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Trigonostigma truncata, a new species of harlequin rasbora from Malay Peninsula (Teleostei: Danionidae)

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Abstract. *Trigonostigma truncata*, new species, is described from the coastal swamp forests along the east coast of the Malay Peninsula. It differs from all congeners, in having a gently sloping lateral head and nape shape, the characteristic black triangular marking, newly termed here as the axine, which is large with its caudal apex not reaching caudal-fin base, presence of orange-red colour on the anal fin, a bluish-lilac coloured sheen on body in life, and a shallower body depth as compared to its most similar congener, *T. heteromorpha*. A key to the genus *Trigonostigma* and a brief redescription of *T. heteromorpha* is also included.

Key words. new species, biodiversity, Southeast Asia, acid waters, Cypriniformes

INTRODUCTION

The genus *Rasbora* has long been known to be a heterogeneous assemblage of lineages, several of them easily separated into species groups or complexes (Brittan, 1954b; Kottelat & Vidthayanon, 1993). A few of these lineages have been recently recognised as separate genera based on morphological grounds (viz. *Boraras* by Kottelat & Vidthayanon, 1993; *Sundadanio* Kottelat & Witte, 1999; and *Trigonostigma* Kottelat & Witte, 1999) and others more recently recognised as separate genera in conjunction with molecular phylogenetic work (*Brevibora*, *Kottelatia*, *Rasbosoma*, *Trigonopoma*) (Liao et al., 2010).

The genus *Trigonostigma* was distinguished from *Rasbora*, by a small adult size (less than 35 mm SL), unique body colour pattern (an axine [see below] consisting of a broad black triangular to dash-shaped pattern along the middle of the body, with a red to pink to orange body colour), an incomplete lateral line which is reduced to 6–9 pored scales, and unique behavioural spawning traits (upside down body positions of both male and female fish, and egg deposition on the underside of leaves of submerged macrophytes) (Kottelat & Witte, 1999; and present study). *Trigonostigma* currently includes four species (Kottelat, 2013): *T. heteromorpha* (Duncker, 1904), *T. hengeli* (Meinken, 1956), *T. somphongsi* (Meinken, 1958a), and *T. espei* (Meinken, 1967); all occurring in freshwater acidic swamp forest habitats. The monophyly of *Trigonostigma* has not been disputed since its inception (see Conway, 2005; Liao et al., 2011), but its phylogenetic position in relation to *Rasbora* and related genera is still inconclusive (Mayden et al., 2007; Rüber et al., 2007; Conway et al., 2008; Britz et al., 2009, 2014; Fang et al., 2009; Liao et al., 2010; Tang et al., 2010).

The type species *T. heteromorpha* was described by Duncker in 1904, based on a series of specimens from several localities (Negri Sembilan, Selangor in Peninsular Malaysia and Singapore). This species is heavily traded in the ornamental fish trade (Ng & Tan, 1997) based mainly on wild caught stock, but several selectively bred aquarium varieties are also available. The subsequent three species were described by Meinken, all based on aquarium trade fishes (Meinken, 1956, 1958a, 1958b, 1967). *Trigonostigma hengeli* is now known from two main locations, one in central Jambi and another in West Kalimantan (Tan & Kottelat, 2009), and appears sporadically in the aquarium trade. *Trigonostigma somphongsi* is the most uncommon of the four species, supposedly from Menam in southern Thailand (Chao Phraya drainage) (Kottelat, 2013). It has only been rarely encountered and always in small numbers during the flood season (Panitvong N, pers. comm.). *Trigonostigma espei* was also described from aquarium trade material, supposedly obtained from specimens imported from Bangkok (Kottelat, 2013). This taxon also exhibits a disjunct distribution. Populations in the eastern range are known from Chantaburi area in eastern Thailand (Panitvong, 2020), Sihanoukville in Cambodia, and Phu Quoc island, Vietnam (Bùi, 2011; Vasil'eva et al., 2013). The disjunct western population is known from Krabi area, in southwestern Thailand (Panitvong, 2020). For now, these populations are considered conspecific, but deserve further investigation. *Trigonostigma espei* is occasionally available in the aquarium trade.

Recently, a series of specimens obtained through the aquarium trade were observed to have a slightly different body shape

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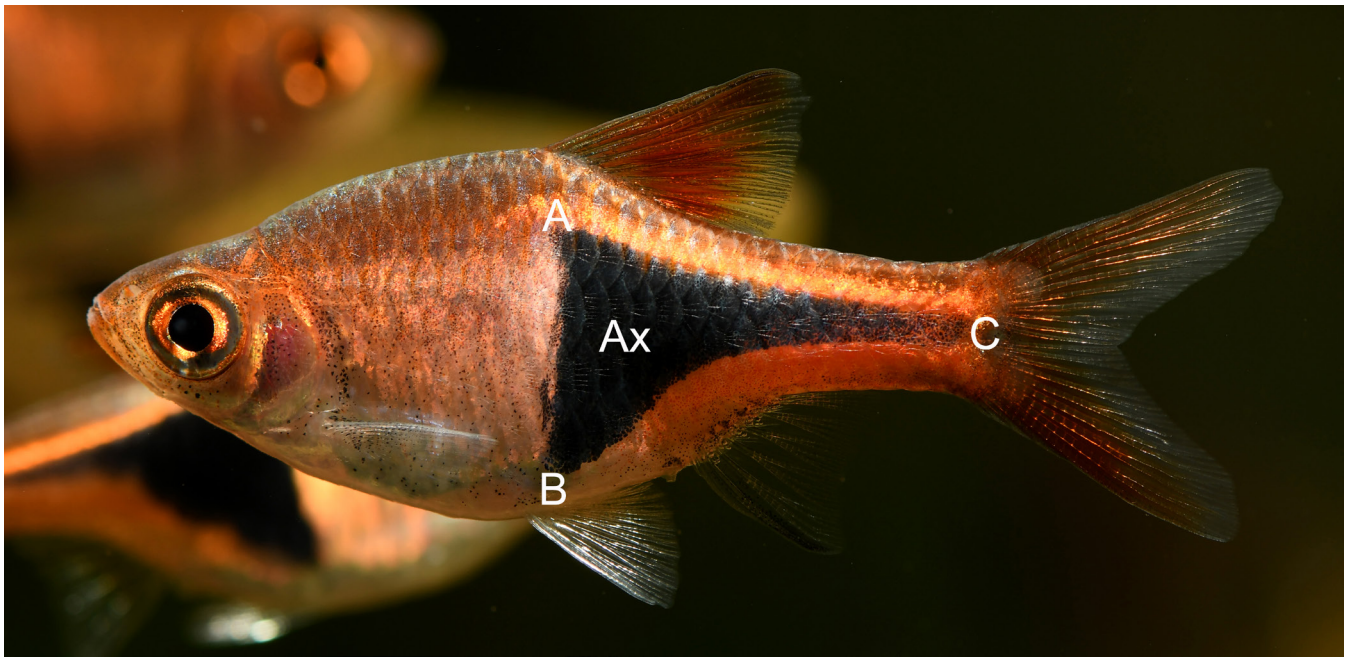

