

Review of the Southeast Asian miniature cyprinid genus *Sundadanio* (Ostariophysi: Cyprinidae) with descriptions of seven new species from Indonesia and Malaysia

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Sundadanio axelrodi is redescribed and seven new species are described: *S. margariton* from the Rajang and Sarawak drainages (Sarawak), *S. echinus* from the Anjungan peat swamp forest and *S. rubellus* from the Kapuas drainage (Kalimantan Barat, Borneo), *S. retiarius* from the Kotawaringin to Kahayan drainages (Kalimantan Tengah, Borneo), *S. goblinus* from the Batang Hari drainage (Sumatra), *S. atomus* from Singkep Island and *S. gargula* from Bangka Island. The eight species are distinguished by characters of colour pattern, tuberculation and squamation.

Introduction

Sundadanio axelrodi, a tiny member of the Cyprinidae, was first described by Brittan (1976) based on aquarium material of “uncertain origin” postulated to have originated somewhere on the Indonesian island of Sumatra. Roberts (1989) later recorded this species from western Borneo, based on material collected from a small peat swamp in southwestern Borneo. It has since been reported from peat swamp forests and blackwater streams throughout much of western and southern Borneo, eastern Sumatra and Banka, Bintan and Singkep islands (Kottelat et al., 1993; Tan & Tan, 1994; Kottelat & Lim, 1995; Lim &

Parenti, 2005; Tan & Kottelat, 2009). Individuals of *Sundadanio* are frequently collected in sympatry with *Paedocypris*, an other genus of the Cyprinidae endemic to the peat swamp forests of Southeast Asia (Kottelat et al., 2006; Britz & Kottelat, 2008). Interestingly, unlike *Paedocypris*, *Sundadanio* is absent from the peat swamp forests of western peninsular Malaysia.

Originally described as a member of *Rasbora*, *S. axelrodi* exhibits remarkable sexual dichromatism and unique sexual dimorphisms that are unknown amongst other South or Southeast Asian cyprinids (Kottelat & Witte, 1999; Conway & Britz, 2007). Of greatest interest are the sexual dimorphisms of the muscoskeletal system, including

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features of the pectoral girdle, axial skeleton and associated musculature, which are hypothesised to be responsible for the production of a croaking sound by males (Conway & Britz, 2007).

Comparison of the type material of *S. axelrodi* with material collected from peat swamp forests across Sundaland (the Great Sunda islands and the southern Malay Peninsula) revealed that *S. axelrodi* actually represents a number of different species. In this paper we provide a revised diagnosis for *Sundadanio*, redescribe *S. axelrodi* and provide descriptions for seven new species.

Materials and methods

All measurements (Fig. 1a) were taken on the left side of specimens to the nearest 0.1 mm using a Zeiss DRC stereomicroscope equipped with an ocular micrometer. Counts were obtained from cleared and stained (c&s) specimens, which were prepared following the protocol of Taylor & van Dyke (1985). Colour pattern terminology (Fig. 1b) generally follows that of Brittan (1954) with the addition of secondary lateral stripe (a narrow but distinct strip of melanophores running along the ventral edge of the anterior half of the dark lateral stripe, often visible as a bright red or orange stripe in live specimens). Selected specimens were initially dehydrated using a graded series of ethanol, critical point dried (Denton DCP-1A), placed on an aluminum stub and coated with gold (Denton Desk IV XLS) for examination with scanning electron microscopy (SEM) using a Philips XL-20 SEM. Two additional specimens were later prepared for SEM examination using the technique outlined in Ellis & Pendleton (2007) and examined using a JEOL JSM-6400 SEM.

Materials examined during the course of this study are housed in the following collections: BMNH, Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; CMK, collection of the second author, Cornell; FMNH, Field Museum of Natural History, Chicago; MZB, Research and Development Centre for Biology (ex Museum Zoologicum Bogoriense), Indonesian Institute of Sciences, Cibinong; TCWC, Texas Cooperative Wildlife Collection, College Station; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZRC, Raffles Museum of Biodiversity Research, National University of Singapore.

Taxonomy

Sundadanio Kottelat & Witte, 1999

Type species. *Rasbora axelrodi* Brittan, 1976.

Diagnosis. A genus of cyprinid fish distinguished from all other genera of the family Cyprinidae by several unique features relating to sexual dimorphism of the pectoral girdle and axial skeleton (as described by Conway & Britz, 2007), including: fifth pectoral-fin ray of males greatly thickened proximally, bearing a small pointed, sometimes serrated, ridge of bone on its dorsal surface; cleithrum of males with extensive membranous flange on posterior edge; scapulo-coracoid cartilage of males completely ossified, without intervening cartilage filled sutures (vs. scapulocoracoid cartilage with two ossifications, the scapula and coracoid); head of 5th rib and outer arm of the os suspensorium of males hypertrophied, up to 10× thicker than that of females; presence of a large hypertrophied bulbous muscle in males, a modification of the hypaxial musculature, attaching to a cup-like depression on enlarged head of fifth rib, extending medially to attach laterally to the head of the outer arm of the os suspensorium.

The following characters are also diagnostic, although not unique to the genus: miniature adult size (maximum size 19.7 mm SL); males with large conical tubercles over most available body surfaces, including the lower and upper jaws, dorsal and ventral surfaces of head (Fig. 2), chest, scales (Fig. 3), fin rays, fin membranes; two distinct clusters of large tubercles on lower jaw of male (Fig. 2), each supported by a bony shelf on lateral face of dentary (Fang, 2003); presence of large pre- and postepiphyseal fontanelle (Fig. 4); anal fin skeleton with elongate middle radials; branching point of branched anal-fin rays close to base of ray (separated only by three segments; Fig. 5); absence of the following bones in the neurocranium (nasal, intercalar, preethmoid), hyopalatine arch (ectopterygoid), pectoral girdle (posttemporal, postcleithrum, mesocoracoid) and axial skeleton (2nd uroneural); cephalic sensory system weakly developed, composed of a short supra-orbital canal (Fig. 4) and proopercular canal only; sensory canals open, not enclosed by canal ossification; absence of body lateral line; well developed free neuromasts over much of body surface,

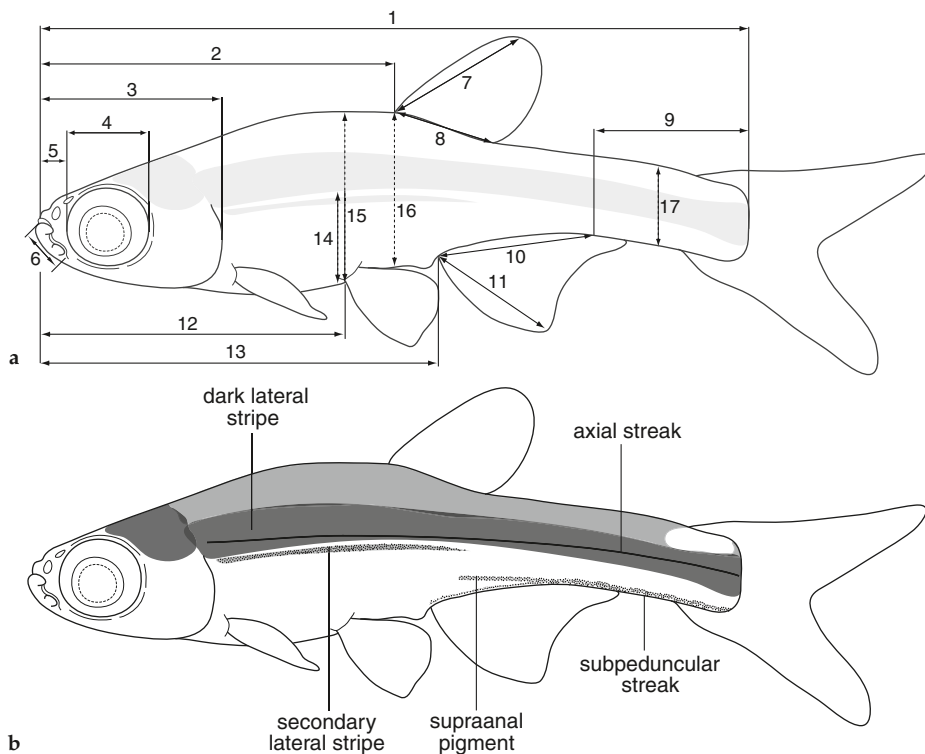
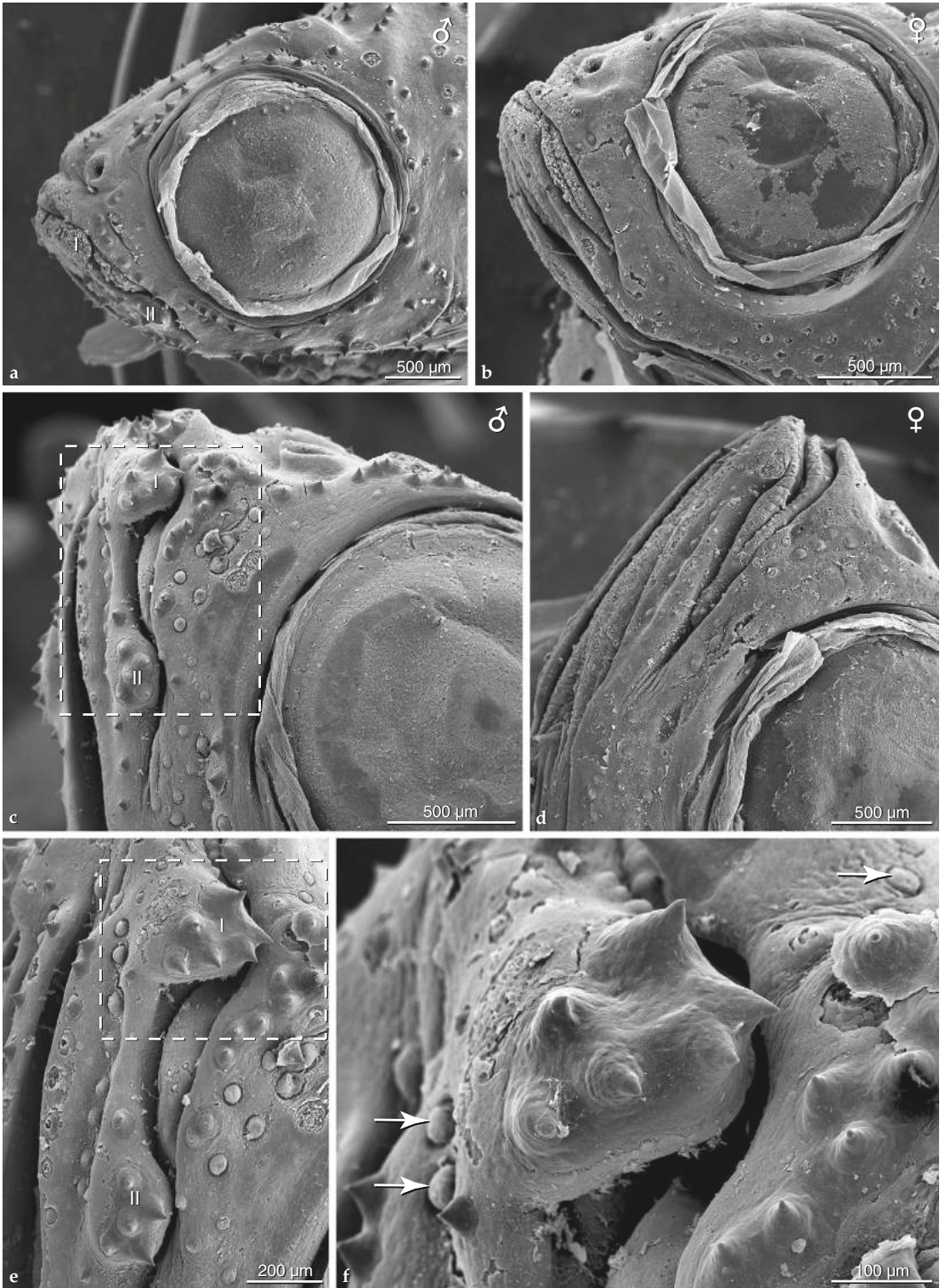


Fig. 1. Morphometric characters (a) and colour pattern terminology (b) used herein. 1, standard length; 2, pre-dorsal length; 3, head length; 4, eye diameter; 5, snout length; 6, length of lower jaw; 7, height of dorsal fin; 8, length of base of dorsal fin; 9, length of caudal peduncle; 10, length of base of anal fin; 11, height of anal fin; 12, prepelvic length; 13, preanal length; 14, dark lateral stripe to ventral midline, vertical distance from ventral-most point of dark lateral stripe to ventralmost edge of body; 15, body depth in front of pelvic fin; 16, body depth in front of dorsal fin; 17, depth of caudal peduncle, taken at narrowest point.

arranged in well defined vertical rows (Fig. 3); scales thin, cycloid; fully scaled species with 32–34 scales along midlateral row, 12 circumpeduncular; scales absent from caudal peduncle in *S. axelrodi* (Fig. 3); scales absent from dorsal midline anterior to dorsal fin and lateral body surface dorsal to anal fin in all species; scales lateral to window (= pseudotypanum) in hypaxial musculature enlarged in males (typically only 2); pharyngeal teeth arranged in two rows, with 1–2 teeth in outer row and 5 in inner row (formula 1–2,5–5,1–2, typically 2,5–5,2); dorsal-fin rays ii–iii.6.i, last two (one branched + one unbranched) articulating with same pterygiophore; anal-fin rays iii.6–7, last two articulating with same pterygiophore; caudal fin with 10+9 principal rays; 9–12 dorsal procurrent rays; 8–11 ventral procurrent rays; 9 pectoral-fin rays (i.5–7.ii–iii); 6–7 pelvic-fin rays (i.4–5.i); 14–15 abdominal + 19–21 caudal = 34–36

total vertebrae; 5–6 hypurals (hypural 6 and its cartilaginous precursor variably absent); variable number of dorsal and ventral caudal radial cartilages supporting bases of procurrent rays (Fig. 6).

