

A synopsis of the South Asian fishes referred to *Puntius* (Pisces: Cyprinidae)

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The tropical Asian cyprinid genus *Puntius*, which contains some 120 valid species, has long been suspected to be polyphyletic. Here, through an examination of external morphology, osteology, and analysis of 16S ribosomal RNA and cytochrome *b* gene fragments from 31 South Asian species hitherto referred to *Puntius*, we show that these fishes represent at least five lineages recognisable as genera. *Puntius sensu stricto* has the rostral barbels absent; last unbranched dorsal-fin ray weak or strong, smooth; and lateral line complete, with 22–28 pored scales. *Systemus* possesses maxillary and rostral barbels; last unbranched dorsal-fin ray stiff ('osseous'), serrated; and lateral line complete, with 27–34 scales. Three new genera are proposed: *Dawkinsia* (type species *Leuciscus filamentosus*) is distinguished by lacking rostral barbels; having the last unbranched dorsal-fin ray smooth; lateral line complete, with 18–22 scales; and a juvenile colour pattern that includes three black bars on the body. *Dra-vidia* (type species *Cirrhinus fasciatus*) is distinguished by having both rostral and maxillary barbels present; lateral line complete, with 18–26 pored scales; dorsal fin with 4 unbranched and 8 branched rays, last unbranched dorsal-fin ray smooth; infraorbital 3 deep, partly overlapping the preoperculum; and free uroneural and post-epiphysal fontanelle absent. *Pethia* (type species *Barbus nigrofasciatus*) is distinguished by having the last unbranched dorsal-fin ray stiff, serrated; infraorbital 3 deep, partially overlapping preoperculum; rostral barbels absent; maxillary barbels absent or minute; a black blotch on the caudal peduncle; and frequently, black blotches, spots or bars on the side of the body. The identities of *Puntius sophore* and *Systemus immaculatus* are clarified through the designation of neotypes; a lectotype is designated for *Neolissochilus bovanicus*; and precedence is given to the spelling *bovanicus* over *bovianicus*.

Introduction

Puntius has long been recognized as a “catch-all” genus for a variety of small tropical Asian cyprinids whose interrelationships are poorly understood (Kortmulder, 1972; Schut et al., 1984; Kottelat & Pethiyagoda, 1989; Kullander & Fang, 2005; Kullander, 2008). The genus, which contains some 220 nominal species (about 120 of these

considered valid), has seen a significant accretion of new species in recent years. The striking coloration of many species of *Puntius* has also led to their popularity as freshwater-aquarium fishes; many species are traded internationally as ornamentals (Collins et al., 2012). As the genus has hitherto been understood (e.g., Menon, 1999; Jayaram, 2010), species of *Puntius* range widely in size, from about 20 to 500 mm SL; possess 18–

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47 lateral-line scales; a complete, incomplete or interrupted lateral line; none, one or two pairs of barbels; a weak or strong, serrated or smooth last unbranched dorsal-fin ray; and a body coloration composed of a spot or blotch at the base of the caudal fin, one or more blotches or bars on the body, one or more lateral stripes, or none at all (Jayaram, 1991). The genus comprised 48 valid species in the South Asian region as at 1990 (Talwar & Jhingran, 1991), since when some 30 additional species have been described.

The first experimental investigation of species groups within *Puntius* appears to have been by Kortmulder (1972). As a result of similarities between their larvae and juveniles, and through a number of hybridization experiments, he suggested close relationships between *P. filamentosus* and *P. arulius*; and between *P. stoliczkanus*, *P. conchoni*, *P. phutunio*, *P. cumingii* and *P. nigrofasciatus*, concluding that “*cumingii*, *phutunio* and *gelius* are more or less neotenus descendants from a *nigrofasciatus* like ancestor.” A single experiment he performed to hybridize *P. conchoni* and *P. filamentosus*, however, produced larvae that died shortly after hatching as a result of being unable to aerate their swim bladders, suggestive of their belonging to different sub-groups within *Puntius*.

Following on this Taki et al. (1978), from an osteological study of 23 mostly Southeast Asian species of *Puntius* s.l., proposed six groups, of which two (their *P. conchoni* group and the *P. arulius* group) comprised South Asian species. In a later study, Shantakumar & Vishwanath (2006) included also *P. sophore*, the type species of *Puntius*, and showed that this species, together with *P. terio* and *P. chola*, possesses a post-epiphysal fontanelle and a smooth, weak last unbranched dorsal-fin ray. Both these characters were absent in the other nine species of *Puntius* s.l. they examined, which included two members of the *P. conchoni* group of Taki et al. (1978). They also proposed a group not sampled by the previous authors, comprising *P. sarana*, *P. jayarami* and *P. orphoides*, which differed from *Puntius* s.s. and the *P. conchoni* group by possessing 35–36 (vs. 29–33) vertebrae and a free uroneural (absent in *Puntius* s.s. and the *P. conchoni* group).

The foregoing work suggests that *Puntius* s.l. comprises a number of species groups that share various combinations of apomorphic characters

and character states. The vast range of the genus (all of tropical South and Southeast Asia), and the large number of included species, has made the resolution of all the species groups of which *Puntius* is presently composed a challenge. The conservative body plan of the included species too, has resulted in analyses of external morphology alone (e.g. Pillay, 1951; Jayaram, 1991; De Silva & Liyanage, 2010) proving to be of limited value in identifying species groups. At the same time, given the steady accretion of new species to *Puntius* s.l., especially from South Asia, an improved understanding of the species-groups that comprise it is desirable. Here, based on an analysis of external morphology and osteology, and a molecular phylogeny constructed from a mitochondrial 16S ribosomal RNA gene fragment (~540 bp) and a cytochrome *b* gene fragment (~550 bp) including 30 putative species of Indian and Sri Lankan *Puntius* s.l., we show that at least five lineages are present within South Asian *Puntius*, which we recognize as distinct genera.

Material and methods

Specimens referred to in this study are deposited in the Australian Museum, Sydney (AMS); the Natural History Museum, London (BMNH); the Collection of Maurice Kottelat, Cornol (CMK); the Raffles Museum of Biodiversity Research, Singapore (ZRC); the collection of the Wildlife Heritage Trust of Sri Lanka (WHT), now deposited in the National Museum of Sri Lanka, Colombo (NMSL); and the Zoological Survey of India, Kolkata (ZSI). Abbreviations: SL, standard length; HL, head length.

Measurements were made with digital Vernier calipers and recorded to the nearest 0.05 mm. Drawings were made using a Motic dissecting microscope fitted with a camera lucida. Methods for taking counts and measurements follow Pethiyagoda & Kottelat (2005a), except that scales in transverse line on body were counted downwards and backwards from dorsal-fin origin to the pelvic-fin origin. Osteological descriptions are based on alizarin-stained specimens (2 from each species, following the method of Taylor & Van Dyke, 1985) and/or x-ray radiographs. Osteological nomenclature follows Conway (2011). Numbers in (square) brackets following a count indicate the frequency of that count.

'South Asia' as used here is the political unit previously referred to as British India, bounded approximately by Pakistan, Myanmar and Sri Lanka. 'Southeast Asia' as used here is tropical continental Asia east of South Asia.

DNA analysis. DNA was extracted from ethanol-preserved tissues extracted from 39 species (see Table 1) using Qiagen tissue extraction kits and manufacturer's protocols. Mitochondrial 16S r-

bosomal RNA gene and cytochrome-b gene fragments were amplified using primers 16Sar and 16Sbr (Palumbi, 1996) which amplified ~540 bp of the 16S rRNA gene and CB-J-10933 (5'-TATGT-TCTACCATGAGGACAAATATC-3'), and BSF4 (5'-CTTCTACTGGTTGCCCTCCGATTCA-3') (Bossuyt & Milinkovitch, 2000), which amplified ~550 bp of cytochrome-b gene.

PCR conditions were as follows: denaturation at 95 °C for 40 s, annealing at 45 °C for 40 s and

Table 1. GenBank accession numbers, species and locations of the 39 species of Cyprinidae included in the molecular analysis.

reference no.	Genbank accession no.		species	location	country
	16s	cytb			
WHT8818_9	JF793558	JF793592	<i>Garra ceylonensis</i>	Homadola	Sri Lanka
WHT8819_31i	JF793559	JF793593	<i>Garra mullya</i>	Chalakudy	India
WHT8820_80	JF793560	JF793594	<i>Labeo dussumieri</i>	Elahera	Sri Lanka
WHT8821_23i	JF793561	JF793595	<i>Labeo dussumieri</i>	Alleppey	India
WHT8822_29i	JF793562	JF793596	<i>Osteochilichthys nashii</i>	Chalakudy	India
WHT8834_28i	JF793574	JF793608	<i>Gonoproktopterus jerdoni</i>	Srirangapatam	India
WHT8851_1i	JF793591	JF793625	<i>Gonoproktopterus curmuca</i>	Chalakudy	India
WHT8848_85	JF793588	JF793622	<i>Tor khudree</i>	Mawanana	Sri Lanka
WHT8849_AQ1	JF793589	JF793623	<i>Barbonymus schwanenfeldii</i>	Aquar. spec.	-
WHT8823_59	JF793563	JF793597	<i>Pethia bandula</i>	Galapitamada	Sri Lanka
WHT8838_64	JF793578	JF793612	<i>Pethia nigrofasciata</i>	Mawanana	Sri Lanka
WHT8812_1	EU604682.1	EU604674.1	<i>Pethia reval</i>	Kelani River	Sri Lanka
WHT8814_46	EU604684.1	EU604676.1	<i>Pethia cumingii</i>	Bentota	Sri Lanka
WHT8816_75	EU604686.1	EU604678.1	<i>Pethia melanomaculata</i>	Kandalama	Sri Lanka
WHT8850_AQ4	JF793590	JF793624	<i>Pethia conchoniis</i>	Aquar. spec.	-
WHT8815_6i	EU604687.1	EU604679.1	<i>Pethia ticto</i>	Boncron	India
WHT8832_20i	JF793572	JF793606	<i>Draavidia fasciata</i>	Chalakudy	India
WHT8852_40i	JF796852		<i>Dawkinsia assimilis</i>	Chalakudy	India
WHT8833_27i	JF793573	JF793607	<i>Dawkinsia filamentosa</i>	Kottayam	India
WHT8843_33	JF793583	JF793617	<i>Dawkinsia singhala</i>	Menik River	Sri Lanka
WHT8844_19	JF793584	JF793618	<i>Dawkinsia srilankensis</i>	Pallegama	Sri Lanka
WHT8824_48	JF793564	JF793598	<i>Puntius bimaculatus</i>	Bentota	Sri Lanka
WHT8825_88	JF793565	JF793599	<i>Puntius cf. bimaculatus</i>	Minneriya	Sri Lanka
WHT8846_11	JF793586	JF793620	<i>Puntius titteya</i>	Kalu River	Sri Lanka
WHT8847_43	JF793587	JF793621	<i>Puntius cf. titteya</i>	Bentota	Sri Lanka
WHT8826_54	JF793566	JF793600	<i>Puntius thermalis</i>	Mawanana	Sri Lanka
WHT8827_24i	JF793567	JF793601	<i>Puntius chola</i>	Boncron	India
WHT8845_217ai	JF793585	JF793619	<i>Puntius sophore</i>	Boncron	India
WHT8828_40	JF793568	JF793602	<i>Puntius layardi</i>	Walawe River	Sri Lanka
WHT8829_69	JF793569	JF793603	<i>Puntius dorsalis</i>	Gin River	Sri Lanka
WHT8830_70	JF793570	JF793604	<i>Puntius kelumi</i>	Gin River	Sri Lanka
WHT8831_35i	JF793571	JF793605	<i>Puntius dorsalis</i>	Mamallapuram	Sri Lanka
WHT8837_16i	JF793577	JF793611	<i>Puntius mahecola</i>	Kottayam	India
WHT8835_21	JF793575	JF793609	<i>Systemus martenstyni</i>	Pallegama	Sri Lanka
WHT8826_76	JF793576	JF793610	<i>Systemus sp. "Richmondi"</i>	Elahera	Sri Lanka
WHT8842_21i	JF793582	JF793616	<i>Systemus sarana</i>	Boncron	India
WHT8840_35	JF793580	JF793614	<i>Systemus timbiri</i>	Menik River	Sri Lanka
WHT8841_45	JF793581	JF793615	<i>Systemus spilurus</i>	Bentota	Sri Lanka
WHT8839_12	JF793579	JF793613	<i>Systemus pleurotaenia</i>	Gin River	Sri Lanka

extension at 72 °C for 40 s, 35 cycles, with a final extension of 72 °C for 5 min for the 16s gene fragment; denaturation at 95 °C for 40 s, annealing at 45 °C for 50 s and extension at 72 °C for 60 s, 35 cycles, with a final extension of 72 °C for 5 min for the cytochrome-b gene fragment. Products were gel purified and sequenced on an ABI 377 or ABI 3100 automated sequencer following manufacturer's protocols.

