28.3-34.1% SL; vertebral formula 2, 9, 21-22 (total 32-33); head short, stout (Fig. 3C, D); lower margin of operculum yellow or brown, operculum with only one or two black spots, without iridescent green scales; throat with two large black spots which join median part of black lower lip forming an inverted U-shaped mark (Fig. 2B); body brown, with broad, submedian brown stripe which runs from just behind eye to caudal peduncle, with broken, narrow brown stripe just above anal fin sheath scales; flanks of males with 10-30 scattered golden scales on front half, golden scales sometimes arranged together in one group; distal part of pelvic rays iridescent yellow; dorsal and caudal fins with ladder-like vertical bars on membranes. Scale counts: lateral 31- 32 (mode 32), transverse $9^1/_2$-$10^1/_2$ (mode $9^1/_2$), dorsal fin begins over lateral scale 16-18 (mode 16), anal fin begins under lateral scale 7-8 (mode 7), predorsal 21-24 (mode 23), subdorsal $6^1/_2$-7 (mode $6^1/_2$) (Fig. 4C, D), postdorsal 9-10

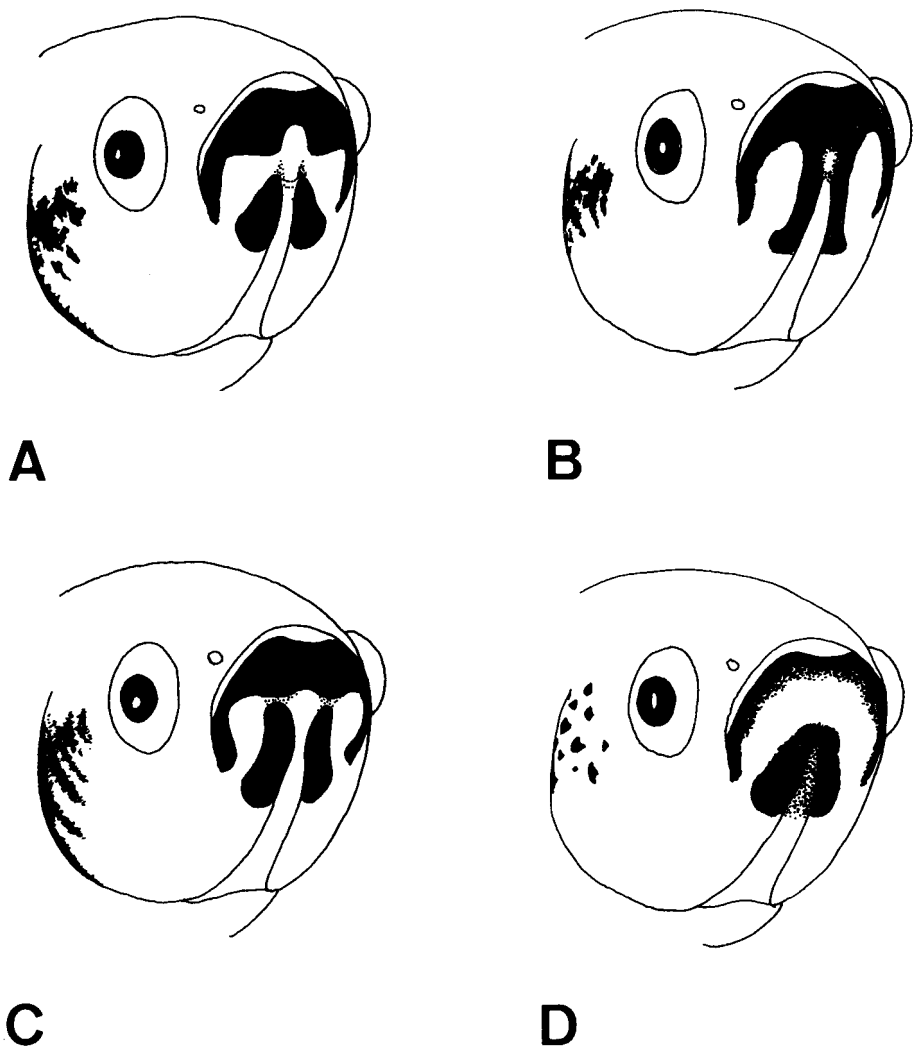

Fig. 2. Schematic figures to show throat patterns. A, *Betta waseri;* B, *B. hipposideros;* C, *B. tomi;* D, *B. spilotogena.*