Coloration pattern in life sexually dimorphic and dichromatic: males with broad pale blue to emerald green or orange to red longitudinal stripe extending on dorsolateral portion of body; wine-red to orange abdominal region and scarlet-red to black blotch on anterior half of anal fin; females transparent with scattering of small melanophores over much of body surface; in preservative, males with distinct dark lateral stripe, varying in thickness and development between species, extending from posterior margin of eye to caudal-fin base in most species; a smaller secondary lateral stripe, running along ventral surface of anterior half of dark lateral stripe varying present; females with



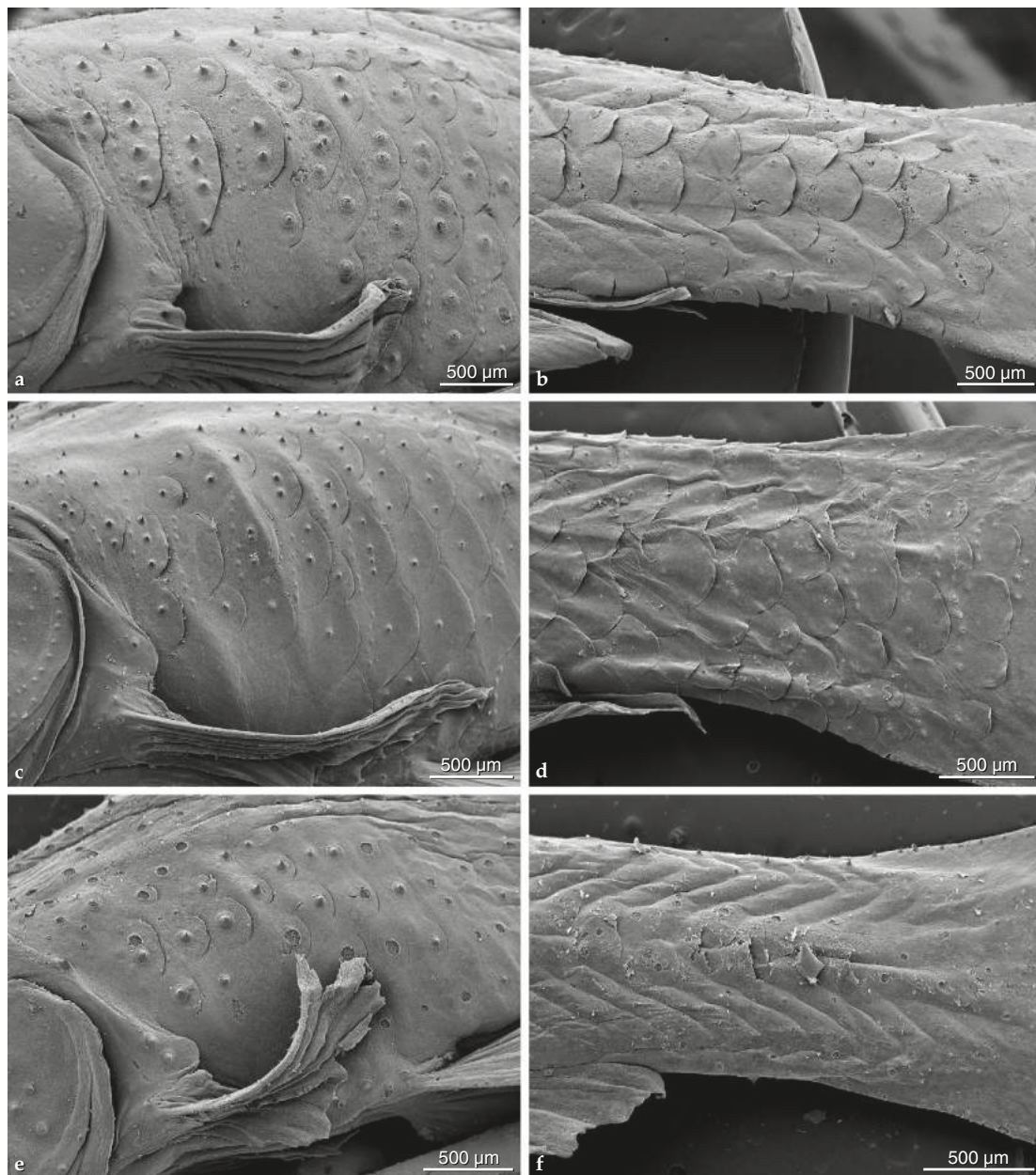


Fig. 3. Scanning electron micrographs of the body of *Sundadanio*; left column: left side of anterior half of body; right column: left side of caudal peduncle in lateral view; **a-b**, *S. gargula*, TCWC 15192.01, male, 17.9 mm SL; **c-d**, *S. retarius*, TCWC 15188.02 male, 16.9 mm SL; **e-f**, *S. axelrodi*, TCWC 15193.02, male, 13.8 mm SL.

◁ **Fig. 2.** Scanning electron micrographs of the mouthparts of *Sundadanio*; **a**, *S. axelrodi*, TCWC 15193.02, male, 13.8 mm SL; **b**, *S. axelrodi*, TCWC 15193.02, female, 13.4 mm SL; **c**, *S. gargula*, TCWC 15192.01, male, 17.9 mm SL; **d**, *S. gargula*, TCWC 15192.01, female, 16.9 mm SL; **e**, close up of lower jaw of *S. gargula* (box in **c**); **f**, close up of anterior most cluster of tubercle of *S. gargula* (box in **e**). Anterior and posterior clusters of tubercles on lower jaw of males indicated with I and II in **a**, **c** and **e**. Free neuromasts indicated with arrows in **f**.

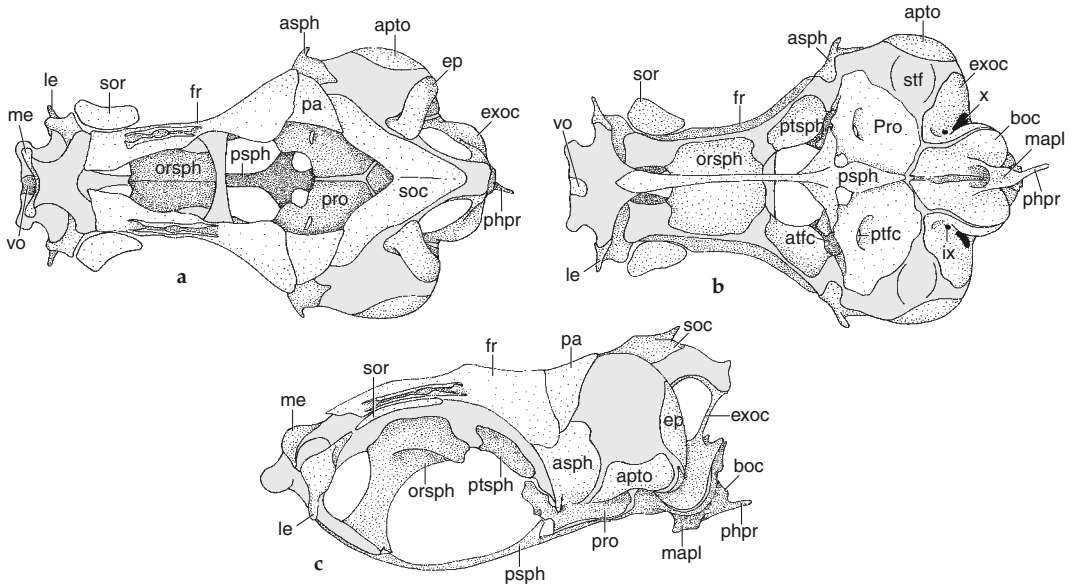


Fig. 4. *Sundadanio echinus*, TCWC 15189.01, male, 16.4 mm SL; neurocranium; **a**, dorsal view; **b**, ventral view; **c**, lateral view, left side. Cartilage grey. Abbreviations: **apto**, autopterotic; **asp**, autosphenotic; **atfc**, anterior opening of trigeminal-facial chamber; **boc**, basioccipital; **ep**, epiotic; **exoc**, exoccipital; **fr**, frontal; **ix**, foramen for glossopharyngeal nerve; **le**, lateral ethmoid; **mapl**, masticatory plate of basioccipital; **me**, mesethmoid; **orsph**, orbitosphenoid; **pa**, parietal; **phpr**, pharyngeal process of basioccipital; **pro**, prootic; **psph**, parasphenoid; **ptfc**, posterior opening of trigeminal-facial chamber; **ptsph**, pterosphenoid; **soc**, supraoccipital; **sor**, supra-orbital; **stf**, subtemporal fossa; **vo**, vomer; **x**, foramen for vagus nerve.

diffuse scattering of melanophores laterally, most dense along dorsolateral portion of body.

Distribution. Endemic to the peat swamp forests and blackwater streams of Southeast Asia (Borneo, Sumatra, Bangka, Bintan and Singkep) (Fig. 7).

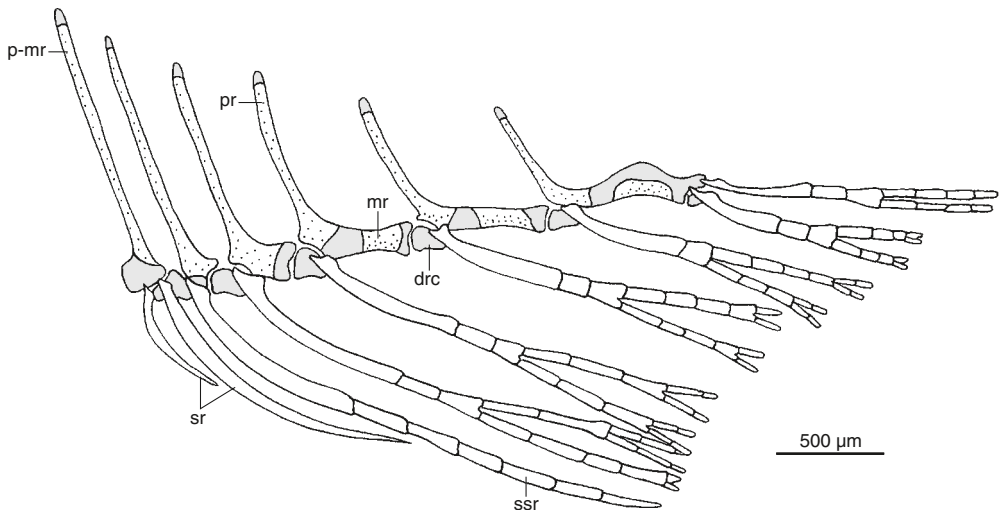


Fig. 5. *Sundadanio echinus*, TCWC 15189.01, male, 16.4 mm SL; anal-fin skeleton. Cartilage grey. Abbreviations: **drc**, distal radial cartilage; **mr**, middle radial; **p-mr**, proximal-middle radial; **pr**, proximal radial; **sr**, supernumerary fin ray; **ssr**, serially associated fin ray.

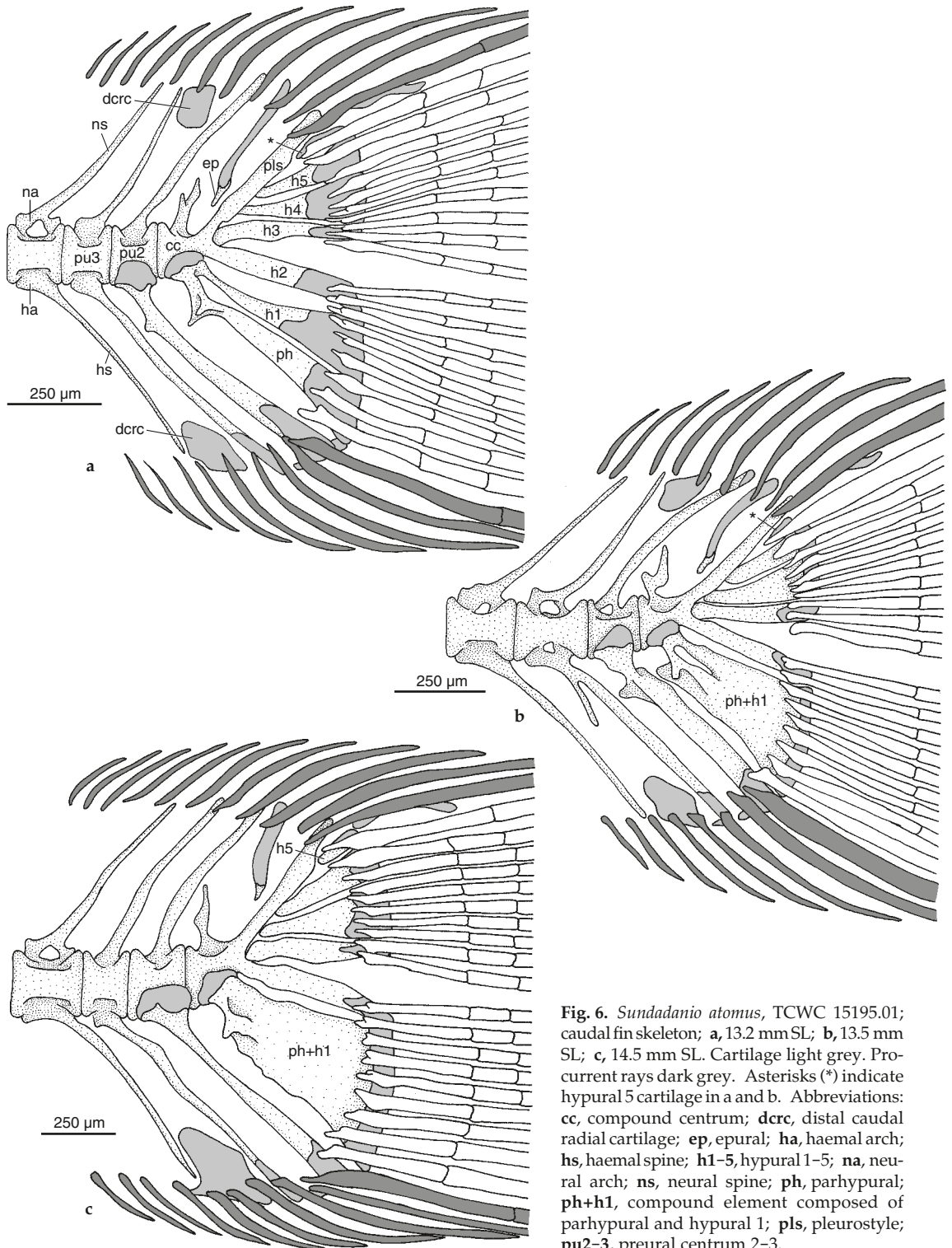


Fig. 6. *Sundadanio atomus*, TCWC 15195.01; caudal fin skeleton; **a**, 13.2 mm SL; **b**, 13.5 mm SL; **c**, 14.5 mm SL. Cartilage light grey. Procurrent rays dark grey. Asterisks (*) indicate hypural 5 cartilage in a and b. Abbreviations: **cc**, compound centrum; **drcr**, distal caudal radial cartilage; **ep**, epural; **ha**, haemal arch; **hs**, haemal spine; **h1-5**, hypural 1-5; **na**, neural arch; **ns**, neural spine; **ph**, parhypural; **ph+h1**, compound element composed of parhypural and hypural 1; **pls**, pleurostyle; **pu2-3**, preural centrum 2-3.