The 16s sequences were aligned using Clustal X (Jeanmougin et al., 1998) and adjusted by eye using Se-Al (ver. 2.0a9; Rambaut, 1996). Positions which were difficult to align and in which we had low confidence in positional homology were excluded from subsequent analyses, leaving a total 411 bp. Cytochrome-b sequences were aligned using translated amino acid sequences using Se-Al (ver. 2.0a9; Rambaut, 1996).

Two *Garra* species (*G. ceylonensis* and *G. mullya*) were used as an outgroup for rooting the tree: the data of Yang et al. (2010) and Zheng et al. (2010) suggest that *Garra* is a closely-related basal genus in relation to most taxa included in this analysis. The data were analyzed using Bayesian and Maximum Parsimony (MP) criteria. We used Bayesian inference as implemented in MrBayes (Huelsenbeck & Ronquist, 2001) to generate a phylogenetic hypothesis of relationships among the taxa and to estimate a general time-reversible model of sequence evolution with gamma-distributed rate variation among sites and a proportion of invariant sites (GTR+I+G). We ran four Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains for 2000 000 generations. The summed likelihood of the four chains converged on a stationary value by 50 000 generations (the burn-in time). We used the frequencies of clades in trees that were sampled every ten generations from the last 250 000 generations as estimates of the posterior probabilities of those clades (Huelsenbeck et al., 2001). Uniform priors were used

throughout and branch lengths, topology, and nucleotide substitution parameters were unconstrained. For tree searches under a Maximum Parsimony criterion (all characters unordered and weighted equally) we used heuristic searches with TBR branch-swapping and random taxon addition as implemented in PAUP*4.0b10. A single tree (tree score 1919 steps) was recorded. A bootstrap analysis to determine node support was also carried out within a maximum parsimony framework. The molecular dataset used for this study can be accessed at: <http://purl.org/phylo/treebase/phyloids/study/TB2:S12407> and <http://web.mac.com/madhavameegaskumbura>.

Results

The original dataset comprised of a 552-bp fragment of *cyt-b* and a 537-bp fragment of 16s. After removing poorly aligned regions of the 16s fragment, a 1060-bp fragment remained, which was used in the analyses.

From our Bayesian analysis, we chose the tree having the highest likelihood value as our best tree (Fig. 1). Maximum Parsimony analysis yielded a single tree (tree length = 1919; not shown because the tree topology from this analysis was very similar to that of the Bayesian analysis).

The Bayesian analysis recovered five well-supported clades within *Puntius* s.l., that we consider to be distinct genera on the basis of external-morphological and osteological characters (see Table 2 for genetic distances and below for diagnoses): *Puntius* s.s., *Systemus*, and three new genera, *Dawkinsia*, *Dravidia* and *Pethia*. The phylogeny shows that (1) *Pethia* is a sister group of *Dravidia* and *Dawkinsia*; (2) *Systemus* is the sister group of *Puntius*; and (3) [*Puntius* + *Systemus*] is sister to [*Dawkinsia* + *Dravidia* + *Pethia*].

Table 2. Percent uncorrected genetic distances between *Dawkinsia*, *Dravidia*, *Pethia*, *Puntius* and *Systemus* for the combined 16s and *cyt-b* fragments analysed.

	<i>Pethia</i>	<i>Dawkinsia</i>	<i>Dravidia</i>	<i>Systemus</i>	<i>Puntius</i>
<i>Pethia</i>	–	7.3–12.0	13.5–14.2	10.4–15.6	10.4–16.3
<i>Dawkinsia</i>		–	12.2–15.6	8.1–15.6	8.4–16.6
<i>Dravidia</i>			–	12.7–15.6	13.0–16.6
<i>Systemus</i>				–	9.5–18.1

Puntius Hamilton, 1822

Type species. *Cyprinus sophore* Hamilton, 1822 (Fig. 2).

Diagnosis. A genus of cyprinid fishes differing from all South and Southeast Asian genera of Cyprininae by the combination of the following characters and character states: adult size usually less than 120 mm SL; maxillary barbels absent or present, rostral barbels absent; dorsal fin with 3–4 unbranched and 8 branched rays; anal fin with 3 unbranched and 5 branched rays; last unbranched dorsal-fin ray weak or strong, apically segmented, not serrated (Fig. 3c); lateral line complete, with 22–28 pored scales on the body; free uroneural present (Fig. 3d); gill rakers simple, acuminate (not branched or laminate); no antrorse predorsal spinous ray; a post-epiphysial fontanelle present (Fig. 3b; but see remarks on *P. bimaculatus* and *P. titteya*, below); supraneurals 4; infraorbital 3 slender (Fig. 3a); 5th ceratobranchial narrow; pharyngeal teeth 5+3+2; 12–14 abdominal and 14–16 caudal vertebrae; and a colour pattern that includes a (sometimes faint) black spot or blotch on the caudal peduncle.

Remarks. Based on the comparisons made herein (Fig. 1) and the data of Shantakumar & Vishwanath (2006) and Kullander (2008), we include the following South Asian species in *Puntius*: *P. chola* (Hamilton, 1822), *P. dorsalis* (Jerdon, 1849), *P. kelumi* Pethiyagoda, Silva, Maduwage & Mee-gaskumbura, 2008, *P. layardi* (Günther, 1868), *P. mahecola* (Valenciennes, in Cuvier & Valenciennes, 1844), *P. pugio* Kullander, 2008, *P. sophore* (Hamilton, 1822), *P. terio* (Hamilton, 1822) and *P. thermalis* (Valenciennes, in Cuvier & Valenciennes, 1844).

Because they share the external characters diagnostic of *Puntius*, we tentatively retain the following South Asian species in that genus: *P. amphibius* (Valenciennes, in Cuvier & Valenciennes 1842), *P. arenatus* (Day, 1878), *P. burmanicus* (Day, 1878), *P. cauveriensis* (Hora, 1937), *P. crescentus* Yazdani & Singh, 1994, *P. kamalika* Silva, Maduwage & Pethiyagoda, 2008, *P. madhusoodani* Krishnakumar, Pereira & Radhakrishnan, 2011, *P. melanostigma* (Day, 1878), *P. mudumalaisis* Menon & Rema Devi, 1992, *P. muzaffarpurensis* Srivastava, Verma & Sharma, 1977, *P. narayani* (Hora, 1937), *P. parrah* (Day, 1865), *P. sahyadriensis* Silas, 1953, *P. vittatus* (Day, 1865) and *P. waa-*

geni (Day, 1872). We also tentatively retain in *Puntius* *P. denisonii* (Day, 1865) and *P. chalakkudensis* Menon, Rema Devi & Thobias, 1999, for which we lacked material for DNA and osteological analysis: they possess a strikingly different coloration and mouth shape to all other congeners (Menon et al., 1999) and are likely to warrant placement in a separate genus in the future.

Two species, *P. bimaculatus* (Bleeker, 1863a) and *P. titteya* Deraniyagala, 1929, that differ from all the other *Puntius* examined by lacking a post-epiphysial fontanelle (Fig. 4b) and possessing only 7 branched dorsal-fin rays, are nevertheless retained in *Puntius* (see Discussion).

Puntius sophore (Hamilton, 1822)

(Fig. 2)

Cyprinus sophore Hamilton, 1822: 310, 389, pl. 19.

Neotype. ZRC 35064, 71.8 mm SL; Bangladesh: Srimangal [= Sreemangal] town market, from Hail Hoar floodplain near Moulvi Bazaar; D. Hoggarth, Mar 1993.

Topotypes. ZRC 35065–35069, 5, 59.4–80.6 mm SL, same data as neotype.

Description of neotype. General body shape and appearance are illustrated in Fig. 2a. Morphometric data of neotype and 5 topotypes are given in Table 3; characters of topotypes, where different from neotype, are given in parentheses. Body stout, standard length about 2.4 times maximum depth, laterally compressed. Dorsal profile of head concave above eye; dorsal profile of body convex, rising steeply from occipital, almost horizontal at dorsal-fin origin. Ventral contour of body convex to anal-fin insertion, almost horizontal at pelvic-fin origin. Dorsal and ventral profiles of caudal peduncle concave to terminal scales on tail base. Caudal peduncle length 1.3 (1.2–1.4) times its depth.

Head short, its length about one-fifth standard length, somewhat compressed laterally. Eyes located forward of centre, superiorly on head, just visible in ventral and dorsal views. Nares dorsolaterally orientated. Mouth U-shaped in ventral aspect, subterminal, small, angle of gape not reaching below anterior nares in lateral aspect. Lips fleshy, entire, adnate to jaws. Upper lip overhanging lower one. Barbels absent.

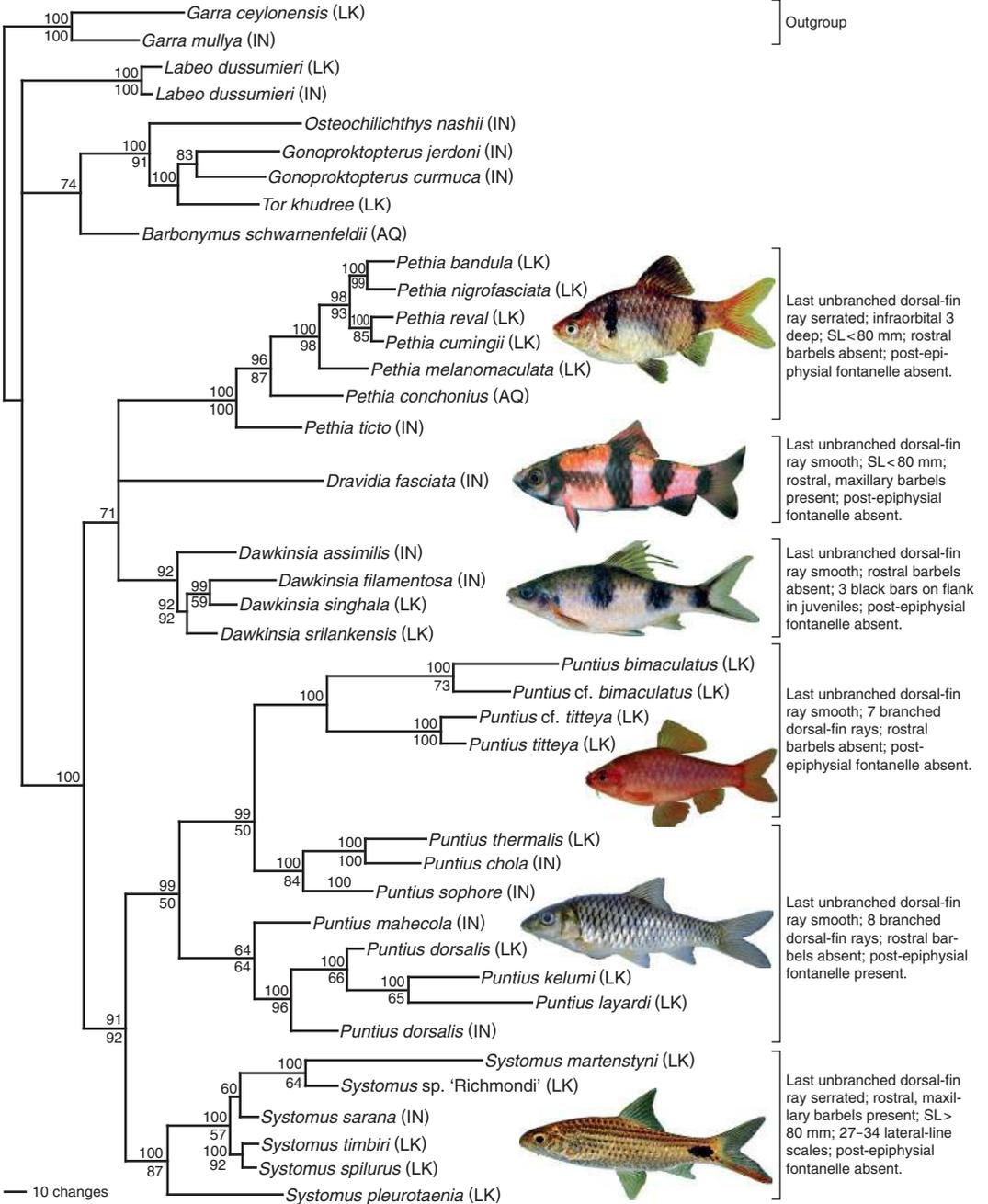


Fig. 1. Bayesian phylogram of the 31 putative species of South Asian *Puntius* s.l. analysed, with key shared morphological and osteological characters for each group. See Table 1 for list of material. Provenance: AQ, aquarium trade; IN, India; LK, Sri Lanka. Posterior probabilities are shown above nodes, parsimony bootstrap values below nodes. Photographs illustrate species within the respective genera: from top, *Pethia bandula*, *Dravidia fasciata*, *Dawkinsia srilankensis*, *Puntius titteya*, *Puntius dorsalis* and *Systemus asoka*.