Fig. 1. *Trigonostigma heteromorpha* with depiction of the axine (Ax) with three apices labelled. A, dorsal apex; B, ventral apex; C, caudal apex. Specimen from Singapore: Central Catchment Nature Reserve, not preserved.

and different black marking on the body from true *T. heteromorpha*. Upon closer examination of these specimens and additional material within the Zoological Reference Collection at Lee Kong Chian Natural History Museum, these were discovered to be distinct from *T. heteromorpha* and represent a new species, described herein.

MATERIAL AND METHODS

The black triangular shape on the posterior half of body is unique to the genus *Trigonostigma* (see comparative notes in Kottelat & Witte, 1999: 54–55), though *T. somphongsi* has a much-reduced marking, that is more of a thick black stripe. Based on its uniqueness, a new term is proposed for this feature — "axine". It is a Greek word, meaning wedge. In reference to the orientation of the axine, there are three apices — dorsal, ventral and caudal. The dorsal apex is below the dorsal-fin origin, the ventral apex is above the pelvic-fin origin, and the caudal apex is near the caudal fin or at caudal-fin base (see Fig. 1).

Specimens were fixed in 10% formalin and later transferred to 75% ethanol for long-term storage. Measurements were obtained with dial calipers from the left side, according to Kottelat (1984). Colour pattern terminology follows Brittan (1954b). Abbreviations used: SL, standard length; HL, head length.

Specimens examined are deposited in the private collection of Maurice Kottelat, Delemont, Switzerland (CMK); Natural History Museum, London (BMNH); and the Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC).

TAXONOMY

An artificial key to the genus *Trigonostigma* (based on freshly preserved mature specimens)

1. Axine large and prominent; distance between dorsal and ventral apices at least ½ or more than ½ of body depth 2
– Axine narrow, resembling a thick stripe, with anterior portion slightly deeper; distance between dorsal and ventral apices around or less than eye width; known from central Thailand ..... *Trigonostigma somphongsi*
2. Caudal apex of axine reaching caudal fin; anal fin with faint or without orange pigment.....3
– Caudal apex of axine not reaching caudal fin, with 1–1½ scale space; anal fin always with orange pigment; known from east coast of Malay Peninsula ....*Trigonostigma truncata*, new species
3. Adult size less than 30 mm SL; axine shallower in depth and not more than ½ body depth; anal fin without anterior black streak.....4
– Adult size up to 35 mm SL; axine large and more than ⅔ body depth; anal fin always with anterior black streak; known from Malay Peninsula, northern Sumatra, and Sumatran islands..... ..... *Trigonostigma heteromorpha*
4. Red/orange pigment restricted to area anterior and dorsal to axine; dorsal fin pale yellow or orange; known from central Sumatra and west Kalimantan ..... *Trigonostigma hengeli*
– Red/orange pigment throughout body, more intense along dorsum and caudal regions; dorsal fin reddish; known from two disjunct populations – eastern Thailand to coastal Cambodia and Vietnamese island of Phu Quoc, and near Krabi in southwestern Thailand .....*Trigonostigma espei*

Fig. 2. *Trigonostigma truncata*, new species, holotype, ZRC 61240, 24.2 mm SL; Thailand: Narathiwat.

Fig. 3. *Trigonostigma truncata*, new species, live specimen of ca. 30 mm SL (trade material, not preserved).

***Trigonostigma truncata*, new species**
(Figs. 2, 3, 4A, 5)

Rasbora heteromorpha (non-Duncker) – Mohsin & Ambak, 1983: 50 (part); Kottelat et al., 1992: 9, table 1; Kottelat et al., 1993: 63, pl. 18 (part).

Rasbora cf. *heteromorpha* – Collins et al., 2012: 10, table 3, supplementary data table S1: 16 (part?).

Trigonostigma heteromorpha (non-Duncker) – Kottelat & Witte, 1999: 54 (part), fig. 10; Kottelat, 2013: 170 (part); Panitvong, 2020: 142.

Trigonostigma aff. *heteromorpha* – Ng et al., 2019: 527 (part).

Material examined. — Holotype: ZRC 61240, 1 ex., 24.2 mm SL; Thailand: Narathiwat Province, stream along road branching West at about 7 km on road from Waeng to Ban Bu Ke Ta; Kottelat M et al., 2 November 1995.