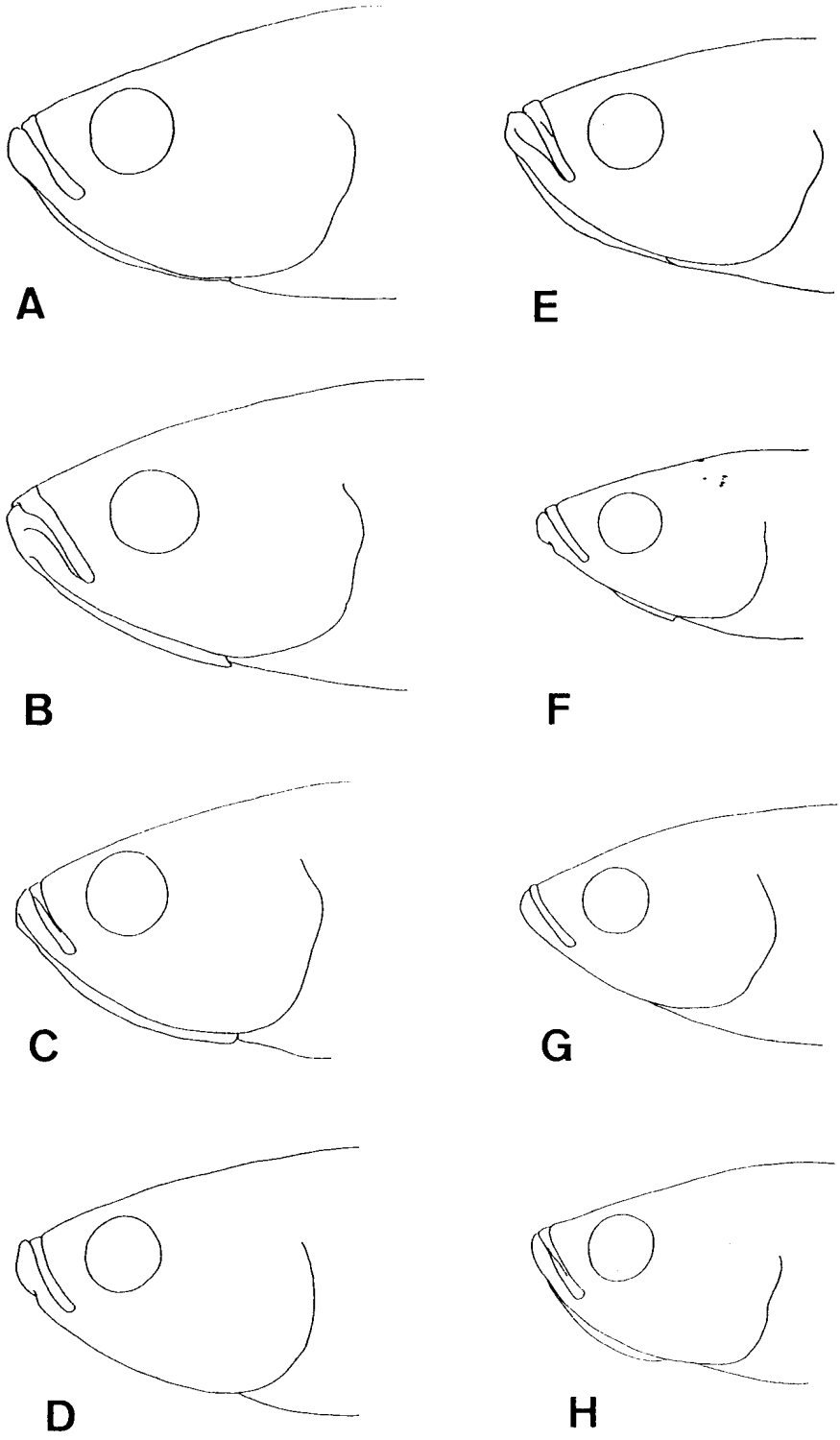

Fig. 3. Head shapes. *Betta waseri:* A, ZRC 35403, 80.3 mm SL, Pahang; B, ZRC 35402, 80.7 mm SL, Pahang. *Betta hipposideros:* C, ZRC 18688, holotype, 69.0 mm SL, Selangor; D, ZRC 18691, paratype, 66.9 mm SL, Selangor. *Betta tomi:* E, ZRC 35409, holotype, 70.4 mm SL, Johor; F, ZRC 35411, paratype, 64.9 mm SL, Johor; G, CAS 133176, 73.0 mm SL, Singapore. *Betta spilotogena:* H, ZRC 35417, holotype, 69.7 mm SL, Pulau Bintan.

(mode $9^1/_2$). Fin ray counts: dorsal I, 8-9 (total 9-10, mode 10), caudal ii,6+7,i, anal I-II, 27-29 (total 28-31, mode 30), pelvic I,1,4, pectoral 13-15 (mode 14) (see Table 2).

Etymology. - The name is derived from the Latin for horseshoe, alluding to the distinctive throat markings of the species. It is used as a noun in apposition.

Remarks. - *Betta hipposideros* has the deepest body depth of the three species, giving the fish a very short and stout appearance. The snout in adult males is also generally blunter. In this respect, it is closer to *B. tomi*.