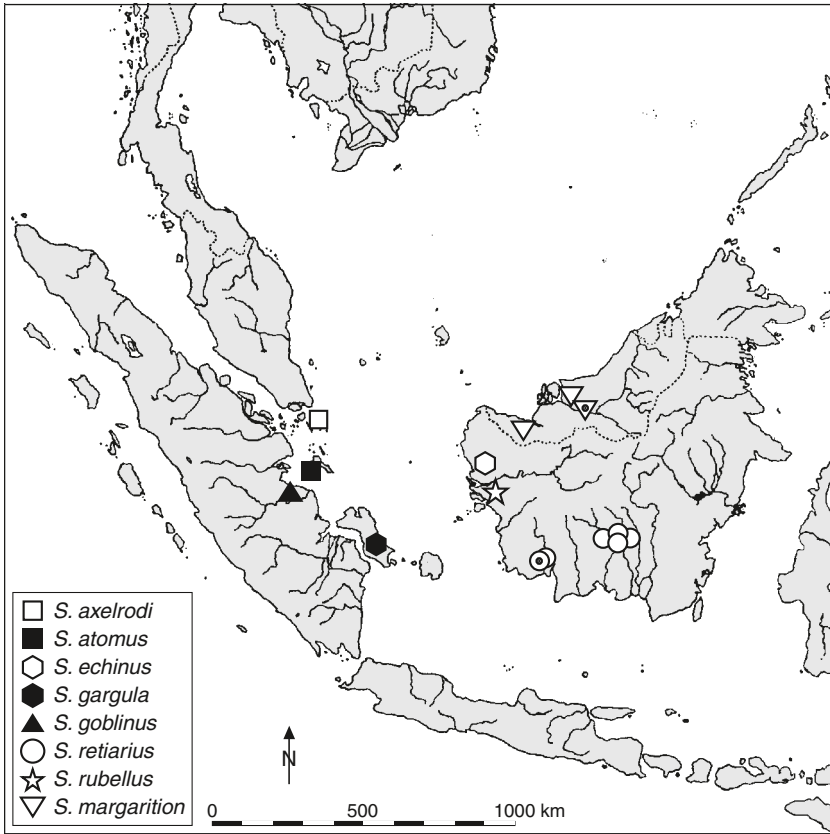


Fig. 7. Distribution of *Sundadanio* species. Open symbols with black dots indicate the type locality for those species known from more than one locality.

Key to the species of *Sundadanio*

Note on using key: The following key is designed to work on mature, fully tuberculate male specimens only and should not be used for female or immature male specimens.

- 1 – Secondary lateral stripe present along lateral side of anterior half of body, ventral to dark lateral stripe. 2
- Secondary lateral stripe absent. 5
- 2 – Dorsal body surface posterior to dorsal-fin origin with weak reticulate pattern; secondary lateral stripe strongly developed. 3
- Dorsal body surface posterior to dorsal-fin origin without reticulate pattern; secondary

lateral stripe weakly developed; live individuals with an emerald green sheen extending along dorsolateral surface of body; from vicinity of Kuching and Sibul, Sarawak.

..... *S. margarition*

- 3 – Horizontal through ventral margin of dark lateral stripe, when brought forward, extending through upper half of eye (Fig. 8a); dorsolateral surface of body with a green/blue-orange sheen in live individuals. 4

- Horizontal through ventral margin of dark lateral stripe, when brought forward, extending through lower half of eye (Fig. 8b); dorsolateral surface of body with an orange/red sheen in live individuals; southern Kalimantan Tengah.

..... *S. retarius*

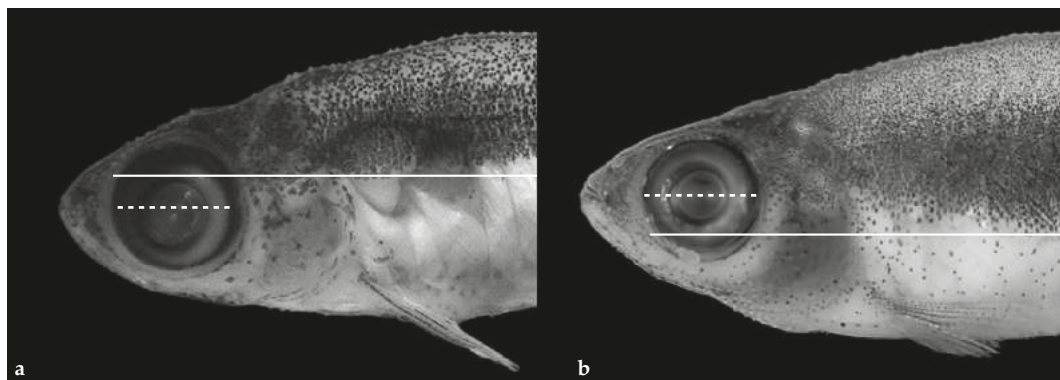


Fig. 8. Ventral margin of dark lateral stripe in relation to center of eye. Horizontal through ventral margin of dark lateral stripe, when brought forward, extending through upper half of eye (a) or lower half of eye (b).

- 4 – Snout length 14–18 % HL; body depth at pelvic-fin origin 25–30 % SL; live individuals with a green/blue-orange sheen extending along dorsolateral surface of body, bordered ventrally by a thin, bright red or brownish stripe; vicinity of Anjungan and Kepayan, western Kalimantan Barat.

..... *S. echinus*

- Snout length 18–21 % HL; body depth at pelvic-fin origin 20–26 % SL; live individuals with a green/blue-orange sheen extending along dorsolateral surface of body, bordered ventrally by a thin, bright orange stripe; vicinity of Ambawang, Kapuas basin, Kalimantan Barat.

..... *S. rubellus*

- 5 – Dark lateral stripe poorly developed.

.....6

- Dark lateral stripe well developed; live individuals with a blue/green sheen extending along dorsolateral surface of body; Bangka Island.

..... *S. gargula*

- 6 – Squamation complete along caudal peduncle; dorsal and caudal fins with or without dusky markings.

.....7

- Squamation incomplete along caudal peduncle; dorsal and caudal fins without dark markings; Bintan Island.

..... *S. axelrodi*

- 7 – Dorsal and caudal fins with dusky markings; maximum known size 19 mm SL; vicinity of Jambi, Batang Hari Basin, Sumatra.

..... *S. goblinus*

- Dorsal and caudal fins without dusky markings; maximum known size less than 16 mm SL; from peat swamp forests and blackwater streams of Singkep Island.

..... *S. atomus*

***Sundadanio axelrodi* (Brittan, 1976)**

(Figs. 9–11)

Rasbora axelrodi Brittan, 1976: 94; Tan & Tan, 2004: 353.

Material examined. 22 specimens including 2 paratypes, plus photograph and radiograph of holotype (CAS 36685): CAS 36686, paratypes, 2, 14.9 mm SL; Indonesia: Sumatra: probably Bintan Island, locality unknown. – ZRC 34255, 36, 8.0–13.6 mm SL; TCWC 15193.01, 2 c&s, 11.8–12.4 mm SL; TCWC 15193.02, 2 prepared for SEM, 13.4–13.8 mm SL; Indonesia: Sumatra: Bintan Island north; N. Sivasothi et al., 12 May 1993.

Diagnosis. *Sundadanio axelrodi* is distinguished from all other species of the genus by its reduced squamation (caudal peduncle devoid of scales or with few small, widely spaced scales situated along horizontal septum vs. caudal peduncle with complete covering of overlapping scales) and from all others except *S. atomus* and *S. goblinus* by its weakly developed dark lateral stripe. It is further distinguished by the following combination of characters: small body size (largest speci-

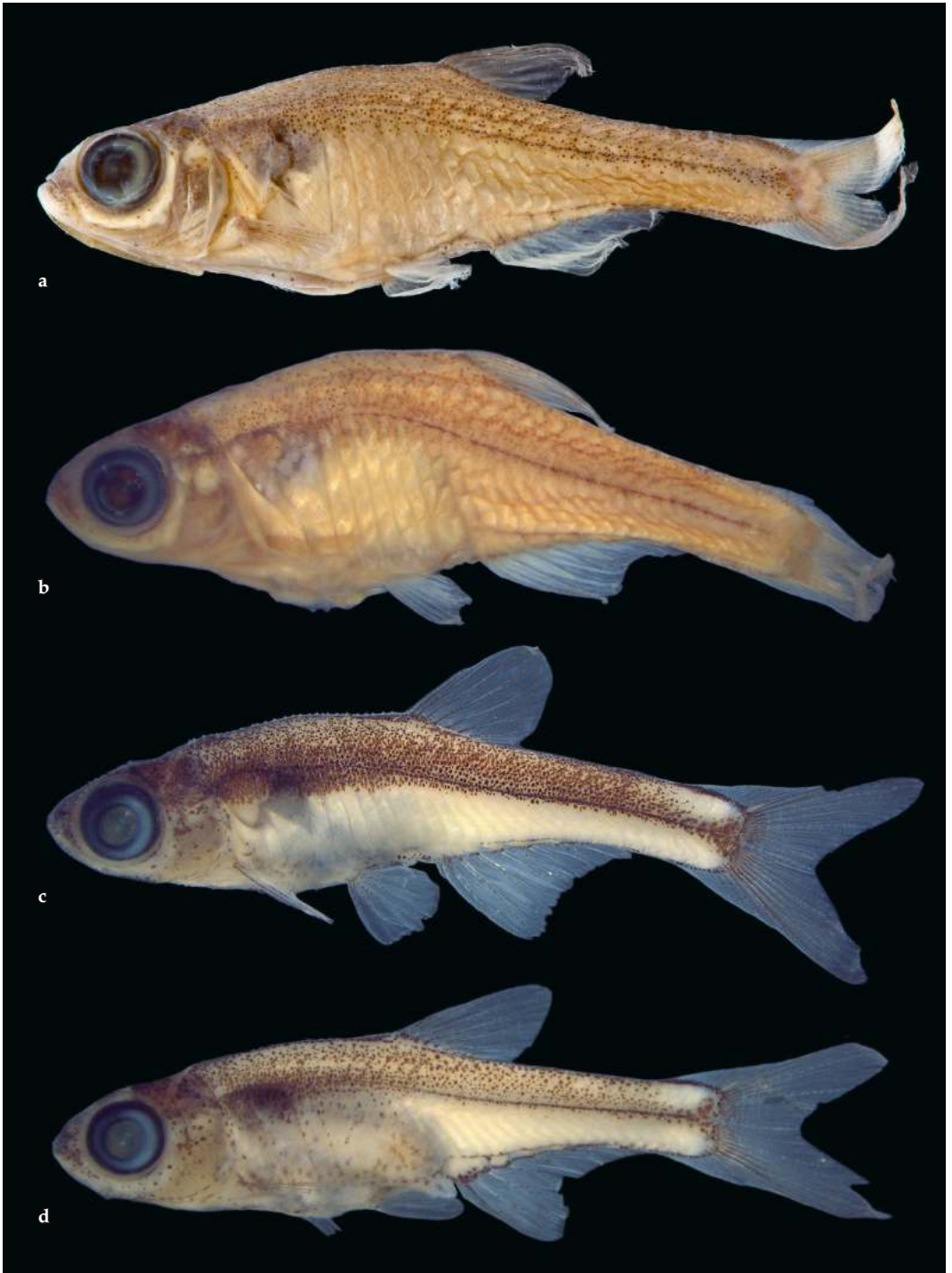


Fig. 9. *Sundadanio axelrodi*; **a**, CAS 36685, holotype, male, 17.1 mm SL; Indonesia: probably Bintan Island; **b**, CAS 36686, paratype, male, 14.9 mm SL; Indonesia: probably Bintan Island; **c-d**, ZRC 34255, male, 13.9 mm SL (**c**) and female, 13.6 mm SL (**d**); Indonesia: Bintan Island.



Fig. 10. *Sundadanio axelrodi*, male, not measured, not preserved; Indonesia: Bintan Island.



Fig. 11. *Sundadanio axelrodi*, male; Indonesia: Bintan Island. Aquarium specimens, not preserved. Photograph by Koji Yamazaki.

men examined 17.1 mm SL); live males with blue to emerald green sheen (this depends on angle of incident light and perception) across dorsal body surface and an intense red colour across anterior portion of anal fin; absence of secondary lateral stripe in males; absence of reticulate pattern along dorsal body surface; absence of dusky markings on dorsal and caudal fins; scales posterior to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre.

Description. Morphometric and meristic data are listed in Tables 1–2 respectively. General body shape as in Figures 8 and 10. Largest specimen examined 17.1 mm SL (range 10.5–17.1 mm, smallest tuberculate male 11.9 mm SL). Head and eye large, mouth terminal. Anterior nostril opening large, separate from smaller posterior opening. Body moderately deep, caudal peduncle slender. Dorsal fin situated mid-body, tip rounded, posterior half level with anterior half of anal fin. Pelvic fin rounded, origin situated anterior to

dorsal-fin origin. Pectoral fin pointed, reaching slightly anterior to or past pelvic-fin origin when depressed. Caudal fin forked, upper and lower lobes rounded, equal in length.

Dorsal procurrent rays 11–12, ventral procurrent rays 9–10. Total number of vertebrae 34–35, consisting of 14 abdominal and 20–21 caudal vertebrae. Males with large conical tubercles scattered over most of body surface, including dorsal and ventral surface of head and chest, dorsum, along leading edge of dorsal and anal fins, along rays of anal fin, along both dorsal and ventral surfaces of outer pectoral and pelvic rays. Caudal

peduncle devoid of scales except for a few, widely spaced separate scales adjacent to horizontal septum. Enlarged scales lateral to window in body musculature with one large conical tubercle at scale apex or two large conical tubercles arranged in a single vertical row across scale centre. Scales posterior to window in body musculature and anterior to anal-fin origin with a single small conical tubercle at centre. Females with small conical tubercles scattered over dorsal surface of head, on scales lateral to window in body musculature, and a single row along pre-dorsal midline.