Paratypes: SOUTH THAILAND — CMK 12049, 21 ex., ZRC 42090, 21 ex., 9.7–24.2 mm SL; same locality as holotype. — ZRC 42131, 2 ex., 17.0–20.3 mm SL; Thailand: Narathiwat Province, stream about 2 km South of Ban Bu Ke Ta on road to Ban Sac; Kottelat M et al., 2 November 1995. — ZRC 42076, 6 ex., 15.1–21.6 mm SL; Thailand: Narathiwat Province, swamp area about 2 km North of Ban Bu Ke Ta, about 8 km South of Waeng; Kottelat M et al., 2 November 1995. PENINSULAR MALAYSIA — CMK 8221, 50 ex., ZRC 24807, 36 ex., 8.2–25.1 mm SL; Malaysia: Terengganu, stream at about 6 km on road from Kuala Brang to Kuala Terengganu; Ng PKL et al., 19 March 1992. — ZRC 40234, 40 ex., 11.9–24.7 mm SL; Malaysia: Terengganu, 5 km Kuala Brang-Kuala Terengganu road; Ng PKL et al., 16 May 1995. — ZRC 41933, 7 ex., 15.1–21.7 mm SL; Malaysia: Terengganu, Kuala Brang; Ng PKL et al., October 1997. — ZRC 1966, 27 ex., 9.5–22.3 mm SL; Malaysia: Terengganu, 17.5 mile Kuala Terengganu-Kuala Brang road; Alfred ER, 8 July 1958. — ZRC 1714, 6 ex., 15.3–20.2 mm SL; Malaysia: Terengganu, Kuala Brang; Tweedie M, August 1950.

Table 1. Meristic and morphometric data for *Trigonostigma truncata*, new species.

Meristics	**Holotype (ZRC61240)**	**Paratypes (ZRC24807, 42131, 42076, 42090) (n=17) and holotype [mode]**
SL (mm)	24.2	17.3–25.1
dorsal fin rays	i, 7	i, 7
anal fin rays	i, 6	i, 6
caudal fin rays (principle rays)	9+9	9+9
pelvic fin rays	i, 5	i, 5
pectoral fin rays	10	10
lateral scales	27	26–30 [27]
no. of pored lateral line scales	6	6–8 [7]
predorsal scales	11	11
transverse scales	7½	7–8 [7½]
transverse scales at dorsal	8½	7½–9 [8½]
caudal peduncular scales	½.4.½	½.4.½
circumpeduncular scales	10	10
dorsal fin origin (lat)	10	8–10 [9]
anal fin origin (lat)	15	14–15 [14]
pelvic fin origin (lat)	9	8–10 [9]
start of axine in relation to lateral scales	12	10½–12½ [11]
scale rows between lateral and pelvic	3	2½–3 [3]

		min	**max**	**mean**	**SD**
% standard length					
total length	130.2	130.2	142.9	138.7	3.34
body length	74.4	68.6	74.4	71.0	1.79
predorsal length	51.7	51.2	56.1	53.3	1.64
preanal length	68.2	64.3	70.7	67.7	1.92
prepelvic length	51.2	48.9	53.3	51.3	1.28
head length	31.0	28.5	31.6	30.2	1.00
body depth at dorsal	33.1	28.3	34.6	32.4	1.88
body depth at anus	24.8	22.5	29.3	25.8	1.68
caudal peduncle depth	14.5	11.0	27.9	14.0	3.98
caudal peduncle length	21.9	15.0	23.7	19.9	2.34
dorsal fin base length	15.3	12.9	16.9	15.0	1.02
anal fin base length	12.0	10.6	15.2	12.4	1.19
pelvic fin length	19.0	15.7	21.6	19.6	1.39
pectoral fin length	17.8	17.8	22.9	20.4	1.84
upper caudal lobe length	38.0	33.2	42.7	38.8	3.14
median caudal length	14.9	12.8	20.5	17.0	2.33
lower caudal lobe length	39.3	36.4	43.6	39.7	1.89
% head length					
head depth	64.0	62.1	76.9	69.6	4.38
head width	46.7	39.4	51.9	46.8	2.89
snout length	22.7	16.4	25.8	22.1	2.93
orbital diameter	38.7	33.8	40.4	36.8	2.23
interorbital width	36.0	30.1	42.3	36.0	2.97

Others: ZRC 54736, 4 ex., 29.7–33.7 mm SL; obtained from aquarium trade, September 2015.

Diagnosis. *Trigonostigma truncata*, new species, is most similar to *T. heteromorpha*, in having a large black axine starting from approximately mid-body with dorsal apex near dorsal-fin origin, ventral apex near pelvic-fin origin, and caudal apex near caudal-fin base; this axine being the largest amongst all congeners. *Trigonostigma truncata* differs from *T. heteromorpha* in the following characters: a gently sloping lateral head profile to pre-dorsal region (vs. a steep convex lateral profile from posterior of head to predorsal region); sub-superior mouth (vs. terminal mouth); caudal apex of axine not reaching caudal-fin base (vs. reaching and extending to hypural plate); dorsal and ventral apices of axine originate posterior to both dorsal-fin and pelvic-fin origins by up to three scale-widths (vs. dorsal apex starting one scale-width posterior to dorsal-fin origin and ventral apex starting at pelvic-fin origin; see Figs. 4, 5); faint or indistinct brown humeral streak just posterior to opercular opening (vs. a distinct black humeral streak); base of dorsal fin hyaline and its middle reddish-orange in life (vs. anterior two-thirds of fin orange-red); presence of distinct orange-red colour on anal fin in life (vs. faint or absence); having a bluish-lilac sheen on the body in life (vs. reddish or purplish sheen); and having a shallower body (depth at dorsal-fin origin 28.3–34.6% SL [mean 32.4], vs. 32.6–38.2% [mean 35.8]).

Description. See Figs. 2–4 for general appearance. See Table 1 for meristic and morphometric data. Head pointed, with sub-superior mouth, barbels absent. Profile of head and anterior of body gently sloping upwards to dorsal-fin origin, absence of distinct notch between occiput and nape. Orbit relatively large (orbital diameter 33.8–40.4% HL). Body compressed, deepest at dorsal-fin origin (body depth 28.3–34.6% SL) and shallowest at caudal peduncle (caudal peduncle depth 11.0–14.5% SL). Dorsal and pelvic fins situated mid-body (predorsal length 51.2–56.1% SL; prepelvic length 48.9–53.3 % SL), triangular and small (dorsal-fin base length 12.9–16.9% SL). Caudal fin forked, symmetrical (upper caudal-fin lobe length 33.2–42.7% SL; lower caudal-fin lobe length 36.4–43.6% SL). Anal fin triangular, situated ⅔ down the body (preanal length 64.3–70.7% SL), and small (anal-fin base length 10.6–15.2% SL). Both pelvic and pectoral fins triangular. Lateral scale series with 26–30 scales (mode 27), lateral line incomplete and leading horizontally away from head, perforated lateral line scales 6–8 (mode 7). Both dorsal-fin and pelvic-fin origins on vertical through lateral scale 8–10 (mode 9), anal-fin origin at 14–15 (mode 14). Axine starting at lateral scale series 10½–12½ (mode 11).