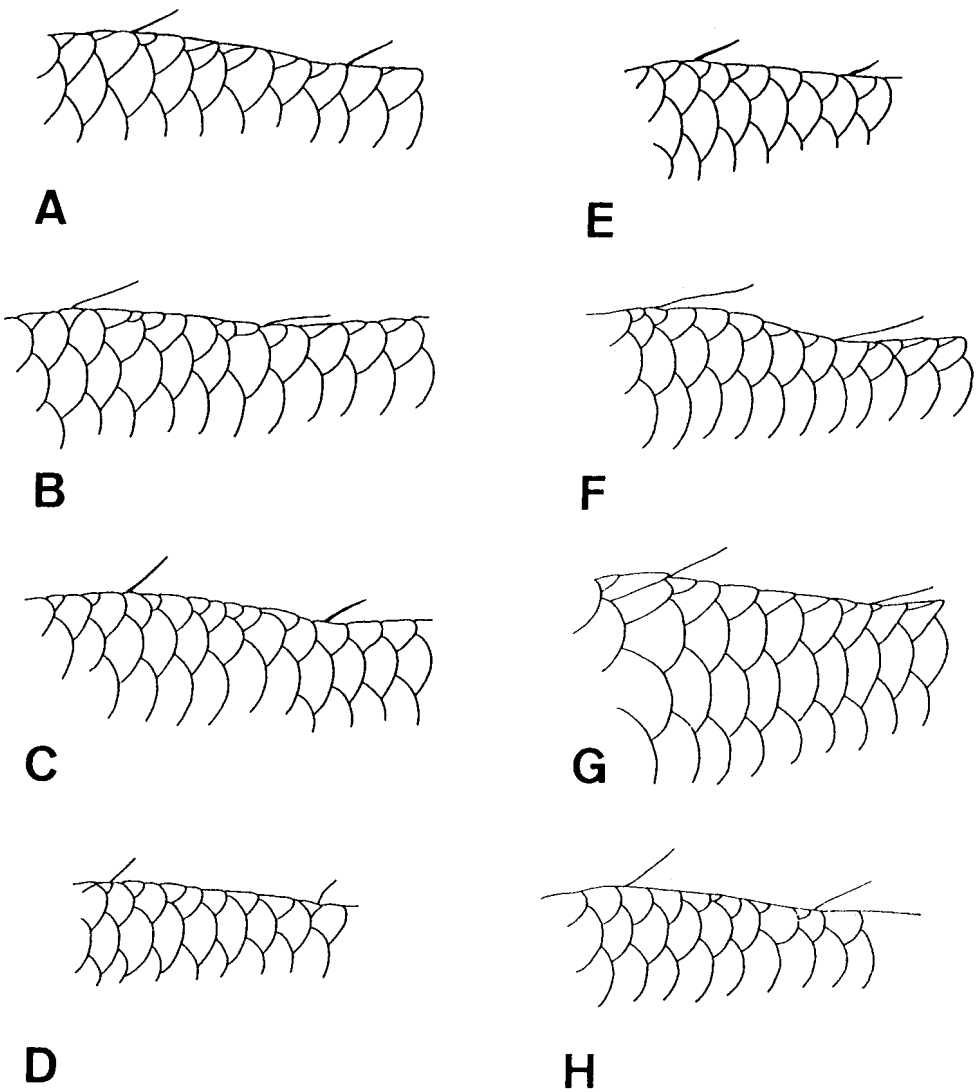

Fig. 4. Subdorsal scalation. *Betta waseri:* A, ZRC 35403, 80.3 mm SL, Pahang; B, ZRC 35402, 80.7 mm SL, Pahang. *Betta hipposideros:* C, ZRC 18688, holotype, 69.0 mm SL, Selangor; D, ZRC 18691, paratype, 66.9 mm SL, Selangor. *Betta tomi:* E, ZRC 35409, holotype, 70.4 mm SL, Johor; F, CAS 133176, 73.0 mm SL, Singapore; G, CAS 133176, 56.0 mm SL, Singapore. *Betta spilotogena:* H, ZRC 35417, holotype, 69.7 mm SL, Pulau Bintan.

The ladder-like pattern of vertical black bars on the caudal membranes are present in adults of both sexes, although they are usually darker and more distinct in males. Smaller specimens occasionally lack these ladder-like caudal membrane patterns or have it less distinct.

Betta waseri was reported from Penang, Peninsular Malaysia by Schmidt (1988: fig. 6) and Witte & Schmidt (1992). The throat markings of the Penang specimen resembles that of *B. hipposideros*, but in the absence of specimens, this cannot be ascertained.

Sexual dimorphism. - Although the snout and head of *B. hipposideros* (Fig. 3C, D) are generally blunter than those of *B. waseri* (Fig. 3A, B), that of adult male *B. hipposideros* are still sharper than that of adult females. The black markings on the head and flanks are more distinct in adult females than that on the adult males. The golden scales on the front half of the flanks are more distinct in males.

Colour notes. - The lack of a black lower margin on the operculum is constant for this species.

Ecological notes. - *Betta hipposideros* has been found only in blackwater peat swamps so far. The pH of the waters are between 3.5-3.7 (Ng *et al.*, 1992). Larger specimens occured

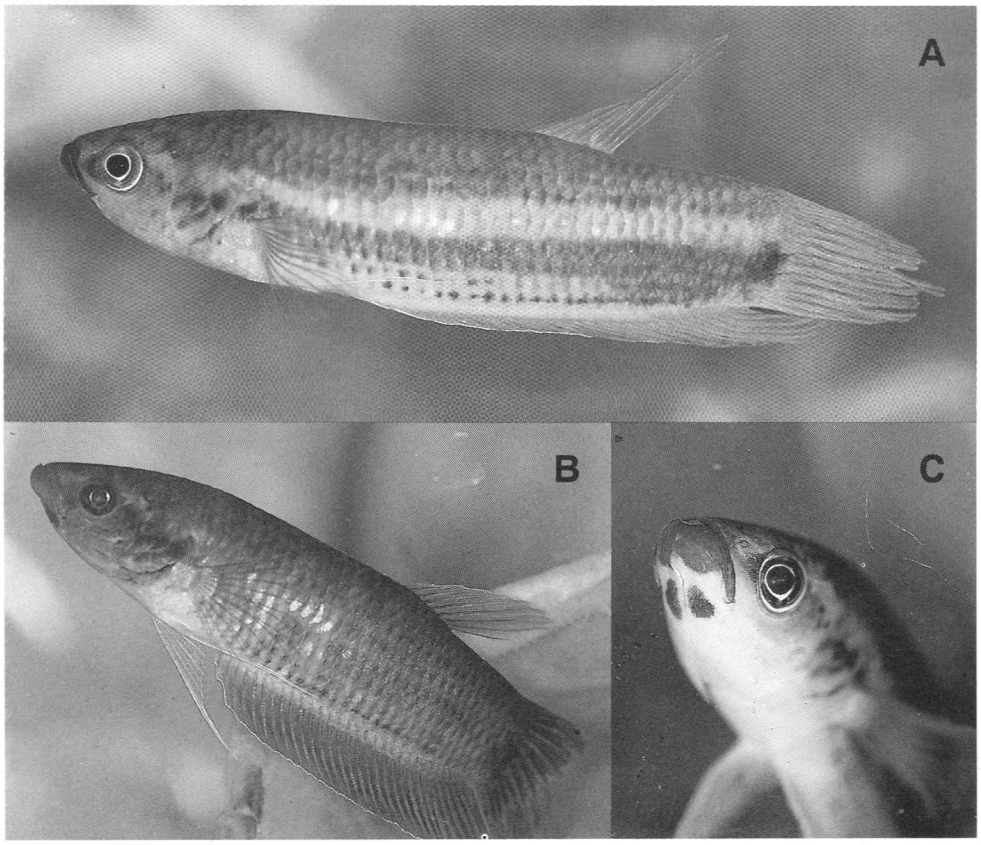

Fig. 5. Betta waseri. A, C, ZRC 35403, 80.3 mm SL, Pahang; C, ZRC 35402, 80.7 mm SL, Pahang.