Pelvic-fin origin slightly anterior to dorsal-fin origin. Posterior margin of dorsal fin slightly concave, that of anal fin straight. Distal margins of pelvic and pectoral fins convex, rounded. Dorsal-fin with 4 unbranched rays (last one smooth, strong) and 8 branched rays, its origin above ninth lateral-line scale. Anal fin with 3 unbranched and 5 branched rays. Pelvic fin with 1 unbranched and 8 branched rays, not reaching anus. Pectoral fin with one unbranched and 15 branched rays, not reaching pelvic-fin origin. Caudal fin deeply forked, its lobes pointed, with 1+9+8+1 principal rays.

Lateral-line pored scales on body 24 (23 [2]), plus 1 on caudal-fin base; 4½ scales in transverse line between lateral line and origin of dorsal fin, 4 (3½ [1]) between lateral line and origin of pelvic fin; ½2/1/2½ scales in transverse line on caudal peduncle; 9 predorsal scales (excluding notched scale at dorsal-fin origin). An axillary scale approximately one-third length of pelvic fin extends backwards from pelvic-fin origin. Dorsal-fin base

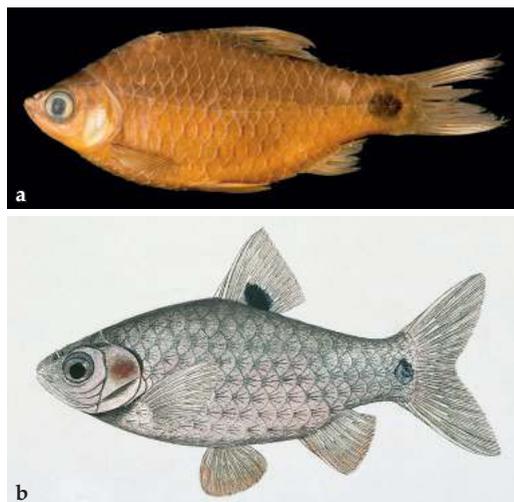


Fig. 2. *Cyprinus sophore*: **a**, ZRC 35064, neotype, 71.8 mm SL; Bangladesh: Hail Hoar floodplain; **b**, copy of Hamilton's drawing, in the collection of the Linnean Society of London (courtesy of Linnean Society of London).

Table 3. Standard length (in millimetres) and proportional measurements as a percentage of standard length or head length of the neotype (ZRC 35064, 71.8 mm SL) and 5 topotypes (ZRC 35065–35069, 59.4–80.6 mm SL) of *Puntius sophore*.

	neotype	range	
		min.	max.
Standard length (mm)	71.8	59.4	80.6
In percent SL			
Total length	130	127	133
Head length	28.6	27.3	29.7
Predorsal length	52.8	52.7	56.1
Preanal length	76.9	71.2	76.9
Prepelvic length	50.3	43.6	50.5
Caudal-peduncle length	19.8	18.0	20.5
Caudal-peduncle depth	14.9	13.8	15.2
Body depth	42.5	40.2	42.5
Dorsal-fin height	27.3	23.8	30.8
Length of stiff portion of last unbranched dorsal-fin ray	17.5	17.1	19.9
Pectoral-fin length	18.9	18.4	23.1
Pelvic-fin length	20.6	19.0	22.6
Distance from dorsal-fin origin to hypural fold	54.5	54.5	58.2
Post-dorsal distance	36.4	36.4	39.8
Maximum body width	17.3	14.0	17.3
Length of dorsal-fin base	18.2	16.1	18.6
Length of anal-fin base	13.9	11.4	14.7
In percent HL			
Snout length	27	27	30
Post-orbital head length	50	49	53
Eye diameter	32	27	32
Internarial width	26	22	27
Interorbital width	42	38	42

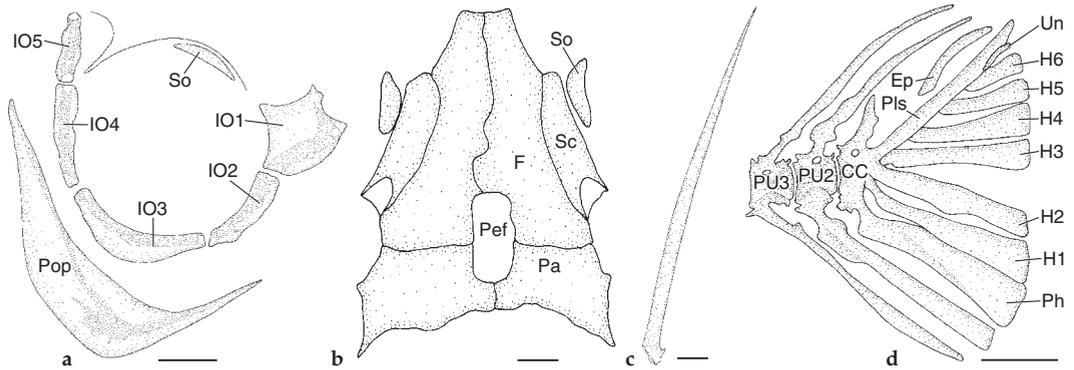


Fig. 3. *Puntius sophore*, WHT11062, 28.9 mm SL; SL: **a**, circumorbital series; **b**, dorsal view of orbital region of cranium; **c**, last unbranched dorsal-fin ray; and **d**, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Pef, post-epiphysial fontanelle; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; Sc, supraorbital sensory canal; So, supraorbital; Un, free uroneural.

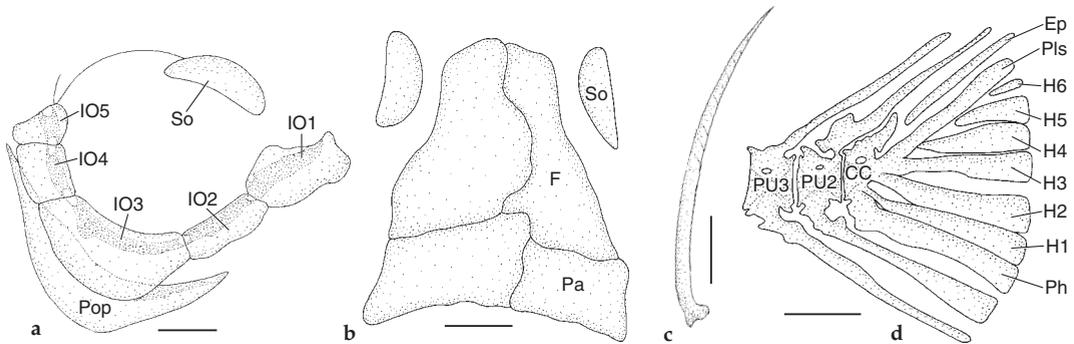


Fig. 4. *Puntius bimaculatus*, WHT 11029, 40.5 mm SL: **a**, circumorbital series; **b**, dorsal view of orbital region of cranium; **c**, last unbranched dorsal-fin ray; and **d**, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; So, supraorbital; supraorbital sensory canal not shown.

sheathed by 8 (7 [2]) scales, anal-fin base by 6 (7 [3]) scales.

In preservative (Fig. 2a), head and body brownish olive, lighter below lateral line; lower body, belly and chest pale cream-yellow. Fin rays light brown, interradial membrane hyaline. A distinct, horizontally-elongate black blotch slightly larger than eye, about 3 scales wide by 2 scales high, at posterior end of caudal peduncle. A smaller black blotch at base of dorsal-fin rays 5-7.

Systemus McClelland, 1838

Type species. *Systemus immaculatus* M' Clelland, 1839.

Diagnosis. A genus of cyprinid fishes differing from all South and Southeast Asian genera of Cyprininae by the combination of the following characters and character states: adult size greater than 80 mm SL (in South Asian species); maxillary and rostral barbels present; dorsal fin with 4+8 rays, its last unbranched ray stiff, strongly serrated (Fig. 5c); lateral line complete, with 27-34 scales on body; gill rakers simple, acuminate (not branched or laminate); no antrorse predorsal

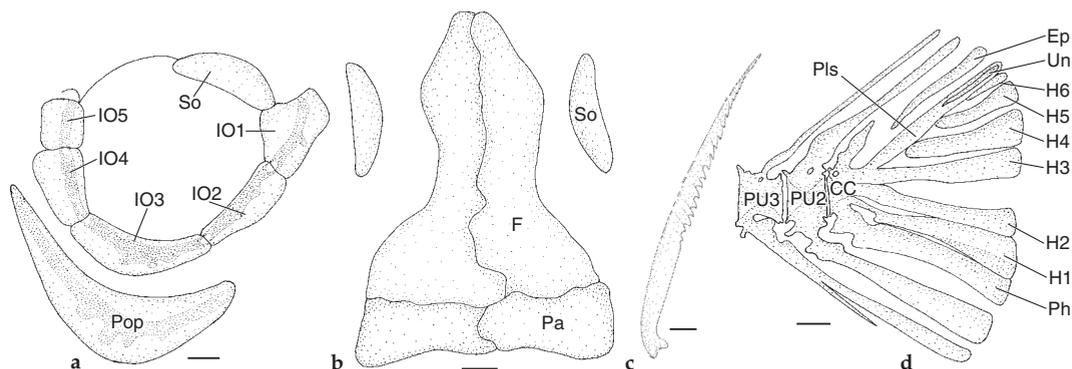


Fig. 5. *Systomus spilurus*, WHT 11028, 61.1 mm SL: a, circumorbital series; b, dorsal view of orbital region of cranium; c, last unbranched dorsal-fin ray; and d, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; So, supraorbital; Un, free uroneural; supraorbital sensory canal not shown.

spinous ray; free uroneural present (Fig. 5d); post-epiphysial fontanelle absent (Fig. 5b); 5 supraneurals; infraorbital 3 slender (Fig. 5a); 14-15 abdominal and 17-19 caudal vertebrae; and colour pattern including a prominent, horizontally-elongate oval black blotch on the caudal peduncle, with no prominent bars or blotches on the body.