Colouration in preservative. See Fig. 2. Base body colour cream, dorsum dark brown, with dark brown stripe across dorsum. Head region above eye dark brown. Eye with silvery iris. Region posterior to opercle opening with faint brown humeral streak. All fins hyaline, thin black margin on distal half of anterior edge of dorsal and anal fins. Black or dark brown axine on mid-body, anterior margin concave to straight edged, dorsal apex starting about three scales posterior to dorsal-fin origin, ventral apex starting above pelvic-fin origin, caudal apex extending length of caudal peduncle stopping about 1–2 scales anterior to caudal-fin base; axine surrounded with distinct margin of 1–1½ scale width. Region of body anterior to triangular marking with diffused melanophores.

Colouration in life. See Figs. 3, 4. Base body colour pale yellowish-brown, dorsum can be a darker shade; sometimes with slight orangish iridescence on anterior half of body and bright orange blotch at caudal-fin base; in fully acclimatised specimens in captivity, a bluish-lilac sheen can be visible on body. Region of head above eye dark brown or brown. Eye with yellowish-orange iris with black dorsal patch, ventral area silver. Region posterior to opercular opening with faint brown humeral streak. Large velvety black axine on mid-body, anterior margin concave to straight edged, dorsal apex at about three scales posterior to dorsal-fin origin, ventral apex at pelvic-fin origin, caudal apex extending length of caudal peduncle to about 1–2 scales anterior to caudal-fin base; whole axine surrounded with distinct margin of 1–1½ scale width. Paired fins hyaline. Dorsal fin base hyaline, thin black margin on distal half of anterior edge, middle section orangish-red, distal margin hyaline. Caudal fin yellowish with hyaline distal margin. Anal fin base hyaline, thin black margin on distal half of anterior edge, middle section orangish-red, distal margin hyaline. Supra-anal region to ventral base of caudal peduncle with dark brown streak.

No sexual dimorphism or dichromatism observed. From hobbyists' observations, males are usually more intensely coloured.

Distribution. *Trigonostigma truncata*, new species, is currently known from the east coast of the Malay Peninsula, from south of the Isthmus of Kra in Narathiwat province of southern Thailand to the Malaysian State of Terengganu (Fig. 6). The map in Fig. 6 also shows the distribution of all five species for comparison.

Field notes. This species is found in lowland freshwater acid swamp-forest stream habitats, usually flowing into riverine habitats. Syntopic species collected from Mae Nam Tod Deng swamp forest in South Thailand include the following: *Notopterus notopterus* (Notopteridae), *Boraras urophthalmoides*, *Trigonopoma gracile* (Danionidae), *Kryptopterus minor* (Siluridae), *Clarias meladerma* (Clariidae), *Monopterus javanensis* (Synbranchidae), *Chaudhuria* sp. (Chaudhuriidae), *Oryzias minutulatus* (Adrianichthyidae), *Indostomus crocodilus* (Indostomidae), *Betta imbellis*, *B. pi*, *Parosphromenus paludicola*, *Trichopodus trichopterus*, *Trichopsis vittata* (Osphronemidae), *Channa limbata*, and *C. lucius* (Channidae).

Syntopic species collected from Kuala Brang in Terengganu include the following: *Osteochilus vittatus* (Cyprinidae), *Rasbora bankanensis*, *R. dusonensis*, *Trigonopoma gracile* (Danionidae), *Acanthopsoides* sp., *Lepidocephalichthys furcatus*, *Pangio cuneovirgata*, *P. piperata*, *P. semicincta*, *P. muraeniformis* (Cobitidae), *Homalopteroides nebulosus* (Balitoridae), *Nemacheilus selangoricus* (Nemacheilidae),

Fig. 4. A, *Trigonostigma truncata*, new species, ZRC 54736, 33.7 mm SL, trade material; B, *T. heteromorpha*, ZRC 61239, 28.4 mm SL, trade material; C, *T. espei*, ZRC uncat, 28.2 mm SL, trade material (obese individual); D, *T. hengeli*, ZRC uncat, 23.3 mm SL, Sumatra: Jambi; E, *T. somphongsi*, not preserved, ca. 15 mm SL (right-side reversed; photograph by N. Panitvong).

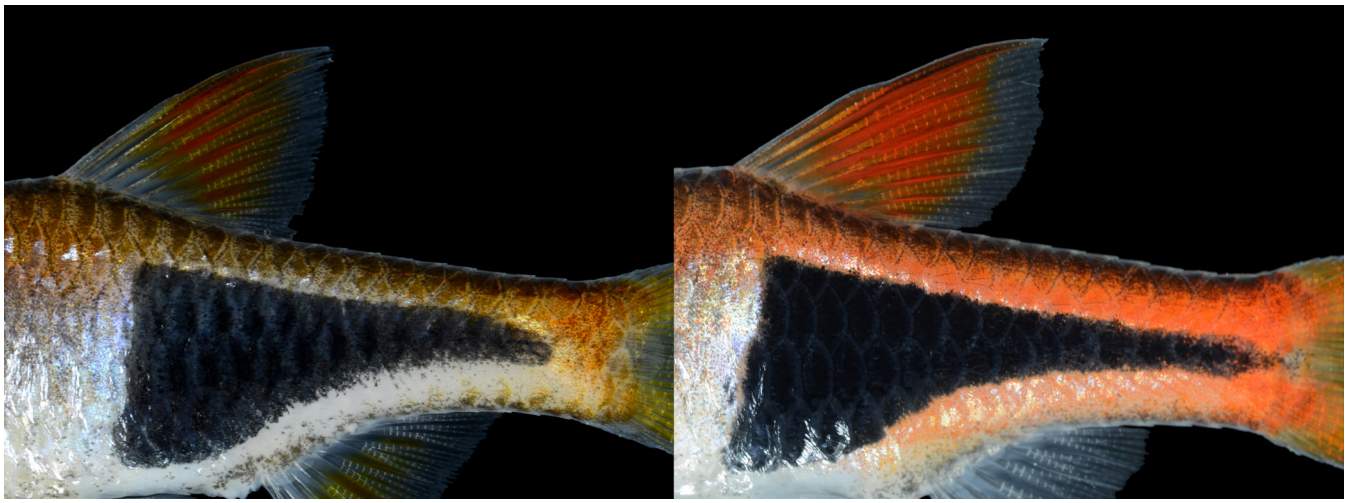

Fig. 5. *Trigonostigma truncata*, new species, ZRC 54736, 33.7 mm SL (left); and *Trigonostigma heteromorpha*, ZRC 61239, 28.4 mm SL (right); detail of body, showing axine.