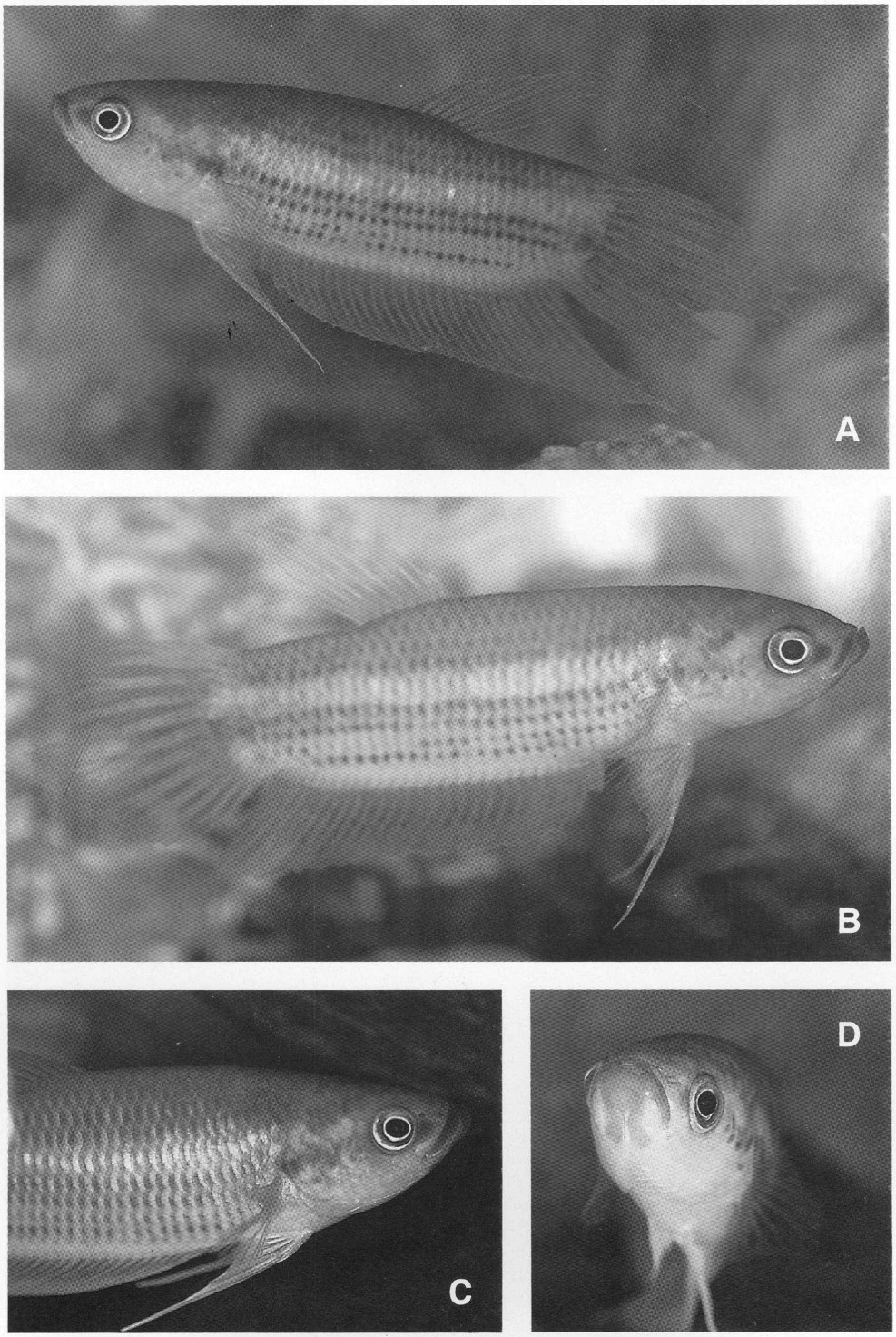

Fig. 6. *Betta hipposideros.* A, C, D, adult male (ca. 65 mm SL), Selangor; B, adult female (ca. 60 mm SL), Selangor. Specimens not preserved.

in the flowing sections of the blackwater streams whereas smaller ones appear to prefer pools and slower flowing waters. The substrate was usually peat and leaf litter. Other belontiid species found sympatrically with *B. hipposideros* were *Betta bellica*, *B. livida*, *Parosphromenus harveyi*, *Sphaerichthys osphromenoides*, *Trichogaster leerii*, *T. pectoralis* (feral), *T. trichopterus* and *Belontia hasselti*.

Distribution. - Known only from the Malaysian states of Selangor and Perak.

Betta tomi, new species
(Figs. 2C; 3E-G; 4E-G; 7)

Material examined. – Holotype - ZRC 35409, male, 70.4 mm SL; PENINSULAR MALAYSIA: JOHOR, tributary of Sungai Mupor, about 15 km on road from Kota Tinggi to Mersing, ca. 1°52'N, 103°56'E, freshwater swamp forest; coll. P.K.L. Ng, viii.1992.

Paratypes - PENINSULAR MALAYSIA: JOHOR, ZRC 35410, 1 ex., 37.6 mm SL; same data as holotype. — CMK 9753, 6 ex., 16.8-60.4 mm SL; same locality as holotype; coll. M. Kottelat, P.K.L. Ng & K. Lim, 22.i.1991. — ZRC 35411-35416, 6 ex., 64.9, 55.9, 37.5, 34.3, 33.2, 24.8 mm SL; tributaries of Sungai Mupor, freshwater swamp forest; coll. P.K.L. Ng *et al.*, 13.i.1993.

Other material - PENINSULAR MALAYSIA: JOHOR, ZRC 18059-18073, 15 ex., 11.8-20.9 mm SL; north of Mersing, 177 km milestone, on road from Johor Bahru to Kuantan; coll. P.K.L. Ng *et al.*, 19.x.1991. SINGAPORE, CAS 133176, 7 ex., 32.5-73.0 mm SL; Mandai Road area, swamp forest; coll. A.W.C.T. Herre, 1937.

Diagnosis. - The differences between *B. tomi*, *B. waseri*, *B. hipposideros* and *B. spilotogena* in their throat markings, markings on the dorsal, anal and caudal fin membranes, number of transverse scales, lateral scales above beginning of anal fin, lateral scales below beginning of dorsal fin, subdorsal scales, postdorsal scales, dorsal fin rays, and proportions of the head, body depth, and distance from edge of operculum to base of first dorsal fin ray or spine, are summarised in Table 1.