Table 1. Morphometric characters for *Sundadanio axelrodi* (n=10), *S. atomus* (n=9), *S. gargula* (n=10) and *S. goblinus* (n=10). STD standard deviation. H, holotype.

	<i>S. axelrodi</i>			<i>S. atomus</i>			
	mean	STD	min-max	H	mean	STD	min-max
Standard length			10.5–17.1	14.5			10.2–15.7
Percent of standard length							
Head length	27.9	0.8	27.0–29.4	29.0	28.2	1.1	27.7–29.5
Predorsal length	55.4	1.2	54.6–57.7	53.8	53.8	0.7	52.9–54.5
Preanal length	58.4	1.9	56.8–61.7	58.6	58.7	1.3	57.4–60.2
Prepelvic length	46.8	1.3	46.3–48.4	45.5	45.9	0.9	45.2–47.2
Body depth at dorsal-fin origin fin	21.8	2.3	19.7–25.7	18.6	19.5	0.5	18.6–20.3
Body depth in front of pelvic fin	23.7	1.9	21.6–26.5	20.7	21.3	1.0	20.5–23.6
Dark lateral stripe to ventral midline	12.3	0.9	11.6–13.6	12.4	12.4	0.7	11.7–13.2
Caudal peduncle length	21.9	0.7	20.4–23.0	24.1	24.5	1.5	22.6–26.8
Caudal peduncle depth	11.0	0.5	10.6–12.2	9.7	9.5	0.4	8.7–10.2
Anal-fin base length	19.0	0.8	17.6–20.0	18.6	17.9	1.1	16.2–19.3
Dorsal-fin base length	9.6	0.5	9.0–10.8	10.3	9.4	0.7	8.3–10.3
Dorsal-fin height	20.4	0.7	19.4–21.3	22.1	23.0	1.8	19.1–25.2
Percents of head length							
Eye diameter	41.4	0.9	40.5–42.4	38.1	40.6	2.0	38.1–44.1
Snout length	19.4	1.4	17.5–21.6	19.0	18.6	1.1	17.8–20.6
Length of lower jaw	40.8	1.2	38.9–42.4	40.5	41.9	1.8	39.5–45.0

Table 2. Meristic characters of *Sundadanio axelrodi* (n=2), *S. atomus* (n=3), *S. gargula* (n=3), *S. goblinus* (n=3), *S. margarition* (n=7), *S. echinus* (n=5), *S. rubellus* (n=3) and *S. retarius* (n=5).

	<i>S. axelrodi</i>	<i>S. atomus</i>	<i>S. gargula</i>	<i>S. goblinus</i>	<i>S. margarition</i>
Dorsal-fin rays	ii.6.i	ii–iii.6.i	ii.6.i	ii.6.i	ii.6.i
Anal-fin rays	iii.6	iii.6–7	iii.6	iii.6	iii.6
Principal caudal-fin rays	10+9	10+9	10+9	10+9	10+9
Pelvic-fin rays	i.5.i	i.5.i	i.5.i	i.5.i	i.5.i
Pectoral-fin rays	i.6.ii	i.6.ii	i.6.ii	i.6.ii	i.6–7.i–ii
Procurrent rays (dorsal+ventral)	11–12+9–10	10–11+9–10	11–12+10	9–11+8–11	10–12+9–11
Abdominal vertebrae	14	14–15	14	15	14–15
Caudal vertebrae	20–21	20	20	20–21	19–20
Total vertebrae	34–35	34–35	34	35–36	34
Pharyngeal teeth	2,5–5,2	1,5–5,1	2,5–5,2	2,5–5,2	1–2,5–5,1–2

Coloration in life. Males with blue-emerald green sheen extending along dorsolateral surface of largely translucent body (Figs. 10–11); lower portion of abdomen deep red to carmine; anterior portion of anal fin intense red, fading posteriorly; other fins translucent. Females translucent with light scattering of melanophores; anterior portion of anal fin with a small patch of intense red at base of 3–4 anteriormost rays.

Coloration in preservative. In mature males (Fig. 8), body colour whitish with following pigmentation features: a weakly developed dark lateral stripe, about width of pupil, running from opercle to caudal-fin base, densest anteriorly. A dense scattering of dark melanophores dorsal

to dark lateral stripe, present over entire dorsal surface, occluding dorsal edge of dark lateral stripe, except for its posterior most point, ventral to base of dorsal procurrent rays. A narrow but distinct axial streak, starting behind opercle and continuing to caudal-fin base. A narrow row of small melanophores along entire length of dorsal midline (equivalent to the dorsal stripe of Brittan, 1954), from neurocranium posteriorly to caudal fin. A similar row of melanophores along ventral midline originating at posterior margin of vent, running along base of anal fin, and continuing posteriorly as a subpeduncular streak along ventral margin of caudal peduncle. Supraanal pigment originating above 3–4th branched anal-fin rays, continuing posteriorly and connecting with the subpeduncular streak. Dorsal area of occipital region heavily speckled with large melanophores, continuous with dorsal pigment row. Dorsal surface of snout between nostrils densely speckled with small melanophores. Light scattering of large dark melanophores on opercle, branchiostegal membranes, lower jaw, and surrounding vent and base of pelvic fin. A thin ventromedian row of small melanophores between pelvic fins and tips of cleithra. Thin streaks of small melanophores along principal caudal-fin rays and along rays of dorsal, anal, pectoral and pelvic fins. Lateral body surface, ventral to dark lateral stripe, devoid of melanophores.

Preserved colouration of mature females as described for males, except for the following differences. Dark lateral stripe absent. Upper surface of body with light scattering of dark melanophores, densest lateral to window in body musculature, absent on dorsal half of caudal peduncle, ventral to base of dorsal procurrent rays. Dark melanophores on outer surface of peritoneal lining visible through body musculature.

Distribution. *Sundadanio axelrodi* is known only from the peat swamp forests of Bintan Island (Fig. 7).

Remarks. *Sundadanio axelrodi* was described on the basis of 3 specimens obtained by H. R. Axelrod in the tanks of an aquarium-fish exporter in Singapore and said to come from Sumatra (Fig. 9a–b). In the 1970s there were very few companies exporting aquarium fishes from Indonesia. The main one was probably Vivaria Indonesia. Its owner (the late Dr. Digdo Yuwono) informed the second author (around 1988–1990)

<i>S. gargula</i>				<i>S. goblinus</i>			
H	mean	STD	min-max	H	mean	STD	min-max
18.7			10.2–19.0	16.0			12.2–19.2
25.7	26.1	0.8	24.7–27.2	26.9	27.5	0.8	26.5–29.0
52.9	54.2	1.0	52.6–55.1	53.1	52.8	0.7	51.7–53.8
57.2	58.6	1.1	57.1–60.1	57.5	57.2	1.2	55.6–58.7
44.4	45.3	0.9	44.1–46.8	43.8	44.2	1.0	42.5–45.8
23.5	23.8	0.8	22.5–24.5	21.9	20.0	1.1	18.0–21.4
25.1	25.5	0.8	24.0–27.0	22.5	21.3	1.1	19.0–22.9
14.0	14.0	0.4	13.5–14.5	–	–	–	–
25.1	23.1	1.3	21.3–25.1	23.1	24.8	1.1	23.1–26.5
9.6	9.8	0.5	9.0–10.6	10.0	9.7	0.5	8.8–10.4
20.9	20.0	1.2	18.5–21.9	19.4	18.2	1.7	15.5–20.1
11.2	10.3	0.6	9.6–11.2	10.6	9.8	0.7	8.9–10.6
19.8	21.7	1.9	19.7–23.9	23.1	21.8	1.2	19.5–23.6
41.7	41.9	1.2	39.1–43.5	37.2	37.6	1.2	36.4–40.4
18.7	18.5	0.9	17.1–19.6	18.6	19.9	0.8	18.6–20.5
41.6	41.4	1.2	39.1–43.9	39.5	42.5	1.8	39.5–45.2

<i>S. echinus</i>	<i>S. rubellus</i>	<i>S. retiarus</i>
ii.6.i	ii.6.i	ii.6.i
iii.6	iii.6	iii.6
10+9	10+9	10+9
i.5.i	i.4–5.i	i.5.i
i.6–7.i–ii	i.5–7.i–iii	i.6.ii
10–11+9	9–10+7–10	10+8–10
14–15	14–15	14–15
19–21	20–21	19–20
34–35	34–36	34–35
2,5–5,2	1–2,5–5,1–2	1–2,5–5,1–2



Fig. 12. *Sundadanio atomus*; Indonesia, Singkep Island: **a**, MZB 17188, holotype, male, 14.5 mm SL; **b**, ZRC 52375, paratype, female, 15.7 mm SL.



Fig. 13. *Sundadanio atomus*; ZRC 52375, male, not measured; Indonesia: Singkep Island.

that he had collected the specimens exported to Singapore to the company that provided them to Axelrod. He had collected them personally on Bintan Island. Dr. Yuwono has been a trustworthy informant who regularly provided locality information that could be checked and there is no reason to doubt this information. The type series

of *S. axelrodi* is characterized by its reduced squamation, with the caudal peduncle devoid of scales or with few small, widely spaced scales. We have observed this feature only in the samples from Bintan and this adds support to the origin of the type series.

Brittan (1976) reported a size of 18.1 mm SL



Fig. 14. *Sundadanio gargula*: Indonesia: Bangka; **a**, MZB 17190, holotype, male, 18.7 mm SL; **b**, CMK 9633, paratype, female, 17.8 mm SL.

for the holotype of *S. axelrodi* and 16.0 and 14.8 mm SL for the two paratypes. Our measurements of the two paratypes are both 14.9 mm SL using an ocular micrometer. David Catania (CAS) measured the holotype for us and found a smaller size than originally reported (17.1 mm SL vs. 18.1). The difference is possibly the result of shrinkage in alcohol. Despite this discrepancy, all members of the type series are roughly 2–3 mm larger than non-type material (the largest specimen of which is 13.9 mm SL). This is possibly because the types had been kept in an aquarium for some time prior to fixation.

***Sundadanio atomus*, new species**
(Figs. 12–13)

Holotype. MZB 17188, male, 14.5 mm SL; Sumatra: Singkep; P. Yap, 18 March 2008.

Paratypes. MZB 17189, 4, 13.0–15.5 mm SL; ZRC 52375, 17, 10.2–15.7 mm SL; TCWC 15195.01, 3 c&s, 13.2–14.5 mm SL; same data as holotype.

Diagnosis. *Sundadanio atomus* is distinguished from all other species of the genus, except *S. axelrodi* and *S. goblinus*, by its weakly developed dark lateral stripe. It is distinguished from *S. axelrodi* by having a complete covering of overlapping scales along caudal peduncle (vs. caudal peduncle devoid of scales or with few small, widely spaced scales situated along horizontal septum) and from *S. goblinus* by the absence (vs. presence) of intense dusky markings on the dorsal and caudal fins. It is further distinguished by the following combination of characters: small adult body size (largest specimen examined 15.7 mm SL); live males with blue to emerald green sheen (this depends on angle of incident light and perception) across dorsal body surface and an intense red colour across anterior portion of anal fin; absence of reticulate pattern along dorsal body surface; scales posterior to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre.

Description. Morphometric and meristic data are listed in Tables 1–2. General body shape as

in Figures 12–13. As described for *S. axelrodi* except for the following differences. Largest specimen examined 15.7 mm SL (range 10.2–15.7 mm). Dorsal procurent rays 10–11 (3). Total number of vertebrae 34–35 (3), consisting of 14–15 abdominal and 20 caudal vertebrae. Caudal peduncle with complete covering of scales. Scales posterior to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre in males.

Coloration in life. As described for *S. axelrodi*.

Coloration in preservative. As described for *S. axelrodi*.

Distribution. *Sundadanio atomus* is known only from the peat swamp forests of Pulau Singkep, Sumatra (Fig. 7).

Etymology. From the latin *atomus*, an indivisible particle, in reference to the small size of this species. In middle English an atomy (pleural atomies) was a diminutive fairy creature or sprite, a team of which drew Queen Mab's carriage in Shakespeare's *Romeo and Juliet* (Shakespeare, 1599). A noun in apposition.

Remarks. *Sundadanio atomus* is very similar to *S. axelrodi*, both of which are small species with a weakly developed dark lateral stripe in preserved males, and a blue-emerald green sheen across the dorsal body surface (Figs. 10, 11, 13). *Sundadanio atomus* is distinguished from *S. axelrodi* by its more slender and more elongate caudal peduncle (caudal peduncle length 23–27 % SL vs. 20–23; depth 9–10 % SL vs. 11–12; caudal peduncle depth in length 2.5 vs. 1.9) and by the presence of scales along the caudal peduncle (vs. absence). *Sundadanio atomus* is distinguished from *S. goblinus*, the only other species of *Sundadanio* to exhibit a weak lateral stripe in mature males, by the absence of dusky pigmentation along the outer margins of the dorsal and caudal fins (vs. presence).

***Sundadanio gargula*, new species**
(Fig. 14)

Sundadanio axelrodi (non Brittan): Conway & Britz, 2007: 1570.

Holotype. MZB 17190, male, 18.7 mm SL; Indonesia: Sumatra: Bangka island: blackwater stream in peat swamp forest, 5.5 km North of Payung on road to Pangkalpinang; M. Kottelat et al., 5 March 1993.

Paratypes. MZB 17191; ZRC 31229, 32, 12.1–18.1 mm SL; CMK 9633, 35, 10.2–19.0 mm SL; TCWC 15191.01, 3 c&s, 15.4–17.2 mm SL; TCWC 15192.01, 2 prepared for SEM, 16.9–17.9 mm SL; same data as holotype.