Barbucca diabolica (Barbuccidae), *Hemibagrus capitulum*, *Nanobagrus fuscus*, *Pseudomystus stenomus* (Bagridae), *Silurichthys hasseltii* (Siluridae), *Parakysis verrucosus* (Akysidae), *Clarias leiacanthus* (Clariidae), *Neostethus smithi* (Phallostethidae), *Bihunichthys* sp. (Chaudhuriidae), *Hemirhamphodon pogonognathus* (Zenarchopteridae), *Xenentodon canciloides* (Belonidae), *Doryichthys martensii* (Syngnathidae), *Brachygobius xanthomelas* (Gobiidae), *Pristolepis grooti* (Pristolepididae), *Luciocephalus pulcher*, and *Parosphomenus paludicola* (Osphronemidae).

Syntopic species collected from Dungun swamp in Terengganu include the following: *Barbodes* cf. *binotatus, Desmopuntius hexazona*, *Osteochilus vittatus*, *O. waandersii* (Cyprinidae), *Boraras maculatus*, *Rasbora einthovenii*, *R. cephalotaenia*, *R. paucisqualis*, *Trigonopoma gracile*, *T. pauciperforatum* (Danionidae), *Lepidocephalichthys furcatus*, *Pangio semicincta* (Cobitidae), *Homalopteroides nebulosus* (Balitoridae), *Nemacheilus selangoricus* (Nemacheilidae), *Neostethus smithi* (Phallostethidae), *Hemirhamphodon pogonognathus* (Zenarchopteridae), *Nandus nebulosus* (Nandidae), *Betta stigmosa*, *Luciocephalus pulcher*, and *Parosphromenus paludicola* (Osphronemidae).

Etymology. From the Latin '*truncus*', meaning cut off, in allusion to the caudal apex of the axine not reaching the base of the caudal-fin. Used as a noun in apposition.

Remarks. *Trigonostigma truncata*, new species, can be further differentiated from *T. heteromorpha* in the following characters: adpressed pectoral fin not reaching pelvic-fin origin (vs. reaching); adpressed pelvic fin not reaching anal-fin origin (vs. surpassing); more lateral scale count (26–30 [mode 27], vs. 25–28 [mode 26]); perforated lateral line scales leading horizontally away from head (vs. curving gently downwards away from head); relatively longer head (head length 28.5–31.6% SL [mean 30.2], vs. 27.2–31.7% [mean 28.9]); relatively slimmer caudal region (body depth 22.5–29.3% SL [mean 25.8], vs. 24.4–30.2% [mean 27.9]; caudal peduncle depth 11.0–14.5% SL [mean 12.9], vs. 12.6–15.8% [mean 13.8]); more slender head (head depth 62.1–76.9% HL [mean 69.6], vs. 68.1–80.6% [mean 74.7]; head width 39.4–51.9% HL [mean 46.8], vs. 42.9–53.5% [mean 49.1]); relatively smaller eye (orbital diameter 33.8–40.4% HL [mean 36.8], vs. 35.6–44.8% [mean 40.2]).

Trigonostigma truncata, new species, can be differentiated from the other congeners (*T. espei*, *T. hengeli*, and *T. somphongsi*) by having a larger adult size (up to 33.7 mm SL, vs. less than 30 mm); large black axine on body with dorsal and ventral borders not exceeding one scale spacing to edge of body (vs. 1½–2½ scale width).

In the naming of the new genus *Trigonostigma* by Kottelat & Witte (1999: 54, fig. 10), they presented a figure of a preserved specimen of *T. heteromorpha* which is from the series ZRC 42076. This is actually part of the type series for the new species, *T. truncata*. The two taxa are so similar that they were misidentified.

Collins' et al. (2012: 6, fig. 4) material of *T. heteromorpha* consist of seven specimens from two genetic populations, with COI divergence of more than 3%. They further commented on the presence of orange pigments on the anal fin (supplementary table 1), which is congruent with the present new species; however all of their material is from the ornamental fish trade, which is without precise locality data, and thus of limited use for taxonomical studies.

***Trigonostigma heteromorpha* (Duncker, 1904)**

(Figs. 1, 4B, 5, 7)

Rasbora heteromorpha Duncker, 1904: 182, pl. 1, fig. 5; Weber & de Beaufort, 1916: 79; Tweedie, 1936: 21; Herre & Myers, 1937: 55; Fowler, 1938: 57; Brittan, 1954a: 152; 1954b: 187, fig. 44; Menon, 1954: 8; Alfred, 1963: 166; 1966: 19; Mohsin & Ambak, 1983: 50 (part); Zakaria-Ismail, 1987: 406; Lim & Ng, 1990: 32; Ng & Lim, 1992: 259, table 3; 1996: 111; 1997: 249; Kottelat et al., 1993: 63, pl. 1; Tan & Tan, 1994: 353; Ng & Tan, 1997: 84; Sim, 2002: 50; Rachmatika et al., 2006: 64; Rüber et al., 2007: figs. 1–3; Collins et al., 2012 (not all molecular phylogenetic studies are included in this synonymy list, as most of them do not include locality data; and many