Remarks. Based on the comparisons made herein, and the data of Shantakumar & Vishwanath (2006) and Kottelat & Pethiyagoda (1989), we include the following nine South Asian species in *Systomus*: *S. asoka* (Kottelat & Pethiyagoda, 1989), *S. compressiformis* (Cockerell, 1913), *S. jayarami* (Vishwanath & Tombi Singh, 1986), *S. martenstyni* (Kottelat & Pethiyagoda, 1991), *S. orphoides* Valenciennes, in Cuvier & Valenciennes 1842, *S. pleurotaenia* (Bleeker, 1863a), *S. sarana* (Hamilton, 1822), *S. spilurus* (Günther, 1868) and *S. timbiri* (Deraniyagala, 1963). An apparently undescribed Sri Lankan species with the label-name 'Puntius sp. Richmondi' too, belongs to *Systomus*. *Barbus clavatus* McClelland, 1844 and *B. shanensis* Hora & Mukerji, 1934 have been variously placed in *Puntius* (e.g., Jayaram, 1991; Talwar & Jhingran, 1991) and *Poropuntius* (e.g., Roberts, 1998; Jayaram, 2010) by previous authors. We have not examined specimens of these and so refer them only tentatively to *Systomus*, though they may bear a closer relationship to the 'Puntius binotatus group' of Southeast Asia (see Discussion).

Systomus immaculatus (Fig. 6)

Systomus immaculatus M'Clelland, 1839: 284, 380, pl. 44, fig. 5.

Neotype. AMS B.7920, 187 mm SL; India: Assam; F. Day.

Topotype. AMS B.7921, 193 mm SL (caudal fin broken); India: Assam; F. Day.

Description of neotype. General body shape and appearance are illustrated in Figure 6a. Morphometric data of neotype and 1 topotype are given in Table 4; characters of topotype, where different from neotype, are given in parentheses. Body elongate, standard length about 2.8 times body depth. Dorsal profile of head rounded; dorsal body profile rising gently to dorsal-fin origin (a post-nuchal hump present), sloping gently downwards thereafter. Dorsal-fin origin slightly posterior to pelvic-fin origin. Ventral body profile curving gently ventrad to pelvic-fin base, almost level from there to anal-fin origin, rising steeply to caudal peduncle; caudal peduncle ventral margin level.

Head relatively long, its length about one-fourth standard length. Eyes located forward of centre, about mid-height on head. Mouth terminal; lips fleshy; lower-lip post-labial groove shallow, uninterrupted. Cheek and interorbital with about 10 sensory pores. Two pairs of barbels present; maxillary barbel long, its length slightly

less than eye diameter; rostral barbel shorter, about half length of maxillary barbel.

Pelvic-fin origin slightly anterior to dorsal-fin origin. Posterior margins of dorsal and anal fins concave. Distal margins of pectoral and pelvic fins convex, rounded. Dorsal-fin origin above 11th lateral-line scale. Dorsal fin with 4 unbranched and 8 branched rays, last unbranched ray stiff, strongly serrated posteriorly in its proximal two-thirds, weak, segmented in its distal one-third. Last unbranched dorsal-fin ray longest, when adpressed not overlapping tip of last branched dorsal-fin ray. Anal fin with 3 unbranched and 5 branched rays. Pelvic fin with 1 unbranched and 8 branched rays. Pectoral fin with 1 unbranched and 15 branched rays. Caudal fin forked, lobes of equal length, longest rays about twice as long as median ones. Caudal fin with 8 upper and 7 lower procurent rays, and 1+9+8+1 principal rays.

Table 4. Standard length (in millimetres) and proportional measurements as a percentage of standard length or head length of the neotype (AMS B.7920) and a topotype (AMS B.7921) of *Systomus immaculatus*.

	B.7920	B.7921
Standard length (mm)	186.0	192.7
Percent standard length		
Total length	127	–
Head length	26.1	25.4
Predorsal length	53.2	54.2
Pre-anal length	75.1	72.1
Pre-pelvic length	41.0	48.2
Caudal-peduncle length	19.4	22.3
Caudal-peduncle depth	15.2	14.8
Body depth	35.9	35.6
Dorsal-fin height	22.7	20.4
Length of stiff portion of last unbranched dorsal-fin ray	15.6	14.7
Pectoral-fin length	19.2	19.3
Pelvic-fin length	19.7	18.8
Dorsal-hypural distance	55.4	56.4
Post-dorsal distance	38.8	40.1
Maximum body width	15.4	14.5
Percent head length		
Snout length	30.1	29.5
Post-orbital head length	53.6	52.2
Head depth	83.1	81.0
Eye diameter	23.0	22.3
Maxillary barbel length	19.3	23.8
Rostral barbel length	8.3	16.8
Internarial width	23.0	23.5
Interorbital width	43.8	42.8

Lateral line present, complete, with 32(33) pored scales on body, 2(3) on caudal-fin base. Lateral line sloping gently downwards for about 7 scales, level thereafter. Flank scales large, their central field (middle one-third) free of annuli, with about 15 irregular polygons. Radii radial, denser anteriorly and posteriorly, less dense in dorsal and ventral fields. 5½ scales in transverse line between lateral line and origin of dorsal fin, 4 between lateral line and origin of pelvic fin; ½3/1/3 scales in transverse line on caudal peduncle; 12(13) predorsal scales. An axillary scale approximately one-fourth length of pelvic fin extends backwards from pelvic-fin origin.

Supraneurals 5(6); 15 abdominal and 17(18) caudal vertebrae (Fig. 6b); free uroneural present; infraorbital 3 slender.

Dravidia, new genus

Type species. *Cirrhinus fasciatus* Jerdon, 1849: 305.

Diagnosis. *Dravidia* differs from all other South and Southeast Asian genera of Cyprinidae by the combination of the following characters and character states: size small, usually less than 60 mm SL; rostral and maxillary barbels present; lateral line complete, with 18–26 pored scales on body; dorsal fin with 4 unbranched and 8 branched rays, the last unbranched ray weak, smooth (Fig. 7c); anal fin with 3 unbranched and 5 branched rays; gill rakers simple, acuminate (not branched or laminate); no antrorse predorsal spinous ray; infraorbital 3 deep, partly overlapping preoperculum (Fig. 7a); free uroneural and post-epiphysal fontanelle absent (Fig. 7b,d); and one or two broad, black bars on flank, between bases of dorsal and anal fins.

Remarks. The following nominal species are referred to *Dravidia*: *D. afasciata* (Jayaram, 1990), *D. fasciata* (Jerdon, 1849), *D. kannikattiensis* (Arunachalam & Johnson, 2003), *D. melanampyx* (Day, 1865) and *D. pradhani* (Tilak, 1973).

Etymology. Named for the Dravidian peoples of the southern peninsular India; gender feminine.



Fig. 6. *Systemus immaculatus*, AMS B.7920, neotype, 187 mm SL; India: Assam; **a**, photograph; **b**, radiograph.

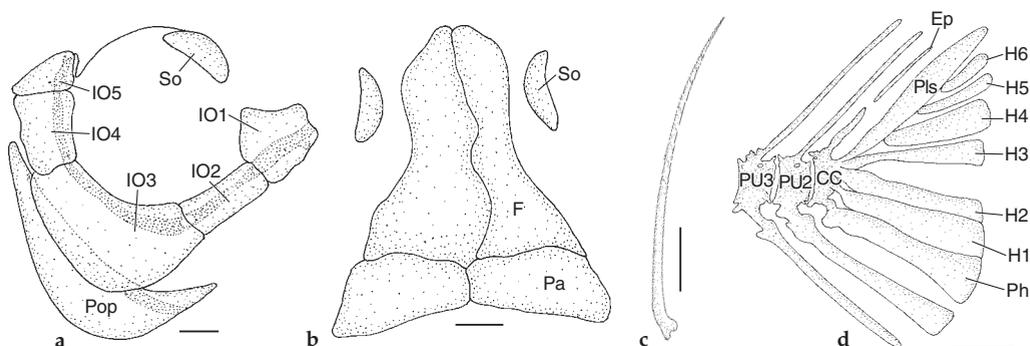


Fig. 7. *Dravidia fasciata*, WHT 11043, 43.0 mm SL: **a**, circumorbital series; **b**, dorsal view of orbital region of cranium; **c**, last unbranched dorsal-fin ray; and **d**, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; So, supraorbital; supraorbital sensory canal not shown.

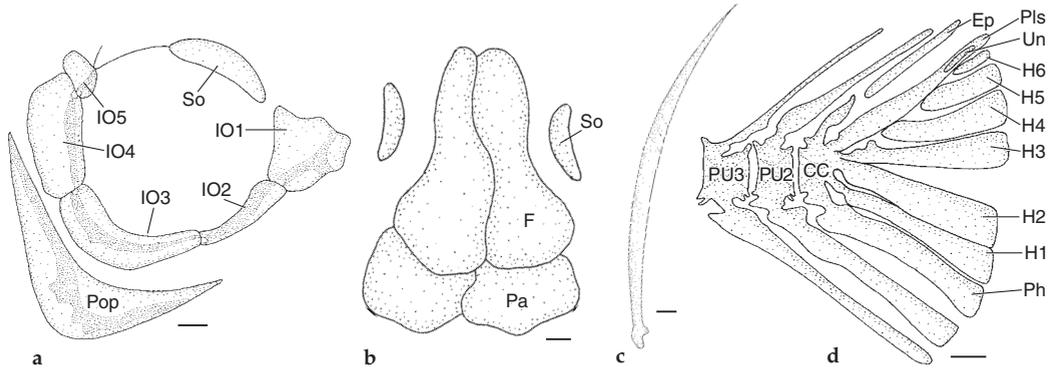


Fig. 8. *Dawkinsia filamentosa*, WHT 11026, 67.1 mm SL: **a**, circumorbital series; **b**, dorsal view of orbital region of cranium; **c**, last unbranched dorsal-fin ray; and **d**, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; So, supraorbital; Un, free uroneural; supraorbital sensory canal not shown.

Dawkinsia, new genus

Type species. *Leuciscus filamentosus* Valenciennes, in Cuvier & Valenciennes, 1844.

Diagnosis. *Dawkinsia* differs from all South and Southeast Asian genera of Cyprinidae by the combination of the following characters and character states: adult size usually 80–120 mm SL; rostral barbels absent, maxillary barbels present or absent; last unbranched dorsal-fin ray smooth (Fig. 8c); 4 unbranched and 8 branched dorsal-fin rays, 3 unbranched and 5 branched anal-fin rays; lateral line complete, with 18–22 scales on body; gill rakers simple, acuminate (not branched or laminate); no antrorse predorsal spinous ray; free uroneural present (Fig. 8d); 4–5 supraneurals; 15 precaudal and 14–17 caudal vertebrae; post-epiphysial fontanelle absent (Fig. 8b); infraorbital 3 slender, not overlapping preoperculum (Fig. 8a); juvenile (<50 mm SL) colour pattern consisting of three black bars on body, persisting to adult stage in some species; a black, horizontally elongate blotch on the caudal peduncle in adults.

Remarks. Based on the comparisons made here-in, and the data of Taki et al. (1978) and Pethiyagoda & Kottelat (2005a), we include the following nine species in *Dawkinsia*: *D. arulius* (Jerdon, 1849), *D. assimilis* (Jerdon, 1849), *D. exclamatio* (Pethiyagoda & Kottelat, 2005b), *D. filamentosa* (Valenciennes, in Cuvier & Valenciennes, 1844), *D. rohani* (Rema Devi, Indra & Marcus Knight, 2010), *D. ru-*

brotinctus (Jerdon, 1849) (see Knight et al., 2011), *D. singhala* (Duncker, 1912), *D. srilankensis* (Senanayake, 1985) and *D. tambraparniei* (Silas, 1954). The genus appears to be restricted to Sri Lanka and southern India.

Etymology. The genus is named for Richard Dawkins, for his contribution to the public understanding of science and, in particular, of evolutionary science; gender feminine.

Pethia, new genus

Type species. *Barbus nigrofasciatus* Günther, 1868.