Diagnosis. *Sundadanio gargula* is distinguished from all other species of the genus by the greater distance between the dark lateral stripe and the ventral midline in males (13.5–14.5 % SL vs. 8.7–13.6) and by its larger and more numerous tubercles (enlarged scales next to window in body musculature with a vertical row of 3–5 large conical tubercles vs. 1–3 [Fig. 3]; scales posterior to enlarged scales next to window in body musculature and anterior to anal-fin origin with 2 large, closely situated conical tubercles at center vs. 1 or 2 small, widely spaced tubercles). It is further distinguished by the following combination of characters: large adult body size (largest specimen examined 19.0 mm SL, smallest tuberculate male 15.2 mm SL); live males with blue to emerald green sheen present across dorsal body surface and an intense red colour across anterior portion of anal fin; preserved males with a highly developed dark lateral stripe of uniform intensity along its entire length, horizontal through ventral border of which, when brought forward, extends through dorsal half of eye; absence of secondary lateral stripe in preserved males; absence of reticulate pattern along dorsal body surface; absence of dusky markings on dorsal and caudal fins; complete covering of scales on caudal peduncle.

Description. Morphometric and meristic data are listed in Tables 1–2. General body shape as in Figure 14. As described for *S. axelrodi* except for the following differences. Largest specimen examined 19.0 mm SL (range 10.2–19.0 mm).

Dorsal procurrent rays 11–12(3), ventral procurrent rays 10(3). Total number of vertebrae 34(3), consisting of 14 abdominal and 20 caudal vertebrae. Caudal peduncle with complete covering of scales.

Males with large conical tubercles scattered over most of body surface, including dorsal and ventral surface of head, upper and lower jaw, upper lip, entire margin of eye, chest, flank, caudal peduncle, dorsal, anal and caudal-fin rays, along both dorsal and ventral surface of outer pectoral and pelvic rays, and scales. Tubercles situated on upper and lower jaws, upper lip, and dorsal margin of eye, in males, larger and more greatly developed than those elsewhere on body. Enlarged scales lateral to window in body musculature with three to five large conical tubercles arranged in a single vertical row at scale apex (Fig. 3a). Scales on side of body posterior to these enlarged scales and anterior to anal-fin origin with 2 large, closely situated conical tubercles at center (Fig. 3a) Females with small tubercles scattered over dorsal surface of head, along ventral margin of eye, chest, caudal fin rays, on scales lateral to window in body musculature, around pelvic-fin origin, and along dorsal midline.

Coloration in life. As described for *S. axelrodi*.

Coloration in preservative. As described for *S. axelrodi* except for the following differences. Mature males with intense dark lateral stripe, originating posterior to neurocranium and dorsal to opercular opening, terminating at caudal fin origin. Dark lateral stripe deepest anteriorly, decreasing in depth gradually towards posterior. A dense scattering of dark melanophores along entire upper half of body, except region ventral to base of dorsal procurrent rays. Lateral body surface, ventral to dark lateral stripe, devoid of melanophores except for a small scattering of large melanophores lateral to cleithrum and those melanophores contributing to supraanal and subpeduncular streaks.

Distribution. *Sundadanio gargula* is known only from the peat swamp forests of Bangka Island, Sumatra (Figs. 7, 15).

Etymology. The name *gargula*, is derived from *gar-*, an onomatopoe common to many ancient European language for boiling water or water

flowing through a gullet, and the Latin *gula*, meaning throat; this gave rise to French gargouille and the English gargoyle; in reference to the somewhat grotesque appearance of the head and throat of tuberculate males of this species. A noun in apposition.

Remarks. *Sundadanio gargula* is most similar to *S. axelrodi* and *S. atomus*, live males of which exhibit a blue-emerald green sheen across the dorsal body surface and an intense red colour across the anterior portion of the anal fin. *Sundadanio gargula* is easily distinguished from both of these species by its larger size (largest specimen examined 19.0 mm SL vs. 17.1 for *S. axelrodi*, 15.7 for *S. atomus*), its more greatly developed dark lateral stripe in preserved males (vs. preserved males with a weakly developed dark lateral stripe), its greater distance between dark lateral stripe and ventral midline (13–14 % SL vs. 11–13), and by its smaller head (head length 25–27 % SL vs. 27–29).

Male specimens of *S. gargula* are more highly tuberculate than any other species of *Sundadanio* examined (Figs. 2–3). Almost all available body surfaces sport large conical tubercles, including the dorsal and ventral surface of the head, upper and lower jaws, upper lip, entire margin of eye, chest, flank, caudal peduncle, dorsal, anal and caudal fin rays, along both dorsal and ventral surfaces of the outer pectoral and pelvic rays, and scales. Tubercles situated on the upper and lower jaws, upper lip, and dorsal margin of eye, are larger and more greatly developed than tubercles present elsewhere on the body (Fig. 2). Males of this species also exhibit two tubercles on those scales situated posterior to the enlarged scales lateral to the window in the body musculature, double the number exhibited by other species for which this character could be checked (Fig. 3). The two enlarged scales situated lateral to the window in the body musculature also appear to exhibit more tubercles in *S. gargula* than they do in other species, with up to five (range 3–5) tubercles arranged in a vertical row on each (vs. 1–3 in other species for which this character could be examined). Female of *S. gargula* exhibit an almost identical pattern of tuberculation as that described for males, but tubercles are much smaller and less developed.



Fig. 15. Blackwater stream in peat swamp forest North of Payung, Bangka, Indonesia; 5 March 1993. Type locality of *Sundadanio gargula*.

Sundadanio goblinus, new species
(Figs. 16–17)

Sundadanio axelrodi (non Brittan): Tan & Kottelat, 2009: 20, table 1.

Holotype. MZB 17192, male, 16.0 mm SL; Sumatra: Jambi, Berbak (Batang Hari Basin); P. Yap, 18 March 2008.

Paratypes. MZB 17204, 5; ZRC 52376, 21, 12.2–19.2 mm SL; TCWC 15196.01, 3 c&s, 14.5–16.0 mm SL; same data as holotype.

Diagnosis. *Sundadanio goblinus* is distinguished from all other species of the genus by the presence of intense dusky markings on the dorsal and caudal fins, and from all others, except *S. axelrodi* and *S. atomus*, by the poorly developed dark lateral stripe of males. It is further distinguished by the following combination of characters: large body size (largest specimen examined 19.2 mm SL); body surface dorsal to dark lateral stripe with light scattering of melanophores in preserved males; absence of secondary lateral stripe in preserved males; absence of reticulate pattern along dorsal body surface; presence of enlarged scales next to window in body musculature; complete covering of scales on caudal peduncle.

Description. Morphometric and meristic data are listed in Tables 1–2, respectively. General body shape as in Figures 16–17. As described for *S. axelrodi* except for the following differences. Largest specimen examined 19.2 mm SL (range 12.2–



Fig. 16. *Sundadanio goblinus*; Sumatra: Jambi: Berbak; **a**, MZB 17192, holotype, male, 16.0 mm SL; **b**, ZRC 52376, paratype, female, 18.5 mm SL.



Fig. 17. *Sundadanio goblinus*, ZRC 52376, paratype, female, not measured; Sumatra: Jambi: Berbak.

19.2 mm). Dorsal procurrent rays 9–11 (3), ventral procurrent rays 8–11 (3). Total number of vertebrae 35–36 (3), consisting of 15 abdominal and 20–21 caudal vertebrae. Caudal peduncle with complete covering of scales.

Coloration in life. Live colouration of males unknown. Females translucent, with peppering of small dark melanophores over entire body surface, densest along caudal peduncle (Fig. 17). Anterior edge and tip of dorsal fin, anterior third



Fig. 18. *Sundadanio rubellus*; Indonesia: Kalimantan Barat: Ambawang; a, MZB 17193, holotype, male, 19.4 mm SL; b, ZRC 52377, paratype, female, 18.0 mm SL.

of anal fin and upper and lower lobes of caudal fin intensely marked with melanophores giving median fins dusky appearance.

Coloration in preservative. As described for *S. axelrodi* except for the following differences. Both sexes with small black melanophores along anterior edge and tip of dorsal fin, anterior third of anal fin and upper and lower lobes of caudal fin, giving median fins dusky appearance.

Distribution. *Sundadanio goblinus* is known from the coastal peat swamp forests along the coast of Jambi province in Central Sumatra (Fig. 7).

Etymology. The name *goblinus* is derived from the Anglo-French word goblin, meaning an ugly or grotesque sprite that is usually mischievous and sometimes evil and malicious; in reference to the small size and somewhat 'gnarled' appearance of the new species. A noun in apposition.

Remarks. *Sundadanio goblinus* is distinguished from all other species of the genus by the presence of dusky black markings on the dorsal and caudal fins (vs. absence). It is further distinguished from all other species, excluding *S. axelrodi* and *S. atomus*, by its weakly developed dark lateral stripe in preserved males. *Sundadanio goblinus* is distin-

guished from *S. axelrodi* and *S. atomus* by its larger size (largest specimen examined 19.2 mm SL vs. 17.1 for *S. axelrodi* and 15.7 for *S. atomus*). It is further distinguished from *S. axelrodi* by having a complete covering of scales on the caudal peduncle (vs. caudal peduncle devoid of scales of with a few small, widely spaced scales along horizontal septum).

The dark lateral stripe in mature males of *S. goblinus* is very poorly developed and is difficult to identify anterior to the dorsal fin. The distance between the ventral margin of the dark lateral stripe and the ventral midline was not measured for this species.

Sundadanio goblinus is the only species of *Sundadanio* known currently from mainland Sumatra (Tan & Kottelat, 2009).

Sundadanio rubellus, new species

(Figs. 18–19)

Sundadanio axelrodi (non Brittan): Conway & Britz 2007: 1570

Holotype. MZB 17193, male, 19.4 mm SL; Indonesia: Borneo: West Kalimantan, Ambawang; H. H. Tan et al., 18 May 2008.

Table 3. Morphometric characters for *Sundadanio echinus* (n=10), *S. rubellus* (n=10), *S. retarius* (n=29) and *S. margination* (n=10). STD, standard deviation. H, holotype.

	<i>S. rubellus</i>				<i>S. echinus</i>			
	H	mean	STD	min-max	H	mean	STD	min-max
Standard length	19.4			15.3–19.4	17.7			9.6–17.8
Percent of standard length								
Head length	27.8	28.6	0.9	27.1–30.2	26.5	28.2	0.7	26.5–29.3
Predorsal length	53.1	53.1	0.8	51.7–54.3	54.2	55.2	1.1	53.2–57.7
Preanal length	56.7	58.1	1.1	56.0–60.0	56.5	58.7	2.0	56.5–63.9
Prepelvic length	43.8	45.3	0.9	43.8–47.2	43.5	45.2	1.4	43.5–47.7
Body depth at dorsal-fin origin	20.6	21.9	1.4	19.3–25.0	23.7	24.5	1.1	22.8–26.5
Body depth in front of pelvic fin	22.7	23.4	1.3	20.5–25.6	26.0	26.7	1.8	24.8–30.5
Dark lateral stripe to ventral midline	11.3	11.9	1.4	10.2–13.7	11.8	12.5	0.7	11.5–13.6
Caudal peduncle length	23.7	23.4	1.0	21.1–24.7	22.6	22.7	0.9	21.6–24.5
Caudal peduncle depth	10.3	10.3	0.5	9.3–11.4	11.3	11.4	0.5	10.5–11.9
Anal-fin base length	19.6	19.3	1.1	17.5–21.4	20.9	19.6	1.0	18.0–20.9
Dorsal-fin base length	9.8	10.5	0.7	9.5–12.1	10.2	11.4	0.8	10.2–12.7
Dorsal-fin height	25.8	24.4	1.0	21.9–25.8	24.8	23.9	0.6	23.0–24.8
Percent of head length								
Eye diameter	38.9	39.1	1.6	36.4–42.5	40.3	40.2	1.3	37.2–41.4
Snout length	20.4	19.9	1.1	18.2–21.8	14.9	16.6	1.2	14.6–18.6
Length of lower jaw	37.0	38.7	1.2	37.3–41.7	40.4	38.9	1.5	37.2–41.5

Paratypes. MZB 17194, 4, 17.0–17.3 mm SL; ZRC 52377, 17, 15.5–19.2 mm SL; TCWC 15197.01, 3 c&s, 15.0–15.7 mm SL; same data as holotype.

Diagnosis. *Sundadanio rubellus* is distinguished from all other species of the genus, except *S. echinus*, by the presence of the secondary lateral stripe in both sexes (vs. secondary lateral stripe present only in males in *S. retiarius* and *S. margarition* or absent in *S. axelrodi*, *S. atomus*, *S. gargulae* and *S. goblinus*). It is further distinguished by the following combination of characters: large adult body size (largest specimen examined 19.4 mm SL); live males with blue-emerald green sheen across dorsal body surface, secondary lateral stripe intense red orange, running along ventral edge of blue-emerald green sheen from posterior to opercular opening to point opposite middle of anal fin, and an intense black-red marking across anterior portion of anal fin; preserved males with a well developed dark lateral stripe of roughly uniform depth along entire length, horizontal through ventral border of which, when brought forward, extending through dorsal half of eye; secondary lateral stripe well developed, consisting of small melanophores running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin; presence of a weak reticulate pattern along dorsal body surface posterior to dorsal fin; absence of dark markings on dorsal and caudal fins; presence of enlarged scales next

to window in body musculature; scales posterior to enlarged scales next to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre; complete covering of scales on caudal peduncle.

Description. Morphometric and meristic data are listed in Tables 2–3. General body shape as in Figures 18–19. As described for *S. axelrodi* except for the following differences. Largest specimen examined 19.4 mm SL (range 15.3–19.4 mm). Dorsal procurrent rays 9–10 (3), ventral procurrent rays 7–10 (3). Total number of vertebrae 34–36 (3), consisting of 14–15 abdominal and 20–21 caudal vertebrae. Tubercles weakly developed in type series, occupying similar positions to those described for *S. axelrodi*. Caudal peduncle with complete covering of scales.

Coloration in life. Males with blue-emerald green sheen extending along dorsolateral surface of largely translucent body (Fig. 19); an intense red-orange stripe (secondary lateral stripe) bordering ventral edge of blue-emerald green sheen from posterior to opercular opening to point opposite middle of anal fin; posterior half of abdomen and lateral body surface dorsal to anterior half of anal fin and ventral to secondary lateral stripe heavily speckled with large dark melanophores; anterior portion of anal fin with an intense black-red marking, fading posteriorly; anterior margin of dorsal fin and dorsal and ventral margins of caudal fin with a bright red-pink colour; paired fins translucent. Females translucent with light scattering of melanophores over entire body surface, densest on lateral body surface dorsal to anterior half of anal fin; a short orange-light red stripe (secondary lateral stripe) running along lateral body surface from just posterior to window in body musculature to a point lateral to middle of posterior swimbladder chamber; anterior portion of anal fin weakly speckled with small melanophores; anterior margin of dorsal fin and dorsal and ventral margins of caudal fin with a weak orange-red colour; paired fins translucent.