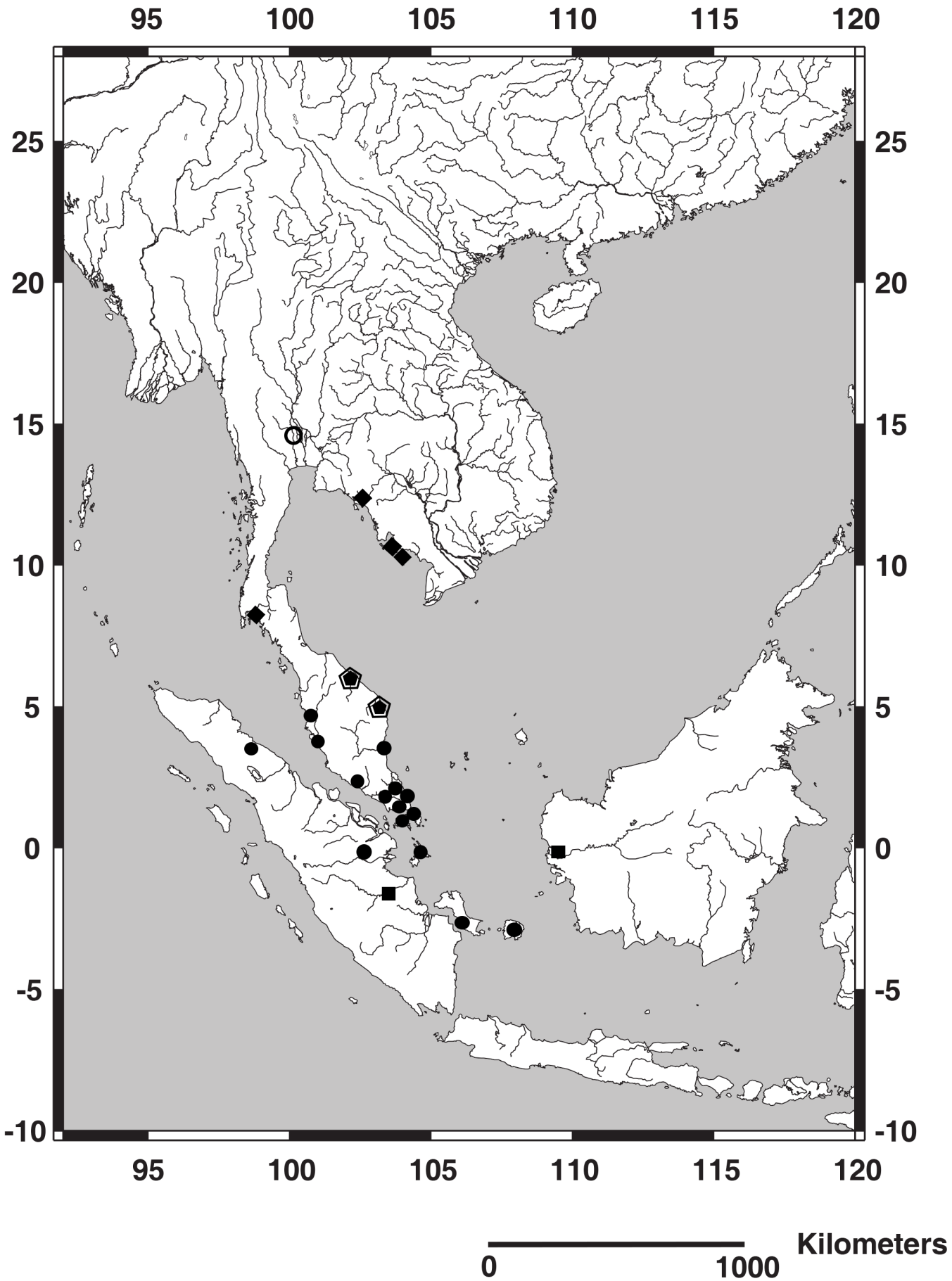

Fig. 6. Map of Southeast Asia showing distribution of *Trigonostigma*: *T. heteromorpha* (solid circle), *T. somphongsi* (hollow circle), *T. espei* (diamond), *T. hengeli* (square), and *T. truncata*, new species (pentagon). Each symbol may represent more than one location.

also suffer from using the same set of sequence data without verification of vouchers, thus perpetuating errors [pers. obs.]).

Trigonostigma heteromorpha (Duncker, 1904): Kottelat & Witte, 1999: 54; Ng & Tan, 1999: 352, table 1; Conway, 2005: table 1, fig. 11; Tan & Kottelat, 2009: 52; Baker & Lim, 2012: 36; Kottelat, 2013: 170 (part); Chow et al., 2014: 56; Fahmi-Ahmad et al., 2015: 34, table 1; Azmai et al., 2020: 74.

Material examined. — ZRC 39918, 2 ex., 19.3–24.2 mm SL; Malaysia: Perak, Sungei Beriang, 21 km milestone from Taiping to Segama; Tan HH et al., 18 November 1995. — ZRC 14383, 1 ex., 28.0 mm SL; Malaysia: Selangor, Sungei Buloh forest reserve, swampy forest stream; Ng PKL & Lim KKP, 6 March 1991. — ZRC 13794 sa, 7 ex., 9.8–25.9 mm SL; Malaysia: Johor, Panti forest stream; Ng PKL, 31 August 1990. — ZRC 4903–4914, 11 ex., 15.6–25.0 mm SL; Malaysia: Johor, Mawai, Sunegi Mupor; Alfred ER, 21 February 1971. — ZRC 55562, 9 ex., 19.0–27.6 mm SL; Singapore: Central Catchment Nature Reserve, channel between Upper Peirce and MacRitchie Reservoirs; Tan HH et al., 18 September 2007 (only the largest specimens were used for meristic counts and morphometric measurements; n=20, SL=21.6–27.6 mm).