Description. - Body relatively long, stout, body depth 24.1-29.8% SL; HL 29.3-37.1% SL; vertebral formula 2, 8, 21 (total 31); head short, stout (Fig. 3E-G); lower margin of operculum black, operculum with several short, black streaks, without iridescent green scales; throat with two black oval spots which do not merge with black lower lip (Fig. 2C); body brown, with broad, submedian brown stripe which runs from just behind eye to caudal peduncle, with broken, narrow black stripe just above anal fin sheath scales; flanks of males with 10-16 scattered golden scales on front half; distal part of pelvic rays iridescent yellow; distal margin of anal fin often with dark green band. Scale counts: lateral 31-32 (mode 31), transverse $9^1/_2$-$10^1/_2$ (mode 10), dorsal fin begins at lateral scale 15-17 (mode 16), anal fin begins at lateral scale 7-8 (mode 7), predorsal 21-23 (mode 23), subdorsal 5-$5^1/_2$ (mode 5) (Fig. 4E, F), postdorsal 10-$10^1/_2$ (mode 10). Fin ray counts: dorsal I, 8-9 (total 9-10, mode 9), caudal ii,6+7,i, anal II, 26-29 (total 28-31, mode 30), pelvic I,1,4, pectoral 13-14 (mode 14) (see Table 2).

Etymology. - The species is named after the head of the Department of Zoology, National University of Singapore, Professor "Tom" Lam Toong Jin, who has generously supported the authors' research over the years.

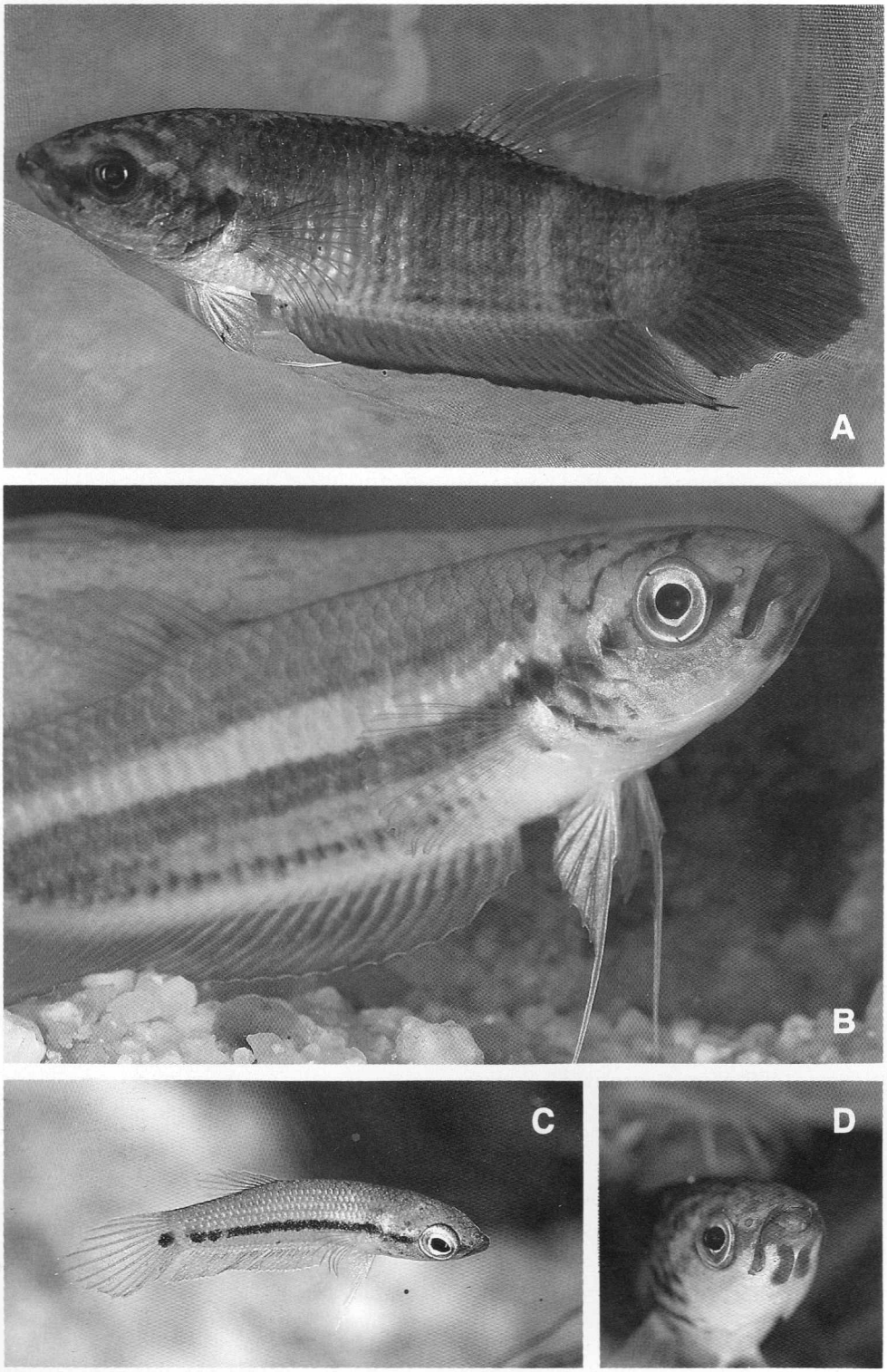

Fig. 7. *Betta tomi.* A, ZRC 35409, holotype, 70.4 mm SL, Johor; B, D, ZRC 35411, paratype, 64.9 mm SL, Johor; C, ZRC 18059, 11.8 mm SL, Johor.

Remarks. - Adult *B. tomi* resembles *B. hipposideros* in body physiognomy, being generally a shorter and stouter fish compared to *B. waseri*. The body depth is generally deeper. The male of *B. tomi* (Fig. 3E) also has a blunter snout like *B. hipposideros* (Fig. 3C). *Betta tomi* has a mixture of characters and it is difficult to ascertain if it is closer to *B. waseri* or *B. hipposideros*. In body form and throat markings, as well as most morphometric features, it is certainly closer to *B. hipposideros*, but in the patterns of the operculum, body and fins, it is closer to *B. waseri*.

Adult *B. tomi* can be distinguished from *B. pugnax* which occurs sympatrically in the type locality in reaching a much larger size (*B. pugnax* does not usually exceed 60 mm SL), having a distinctly stouter body, more anal fin rays (26-29, against 25 or less in *B. pugnax*), absence of iridescent green or blue scales on the operculum or flanks, and the presence of two black tear drop-like black markings on the throat (Fig. 2C) (a chin- bar present in *B. pugnax*). The distinct dark green distal band present in some specimens of *B. tomi* is also always absent in *B. pugnax*. Juvenile *B. tomi* can also be easily distinguished from *B. pugnax* in having a thick black median stripe on the flanks (against broken or scattered black patches).