Diagnosis. *Pethia* differs from all South and Southeast Asian genera of Cyprinidae by the combination of the following characters and character states: small adult size (usually less than 50 mm SL, exceptionally to 80 mm SL); rostral barbels absent; maxillary barbels usually absent, minute if present; last unbranched dorsal-fin ray stiff, serrated (Fig. 9c); 3 or 4 unbranched and 8 branched dorsal-fin rays, 3 unbranched and 5 branched anal-fin rays; gill rakers simple, acuminate (not branched or laminate); no antrorse predorsal spinous ray; infraorbital 3 deep, partially overlapping the cheek and preoperculum (Fig. 9a); free uroneural absent (Fig. 9d); 4 supraneurals; 11–13 precaudal and 13–16 caudal vertebrae; post-epiphysial fontanelle absent (Fig. 9b); lateral line complete, interrupted or

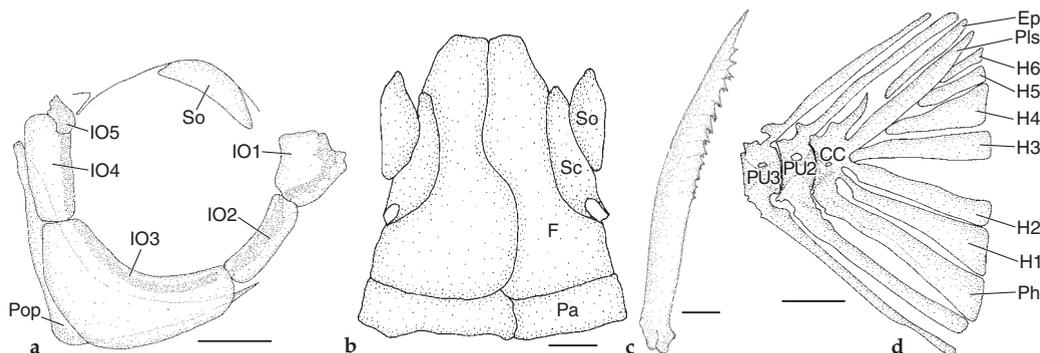


Fig. 9. *Pethia nigrofasciata*, WHT 11022, 35.9 mm SL: **a**, circumorbital series; **b**, dorsal view of orbital region of cranium; **c**, last unbranched dorsal-fin ray; and **d**, caudal skeleton (scale bar 1 mm). Abbreviations: CC, compound centrum; F, frontal; Ep, epural; H1-6, hypurals 1-6; IO1-5, infraorbitals 1-5; Pa, parietal; Ph, parhypural; Pls, pleurostyle; Pop, preopercle; PU2, PU3, preural centra 2, 3; Sc, supraorbital sensory canal; So, supraorbital.

incomplete (usually incomplete), with 19–24 scales on body in lateral series; and colour pattern consisting of a black blotch on caudal peduncle and frequently also other black blotches, spots or bars on side of body.

Remarks. Based on the comparisons made herein, and the data of Taki et al. (1978), Kullander & Fang (2005), Shantakumar & Vishwanath (2006), Kullander (2008) and Kullander & Britz (2008) we allocate the following 23 species to *Pethia*: *P. atra* (Linthoingambi & Vishwanath, 2007), *P. bandula* (Kottelat & Pethiyagoda, 1991), *P. conchoniis* (Hamilton, 1822), *P. cumingii* (Günther, 1868), *P. didi* (Kullander & Fang, 2005), *P. erythromycter* (Kullander, 2008), *P. gelius* (Hamilton, 1822), *P. khugae* (Linthoingambi & Vishwanath, 2007), *P. macrogramma* (Kullander, 2008), *P. manipurensis* (Menon, Rema Devi & Viswanath, 2000), *P. melanomaculata* (Deraniyagala, 1956), *P. nankyweensis* (Kullander, 2008), *P. nigripinnis* Knight, Rema Devi & Arunachalam, 2012, *P. nigrofasciata* (Günther, 1868), *P. padamyia* (Kullander & Britz, 2008), *P. phutunio* (Hamilton, 1822), *P. pookodensis* (Mercy & Jacob, 2007), *P. punctata* (Day, 1865), *P. reval* (Meegaskumbura, Silva, Maduwage & Pethiyagoda, 2008), *P. shalyinius* (Yazdani & Talukdar, 1975), *P. stoliczkana* (Day, 1871), *P. thelys* (Kullander, 2008), *P. tiantian* (Kullander & Fang, 2005) and *P. ticto* (Hamilton, 1822). Based on characters provided in their original descriptions, and as pointed out by Kullander & Fang (2005), other species such as *Puntius meingangbii* Arunkumar & Tombi Singh, 2003, *P. murvattupuzhaensis* Jamee-

la Beevi & Ramachandran, 2005, *P. narayani* (Hora, 1937), *P. ornatus* Vishwanath & Laisram, 2004, *P. setnai* Chhapgar & Sane, 1992, and *P. yuensis* Arunkumar & Tombi Singh, 2003 too, likely warrant placement in *Pethia* (though *Puntius narayani* differs from *Puntius* s.s. and *Pethia* by having 9 branched dorsal-fin rays and 6 branched anal-fin rays: Hora, 1937).

Etymology. *Pethia* is the generic vernacular name for small cyprinids in Sinhala; gender feminine.

Discussion

The mitochondrial DNA phylogeny based on *cyt-b* and 16s gene fragments (Fig. 1) shows that there are five well supported clades that can be recognized as distinct genera also on the basis of shared external-morphological and osteological characters and character states within South Asian *Puntius* as previously understood. These generic allocations are also supported by (uncorrected) genetic distances in the range 7.3–18.1 % (Table 2). Except as mentioned below, we believe the present analysis to include all the major lineages represented by the South Asian fishes until now included in *Puntius*. We also comment below on several species with distinctive characters for which we do not have tissue for molecular analysis. By presenting a clearer definition of *Puntius* s.s., the present study also opens the way for the recognition of distinct genera for many of the Southeast Asian fishes hitherto referred to

Puntius. Our results also corroborate the phylogenetic relationships recovered by Bossuyt et al. (2004) involving some of the same species and analysing the same ~590 bp segment of the 16S rRNA gene and a ~540 bp segment of the *cyt-b* gene.

None of the genus-group names hitherto in the synonymy of *Puntius* have type species potentially referable to *Puntius* s.s., *Systemus* s.s., *Dawkinsia*, *Dravidia* or *Pethia*. The only contending genus-group names are *Cephalakompsus* Herre, 1924a, *Mandibularca* Herre, 1924a, *Ospatulus* Herre, 1924b, and *Spratellicypris* Herre & Myers, 1931, all of which have type species endemic to the Philippines. These possess both rostral and maxillary barbels, by which they are immediately distinguished from *Puntius*, *Dawkinsia* and *Pethia* (which lack rostral barbels). *Puntius* and *Systemus* are in any event not threatened by *Cephalakompsus*, *Mandibularca*, *Ospatulus* and *Spratellicypris*, which are junior. On the basis of the original descriptions of their type species in Herre (1924a), *Dravidia* differs from *Cephalakompsus*, *Ospatulus* and *Spratellicypris* by having a smooth (vs. serrated) last unbranched dorsal-fin ray; and from *Mandibularca* by its smaller size (up to 80 mm total length, vs. 220 mm in *Mandibularca*), having the lower jaw horizontal (vs. strongly curved upwards) and habitus (see Herre, 1924a: pl. 1).

South Asian *Puntius*. The recognition of additional genera within *Puntius* as previously understood makes it imperative that the identity of *P. sophore* (Hamilton, 1822), the type species of *Puntius*, be stabilised. Hamilton's description and figure of *P. sophore* do not allow this species to be unambiguously distinguished from other valid species, e.g., *P. chola*, *P. dorsalis*. No type specimens of fishes described by Hamilton have come to light in the 190 years since the publication of this work; nor has the existence of such types been alluded to in the subsequent literature. They must therefore be presumed lost. Hamilton (1822) did not specify the type locality of *S. sophore* in his account of that species, but it can be inferred from his preceding account of *Puntius* that it was Bengal. We selected ZRC 35064, a 71.8 mm SL specimen, as neotype because it was collected within the Ganges floodplain in Bengal (now Bangladesh); it is consistent with the original description (Hamilton, 1822: pl. 19, fig. 86); and it is accompanied by a series of five topotypes that facilitate a more representative description.

The coloration of the neotype also matches that delineated in a copy of Hamilton's figure in the archives of the Linnean Society of London (Fig. 2b). This illustrates a specimen with 17 lateral-line scales, 2 unbranched and 8 branched dorsal-fin rays, 2 unbranched and 6 branched anal-fin rays, 1+7+7+1 principal caudal-fin rays, and 1 unbranched and 7 branched pelvic-fin rays. Although, as pointed out by Silva et al. (2010), Hamilton's drawings contain many inaccuracies in their detail, the neotype matches Hamilton's figure in general appearance. Based on the neotype and topotypes described herein, *P. sophore* may be distinguished from *P. chola* by the characters given in Talwar & Jhingran (1991) and Jayaram (2010), and from *P. dorsalis* by the characters given in Pethiyagoda et al. (2008).

Because of a lack of material, we have been unable to assign several other Indian species with 40 or more lateral-line scales, hitherto in *Puntius*, to any of the above genera: their generic placement must depend on future work. Perhaps most prominent among these are '*P. deccanensis*', '*P. fraseri*', and *P. sharmai*, which lack rostral barbels but possess a pair of maxillary barbels, a stiff, strongly serrated last unbranched dorsal-fin ray, and 42–47 lateral-line scales, though the first species differs from the latter two by having 9 branched dorsal-fin rays and 7 branched anal-fin rays, vs. 8 and 5 in *Puntius* (Hora & Misra, 1938; Yazdani & Babu Rao, 1976; Menon & Rema Devi, 1993). Also with a high lateral-line scale count (43) is *Puntius punjaubensis* (Day, 1871), which has no barbels and possesses a smooth last unbranched dorsal-fin ray: it is almost certainly not a member of any of the preceding genera. We note in passing that the original spelling '*punjaubensis*' is not a lapsus for '*punjabensis*', the spelling adopted in the current literature (e.g., Jayaram, 1991, 2010; Talwar & Jhingran, 1991): Day retained the original spelling also in his 'Fishes of India' (1878), 'Punjaub' having been an accepted contemporaneous spelling.

Another intriguing taxon is '*Puntius* *ophicephalus*', for which Menon (1999) created the genus *Eechathalakenda*. Possessing both maxillary and rostral barbels, a smooth last unbranched dorsal-fin ray and 40–42 lateral-line scales, this species does not fit within any of the preceding genera. Menon (1999) diagnosed *Eechathalakenda* from *Gonoproktopterus* by its "elongated *Channa* like appearance, 7 branched rays in the dorsal fin (9 in *Gonoproktopterus*), a slightly elongated but

weak, smooth and segmented last undivided ray to the dorsal fin, four barbels and 40–42 scales along the lateral line”. We tentatively treat *Eechathalakenda* as valid.

The relationships of ‘*P.* *guganio* (Hamilton, 1822) and ‘*P.* *nangalensis* Jayaram, 1990 (barbels absent; last unbranched dorsal-fin ray stiff, serrated; lateral line incomplete, with 36–39 and 31–33 scales respectively, in lateral series), remain to be elucidated. Jayaram (1990) considered these two species to be closely related. In the absence of material for comparison, we retain both species in ‘*Puntius*’ for the present, although they do not belong to this or any of the genera discussed herein.

Unlike all the other species of *Puntius* examined in this study, *P. bimaculatus* (restricted to southern India and Sri Lanka) and *P. titteya* (a Sri Lankan endemic) lack a post-epiphysial fontanelle. These two species also group separately from all the other species of *Puntius* examined (Fig. 1) and share a suite of additional distinguishing characters: only 7 (vs. 8) branched dorsal-fin rays; $\frac{1}{2}3$ (vs. $\frac{1}{2}4$ – $\frac{1}{2}5$) scale rows between dorsal-fin origin and lateral-line row; a lateral line that is in *P. titteya* incomplete and in *P. bimaculatus* occasionally interrupted or incomplete; and a coloration which includes a red lateral stripe – unusual in *Puntius*. Although they appear to warrant placement in a separate genus, we refrain from doing so as this would render *Puntius* paraphyletic (the two lower clades of *Puntius* in Fig. 1 evidently do not possess a suite of external characters that distinguish them). We feel this problem is best resolved once a wider sample of species is available for analysis.