The following material was also examined but no measurements or counts taken — BMNH 1905.5.6:2–3 (2 paralectotypes), 22.3–23.2 mm SL; Malaysia: Selangor, Kuala Lumpur; Robinson HC, 1905. PENINSULAR MALAYSIA — ZRC 27602, 1 ex., 18.0 mm SL; Malaysia: Selangor, Sabak Bernam, Sungei Bernam; Ng PKL et al., 19 September 1992. — ZRC 13547, 2 ex., 27.9–28.3 mm SL; Malaysia: Johor, Pontian, stream adjacent to Gunung Pulai reservoir I; Ng PKL & Yeong R, 9 September 1988. — ZRC 21243, 4 ex., 17.9–22.9 mm SL: Malaysia: Johor, Sungei Selangi, 15 km Kota Tinggi-Tanjung Sedili Road; Ng PKL et al., 22 April 1992. SINGAPORE — ZRC 2314 (6 paralectotypes); Singapore: Botanical Garden pond. — ZRC 12405, 4 ex., 18.4–21.0 mm SL: Singapore: Sime Road forest; Ng PKL & Lim KKP, 27 October 1989. — ZRC 34601, 18 ex., 9.0–18.9 mm SL; Singapore: Sime Road forest; Lim KKP et al., May 1992. — ZRC 34623, 2 ex., 23.0–24.1 mm SL; Singapore Rifle Range road stream; Chang CY et al., 27 May 1993. — ZRC 12386, 4 ex., 17.9–27.0 mm SL; Singapore Nee Soon swamp forest, second track; Lim KKP & Ng PKL, 14 April 1990. — ZRC 38248, 7 ex., 17.0–28.5 mm SL; Singapore Nee Soon swamp forest; Lim KKP, 20 June 1994. INDONESIA: Riau Archipelago — ZRC 14044, 8 ex., 19.6–30.3 mm SL: Indonesia: Pulau Batam, north-western part; Ng PKL & Lim KKP, 25 February 1991. — ZRC 33215, 5 ex., 10.0–28.0 mm SL; Indonesia: Pulau Bintan North; Tan THT et al., 11 May 1993. — ZRC 31540, 10 ex., 19.1–31.2 mm SL; Indonesia: Pulau Lingga, Daik; Searby M, November 1996. INDONESIA: Sumatra — ZRC 41950, 8 ex., 11.3–25.1 mm SL; Indonesia: Sumatra: Riau, upper Indragiri; Tan HH et al., November 1996. — Others: ZRC 61239, 1 ex., 27.8 mm SL; obtained from aquarium trade, September 2015.

Diagnosis. *Trigonostigma heteromorpha* shares with *T. truncata*, new species, a large black axine starting from approximately mid-body with dorsal apex near dorsal-fin origin, ventral apex near pelvic-fin origin, and caudal apex near caudal-fin base; this axine being the largest amongst all congeners. *Trigonostigma heteromorpha* differs from all congeners in the following combination of characters: a steep sloping lateral head to pre-dorsal region (shared with *T. espei*, vs. a gentle sloping lateral profile from posterior of head to predorsal region for *T. truncata*, *T. hengeli*, and *T. somphongsi*); terminal mouth (shared with all except *T. truncata* with a sub-superior mouth); caudal apex of axine reaching caudal-fin base (shared with all except *T. truncata* with caudal apex not reaching); dorsal and ventral apices of axine originate near to both dorsal-fin and pelvic-fin origins (shared with *T. truncata*, vs. dorsal apex starting up to three scale-width posterior to dorsal-fin origin and ventral apex starting two scale-width after pelvic-fin origin in *T. espei* and *T. hengeli*; axine reduced to thick black stripe in *T. somphongsi*); dorsal fin with distinct orange/red pigments (shared with *T. truncata* and *T. espei*, vs. both *T. hengeli* and *T. somphongsi* with almost hyaline dorsal fin); and the largest adult size (up to 35 mm SL).

Fig. 7. *Trigonostigma heteromorpha*, BMNH 1905.5.6:2–3, paralectotypes, 22.3 mm SL (top), 23.2 mm SL (bottom); Peninsular Malaysia: Selangor (copyright of Natural History Museum, London).

Description. See Figs. 1, 4B, 7 for general appearance. See Table 2 for meristic and morphometric data. Head pointed, with terminal mouth, barbels absent. Profile of head and anterior of body with a steep slope upwards to dorsal-fin origin, presence of distinct notch between occiput and nape. Orbit relatively large (orbital diameter 35.6–44.8% HL). Body compressed, deepest at dorsal-fin origin (body depth 32.6–38.2% SL) and shallowest at caudal peduncle (caudal peduncle depth 12.6–15.8% SL). Dorsal and pelvic fins situated mid-body (predorsal length 46.8–54.8% SL; prepelvic length 47.9–52.5% SL), triangular and small (dorsal-fin base length 13.1–18.4% SL). Caudal fin forked, symmetrical (upper caudal-fin lobe length 32.6–39.1% SL; lower caudal-fin lobe length 33.5–41.6% SL). Anal fin triangular, origin situated ⅔ down body (preanal length 64.6–70.2% SL), and small (anal-fin base length 10.5–15.2% SL). Both pelvic and pectoral fins triangular. Lateral scale series with 25–30 scales (mode 26), lateral line incomplete

Table 2. Meristic and morphometric data for *Trigonostigma heteromorpha*.