The specimens from Singapore in the CAS are tentatively referred to *B. tomi*. The largest specimen (73.0 mm SL), apparently a female, resembles the type series of *B. tomi* from Johor quite well, although its colour markings (especially the throat markings) are not clearly discernible. In the stoutness of the head, most of the scale and fin ray counts, as well as morphometrics, they are closer to *B. tomi* than *B. spilotogena*. One difference observed is in the number of subdorsal scales. The specimens of *B. tomi* from Johor all have between 5-5$^{1}/_{2}$ scales (mode 5) (Fig. 4E), whereas the specimens from Singapore have six subdorsal scales (Fig. 4F, G). It cannot be dismissed however, that Singapore previously had a species distinct from both *B. tomi* and *B. spilotogena*. The area in Singapore where Herre collected his specimens has been completely changed and the best swamp forest in that area has already been lost to development and reservoir expansion. The authors and their colleagues have never encountered this species in Singapore. Collections in the only extant freshwater swamp forest left in Singapore (see Ng & Lim, 1992) have failed to uncover any specimens, juvenile or otherwise, belonging to the *B. waseri* group.

Sexual dimorphism. - The heads of the adult male appears shorter and the snout blunter than adult females which appear sharper. The dark stripes and markings on the head, operculum and flanks are also more pronounced in females. Only males apparently possess scattered gold scales on the front half of the flanks. The broad dark green margin on the anal fin may be a sexual character, present only in males.

Colour notes. - The males of *B. tomi* has the most intense colour pattern of the four species of the *waseri* group. In life, the lower margin of the operculum in all the specimens was black. None of the specimens examined has vertical black bars on the dorsal or caudal fin membranes.

Ecological notes. - The type specimens of *B. tomi* (from Johor, Malaysia) were collected in well shaded shallow streams in a freshwater swamp forest draining into a large stream. The substrate was very soft mud with a great deal of leaf litter and detritus. The water in the streams was clear, had a pH of about 5.5, and was very pale tea-coloured. Only two species of belontiids were found sympatrically with *B. tomi*: *Betta pugnax* and *Trichogaster trichopterus*.

Distribution. - Known only from eastern Johor, Peninsular Malaysia, and possibly from Singapore previously.

Betta spilotogena, new species
(Figs. 2D; 3H; 4H; 8)

Material examined. - Holotype - ZRC 35417, male, 69.7 mm SL; INDONESIA: RIAU ARCHIPELAGO, small stream, northern Pulau Bintan; coll. N. Sivasothi *et al.*, 13.v.1993.

Paratypes - INDONESIA: RIAU ARCHIPELAGO, ZRC 35418-35420, 3 ex., CMK 10021, 2 ex., 35.4-66.0 mm SL; same data as holotype. — ZRC 35421-35431, 11 ex., MZB, 3 ex., 15.0-62.8 mm SL; northeastern Pulau Bintan, Tanjong Bintan, freshwater swamp, coll. P.K.L. Ng *et al.*, 10-15.v.1993. — ZRC 34783, 1 ex., 58.0 mm; northern Pulau Bintan, 1°09'34.6"N 104°31'57"E; coll. N. Sivasothi *et al.*, 13.v.1993. — ZRC 34748, 1 ex., 57.9 mm SL; northern Pulau Bintan; coll. N. Sivasothi *et al.*, 12.v.1993.

Other material - ZRC 35394, 35395, 2 ex., 49.4, 54.4 mm SL; northern Pulau Bintan, stream after Uban Pinang road, 56 km stone, near Gunung Demit; coll. P.K.L. Ng *et al.*, 11-15.v.1993. — ZRC 35396-35400, 5 ex., 11.4-42.1 mm SL; northern Pulau Bintan, stream after Uban Pinang road, 56 km stone, near Gunung Demit; coll. P.K.L. Ng *et al.*, 11-15.v.1993. — ZRC 35401, 1 ex., 63.2 mm SL; northern Pulau Bintan, stream after Uban Pinang road, 56 km stone, near Gunung Demit; coll. P.K.L. Ng *et al.*, 11-15.v.1993.

Diagnosis. - The differences between *B. spilotogena* and the other species in the *B. waseri* group in their head proportions, throat and opercular markings, markings on the dorsal, anal and caudal fin membranes, lateral scales above beginning of anal fin, lateral scales below beginning of dorsal fin, subdorsal scales, postdorsal scales, dorsal fin rays, and proportions of the head, body depth, distance from edge of operculum to beginning of dorsal fin are summarised in Table 1.

Description. - Body relatively long, stout, body depth 25.6-28.7% SL; HL 25.6-33.4% SL; vertebral formula 2, 9, 22 (total 33); head stout (Fig. 3H); lower margin of operculum black, operculum distinctly covered with several large black spots in adults, without iridescent green scales; throat with two very broad black oval spots which may appear joined medially, spots do not merge with black lower lip (Fig. 2D); body brown, with broad, submedian brown stripe which runs from just behind eye to caudal peduncle, with broken, distinct black stripe just above anal fin sheath scales; flanks of males with scattered golden scales on front half; distal part of pelvic rays iridescent yellow. Scale counts: lateral 31-32 (mode 32), transverse 9-9$^1/_2$ (mode 9$^1/_2$), dorsal fin begins at lateral scale 16-17 (mode 17), anal fin begins at lateral scale 7-8 (mode 7), predorsal 23-25 (mode 24), subdorsal 5$^1/_2$-6 (mode 5$^1/_2$) (Fig. 4H), postdorsal 10-10$^1/_2$ (mode 10). Fin ray counts: dorsal 0-I, 8-9 (total 8-10, mode 9), caudal ii,6+7,i, anal II-III, 27-29 (total 29-31, mode 30), pelvic i,1,4, pectoral 12-13 (mode 13) (see Table 2).

Etymology. - The name is derived from the Latin for "spotted cheeks", alluding to the distinctive spotted pattern on the operculum of adults. The name is a noun in apposition.

Remarks. - *Betta spilotogena* seems to be closest to *B. tomi* from Johor and Singapore, but can easily be distinguished by its proportionately longer and more slender head, more elongate body, as well as the spotted operculum in life.