South Asian *Systemus*. Having long been treated as a synonym of *Puntius* (Bleeker, 1863b; Day, 1878; Banareescu, 1997), *Systemus* was revived as a valid genus by Rainboth (1996), who assigned six Cambodian species previously in *Puntius* to it on the basis of the finely-serrated last unbranched dorsal-fin ray, possession of rostral and/or maxillary barbels, and gill rakers fewer than 12 on the first arch. Further species were added by subsequent authors (e.g. Ng & Tan, 1999; Parenti & Lim, 2005; Kottelat & Tan, 2011; see also Roberts & Catania, 2007). Given that some species of *Systemus* sensu Rainboth (1996) are popular aquarium fishes (e.g., ‘*S.* *johorensis*, ‘*S.* *lateristriga*, ‘*S.* *partipentazona*), the genus-name is in wide use despite other authors (e.g., Kottelat,

2000, 2001; Kottelat & Widjanarti, 2005) retaining it as a junior synonym of *Puntius*, because removing these six species out of a large, heterogeneous genus without resolving the generic identity of the remaining species would likely cause confusion.

This confusion is in part because the type species of *Systemus*, *S. immaculatus*, considered a synonym of *S. sarana* since Day (1878), is poorly known. M’Clelland (1839) characterized *Systemus* as follows: “Intermaxillaries protractile, dorsal and anal short, the former opposite to the ventrals and preceded by a spinous ray; body elevated and marked by two or more distinct dark spots, or diffuse spots either on the fins or opercula, prominence on the apex of the lower jaw obscure”. The first of the eight species he included in the first division of the genus (characterized by “depth of the body ... equal to about half the length, and the spiny ray of the dorsal ... serrated behind”) was *S. immaculatus*, subsequently designated as type species by Jordan (1919). This species he described as having “four cirrhi, a slight golden tinge on the opercula, fins dark, thirty-two scales on the lateral line and ten in an oblique line from the base of the ventrals to the dorsum”. He gave the type locality of *S. immaculatus* as “Small streams with sandy bottoms in Assam, and probably occasionally in the large rivers” adding that *S. chrysosomus* (a junior synonym of *S. sarana*) “is probably a variety only of this species, which is generally distributed throughout the rivers and ponds of all parts of India, sometime weighing as much as two pounds [0.9 kg]”.

The type/s of *S. immaculatus*, however, are apparently lost. A search for possible types of this species in the collections of BMNH and SMF, the only repositories known to contain fish types of M’Clelland, proved fruitless (J. Maclaine, BMNH; and H. Zetzsche, SMF, pers. comms.). A search of the fish collections of ZSI too, failed to reveal any cyprinid specimens attributable to M’Clelland (RP, pers. obs.). Given the confusion that exists with regard to the identity of the genus, it is necessary that the identity of *S. immaculatus*, its type species, be clarified through the designation of a neotype: we here designate AMS B.7920 (locality Assam, India), as neotype of *Systemus immaculatus* M’Clelland, 1839. The specimen is illustrated in Fig. 6 and its morphometric and meristic data given in Table 2, which supplement the description and diagnosis of M’Clelland (1839).

M'Clelland's (1839) description of *S. immaculatus* matches that of 'Puntius' *sarana* (type locality 'ponds and rivers of Bengal') (Jayaram, 1991; Talwar & Jhingran, 1991). As shown here (Figs. 1, 6) and corroborated also by Shantakumar & Vishwanath (2006), '*P.* *sarana*' belongs to a lineage distinct from the one that includes *Puntius siphore* (the type species of *Puntius*): the former possess both rostral and maxillary barbels, a stiff, strongly serrated last unbranched dorsal-fin ray, a complete lateral line with 27–34 scales on the body, and a horizontally elongate oval black blotch on the caudal peduncle. This adds confidence to our selection of a neotype for *S. immaculatus* from among specimens nominally identified as '*Puntius sarana*' from Assam. *Systemus immaculatus* (= *S. sarana*) may be distinguished from the other species here included in *Systemus* based on the characters provided above for the neotype and topotype, and those provided in the works cited in Remarks under the diagnosis of *Systemus*.

Barbodes, *Barbonymus* and *Poropuntius* resemble *Systemus* in possessing two pairs of barbels and a serrated last unbranched dorsal-fin ray. Indeed, Menon (1999) placed *S. sarana* in *Barbodes*, the type species of which is *Barbus maculatus* Valenciennes, in Cuvier & Valenciennes 1842 (see Kottelat, 1999), which is considered a synonym of *B. binotatus* Valenciennes, in Cuvier & Valenciennes 1842 (Kottelat, 1999; Pethiyagoda & Kottelat, 2005b). *Barbus binotatus*, however, differs from species of *Systemus* by possessing 23–27 lateral-line scales on body and $\frac{1}{4}$ scale rows between the dorsal-fin origin and lateral line (vs. 32–33 lateral-line scales and $\frac{1}{2}$ scale rows between the dorsal-fin origin and lateral line in *S. immaculatus*, the type species of *Systemus*), and having a distinctive colour pattern (see Kottelat et al., 1993, pl. 15) not observed in any other species here allocated to *Systemus* s.s. *Systemus* differs from *Barbonymus* by having fewer than 6 rows of scales between the dorsal-fin origin and lateral line (7 or more in *Barbonymus*); and from *Poropuntius* by lacking an accessory pore on the canals of the lateral-line system (accessory pore present in *Poropuntius*: Kottelat et al., 1993; Roberts, 1998; Kottelat, 2001).

Southeast Asian *Puntius*. The recent literature refers around 45 species of Southeast Asian cyprinids to *Puntius*. Only one of these, however, belongs to the genus as it is now understood:

P. brevis (Bleeker, 1849). Widespread through Southeast Asia (Mekong basin of Laos, Thailand and Cambodia; Chao Phraya basin; Malay peninsula and Java: Kottelat, 2001) it has the last unbranched dorsal-fin ray smooth, a pair of maxillary (and no rostral) barbels, 23–26 lateral-line scales and a black spot on the caudal peduncle. Taki et al. (1978) included *P. brevis* in their *P. binotatus* group, though the former species lacks rostral barbels (present in *P. binotatus*) and has the last unbranched dorsal-fin ray smooth (vs. posteriorly serrated).

Only one other Southeast Asian *Puntius* has the last unbranched dorsal-fin ray smooth, *Puntius oligolepis* (Bleeker, 1853). This species, however, is distinguished from *Puntius* s.s. by having an incomplete lateral line, only 17 scales in the lateral series, and $\frac{1}{2}$ scale rows between the dorsal-fin origin and lateral-line scale row. Its relationships remain to be investigated.

All the other Southeast Asian species presently referred to *Puntius* require new generic assignments. Although this is beyond the scope of the present work for want of material, for convenience of discussion and based on data on external characters available in the literature (Kottelat et al., 1993; Kottelat, 2001; Rainboth, 1996; Roberts, 1989; Weber & de Beaufort, 1916; and the original species descriptions), we here refer these to a number of species groups (see also Southeast Asian *Systemus*, below).

The '*Puntius trifasciatus* group' comprises three species (*P. gemellus* Kottelat, 1996, *P. johorensis* (Duncker, 1904), and *P. trifasciatus* Kottelat, 1996) distinguished by possessing both rostral and maxillary barbels, 25–27 scales in the lateral line on body, 7–11 gill rakers on the anterior gill arch, and a juvenile coloration consisting of 4–5 black bars on the body, changing to 3–6 black stripes on the body as adults (Kottelat, 1996); these characters combine to distinguish the members of this group from *Puntius*, *Systemus*, *Pethia* and *Dravidia*. The members of the *P. trifasciatus* group appear to belong to a lineage distinct also from the only other similarly-coloured species of Southeast Asian '*Puntius*', *P. lineatus* (Duncker, 1904), which possess no or only a single pair of rudimentary barbels and the adults of which have the lower lip forming a complete post-labial groove, distinguishing it from all *Puntius* (in either its previous or present conception). Kottelat (1996) proposed that it be placed in a separate genus (for the present referred to as the '*P. lineatus*' group).

Southeast Asian *Systemus*. Of the five species referred to *Systemus* by Rainboth (1996) only *S. orphoides* appears to be a *Systemus* as the genus is now understood. The other four included species possess characters that suggest they belong to different lineages: '*S. aurotaeniatus* (Tirant 1885) lacks rostral barbels and has a coloration consisting of black spots at the dorsal-fin origin and on the side of the body; '*S. johorensis* (Duncker, 1904) lacks rostral barbels and has a striking colour pattern consisting of six black lateral bars; '*S. partipentazona* (Fowler, 1934a) lacks rostral barbels, has the lateral line incomplete and a colour pattern consisting of five black lateral bars including one across the dorsal fin; and '*S. binotatus* has a dark spot at the dorsal-fin origin, fewer scale rows on the body (23–27, vs. 27–34 in *Systemus*) and caudal peduncle (12 circumpeduncular scale rows, vs. 16) and a different head and mouth shape. Among Southeast Asian cyprinids, only *S. orphoides* and *Barbus jacobusboehlkei* Fowler, 1958 appear to belong to *Systemus* s.s. We here place the remaining species referable to *Systemus* sensu Rainboth (1996) tentatively in two species groups that are, however, unlikely to be monophyletic (e.g., see Kottelat, 1992).

Members of the '*Puntius binotatus* group' possess both rostral and maxillary barbels, and a last unbranched dorsal-fin ray the posterior margin of which is more or less strongly serrated. Roberts (1989) regarded *P. binotatus* to be "the most widely distributed and perhaps most variable species of *Puntius* in southeast Asia", noting that it "occurs from sea level to at least 2,000 m... and on small islands inhabited by few other freshwater fishes." Close examination will likely show at least some of the 13 nominal species from time to time in its synonymy (see Roberts, 1989: 60–61) to be valid, closely-related species, as are *P. banksi* Herre, 1940 (see Kottelat & Lim, 1996: 232), and *P. sealei* (Herre, 1933) (see Inger & Chin, 1990: 73). Additionally, as pointed out by Roberts (1989), *P. binotatus* is regarded as the "parent stock" for the endemic '*Puntius*' species of Lake Lanao and the Lanao Plateau of Mindanao in the Philippines: *P. amarus* (Herre, 1924a), *P. disa* (Herre, 1932), *P. flavifuscus* (Herre, 1924a), *P. herrei* (Fowler, 1934b), *P. joaquiniae* Wood, 1968, *P. katolo* (Herre, 1924a), *P. lanaoensis* (Herre 1924a), *P. lindog* (Herre 1924a), *P. manalak* (Herre, 1924a) and *P. sirang* (Herre, 1932). The Lanao '*Puntius*' share these characters also with other '*Puntius*' from Mindanao (*P. cataractae* (Fowler, 1934b), *P. tumba*

(Herre, 1924a) and *P. umalii* Wood, 1968), as well as those from Lake Manguao on Palawan (*P. manguaoensis* (Day, 1914) and *P. bantolanensis* (Day, 1914)) and Mindoro (*P. hemictenus* (Jordan & Richardson, 1908)). Ranging from about 6–24 cm and possessing 22–32 lateral-line scales most of these species show a coloration that includes a hazy dark stripe on the side of the body, in *P. binotatus* accompanied by a dark spot on the caudal peduncle and dorsal-fin origin, accompanied in some cases by numerous other dark spots and/or blotches on the body (see Kottelat et al., 1993, pl. 15). '*Systemus*' *dunckeri* (Ahl, 1929), '*S. everetti* (Boulenger, 1894), '*S. kuchingensis* (Herre, 1940), '*S. lateristriga* (Valenciennes, in Cuvier & Valenciennes, 1842), '*S. xouthos* Kottelat & Tan, 2011, '*Puntius*' *rhombeus* Kottelat, 2001 and '*P. semifasciatus* (Günther, 1868) too, are apparently members of this group. The genus name *Barbodes* is available for the '*Puntius binotatus* group', with *Cephalakompsus*, *Mandibularca*, *Ospatulus* and *Spratellicypris* as synonyms.