Meristics	**ZRC55562, 4903, 14383, 39918, 13794 (n=20) [mode]**			
SL (mm)	21.6–27.6			
dorsal fin rays	i, 7			
anal fin rays	i, 6			
caudal fin rays (principle rays)	9+9			
pelvic fin rays	i, 5			
pectoral fin rays	12			
lateral scales	25–28 [26]			
no. of pored lateral line scales	5–9 [7]			
predorsal scales	11			
transverse scales	7½			
transverse scales at dorsal	8½			
caudal peduncular scales	½.4.½			
circumpeduncular scales	10			
dorsal fin origin (lat)	7–9 [8]			
anal fin origin (lat)	14–16 [15]			
pelvic fin origin (lat)	8–9 [9]			
start of axine in relation to lateral scales	9½–11 [11]			
scale rows between lateral and pelvic	2–4 [3]			
	min	**max**	**mean**	**SD**
% standard length				
total length	133.0	142.7	137.2	2.82
body length	67.5	75.0	71.0	1.92
predorsal length	46.8	54.8	52.0	2.19
preanal length	64.6	70.2	67.6	1.69
prepelvic length	47.9	52.5	50.1	1.49
head length	27.2	31.7	28.9	1.18
body depth at dorsal	32.6	38.2	35.8	1.64
body depth at anus	24.4	30.2	27.9	1.55
caudal peduncle depth	12.6	15.8	13.8	0.89
caudal peduncle length	18.6	23.3	21.7	1.24
dorsal fin base length	13.1	18.4	15.5	1.38
anal fin base length	10.5	15.2	13.1	1.36
pelvic fin length	17.6	23.7	20.0	1.60
pectoral fin length	17.3	22.9	20.3	1.57
upper caudal lobe length	32.6	39.1	36.4	1.83
median caudal length	13.4	20.2	17.4	1.76
lower caudal lobe length	33.5	41.6	37.8	2.10
% head length				
head depth	68.1	80.6	74.7	3.35
head width	42.9	53.5	49.1	2.86
snout length	20.9	28.6	23.8	2.39
orbital diameter	35.6	44.8	40.2	2.63
interorbital width	35.0	41.3	38.6	1.84

and leading horizontally away from head and sloping downwards, perforated lateral line scales 5–9 (mode 7). Both dorsal-fin and pelvic-fin origins on vertical through lateral scale 7–9 (mode 8) and 8–9 (mode 9) respectively, anal-fin origin at 14–16 (mode 15). Axine starting at lateral scale series 9½–11 (mode 11).

Colouration in preservative. See Fig. 7. Base body colour cream, dorsum dark brown, with dark brown stripe across dorsum, ventrum cream; freshly preserved specimens can be flushed orange or reddish. Head region above eye dark brown. Eye with silvery iris. Region posterior to opercle opening with distinct dark brown humeral streak. All fins hyaline, thin black margin on distal half of anterior edge of dorsal and anal fins; for freshly preserved specimens, dorsal and caudal fins orange or red, anal fin with middle portion orange, paired fins hyaline. Black axine on mid-body, anterior margin straight edged, dorsal apex starting about one scale

posterior to dorsal-fin origin, ventral apex starting above pelvic-fin origin, caudal apex extending length of caudal peduncle reaching base of caudal fin; axine surrounded with distinct margin of 1–1½ scale width. Region of body anterior to triangular marking with diffused melanophores.

Colouration in life. See Figs. 1, 4. Base body colour orange-red, dorsum can be a darker shade, belly lighter shade or silvery; sometimes with slight bluish iridescence on anterior half of body and bright orange blotch at caudal-fin base; in fully acclimatised specimens in captivity, a purplish sheen can be visible on body. Region of head above eye dark brown. Eye with orange iris with black dorsal patch and ring. Region posterior to opercular opening with diffused black humeral streak. Large velvety black axine on mid-body, anterior margin straight edged, dorsal apex at about one scale posterior to dorsal-fin origin, ventral apex at pelvic-fin origin, caudal apex extending length of caudal peduncle to caudal-fin base; whole axine with distinct margin of 1–1½ scale width. Paired fins hyaline. Dorsal fin base flushed red or orange, thin black margin on distal half of anterior edge, distal margin hyaline. Caudal fin reddish-orange with hyaline distal margin. Anal fin base hyaline, thin black margin on distal half of anterior edge, middle section sometimes with small patch of orangish-red, rest of fin hyaline. Supra-anal region to ventral base of caudal peduncle with diffused black streak.

Distribution. *Trigonostigma heteromorpha* is the most widely distributed species of the genus, occurring in Malay Peninsula (Perak, Selangor, Negri Sembilan, Johor, Pahang), Singapore, Sumatra (North Sumatra and Riau provinces), Riau archipelago islands of Batam, Bintan, and Lingga, Bangka island and Belitung island (see Fig. 5). In Sumatra, *T. heteromorpha* is found only in North Sumatra and Riau provinces and is replaced by *T. hengeli* in Jambi and South Sumatra provinces (Kottelat & Witte, 1999; Tan & Kottelat, 2009).

Remarks. Duncker's (1904) description of *T. heteromorpha* was based on material collected from Selangor, Negri Sembilan, and Singapore. Locality data for the type series was from Negri Sembilan and this had been clarified by Alfred (1963). No holotype was designated at the time of publication. Ladiges et al. (1958) selected a lectotype from Negri Sembilan, based in Zoological Museum Hamburg (Kottelat, 2013). The locality where Duncker collected *T. heteromorpha* in Singapore is the Botanical Garden pond (not specified which pond) which is now depleted of *T. heteromorpha* as the surrounding swamp forest habitats have been destroyed. Surviving populations occur in forest streams and a remnant swamp forest habitat within the Central Catchment Nature Reserve (Ng & Lim, 1997; Ho et al., 2016).

Both *T. heteromorpha* and *T. truncata*, new species, are the largest-sized representatives of the genus. The current largest documented *T. heteromorpha* is 35 mm SL (Weber & de Beaufort, 1916: 80) and for *T. truncata* is 33.7 mm SL (present study – ZRC 54736; this specimen has been kept in captivity before preservation).

Comparative material. *Trigonostigma espei* — ZRC 40766, 10 ex., 12.3–19.2 mm SL; Thailand: Trat Province, aquarium material; donor Kubota K, 13 January 1997. *Trigonostigma hengeli* — ZRC 38687, 4 ex., 12.4–20.3 mm SL; Indonesia: Sumatra; Jambi, Pijoan, Sungai Pijoan; aquarium fish collectors, 28 May 1994. — ZRC 37705, 18 ex., 18.8–24.4 mm SL; Indonesia: Sumatra; Jambi, aquarium material; Lim KKP et al., June 1994. — ZRC 47139, 47 ex., 13.5–17.2 mm SL; Indonesia: Kalimantan Barat; Pontianak, aquarium trade; donor Yap P, 8 July 1998.

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This species is described in fond memory of the many occasions on which Tony Whitten (1953–2017) visited the National University of Singapore and ZRC, always engaging in stimulating discussions on the taxonomy, ecology, and biogeography of Southeast Asian fishes, amongst other fauna.

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