Sexual dimorphism. - Males have somewhat blunter snouts compared to the females, and the fins are also distinctly longer and richer in coloration.

Colour notes. - The spotted operculum in *B. spilotogena* is present in both sexes and distinct even in small specimens.

Ecological notes. - The species occurs in freshwater swamps as well as in adjacent streams, usually in relatively shallow water about a metre or so in depth with dense vegetation growing along the banks and under shade. The water was typically clear or tea-coloured with a pH between 4.9-5.5. Belontiids collected with *B. spilotogena* include *Betta edithae*, *B. miniopinna* and *B. fusca*.

Distribution. - Known only from northern part of Pulau Bintan.

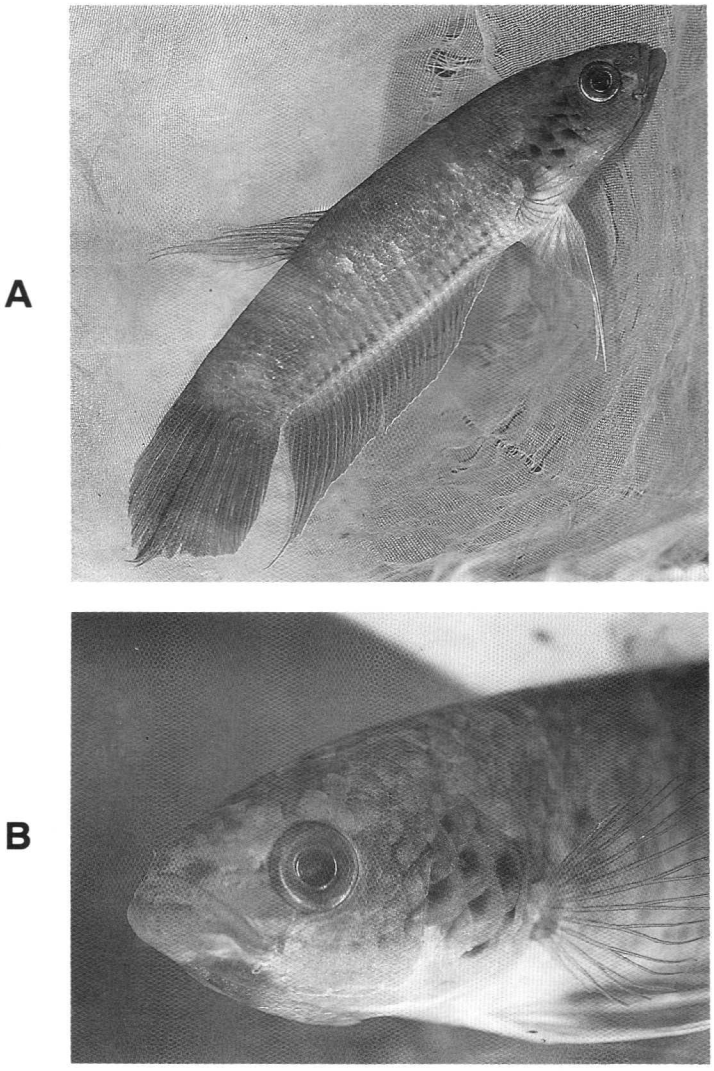

Fig. 8. *Betta spilotogena.* A, B, adult male (ca. 70 mm SL), Pulau Bintan. Specimen not preserved.

Table 1. Differences between *Betta waseri, B. hipposideros, B. tomi* and *B. spilotogena*

	B. waseri	*B. hipposideros*	*B. tomi*	*B. spilotogena*
black throat marking type	"tear-drop" type (Fig. 2A)	"horseshoe" type (Fig. 2B)	"semi-horseshoe" type (Fig. 2C)	black median spot type (Fig. 2D)
dorsal fin membrane (adult male)	without horizontal bars	usually with horizontal bars	without horizontal bars	without horizontal bars
caudal fin membrane (adult male)	without vertical black bars, not ladder-like	usually with distinct vertical black ladder-like bars	without vertical black bars, not laddder-like	without vertical black bars, not ladder-like
edge of anal fin	hyaline, if dark green margin present, very narrow	hyaline, if dark green margin present, very narrow	usually with narrow dark green margin, sometimes broad and distinct	hyaline, if dark margin present, narrow
operculum	lower margin black	lower margin yellow/brown	lower margin black	surfaces spotted, lower margin black
Transverse scales (mode)	9 1/2-10 (9 1/2)	9 1/2-10 1/2 (9 1/2)	9 1/2-10 1/2 (10)	9-9 1/2 (9 1/2)
Lateral scales below dorsal fin (mode)	17-18 (17)	16-18 (16)	15-17 (16)	16-17 (17)
Lateral scales above anal fin (mode)	8-9 (8)	7-8 (7)	7-8 (7)	7-8 (7)
Subdorsal scales (mode)	6-6 1/2 (6)	6 1/2-7 (6 1/2)	5-5 1/2 (5)	5 1/2-6 (5 1/2)
Postdorsal scales (mode)	10 1/2-12 (11)	9-10 (9 1/2)	10-10 1/2 (10)	10-10 1/2 (10)
Dorsal rays (mode)	I,8-9 (I,8)	I,8-9 (I,9)	I,8-9 (I,8)	0-I,8-9 (I,8)
Head length (% SL) - range (mean)	28.6-33.3 (31.6)	28.3-34.1 (31.2)	29.3-37.1 (33.1)	30.6-33.4 (32.0)
Body depth (% SL) - range (mean)	23.1-27.6 (25.7)	23.8-33.1 (28.5)	24.1-29.8 (26.6)	25.6-28.7 (27.5)
Distance from operculum to dorsal fin (% SL) - range (mean)	34.8-39.9 (36.7)	30.2-37.8 (34.3)	32.7-40.1 (36.1)	37.0-40.0 (39.0)
Distance from operculum to dorsal fin (% HL) - range (mean)	106.4-137.0 (118.2)	88.4-129.7 (108.9)	88.0-132.4 (110.6)	110.7-125.1 (121.9)

Table 2. Meristics and morphometrics of holotype and largest recent specimen of *Betta waseri*, and holotypes of *B. hipposideros*, *B. tomi* and *B. spilotogena*