The remaining Southeast Asian '*Systemus*' sensu Rainboth (1996) we place in the '*Puntius tetrazona* group' because they possess a posteriorly serrated last unbranched dorsal-fin ray, maxillary barbels, and a striking coloration that includes 3–6 black bars and/or blotches on the body; the lateral line may be complete or incomplete, and rostral barbels present or absent. These species share a strikingly barred or blotched coloration, which resembles that of some species of *Pethia* (e.g. *P. nigrofasciata*) and *Dravidia* (e.g. *D. fasciata*), as does their small size. They differ from the former genus, however, in possessing a complete lateral line and at least maxillary barbels; and the latter in possessing a serrated posterior edge to the last unbranched dorsal-fin ray. Additionally, at least some of the included species have a slender infraorbital 3 (Taki et al., 1978), which serves to distinguish them from species of *Pethia*. The *Puntius tetrazona* group includes '*S. anchisporus* (Vaillant, 1902), '*S. endecanalis* (Roberts, 1989), '*S. foerschii* (Kottelat, 1982), '*S. hexazona* (Weber & de Beaufort, 1912), '*S. partipentazona*, '*S. pentazona* (Boulenger, 1894), '*S. pulcher* (Rendahl, 1922), '*S. rhomboocellatus* (Koumans, 1940) and '*S. tetrazona* (Bleeker, 1855). Kottelat's (1992) observation that 'tiger barbs' belong to "at least two lineages which are not obviously related" is supported also by the data of Taki et al. (1978), whose '*tetrazona* group' ('*S. tetrazona* and '*S. partipentazona*) lacks rostral barbels whereas



Fig. 10. *Barbus bovanicus*, AMS B.7829, lectotype, 95.1 mm SL; India: Bhavani River, Tamil Nadu; a, photograph; b, radiograph.

their ‘pentazona group’ (*S. everetti*, *S. lateristriga*, *S. pentazona* and *S. rhomboocellatus*) possesses them; Taki et al. (1978) also distinguished the two groups by their colour patterns.

Dravidia. Menon (1999) chose the junior name *Labeo melanampyx* Day, 1865 over its senior subjective synonym, *Cirrhinus fasciatus* Jerdon, 1849 (the type species of *Dravidia*) citing Art. 23(b) of ICZN (1985), on the grounds that the former was “a favourite aquarium fish and several aquarium journals mention this species as *Puntius melanampyx*. A change is not considered desirable.” However, Art. 23(b) of ICZN (1985) requires that such a case is to be referred to the Commission for a ruling, which has not been done in the 13 years following Menon (1999). As such, we follow Arts. 23.1 and 22.9.3 of ICZN (1999) and use the senior synonym *C. fasciatus*, which anyway is also the name in prevailing usage (e.g., Silas, 1956; Jayaram, 1991; Talwar & Jhingran, 1991; Arunachalam, 2000; Bhat, 2005).

Three additional South Asian species included in *Puntius* by previous authors (e.g., Jayaram, 1991; Talwar & Jhingran, 1991) bear two pairs of barbels and a smooth last unbranched dorsal-fin ray: *P. bovanicus*, *P. carnaticus* and *P. jerdoni*. *Barbus bovanicus* (AMS B.7829, syntype, 95.1 mm SL, here designated lectotype; Fig. 10) has 9 branched dorsal-fin rays, 23 lateral-line scales on body, eye in upper half of head, thick, fleshy lips, and the lower lip present medially: it is apparently a *Neolissochilus*. It further differs from all species of *Puntius*, *Systemus*, *Dawkinsia*, *Pethia* and *Dravidia* in possessing 22 (vs. 13–19) caudal vertebrae and 6 (vs. 3–5) supraneurals. We note in passing that the spellings *bovanicus* and *bovianicus* were published simultaneously, in plate 138 fig. 1, and on page 566, of Day (1878), both of which were released on 1 December 1878 (see Whitehead & Talwar, 1976: 54 and references therein). In keeping with subsequent usage, as first reviser we give *B. bovanicus* precedence over *B. bovianicus*.



Fig. 11. *Barbus jerdoni*, AMS B.7935, syntype, 179.3 mm SL; India: Canara [Karnataka].

Pethiyagoda & Kottelat (2005b) noted that the figure of *Barbus carnaticus* in Day (1878: pl. 137) “possibly illustrates a species of *Neolissochilus*”. Jerdon’s (1849) description of *B. carnaticus* is uninformative, and there is no known surviving type material. As a result, subsequent authors have followed Day’s (1878: 563, pl. 137) conception of the species. Two of Day’s specimens in the AMS collection (B.7963, 103.3 mm SL; B.7626, 230 mm SL) have 28 and 29 lateral-line scales on the body plus 2 on the base of the caudal fin; $\frac{1}{2}5 + 1 + 4$ scales in transverse line from dorsal-fin origin to pelvic-fin origin; 4 smooth, unbranched and 8 branched dorsal-fin rays; 3 unbranched and 5 branched anal-fin rays; both rostral and maxillary barbels; and the anal fin, when adpressed, reaching just beyond the hypural fold. This is additionally a large cyprinid, reported to reach a total length of 60 cm (Talwar & Jhingran, 1991). It differs from *Neolissochilus*, however, by having the last unbranched dorsal-fin ray stiff (vs. weak and segmented: Rainboth, 1985) and the lower jaw exposed medially, which characters distin-

guish it also from *Hypsibarbus* and *Gonoproktopterus*, genera it otherwise resembles superficially. Its generic allocation remains uncertain.

We hesitate to follow Menon (1999) in allocating *Barbus jerdoni* to *Gonoproktopterus* (for which he incorrectly used *Hypselobarbus*: see Jayaram, 1997). Although the AMS syntype of *G. jerdoni* (B.7935, 179.3 mm SL; Fig. 11) has 9 branched dorsal-fin rays, the last unbranched ray weak, segmented; rostral and maxillary barbels; and $6 + 1 + 3$ scales in transverse line between dorsal-fin origin and pelvic-fin origin, which are consistent with *Gonoproktopterus* as presently understood (Talwar & Jhingran, 1991; Jayaram, 1997), it possesses 25 lateral-line scales, substantially lower than the 31–45 lateral-line scales observed in other species of this genus. Its generic placement too deserves further investigation.

Dawkinsia. Arguing against the monophyly of the ‘filamentosus complex’ of Jayaram (1991), who did not point to any putative synapomorphies, Pethiyagoda & Kottelat (2005a) proposed the

'*Puntius filamentosus* group' for those species of *Puntius* s.l., the juveniles of which possess a unique shared colour pattern of three black bars on the side. This was demonstrated first by De Silva et al. (1981) in a comparative study of the ontogeny of *Dawkinsia singhala* and *Dravidia fasciata*, since when the genus has expanded considerably (Pethiyagoda & Kottelat, 2005a; Rema Devi et al., 2010; Marcus Knight et al., 2011). Figure 1 suggests that the general coloration of the sister-genera *Dawkinsia*, *Dravidia* and *Pethia* derive from a common ancestry which, taken together with apparent relationships within the *P. tetrazona* group and *P. trifasciatus* group, suggests that coloration could be a relatively conservative character useful in identifying relationships among these fishes (see also Kortmulder, 1986; Kortmulder & van der Poll, 1981).

***Pethia*.** *Pethia* (as the '*Puntius conchoni* group') has been a group of fishes long recognized as having a separate identity within *Puntius* as previously understood. Following on the earlier work of Kortmulder (1972), and the osteological studies of Taki et al. (1978), Kullander & Fang (2005) described the '*Puntius conchoni* group' as being characterized by small adult size, broad infraorbital 3, absence of rostral barbels, minute or absent maxillary barbels, a stiff and serrated last unbranched dorsal fin ray, an often abbreviated lateral line, a colour pattern including a black blotch or spot anteriorly on the side (absent in *P. conchoni*) and a black blotch on the caudal peduncle, and a broad 5th ceratobranchial characterized by a pointed dorsal tip, spaced moderate-sized teeth, and absence of dorsal angle. Our results agree broadly with this characterization except that the 5th ceratobranchial is slender in *P. punctata*, and with an obtuse tip in *P. nigrofasciata*, *P. reval* and *P. cumingii*.

Distribution. The present results suggest a greater degree of generic endemism in South Asian cyprinids than previously suspected. Several cyprinid genera are already known to be endemic to the peninsula of India, including *Betadevario*, *Horallabiosa*, *Gonoproktopterus*, *Lepidopygopsis*, *Parapsilorhynchus* and *Rohtee*. To these are now added *Dawkinsia* and *Dravidia*, which are restricted to Sri Lanka and the southern region of the Indian peninsula. *Puntius* s.s. too, turns out to be largely restricted to South Asia, only a single species, *P. brevis*, extending its range through

Indochina to Java. *Pethia* too, appears mostly restricted to South Asia, with only *P. stoliczkanus* extending its range to Laos (Kottelat, 2001) and Thailand (Smith, 1945, as *Puntius stoliczkae*). Likewise, *Systemus* s.s. is represented in Southeast Asia only by *S. jacobusboehlkei* and *S. orphoides*.

Character states. Some of the character states we report here are variable between closely-related species and even within species. Silva et al. (2008), for example, reported that one of the specimens of *Puntius kamalika* they studied possessed a free uroneural while another did not, and that free uroneurals were altogether absent in its sister species, *P. mahecola*. Similarly, while free uroneurals are present in each of the two specimens of *P. sophore* and *P. chola* cleared and stained by us, Shantakumar & Vishwanath (2006) reported them to be absent in both these species. Although we have included this character in the generic diagnoses above, it is important to note that it may be variable.

While the deep infraorbital 3 is synapomorphic in *Pethia*, this character state occurs also in some species of *Puntius* as understood here, including *P. bimaculatus*, *P. kelumi*, *P. mahecola* and *P. titteya*.

Similarly, character states that are synapomorphic in other cyprinine genera sometimes present themselves as apomorphies in individual species of *Puntius* as presently defined. For example, a few species retained in *Puntius* possess numerous rows of sensory papillae on the head, apparently an apomorphy shared by the closely-related species-group *P. cauveriensis*, *P. dorsalis*, *P. kelumi* and *P. layardi* (Pethiyagoda et al., 2008), but not other species of *Puntius*. Among Asian cyprinine genera, this character-state occurs also in *Cylocheilichthys*, *Eirmotus*, *Neobarymotus* and *Oreichthys* (Kottelat, 1996; Tan & Kottelat, 2008; Schäfer, 2009). Likewise, some species of *Dawkinsia* develop nuptial tubercles on the snout and cheeks (Pethiyagoda & Kottelat, 2005a), a character that occurs also in many other cyprinid genera. The dense tuberculation of the body in sexually mature males of *Puntius kelumi*, however (Pethiyagoda et al., 2008), while not reported from any other member of the *Puntius*, occurs in several cyprinid lineages.

Nevertheless, the five genera into which the South Asian species previously in *Puntius* are now allocated are distinguishable from one another by reliable external characters: *Puntius*, smooth last unbranched dorsal-fin ray, no rostral

barbels, no bars on flank in juveniles; *Systemus*, serrated last unbranched dorsal-fin ray, rostral barbels present; *Dravidia*, smooth last unbranched dorsal-fin ray, rostral barbels present; *Dawkinsia*, smooth last unbranched dorsal-fin ray, rostral barbels absent, black bars on flank in juveniles; *Pethia*, serrated last unbranched dorsal-fin ray, rostral barbels absent. All these species possess fewer than 40 lateral-line scales.

A key to South Asian *Puntius* s.l.

The following key allows generic allocation of South Asian fishes included in *Puntius* by Jayaram (1991, 2010), Talwar & Jhingran (1991), Menon (1999) and authors of new species from the region from 1990–2010. Generic names in quotes indicate provisional assignment pending future revision; such species are unlikely members of the stated genera.