Coloration in preservative. As described for *S. axelrodi* except for the following differences. In males, scales situated along dorsal surface between dorsal fin origin and caudal-fin base weakly reticulate (Fig. 18). Dark lateral stripe well developed but narrow, of roughly uniform depth along entire length. A well developed secondary

<i>S. retiarius</i>				<i>S. margarition</i>			
H	mean	STD	min-max	H	mean	STD	min-max
18.0			11.4–19.4	18.9			8.6–19.7
27.2	27.6	0.9	25.7–29.4	27.4	27.9	0.8	26.3–29.4
52.8	53.9	0.9	51.7–55.8	54.8	54.1	1.1	51.5–55.9
56.7	58.2	1.7	54.7–61.0	57.1	58.7	1.0	56.9–60.5
45.0	45.7	1.6	43.1–48.2	42.8	46.2	1.4	42.8–49.5
25.6	23.1	1.6	18.3–25.6	22.8	22.1	1.3	21.5–24.4
26.7	24.7	1.2	21.7–26.7	24.6	24.3	1.3	21.1–26.9
10.6	9.7	0.8	8.3–11.0	11.4	12.2	0.7	11.2–13.1
22.2	22.6	1.1	20.4–25.3	23.4	22.9	0.8	21.1–24.5
11.7	10.5	0.6	9.5–12.3	10.8	9.4	0.6	8.7–10.8
22.2	20.0	1.1	18.2–22.2	19.4	19.3	0.9	17.0–20.6
10.6	10.6	0.6	9.5–12.3	8.6	9.7	1.2	7.7–11.5
26.1	24.6	1.0	22.9–26.4	22.3	22.0	1.0	20.9–23.2
38.7	39.4	1.3	37.3–43.2	37.5	36.7	1.0	34.8–38.6
20.4	19.4	1.4	16.7–21.6	20.8	19.9	1.6	17.1–21.7
38.7	39.2	1.7	36.4–41.9	37.5	39.6	1.6	37.2–43.2



Fig. 19. *Sundadanio rubellus*; Indonesia: Kalimantan Barat: Ambawang; ZRC 52377, paratypes, not measured; a, male; b, female.



Fig. 20. Aquarium specimen of *Sundadanio* from Borneo, probably *S. rubellus*. Not preserved. Photograph by Koji Yamazaki.



Fig. 21. *Sundadanio echinus*; Indonesia: Kalimantan Barat: Sungei Pinyuh; a, MZB 17195, holotype, male, 17.7 mm SL; b, MZB 3320, paratype, female, 17.8 mm SL.

lateral stripe of small melanophores running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin. Large dark melanophores scattered on posterior half of abdomen and lateral body surface dorsal to anterior half of anal fin and ventral to secondary lateral stripe. Reticulate pattern weakly developed in females. Secondary lateral stripe of females shorter than that of males, consisting of small melanophores running along lateral body surface from just posterior to window in body musculature to a point lateral to middle of posterior swimbladder chamber.

Distribution. *Sundadanio rubellus* is presently known only from the peat swamp forests of the Southern Kapuas River Delta, in the vicinity of Pontianak and Ambawang, West Kalimantan (Fig. 7).

Etymology. From the Latin *rubellus*, reddish, in reference to the live coloration of the fins of males. An adjective.

Remarks. Adult males of all four Bornean species of the genus, viz. *S. echinus*, *S. margarition*, *S. retiaris* and *S. rubellus*, exhibit a secondary lateral stripe. In *S. echinus*, *S. retiaris* and *S. rubellus* this stripe is obvious in life as a bright orange or red stripe along the centre of the body side. The secondary lateral stripe of *S. margarition* is not obvious in live males and visible only in preserved specimens (see remarks below under that species). Unlike *S. margarition* and *S. retiaris*, females of *S. rubellus* and *S. echinus* also exhibit a secondary lateral stripe that is visible in both live and preserved specimens. In both species the secondary lateral stripe exhibits an identical colour in life (orange-light red in *S. rubellus*; blood red in *S. echinus*) in both sexes, but differs in terms of

length between the sexes (being shorter in females vs. males; Fig. 19). Based on preserved material that we have been able to examine, the secondary lateral stripe appears to be much shorter in females of *S. rubellus* compared to females of *S. echinus* (running along middle of body surface from just posterior to window in body musculature to a point lateral to middle of posterior swimbladder chamber vs. along middle of body surface from just posterior to window in body musculature to a point opposite the origin of the anal fin).

Both *S. rubellus* and *S. echinus* inhabit southwestern Borneo, in the Kapuas basin and the adjacent Anjungan peat swamp forest, respectively. Though superficially similar, the two are easily distinguished based on two morphometric characters: body depth (body depth at pelvic-fin origin 20–26 % SL in *S. rubellus* vs. 25–30 in *S. echinus*) and snout length (snout length 14–18 % HL in *S. rubellus* vs. 18–21 in *S. echinus*). *Sundadanio rubellus* is easily distinguished from *S. retiarius* by its shallower lateral stripe, as evidenced by the greater distance between lateral stripe and ventral midline (10–14 % SL in *S. rubellus* vs. 8–11 in *S. retiarius*) and by the relation of the ventral border of dark lateral stripe to the eye (horizontal through dark lateral stripe extending through dorsal half of eye when brought forward in *S. rubellus* vs. extending through ventral half of eye in *S. retiarius*; Fig. 8). The two are further distinguished by the extent of the weak reticulated pattern over the dorsal body surface, which is more extensive in *S. retiarius* (see comments below under *S. retiarius*).

Sundadanio rubellus is common in the aquarium trade and individuals of this species are most likely conspecific with those referred to as the “red morph” or “*Sundadanio axelrodi* red” in aquarium circles. Anecdotal accounts by aquarium exporters indicate that *S. rubellus* attains a larger size than *S. echinus*. Our observations lend some support to this; the largest specimen of *S. echinus* examined was 17.7 mm SL whereas the largest specimen of *S. rubellus* was 19.4 mm SL.

Sundadanio echinus, new species
(Figs. 21–22)

Rasbora axelrodi (non Brittan): Roberts, 1989: 67, figs. 47–48.

Sundadanio axelrodi (non Brittan): Conway & Britz, 2007: 1570.

Holotype. MZB 17195, male, 17.7 mm SL; Indonesia: Borneo: West Kalimantan: Sungei Pinyuh, 8 km SE of Anjungan on road to Pontianak, 13 July 1976, T. R. Roberts & S. Wirjoatmodjo.

Paratypes. BMNH 1982.3.29.50–54, 5 (2 c&s), 13.9–14.9 mm SL; FMNH 94218, 5, 9.5–17.1 mm SL; MZB 3320, 21, 7.7–17.8 mm SL; USNM 230220, 8, 6.6–13.9 mm SL; same locality as holotype. – CMK 6652, 52, 13.1–16.2 mm SL; TCWC 15189.01, 3 c&s, 15.9–16.4 mm SL; same locality as holotype; M. Kottelat et al., 21 May 1990. – ZRC 49907, 125, 9.4–20.7 mm SL; West Kalimantan: Sungei Kepyayan, blackwater brook at km 58 on Pontianak–Anjungan road (0°18.84' N 109°8.09' E); H. H. Tan et al., 29 April 1998.

Diagnosis. *Sundadanio echinus* is distinguished from all other species of the genus by its shorter snout (snout length 15–19 % HL vs. 17–22) and by its deeper body (body depth at pelvic-fin origin 25–30 % SL vs. 20–28), and from all other species, except *S. rubellus*, by the presence of the secondary lateral stripe in both sexes (vs. secondary lateral stripe present only in males in *S. retiarius* and *S. margarition* or absent in *S. axelrodi*, *S. atomus*, *S. gargulae* and *S. goblinus*). It is further distinguished by the following combination of characters: large adult body size (largest specimen examined 17.8 mm SL); live males with emerald green sheen present across dorsal body surface, an intense red secondary lateral stripe, running along ventral edge of emerald green sheen from posterior to opercular opening to point opposite middle of anal fin, and an intense black marking across anterior portion of anal fin; preserved males with a well developed dark lateral stripe of roughly uniform depth along entire length, horizontal through ventral border of which, when brought forward, extending through dorsal half of eye (Fig. 8a); presence of a distinctive secondary lateral stripe of small melanophores running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin; presence of

reticulate pattern along dorsal body surface posterior to dorsal-fin origin; absence of dusky markings on dorsal and caudal fins; presence of enlarged scales next to window in body musculature; complete covering of scales on caudal peduncle; scales posterior to enlarged scales next to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre.

Description. Morphometric and meristic data are listed in Tables 2–3. General body shape as in Figures 21–22. As described for *S. axelrodi* except for the following differences. Largest specimen examined 17.8 mm SL (range 9.6–17.8 mm). Dorsal procurrent rays 10–11 (3), ventral procurrent rays 9 (3). Total number of vertebrae 34–35 (3), consisting of 14–15 abdominal and 19–21 caudal vertebrae. Caudal peduncle with complete covering of scales. Tubercles weakly developed in type series, occupying similar positions to those described for *S. axelrodi*.

Coloration in life. As described for *S. rubellus* with the following differences. Secondary lateral stripe intense blood red and of similar length in both sexes; bordering ventral edge of blue-emerald green sheen from posterior to opercular opening to point opposite middle of anal fin in males (Fig. 22); extending along middle of body side from just posterior to window in body musculature to point opposite the origin of anal fin in females.

Coloration in preservative. As described for *S. rubellus* with the following differences. Secondary lateral stripe of females composed of small melanophores, extending along middle of body side from just posterior to window in body musculature to point opposite the origin of anal fin (Fig. 21).

Distribution. *Sundadanio echinus* is known only from the peat swamp forests of the vicinity of Anjungan and Kepayan, West Kalimantan (Figs. 7, 23). We have seen pictures of *Sundadanio* from western Sarawak that we have tentatively identified as *S. echinus* indicating that this species may have a wider distribution than is known presently.

Etymology. From the Latin *echinus*, hedgehog, in reference to the large, spiny tubercles on the

lower jaw of *Sundadanio*, which were first discovered in this species (Roberts, 1989). A noun in apposition.

Remarks. *Sundadanio echinus* is most similar in general appearance to *S. rubellus*, which occur in adjacent drainages. See comments under *S. rubellus* above.

***Sundadanio retiarius*, new species**
(Figs. 24–25)

Sundadanio cf. *axelrodi*: Tan, 2009: 52

Holotype. MZB 17196, male, 18.0 mm SL; Indonesia: Borneo: Kalimantan Tengah: Kumai drainage: Sungei Nyeri, blackwater stream near Kampung Seitendang, 2°42.730' S 111°43.274' E, 12 m asl; M. Kottelat & H. H. Tan, 12 March 2008.

Paratypes. All from Indonesia: Borneo: Kalimantan Tengah: MZB 17197, 50; ZRC 52381, 44, 11.8–18.3 mm SL; ZRC 53239, CMK 20467, 177; TCWC 15188.01, 3 c&s, 16.5–17.0 mm SL; TCWC 15188.02, 2 prepared for SEM, 16.0–16.9 mm SL; same data as holotype. – ZRC 52380, 20, 12.0–19.4 mm SL; ZRC 53240, 112; CMK 20442, 131; Kotawaringin drainage: Sungei Pasir Panjang, outskirts of Pangkalan Bun, along road to Kumai, 2°43.916' S 111°39.574' E, 21 masl; M. Kottelat & H. H. Tan, 11 March 2008. – CAS 93213, 1, female, 17.6 mm SL; Mentaya drainage, blackwater tidal creek on left bank of Sungai Mentaya, ½ hour by speedboat upriver from Sampit; T. R. Roberts, 10 June 1992. – CAS 95435, 5, 2 males, 3 females, 11.4–16.7 mm SL; Mentaya drainage, blackwater tidal tributary of lower Mentaya, two hours by speedboat downstream from Sampit; T. R. Roberts, 8 June 1992. – CAS 95446, 1, female, 16.5 mm SL; Mentaya drainage, Sungai Rambah, 22 km West of Sampit on road to Pembuanghulu; T. R. Roberts, 11 June 1992. – CAS 95449, 2, males, 17.0–18.5 mm SL; Mentaya drainage, roadside swamp and ditches from Sampit North to Kotabesi; T. R. Roberts, 9 June 1992. – ZRC 52382, 5, 1 male, 15.7 mm SL, 3 females, 12.9–15.5 mm SL; Mentaya drainage: Pundu–Plantarang area, stream at km 142 on road from Palangka Raya to Sampit, 2°01.665' S 112° 59.804' E; M. Kottelat & H. H. Tan, 14 March 2008. – ZRC 52378, 18, 13.6–18.9 mm SL; ZRC 53241, 21; CMK 20418, 38; TCWC 15187.01, 2 c&s, 16.1–16.7 mm SL; Kahayan drainage, Rungan system;



Fig. 22. *Sundadanio echinus*, ZRC 49907, paratype, male, not measured; Indonesia: Kalimantan Barat: Anjungan.

blackwater stream at km 80 on road from Palangka Raya to Tumbang Telakian (35 km after turn-off at km 45 on road from Palangka Raya to Kasongan), 1°37.324' S 113°37.569' E, 28 m asl; M. Kottelat & H. H. Tan, 8 March 2008. – ZRC 52379, 5, 13.5–18.0 mm SL; Bukit Gelaga (village), stream at about 15 km on road turning north off road from Palangka Raja to Bargugus, 1°53.001' S 113°57.367' E; M. Kottelat & H. H. Tan, 7 March 2008.