	B. waseri	*B. waseri*	*B. hipposideros*	*B. tomi*	*B. spilotogena*
	holotype ZMZ 129201	ZRC 35402	holotype ZRC 18688	holotype ZRC 35409	holotype ZRC 35417
SL	90.8 mm	80.7 mm	69.0 mm	70.4 mm	69.7 mm
TL	137.0 mm	107.4 mm	113.1 mm	97.6 mm	99.1 mm
HL	28.8 mm	23.6 mm	21.9 mm	21.3 mm	21.3 mm
			Meristics		
Vertebrae	2,9,22	2,9,22	2,9,22	2,9,22	2,9,22
Lateral scales	32	32	32	31	31½
Transverse scales	9½	9½	9½	10	9½
Transverse scales below first dorsal spine	17	17	16	16	16
Lateral scales above first anal spine	9	8	7	7	7
Predorsal scales	24	24	23	23	25
Subdorsal scales	6½	6	6½	5	5½
Postdorsal scales	12	11	9½	10	10½
			Fin rays		
Dorsal	I,8	I,8	I,8	I,8	I,8
Caudal	ii,6+7,i	ii,6+7,i	ii,6+7,i	ii,6+7,i	ii,6+7,i
Anal	total 30	II,29	II,28	II,27	II,29
Pelvic	i,1,4	i,1,4	i,1,4	i,1,4	i,1,4
Pectoral	13	15	15	14	12
			Morphometrics		
			% SL		
Head length	31.7	29.2	31.7	30.3	30.6
Distance from edge of operculum to base of first dorsal fin ray	38.1	39.9	33.3	40.1	37.0
Distance from base of last dorsal fin ray to caudal peduncle	26.3	23.7	22.3	24.0	21.4
Eye diameter	6.7	7.9	8.1	8.4	8.6
Body depth	29.1	26.8	30.1	29.8	27.0
			% HL		
Distance from edge of operculum to base of first dorsal fin ray	120.1	136.4	105.0	132.4	119.4
Distance from base of last dorsal fin ray to caudal peduncle	83.0	80.9	70.3	79.3	69.0
Body depth	91.7	91.5	95.0	98.6	87.5

GENERAL REMARKS

There are probably more species belonging to the *B. waseri* group than what is described here. Linke (1990: 48) and Kottelat & Whitten (1993: cover photograph) illustrated a species of this group from Borneo under the name *B.* cf. *anabatoides*. Similarly, Schmidt (1988) figured specimens of what was incorrectly identified as *B. macrophthalma* from Pekan Nanas in southwestern Johor which appear quite distinct from *B. tomi* or *B. hipposideros*. Kottelat & Whitten (1993: 163) lists *B. waseri* from Pekanbaru, Sumatra on the basis of a personnal communication by K.-E. Witte. This record is based on the fish illustrated as "*B. macrophthalma* Sumatra" in Schmidt (1988: fig. 7). The actual specimen(s) could not be examined and the photograph does not allow a proper identification; it might be a specimen of *B. spilotogena*. The photograph in Kottelat & Whitten (1993: pl. 77) actually shows the Pekan Nanas specimens discussed above.

The throat markings of the four described species in the *B. waseri* species group are diagnostic for each species. *Betta hipposideros* has the "horseshoe" type, in which the black lower lip marking is continuous with the two parallel bars on the throat, forming a distinct inverted U-shaped pattern (Fig. 2B). Often, the black throat and lower lip markings are connected by a narrow black band, giving the pattern a waist-like shape. In *B. tomi*, the black throat spots are relatively broader and are very close to the lower lip, occasionally merging slightly (Fig. 2C). In *B. spilotogena*, the throat spots are so broad in adults that they may join medially, but never joined to the lower lip, giving the appearance of a single large black median throat spot (Fig. 2D). *Betta waseri* has the "tear-drop" type of throat pattern, in which the throat markings consist of two tapering oval spots usually not connected to the lower lip marking at all (Fig. 2A) (occasionally by a very narrow black stripe when the specimens are stressed). Disturbed specimens of *B. hipposideros* may have a "tear-drop" type of marking instead, but this is always only temporary and the specimens revert back to their original form fairly fast. On the other hand, the Pahang specimens of *B. waseri* ("tear-drop" type) almost never develop the "horseshoe" type of throat marking. In acclimatised adults and sub-adults of the four species, the shape and arrangement of the throat markings are very distinctive and allow the four species to be easily separated.

The band of dark green on the distal part of the anal fin is distinct in male *B. tomi* (Fig. 7A). The anal fin margins of all three species are iridescent pale green, sometimes with a narrow dark green band, but only in *B. tomi* is the band very broad and distinct.

The vertical bars present on the caudal membranes of male *B. hipposideros* and *B. spilotogena* is a useful character, although it may become indistinct when the fish is stressed or after prolonged storage in alcohol. These bars, which give a ladder-like effect, are also evident in freshly preserved specimens. The ladder-like pattern is absent on *B. waseri* and *B. tomi* (Figs. 5A; 7A). The segmented caudal rays of *B. waseri* and *B. tomi* may give such an effect when viewed from a distance because of the segmented rays, but closer scrutiny shows the caudal membranes to be clear.

The ecological niches of *B. waseri*, *B. hipposideros*, *B. tomi* and *B. spilotogena* are worth noting. *Betta waseri* and *B. hipposideros* are both stenotopic blackwater species, and appear to be confined to the peat swamps of northeastern (Pahang and Terengganu) and northwestern Malaysia (Selangor and Perak) respectively (Fig. 1). These two swamps are separated by an extensive ridge of highlands (the Main Range) which runs through most of the length of Peninsular Malaysia. *Betta tomi* and *B. spilotogena* however, occur in acid

water freshwater swamps, and the associated fish fauna of its habitat is of the acid water tree country type (sensu Johnson, 1967). On the other hand, the fish fauna associated with *B. waseri* and *B. hipposideros* are typically blackwater taxa, with many species present or common only in such habitats (Johnson, 1968; Ng *et al.*, 1992). It is possible however, that some of the habitats in the type locality of *B. tomi* and *B. spilotogena* are simply degenerated peat swamp forests, and the present fauna contains both relict peat swamp elements as well as true acid water species.

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