1. – 18–39 scales in lateral line (or if incomplete, in lateral series) on body.2
– 40–47 scales in lateral line on body.10
2. – Last unbranched dorsal-fin ray serrated posteriorly.3
– Last unbranched dorsal-fin ray smooth.5
3. – Lateral line complete; a black blotch on caudal peduncle; adults exceed 80 mm SL. *Systemus*
– Lateral line abbreviated; maximum SL <80 mm.4
4. – 19–24 scales in lateral series; one or more black spots, blotches or bars on body.*Pethia*
– 31–39 scales in lateral series; no black markings on body. '*Puntius*' *guganio*, '*P.*' *nangalensis*
5. – Juveniles (<50 mm SL) with two or more black bars on body.6
– No black bars on body at any stage.7
6. – Both rostral and maxillary barbels present. *Dravidia*
– Rostral barbels absent.*Dawkinsia*
7. – 9 branched dorsal-fin rays.8
– 7 or 8 branched dorsal-fin rays.9
8. – Last unbranched dorsal-fin ray stout, heavily ossified. '*Neolissochilus*' *bovanicus*
– Last unbranched dorsal-fin ray weak, segmented. '*Gonoproktopterus*' *jerdoni*
9. – Rostral barbels present; when adpressed, anal fin reaching beyond hypural notch. '*Gonoproktopterus*' *carnaticus*
– Rostral barbels absent; when adpressed, anal fin falling short of hypural notch.*Puntius*
10. – Both rostral and maxillary barbels present. *Eechathalakenda* *ophicephala*
– Rostral barbels absent.11
11. – Last unbranched dorsal-fin ray serrated; maxillary barbels present.12
– Last unbranched dorsal-fin ray smooth; maxillary barbels absent. '*Puntius*' *punjaubensis*
12. – Lateral line complete; 9 branched dorsal-fin rays; 7 branched anal-fin rays. '*Puntius*' *deccanensis*
– Lateral line incomplete; 8 branched dorsal-fin rays; 5 branched anal-fin rays. '*Puntius*' *sharmai*, '*P.*' *fraseri*

Material examined. *Dawkinsia arulius*, BMNH 1980.11.25:73–74, 2, 88.0–90.9 mm SL; BMNH 89.2.1.664–5, 2, 67.1–67.6 mm SL; India: Tamil Nadu: Cauvery River at Coorg.

Dawkinsia assimilis, WHT 6250, 5, topotypes, 43.3–53.2 mm SL; India: Karnataka: Netravati River, 42 km from Madikeri on Mangalore–Mysore Road.

Dawkinsia exclamatio, WHT 6255, holotype, 70.4 mm SL; WHT 6249, 3 paratypes, 62.3–71.9 mm SL; WHT 11056, 1, 63.5 mm SL, c&s; WHT 11076, 1, 70.4 mm SL, c&s; India: Kerala: Kallada River at Thenmalai.

- Dawkinsia filamentosa*, MNHN 3908, lectotype, 82.7 mm SL; India: Kerala: Alleppey. – AMS B.7869, 94.9 mm SL; India: Madras. – MNHN 3908, 2 paralectotypes, 76.4–85.4 mm SL; India: Alleppey. – WHT 11026, 1, 67.1 mm SL, c&s; WHT 11040, 1, 63.0 mm SL, c&s; India: Kerala: Chalakkudy.
- Dawkinsia singhala*: ZMH 364, lectotype, 24.0 mm SL; ZMH 365, 2, paralectotypes, 54.1–63.3 mm SL; WHT 6245, 4, 54.1–63.3 mm SL; Sri Lanka: Gin River at Wakkwella. – WHT 11037, 1, 62.1 mm SL, c&s; WHT 11042, 1, 55.0 mm SL, c&s; Sri Lanka: Morawaka.
- Dawkinsia srilankensis*, BMNH 1976.2.10.2, holotype, 79.0 mm SL; BMNH 1976.2.10.2, 1, paratype, 63.3 mm SL; WHT 11053, 1, 61.0 mm SL, c&s; WHT 11063, 1, 60.7 mm SL, c&s; Sri Lanka; 3 miles N of Pallegama.
- Dawkinsia tambraparniei*, ZSI 735, 1, paratype, 68.7 mm SL, India: Tamil Nadu: tributary of Tambraparni River 7 km from Kalladi Kuruchi; ZSI-SRS 4452, 2, 52.9–64.6 mm SL; India: Tamil Nadu: Tirunelveli.
- Dravidia fasciata*, WHT 11043, 1, 43 mm SL, c&s; WHT 11034, 1, 39.1 mm SL, c&s; India: Kerala: Chalakkudy.
- Gonoproktopterus carnaticus* AMS B.7963, 1, 103.3 mm SL; AMS B.7626, 1, 225 mm SL; India: Bhavani River, Tamil Nadu, F. Day.
- Gonoproktopterus jerdoni*, AMS B.7935, 1, syntype, 179.3 mm SL, India: Canara [Karnataka], F. Day.
- Gonoproktopterus kolus* AMS B.7518, 1, 153.9 mm SL, India: Deccan, F. Day.
- Gonoproktopterus lithopidos* AMS B.8374, 1, syntype, 282 mm SL, India: Canara, F. Day.
- Neolissochilus bovanicus*, AMS B.7829, lectotype, 95.1 mm SL, India: Bhavani River, Tamil Nadu, F. Day.
- Neolissochilus wynaadensis* AMS B.7989, 1, syntype, 137.1 mm SL, India: Wynaad, F. Day.
- Pethia bandula*, ZRC 38483, holotype, 34.8 mm SL; CMK 7146, 7, paratypes, 29.6–38.5 mm SL; Sri Lanka: Galapitamada.
- Pethia conchoniuis*, AMS IA.6883, 41.8 mm SL; aquarium specimen. – AMS IA.6518, 46.5 mm SL; aquarium specimen.
- Pethia cumingii*, BMNH 1859.10.19.101, lectotype, 33.4 mm SL; BMNH 1859.5.31.47–48, 3, paralectotypes; Sri Lanka. – WHT 7685, 1, 37.0 mm SL, c&s; WHT 11047, 1, 35.6 mm SL, c&s; Sri Lanka: Mawanana.
- Pethia melanomaculata*, WHT 1681, 2, 37.0–38.7 mm SL; WHT 218, 2, 30.6–31.8 mm SL; WHT 11066, 1, 62.8 mm SL, c&s; WHT 11068, 1, 37.8 mm SL, c&s; Sri Lanka: Mahawelia basin: Hasalaka.
- Pethia nigrofasciata*, BMNH 1859.10.19.99–100, 2, syntypes, 32.1–45.5 mm SL; Sri Lanka. – WHT 7677, 3, 41.0–44.4 mm SL; Kelani River at Kitulgala. – WHT 11022, 1, 35.9 mm SL, c&s; WHT 11023, 1, 35.6 mm SL, c&s; Sri Lanka, Mawanana.
- Pethia punctata*, WHT 7716, 3, 35.1–37.0 mm SL; WHT 11071, 1, 29.3 mm SL, c&s; WHT 11077, 1, 28.7 mm SL, c&s; India: Kerala: Calicut. – WHT 7715, 4, 29.7–34.2 mm SL; India: Kerala: Thenmalai.
- Pethia reval*, WHT 677, holotype, 30.5 mm SL; WHT 7536, 3, 28.8–36.6 mm SL; Sri Lanka: Kelani Basin: Labugama. – WHT 11033, 1, 25.6 mm SL, c&s; WHT 11044, 1, 28.3 mm SL, c&s; Sri Lanka: Ingiriya.
- Pethia stoliczkanana*, AMS B.7542, 1, 34.7 mm SL; India: West Bengal: Darjeeling.
- Pethia ticto*, WHT 7718, 5, 30.8–34.6 mm SL; India: West Bengal: Nadia. – AMS B.7974, 2, 49.5–58.6 mm SL; India: Ganjam. – WHT 11054, 1, 37.0 mm SL, c&s; WHT 11065, 1, 37.4 mm SL, c&s; India: W Bengal: Nadia.
- Puntius amphibiis*, MNHN 73, lectotype, 92.5 mm SL; MNHN 2005-0006, 1, paralectotype, 74.3 mm SL; India: Maharashtra: Bombay.
- Puntius bimaculatus*, WHT 79, 2, 37.0–46.2 mm SL; Sri Lanka: Pallegama. – WHT 1065, 8, 40.2–46.0; Sri Lanka: Mee Oya [River].
- Puntius brevis*, AMS I.43487-006, 43.2 mm SL; Cambodia: Tonle Sap River, 3–5 km downstream of Kompung Chhnang.
- Puntius chola*, AMS B.7887, 89.3 mm SL; India: Madras.
- Puntius everetti*, AMS I.30463-001, 3, 32.5–39.4 mm SL; Malaya.
- Puntius denisonii*, AMS B.7913, 1, 88 mm SL; India: Travancore Hills.
- Puntius dorsalis*, WHT 2153, 4, 68.4–115.3 mm SL; India: Tamil Nadu: Mamallapuram. – AMS B.7634, 112.4 mm SL; India: Madras. – WHT 1900, 6, 93.3–133.5; Sri Lanka: Minneriya. – WHT 7646, 2, 56.7–65.0 mm SL, c&s; Sri Lanka: Tissamaharamaya.
- Puntius kamalika*, WHT 7639, holotype, 50.2 mm SL; WHT 7640, 11, paratypes, 39.3–55.4 mm SL; Sri Lanka, Kalu River at Walandure near Kuruwita.
- Puntius kelumi*, WHT 7629, holotype, 70.4 mm; WHT 7630, 4, 57.2–68.6 mm SL; Sri Lanka: Kalu River: Madakada Aranya, near Ingiriya. – WHT 7645, 2, 55.1–63.2 mm SL, c&s; Sri Lanka: Homadola.
- Puntius layardi*: BMNH 1853.12.27.5, syntypes, 2, 92.5–112.7 mm SL; Sri Lanka.
- Puntius mahecola*, MNHN 3896, lectotype, 50.7 mm SL; MNHN 2005-0007, paralectotypes, 5, 48.7–56.5 mm SL; India: Kerala: Mahe. – WHT 7681, 2, 56.8–66.8 mm SL, c&s; India: Kerala: Kottayam.
- Puntius partipentazona*, AMS I.43747-007, 32.1 mm SL; Cambodia: Tonle Sap River.
- Puntius sealei*, AMS I.22131-006, 9, 45.8–62.4 mm SL; Northwest Borneo: Kembang River.
- Puntius sophore*, ZRC 35064, neotype, 71.8 mm SL; ZRC 35065–35069, 5, 59.4–80.6 mm SL; Bangladesh: Srimangal, from Hail Hoar floodplain near Moulvi Bazaar. – WHT 11060, 1, 36.6 mm SL, c&s; WHT 11062, 1, 28.9 mm SL, c&s; India: West Bengal: Boncron.
- Puntius thermalis*, WHT 158, 4, 74.6–76.0 mm SL; WHT 11027, 1, 55.8 mm SL, c&s; WHT 11035, 1, 48.9 mm SL, c&s; Sri Lanka: Attidiya.
- Puntius titteya*, WHT 8013, 1, 32.1 mm SL, c&s; WHT 8014, 1, 44.2 mm SL, c&s; Sri Lanka: Kelani River near Ginigathena.
- Puntius vittatus*, WHT 11036, 1, 27.5 mm SL, c&s; WHT 11038, 1, 28.5 mm SL, c&s; Sri Lanka: Navinna.
- Systemus immaculatus*, AMS B.7920, neotype,

186.9 mm SL; AMS B.7921, 1, topotype, 192.7 mm SL; India: Assam.

Systemus martenstyni, ZRC 38482, holotype, 136.0 mm SL; CMK 7168, 11, 67.2–116.8 mm SL; Sri Lanka: 2 km N of Pallegama.

Systemus orphoides, AMS L43487-062, 2, 106–136 mm SL; Cambodia: Tonle Sap River, 3–5 km downstream of Kompong Chhnang.

Systemus pleurotaenia, WHT 11031, 1, 66.2 mm SL, c&s; Sri Lanka: Akuressa.

Systemus sp. 'Richmondi' [manuscript name for an as yet undescribed species], WHT 9861, 6, 121.5–127.0 mm SL; Sri Lanka: Elahera.

Systemus spilurus, WHT 11028, 1, 61.1 mm SL; Sri Lanka, Kuruwita.

Systemus timbiri, NMSL FF801, holotype, 178 mm SL; Sri Lanka: Timbirigasmankada. – WHT 11107, 5, 127–200 mm SL; Sri Lanka: Walawe River.

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