Diagnosis. *Sundadanio retiaris* is distinguished from all other species of the genus by its smaller distance between dark lateral stripe and ventral midline in males (distance fitting 2.6 times into body depth at pelvic-fin origin vs. 1.7–2.1 in other species) and horizontal through ventral border of dark lateral stripe extending through ventral half of eye (vs. extending through dorsal half of eye; Fig. 8). It is also distinguished from all, except *S. rubellus* and *S. echinus*, by the presence of a weak reticulate pattern over the dorsal



Fig. 23. Sungei Pinyuh, Anjungan, Kalimantan Barat, Indonesia; 21 May 1990. Type locality of *Sundadanio echinus*.

and lateral body surfaces (vs. absence). It is further distinguished by the following combination of characters: large adult body size (largest specimen examined 19.4 mm SL); live males with orange-light green sheen present across dorsal body surface, an intense red-orange secondary lateral stripe, bordering ventral edge of orange-light green sheen from point posterior to opercular opening to point opposite middle of anal fin, and an intense black-red marking across anterior portion of anal fin; preserved males with a well developed dark lateral stripe, deepest anteriorly, covering entire window in body musculature; presence of a secondary lateral stripe of small melanophores running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin, often occluded by ventral edge of dark lateral stripe in mature males; absence of dusky markings on distal tips of dorsal and caudal fins; presence of enlarged scales next to window in body musculature; scales posterior to enlarged scales next to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre; complete covering of scales on caudal peduncle.

Description. Morphometric and meristic data are listed in Tables 2–3. General body shape as in Figures 24–25. As described for *S. axelrodi* except for the following differences. Largest specimen examined 19.4 mm SL (range 11.4–19.4 mm). Dorsal procurrent rays 10, ventral procurrent rays 9.

Males with large conical tubercles restricted to upper and lower jaws, dorsal surface of head, dorsal midline, enlarged scales covering window in body musculature, and surrounding scales. Enlarged scales lateral to window in body mus-



Fig. 24. *Sundadanio retiaris*; Indonesia: Kalimantan Tengah; **a**, MZB 17196, holotype, male, 18.0 mm SL; Kumai drainage; **b**, ZRC 52381, paratype, female, 17.8 mm SL; Kumai drainage; **c**, CAS 95449, paratype, male, 17.0 mm SL; Mentaya drainage; **d**, CAS 95446, paratype, female, 16.5 mm SL; Mentaya drainage.

culature with two to three large conical tubercles arranged in a single vertical row at scale apex. Scales elsewhere with a single tubercle at scale apex. Females with small tubercles scattered over

dorsal surface of head and along dorsal midline only. Caudal peduncle with complete covering of scales.

Coloration in life. Males with orange-light green longitudinal sheen extending along dorsolateral surface of largely translucent body (Fig. 25); an intense red-orange stripe (the secondary lateral stripe) bordering ventral edge of orange-light green sheen from posterior to opercular opening to point opposite middle of anal fin; posterior half of abdomen and lateral body surface dorsal to anal fin and ventral to secondary lateral stripe heavily speckled with large dark chromatophores; anterior portion of anal fin intensely black-dark red, fading posteriorly; other fins translucent. Females translucent with light scattering of melanophores over entire body surface, densest on lateral body surface dorsal to anterior half of anal fin (Fig. 25); anterior portion of anal fin weakly to intensely black-dark red; remaining fins translucent.

Coloration in preservative. As described for *S. rubellus* except for the following differences. In males, all scales, except for those situated between anterior half of anal fin and ventral margin of the dark lateral stripe, with a dark brown edge, forming a weakly reticulate pattern over body surface (Fig. 24). Reticulate pattern most pronounced dorsal to dark lateral stripe, between dorsal-fin origin and caudal-fin base. Dark lateral stripe very contrasted, deep, markedly deeper anteriorly, decreasing in depth towards posterior, ventral margin completely covering window in body musculature anteriorly. Large dark melanophores scattered on lateral body surface ventral to dark lateral stripe, except for area above anal fin, which is devoid of pigmentation. Reticulate pattern weakly developed in females.

Distribution. Known only from the peat swamps and blackwater streams of the southern part of Central Kalimantan, from the Kotawaringin to Kahayan drainages (Figs. 7, 26).

Etymology. From the latin *retiarus*, in ancient Rome a gladiator armed with a piece of netting and a trident, in reference to the reticulated pattern along the dorsal surface. A noun in apposition.

Remarks. *Sundadanio retiarus* is easily distinguished from the other members of the genus by its deep, well developed and very contrasted dark lateral stripe. In *S. retiarus*, the horizontal through the ventral margin of the dark lateral stripe, when

brought forward, extends through the lower half of the eye (Fig. 8b). In all other members of the genus, the horizontal through the ventral margin of the dark lateral stripe, when brought forward, extends through the upper half of the eye (Fig. 8a). Preserved male specimens of *S. retiarus* also exhibit a pronounced reticulated pattern over much of their body surface. *Sundadanio echinus* and *S. rubellus* are the only other members of the genus known to exhibit this reticulated pattern (Figs. 18, 21). In these latter species the reticulated pattern is restricted to the dorsal body surface, starting below the dorsal fin and extending along the dorsal edge of the caudal peduncle to the caudal fin base; it is absent from the lateral body surface below the dark lateral stripe. One male specimen from the Mentaya drainage (CAS 95449; Fig. 24) exhibits a particularly pronounced reticulate pattern, more so than any other specimen of this species.

Sundadanio retiarus has the widest distribution of any species of the genus described to date. It is distributed across five river drainages in southern Central Kalimantan, from the Kotawaringin eastwards to the Kahayan. Its range is almost identical to that reported for *Paedocypris carbunculus* by Britz & Kottelat (2008) and may reflect connectivity of these basins during periods of flooding. These two species have similar habitat requirements and are commonly found together. We have examined immature specimens from the Barito drainage (CMK 16731) that may also represent *S. retiarus* but this identification must be confirmed by the examination of mature specimens.

Sundadanio margariton, new species
(Figs. 27–29)

Sundadanio axelrodi (non Brittan): Kottelat & Lim, 1995: 233; Parenti & Lim, 2005: 18; Conway & Britz, 2007: 1570.

Holotype. ZRC 52383, male, 18.9 mm SL; Sarawak: Sibul, Sungei Nibung, just north of Durin bridge over Rajang River, 2°10'04.98" N 112°00'55.50" E; H. H. Tan, 14 & 16 May 2008.

Paratypes. All from Malaysia: Sarawak: ZRC 37865, 30, 14.0–15.5 mm SL; CMK 10876, 27, 9.4–16.9 mm SL; TCWC 15186.01, 2 c&s, 17.5–18.1 mm SL; Sungei Nibung, about 1 km North of Durin

Ferry on Sungai Rajang, on road from Sri Aman to Sibul, 2°09'53" N 112°00'59" E, M. Kottelat et al., 7 May 1994. – ZRC 37966, 5, 13.5–15.9 mm SL; CMK 10978, 5, 13.2–17.0 mm SL; Sungai Tebu, 8 km on road from Daro to Matu, blackwater stream in 10 year old sagu plantation; M. Kottelat & T. Tan, 14 June 1994. – ZRC 52392, 666, 7.8–17.5 mm SL; TCWC 15198.01, 1 prepared for SEM, 15.9 mm SL; same data as holotype. – ZRC 37970, 4, 12.7–16.5 mm SL; TCWC 15194.01, 2 c&s, 13.0–14.5 mm SL; Parit Nyadok, 200 m after 10 km-stone, on road from Daro to Matu; M. Kottelat & T. Tan, 14 June 1994.

Other material. All from Malaysia: Sarawak: ZRC 52393, 19, 9.0–17.9 mm SL; CMK 8424, 21, 8.0–18.9 mm SL; TCWC 15190.02, 3 c&s, 17.1–19.7 mm SL; TCWC 15190.02, 1 prepared for SEM, 17.3 mm SL; blackwater stream in forest at km 7 on road from Kuching to Batu Kawa, 1°31' N 110°18' E; M. Kottelat et al., 3 July 1992. – ZRC 39890, 44, 10.6–18.5 mm SL; Batu Kawa-Matang area, about 50 m before blackwater stream, 1°34'27.1" N 110°17'34.9" E; H. H. Tan et al., 14 January 1996.

Diagnosis. *Sundadanio margarition* is distinguished from all other species of the genus by the following combination of characters: large adult size (largest specimen examined 19.7 mm SL); live males with emerald blue-green sheen present across dorsal body surface and an intense black-red marking across anterior portion of anal fin; preserved males with a well developed dark lateral stripe of roughly uniform depth along entire length, horizontal through ventral border of which, when brought forward, extending through dorsal half of eye (Fig. 8a); presence of a weak secondary lateral stripe of small melanophores running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin; secondary lateral stripe of males not visible in live specimens; absence of reticulate pattern over dorsal body surface; absence of dusky markings on distal tips of dorsal and caudal fins; presence of enlarged scales next to window in body musculature; scales posterior to enlarged scales next to window in body musculature and anterior to anal-fin origin with a single small tubercle at centre; complete covering of scales on caudal peduncle.

Description. Morphometric and meristic data are listed in Tables 2–3. General body shape as in Figures 27–28. As described for *S. axelrodi* ex-

cept for the following differences. Largest specimen examined 19.7 mm SL (range examined 8.6–19.7 mm). Dorsal procurent rays 9 (2), 10 (5), 11 (1) or 12 (1), ventral procurent rays 9 (3), 10 (5) or 11 (1). Total number of vertebrae 34 (3), consisting of 14 (8) or 15 (1) abdominal and 19 (1) or 20 (8) caudal vertebrae. Tubercles weakly developed in type series, occupying similar positions to those described for *S. axelrodi*. Caudal peduncle with complete covering of scales.

Coloration in life. As described for *S. axelrodi* except for the following differences. Males largely translucent, with emerald green-blue sheen extending along dorsolateral surface of body (Figs. 28–29); anterior portion of anal fin dark red-black; other fins translucent. Secondary lateral stripe not obvious in life (typically represented by a bright red or orange stripe along lateral side of body when present). Females translucent with light speckling of black melanophores over lateral body surface (Fig. 28b).

Coloration in preservative. As described for *S. axelrodi* except for the following differences. Dark lateral stripe well developed (Fig. 27), but narrow, of roughly uniform depth along entire length. Dorsal surface of body with weak scattering of small melanophores. Weakly developed secondary lateral stripe present, running parallel to dark lateral stripe along its ventral margin from posterior to opercular opening to point opposite middle of anal fin.

Distribution. Known to date only from the peat swamp forests and blackwater streams from the Rajang and Sarawak River drainages and probably in between (Figs. 7, 30).

Etymology. From the Latin *margarition*, a small jewel, in reference to the shimmering live coloration of members of the genus. A noun in apposition.

Remarks. *Sundadanio margarition* can be easily distinguished from other species of *Sundadanio* with a secondary lateral stripe (viz. *S. echinus*, *S. retarius*, *S. rubellus*) by the absence (vs. presence) of a weak reticulate pattern along the dorsal surface of the body. Interestingly, the secondary lateral stripe of male *S. margarition* is not obvious in live individuals. In males of *S. retarius* and males and females of *S. echinus* and *S. rubel-*

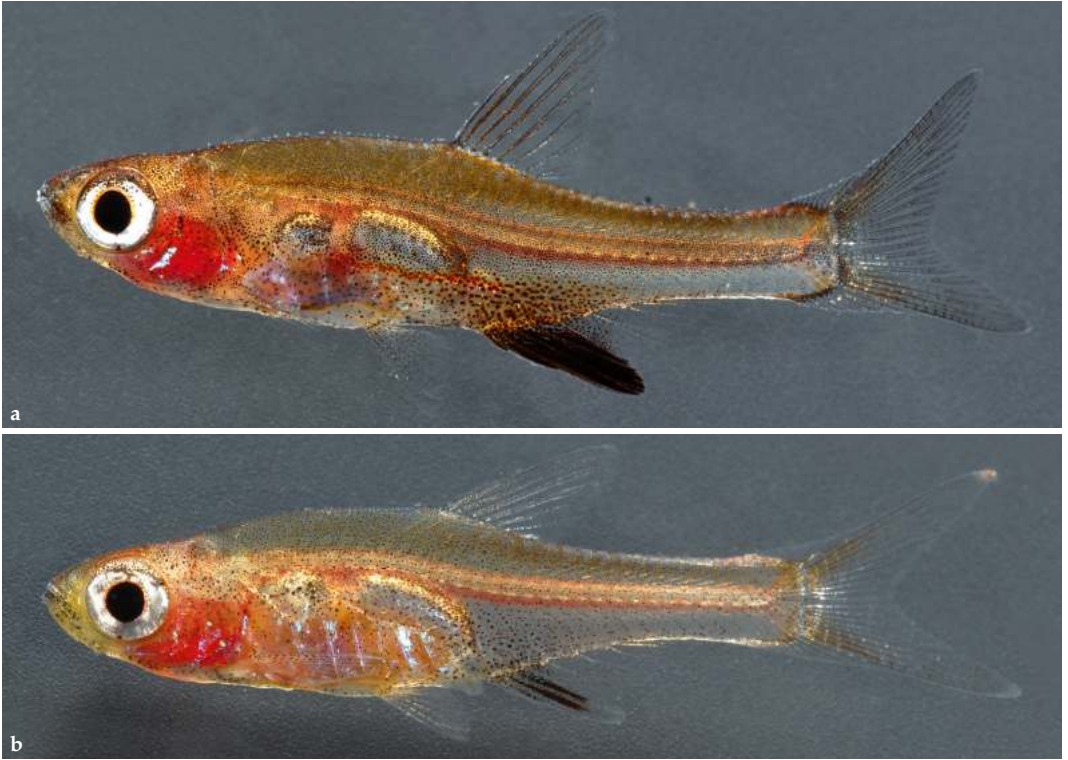


Fig. 25. *Sundadanio retiarius*; Indonesia: Kalimantan Tengah: Kumai drainage; ZRC 52381, paratypes, not measured; **a**, male; **b**, female.

lus the secondary lateral stripe is represented by a bright orange or red stripe in life, obvious from all angles.

Like *S. retiarius*, *S. margarition* has a particularly wide distribution when compared to other

members of the genus, being present in the peat swamp forests and blackwater streams of two major river drainages along the northern edge of Borneo, the Sarawak and Rajang basins and probably in between. A clear biogeographic break between the Sarawak and Rajang basins is exhibited in putative close relatives (sister groups) in several fish genera, for example the pairs *Rasbora kalochroma* and *R. kottelati* (Lim, 1995), *Betta ibanorum* and *B. akarensis* (Tan & Ng, 2004), and *Hemirhamphodon kuekenthali* and *H. pogonognathus* (Anderson & Collette, 1991). Though we could not detect any obvious, consistent differences between *S. margarition* populations from within or between the Rajang and Sarawak drainages, given the clear biogeographic break present across these drainages in species of other genera of freshwater fishes and the probable poor vagility of *Sundadanio*, *S. margarition* as recognised here may represent more than one species. In order to reflect this we have chosen to designate only those specimens from the Rajang basin as type material.



Fig. 26. Sungei Nyeri, blackwater stream near Kampung Seitendang, Kalimantan Tengah, Indonesia; 12 March 2008. Type locality of *Sundadanio retiarius*.



Fig. 27. *Sundadanio margaritum*; Sarawak: Sungei Nibung; a, ZRC 52383, holotype, male, 18.9 mm SL; b, ZRC 52392, paratype, female, 17.9 mm SL.

Discussion

Species of *Sundadanio* exhibit remarkable sexual dichromatism and dimorphism and the taxonomy of the genus presented herein is based almost entirely on characteristics of mature males. Like its putative sister group *Paedocypris* (sensu Rüber et al., 2007; Tang et al., 2010), elements of the colour pattern appear to be the most useful and consistent characteristics in terms of species diagnosis (Britz & Kottelat, 2008). Mature males of all eight species can be distinguished based on a combination of preserved colour pattern characters, including the development of the dark lateral stripe, the relation of the ventral margin of the dark lateral stripe to the eye, the presence/absence of pigmentation on the dorsal and caudal fins, the presence/absence of a secondary lateral stripe, and the presence/absence/extent of a reticulated pattern over the dorsal and lateral body surface. Features of live male coloration also differ between the species of *Sundadanio*, with males exhibiting either a metallic blue, metallic

green, orange-red or combination thereof in life. An intense orange-red secondary lateral stripe is also present in live males of three species (*S. echinus*, *S. retarius*, *S. rubellus*). The coloration of females appears to be relatively uniform across the genus, with the exception of *S. echinus* and *S. rubellus*, in which females also exhibit a secondary lateral stripe, visible in both live and preserved specimens (vs. absent in the other species).

Mature male specimens of *Sundadanio* exhibit extensive tuberculation (Roberts, 1989; Kottelat & Witte, 1999) and tubercle characteristics were found to be of utility in distinguishing between *S. gargula* and other members of the genus. Mature male specimens of *S. gargula* consistently exhibit two large tubercles on those scales situated on the lateral side of the body, posterior to the large modified scales (opposite the window in the lateral body musculature) and anterior to the pelvic fin (Fig. 3a). Males of other species typically exhibited only a single tubercle per scale, on those scales situated in the aforementioned region (Fig. 3b–c). Interestingly, though some

variation in the size of individual tubercles was obvious across the body surface (tubercles contributing to the tubercle clusters on the lower jaw where typically the largest on the body in all of the specimens examined), no differences in the shape of individual tubercles could be discerned using SEM. Using the classification scheme of Chen & Arratia (1996), tubercles of *Sundadanio* are best described as type A (i. e. smooth tubercles with sharp tip that are not surrounded by a “ring” like structure). Tubercle morphology has been relatively ignored in studies of danionine cyprinids, possibly due to their seasonal variation, but can be informative when examined in detail (e. g. Lumbantobing, 2010). Examination of additional (preferably reproductively active) male specimens from each species of *Sundadanio* is warranted to further quantify features of this character complex.

The most surprising outcome of our limited SEM investigation of *Sundadanio* external morphology was the variation in lateral body squamation. Contrary to Brittan (1976) and Roberts (1989) the predorsal midline is devoid of scales in all members of the genus and a variable covering of scales is present over the lateral body surface (Fig. 3), a relatively incomplete covering of scales (as in *S. axelrodi*) or complete covering (in all other species). The scales of *S. axelrodi* are also much smaller than those of other members of the genus (Fig. 3e), are widely spaced, and fail to form the typical overlapping scale pattern characteristic of other cyprinids, and teleosts in general. The caudal peduncle of *S. axelrodi* has a very reduced squamation, being either completely devoid of scales, or with a single row of small, widely spaced scales along the centre, parallel to the horizontal septum (Fig. 3e). Ontogenetic studies of scale formation patterns in members of the Cyprinidae indicate that the predorsal midline scales are typically the last to develop, regardless of the direction (i. e. anteroposterior or posteroanterior) of lateral body scale development (Sire et al., 1997; Sado & Kimura, 2005a–b). The absence of scales along the predorsal midline in *Sundadanio* is therefore easily attributed to developmental truncation. The greatly reduced squamation of *S. axelrodi*, the smallest member of the genus, may represent a more advanced state of developmental truncation.

Miniaturization and morphological variation.

Miniaturization, the evolution of tiny adult body

size, is a common phenomenon in animal taxa, particularly amongst non-amniote vertebrates (Hanken & Wake, 1993). Miniature taxa frequently exhibit high levels of morphological variability and unique blends of characters, combining morphological reductions and structural simplifications with novel characteristics that are absent from larger relatives (Hanken & Wake, 1993; Hanken 1993). With maximum sizes ranging from ~16–20 mm SL, all members of *Sundadanio* are clearly miniature fishes (sensu Weitzman & Vari, 1988) and provide an excellent opportunity to investigate the effects of miniaturization on the vertebrate body. Previous studies have commented on the morphological reductions (Fang, 2003; Britz & Conway, 2009) and novelties (Conway & Britz, 2007; Rüber et al., 2007; Britz & Conway, 2009) exhibited by *Sundadanio* and we take this opportunity to comment on the morphological variability present in the skeletal system and ask whether this ‘variability’ can be considered to be ‘increased’ compared to that of larger close relatives.

Examination of 28 cleared and stained specimens of *Sundadanio*, representing six species, revealed both intraspecific variation (between individuals of the same species) and individual variation (asymmetry) in a number of skeletal elements. Those found to exhibit intraspecific variation included: (1) supraneurals, ranging from 0–3 for each species (representing supraneurals 5–7); (2) presence/absence of hypural 6 and its cartilaginous precursor (reported previously by Britz & Conway, 2009; Fig. 6); (3) presence/absence of the upper distal caudal radial cartilage (lower present in all specimens examined; Fig. 6); and (4) the parhypural, which is either separate from, or fused to, hypural 1 (latter condition observed only in *S. atomus*; Fig. 6). Individual variation (asymmetry) of skeletal elements was less common in the material examined and observed only in elements of the shoulder girdle and gill arches. The posttemporal, an exoskeletal ossification of the shoulder girdle typically absent in *Sundadanio* (Conway & Britz, 2007; Britz & Conway, 2009), was present on the right side only, lateral to the tip of the supracleithrum, in a single specimen of *S. gargula*. Asymmetry in the number of teeth present in the inner pharyngeal tooth row on ceratobranchial 5 was observed in *S. margarithion*, *S. retiarius* and *S. rubellus* (Table 2). Pharyngeal teeth asymmetry was recently reported for *Sundadanio* by Pasco-Viel et al. (2010), not only in

the number of teeth per row (as described here) but also in the number of rows (3 vs. 2 rows on the left vs. right side of the single specimen examined; Pasco-Viel et al., 2010: fig. 4a). A third pharyngeal tooth row was absent from all material examined as part of this study and we prefer to report two rows as diagnostic for the genus in our generic diagnosis above.

In their review of miniaturization, Hanken & Wake (1993) listed increased morphological variability as one of three “organismal consequences” of miniaturization but noted that there were few published examples (majority of which were restricted to salamanders, e.g., Hanken, 1984, 1985). Our cursory investigation of *Sundadanio* osteology has revealed that intraspecific variation is quite common throughout the skeleton, particularly in elements of the axial skeleton. For example, all three individuals of *S. atomus* (all from the same locality and of similar size) that were randomly selected to be cleared and stained for bone and cartilage study exhibited distinctly different caudal skeletons, differing in number of distal caudal radial cartilages, whether the parhypural and hypural 1 were separate or fused, and whether hypural 6 cartilage was ossified to form hypural 6 or not (Fig. 6). Specimens of *S. echinus*, *S. gargula* and *S. retiarius* exhibited additional variation of the caudal skeleton in the presence/absence of hypural 6 cartilage (variation first reported for *Sundadanio* by Britz & Conway, 2009). Is this variability in the caudal skeleton of *Sundadanio* exhibited at ‘increased’ levels compared to its larger relatives? Unfortunately, few studies appear to have investigated variation in the skeleton of danionine cyprinids and without information on the variability present in the skeletons of close relatives this is a difficult question to answer. The results of the single study (Ferrerri et al., 2000), which we are aware of, to have investigated skeletal variation in *Danio rerio* (a putative close relative) indicate that levels of skeletal variation (quantified as number of “abnormalities”) are significantly higher in the caudal region than more anterior regions of the axial skeleton. These results suggest that the variation present in the caudal skeleton of *Sundadanio* may be within the normal levels of intraspecific variation exhibited by the caudal skeleton of danionins and not necessarily attributed to miniaturization. Additional investigations of variation in the skeletal system of cyprinids (and other teleosts) exhibiting a range of different adult body

sizes are needed to more elegantly test whether miniature cyprinids exhibit increased levels of morphological variability than their larger relatives, as has been suggested for salamanders (Hanken, 1984, 1985; Hanken & Wake, 1993).

Notes on the phylogenetic position of *Sundadanio*. *Sundadanio axelrodi* was originally described as a member of *Rasbora* by Brittan (1976). Roberts (1989) questioned its placement within *Rasbora* due to the presence of sexual dichromatism and extensive development of “large specialized tubercles in males”, features not known in other species of *Rasbora* at that time (but see Kottelat, 1995; Hadiaty & Kottelat, 2009). Through examination of the jaws of *S. axelrodi* (herein identified as *S. echinus*), Roberts (1989) suggested that it was more closely related to danionin cyprinids than to other species of *Rasbora*. Kottelat & Vidthayanon (1993) explicitly excluded *S. axelrodi* from *Rasbora* but refrained from placing it in any genus. Subsequently, Kottelat & Witte (1999) later erected *Sundadanio* for *R. axelrodi* and suggested a possible danionin affiliation following Roberts (1989).

Fang (2003) investigated the intra-relationships of certain danionin taxa (including *Sundadanio*) using characters of morphology. In that particular analysis *Sundadanio* was recovered as part of a clade of miniature (sensu Weitzman & Vari 1988) taxa, including *Danionella*, *Microrasbora rubescens* and *Danio erythromicron*. Based on low branch support values Fang (2003:719) doubted the validity of this clade and concluded that *Sundadanio* was “apparently a danionin taxon, but a precise phylogenetic placement is presently elusive”. A more recent study on the osteology of miniature cyprinids hypothesized that *Sundadanio* formed the sistergroup to a clade composed of *Paedocypris* + *Danionella* based on a number of apomorphic, reductive characteristics of the skeletal system (Britz & Conway, 2009).

A number of recent molecular phylogenetic studies, focused on various aspects of cyprinid systematics, have included *Sundadanio* (reviewed by Britz & Conway, 2011). The phylogenetic placement of *Sundadanio* inferred by such studies is conflicting, with as many as six alternative hypotheses published to date (Britz & Conway, 2011). Despite this conflict, some patterns are emerging and in the majority of these molecular phylogenetic hypotheses *Sundadanio* is recovered as a member of the Danioninae (e.g. Rüber et al.,



Fig. 28. *Sundadanio margaritum*; Sarawak: Sungei Nibung; ZRC 52392, paratypes, not measured; **a**, male; **b**, female.

2007; Conway et al., 2008; Fang et al., 2009; Conway et al., 2009; Britz et al., 2009; Tang et al., 2010, 2011), with four separate studies supporting a sister group relationship between *Sundadanio* and *Paedocypris* (Rüber et al., 2007; Fang et al., 2009; Tang et al., 2010, 2011). One recent molecular phylogenetic study that included *Sundadanio* (Mayden & Chen, 2010) concluded that it was not a member of the Danioninae (their rasborine clade) and erected the Sundadanionidae for its inclusion. We regard this taxonomic decision as irrational, given the conflicting placement of *Sundadanio* in molecular phylogenetic studies, and regard Sundadanionidae Mayden & Chen as a synonym of Danioninae Bleeker.

Britz et al. (in press) describe a number of derived osteological characters unique to *Sunda-*

danio and *Fangfangia*, the latter a new monotypic genus of miniature cyprinid from the peat swamp forests of southern Borneo. These derived osteological characters are: (1) the middle radials of the anal fin greatly elongated, reaching up to 50 % of the length of the proximal radials; (2) only one segment between the long basal element of branched anal-fin rays and the branching segments of those rays; (3) lateral process of the first centrum directed ventrally and connected to the pharyngeal process of the basioccipital process; and (4) high number of procurrent rays of caudal fin. These shared characters are suggestive of a sister group relationship between *Sundadanio* and *Fangfangia* (Britz et al., in press). Future studies should focus on testing this hypothesis.



Fig. 29. Aquarium specimen of *Sundadanio* from Borneo, probably *S. margarition*. Not preserved. Photograph by Koji Yamazaki.

Conclusions

Evidence presented herein indicates that *Sundadanio*, a genus considered until now to include a single, widespread species, is actually composed of multiple species. Like *S. axelrodi*, the new species described are endemic to the highly acidic peat swamp forests and blackwater streams of

Southeast Asia and further emphasize the link between miniature fishes and low pH aquatic environments (Weitzman & Vari, 1988; Kottelat & Vidthayanon, 1993; Kottelat et al., 2006; Bennett & Conway, 2010). Southeast Asian peat swamp forests represent some of the World's most vulnerable freshwater habitats (Ng et al., 1994; Kottelat et al., 2006). Most peat swamps visited by



Fig. 30. a, Sungai Nibung, southwest of Sibul, Sarawak; 7 May 1994. Type locality of *Sundadanio margarition*. b, Sungai Tebu, blackwater stream in 10 year old sagu plantation, road from Daro to Matu, Sarawak; 14 June 1994. Degraded habitat of *S. margarition*.

the authors in the 90s are no longer existent, and those which remain are under tremendous threat from anthropogenic activities such as deforestation, conversion into plantations, water extraction and draining. Habitat at the localities of many of the species of *Sundadanio* described herein is already heavily degraded (Figs. 26, 30b) or entirely destroyed. Extirpation of entire populations of *Sundadanio* has occurred and extinction may become a reality in the future given the restricted ranges and stenotopic nature of these unique cyprinids.

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