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Fangfangia spinicleithralis, a new genus and species of miniature cyprinid fish from the peat swamp forests of Borneo (Teleostei: Cyprinidae)

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Fangfangia spinicleithralis, new genus, new species, is described from peat swamp forest habitats in Kalimantan Tengah, Borneo, Indonesia. It differs from all other cyprinids in having the anteroventral tip of the left cleithrum projecting into a strong anteriorly directed spine and a pointed posteriorly directed spine at the posteroventral aspect of each cleithrum. In addition, it can be diagnosed by the following characters: the base of the dorsal hemitrich of the first pectoral-fin ray with serrated margin, multicuspid pharyngeal teeth, ventrally directed lateral processes on vertebra 1, the high number of procurrent caudal-fin rays (14–18 dorsally, 11–15 ventrally), absence of scales with the exception of six or seven tubular lateral line ossicles, and the greatly elongated middle radials in the anal fin, which may reach half the length of proximal radials.

Introduction

Peat swamp forests in Southeast Asia harbour an exceptionally large number of miniature fishes, the majority of which is made up of species of the family Cyprinidae (Kottelat et al., 2006).

During a recent collecting trip, a tiny cyprinid was found, which was thought in the field to be a member of the genus *Sundadanio*. A closer inspection, however, revealed that it differs significantly from *Sundadanio* and exhibits several unique anatomical modifications. The present paper describes it as a new genus and species of the family Cyprinidae and highlights again the link between miniaturization and evolutionary novelty.

Material and methods

The number of fin rays were counted in transmitted light under a Zeiss DRC stereomicroscope at magnifications of 10–80× in the holotype, the well-preserved paratypes of lots ZRC 52074 and CMK 20388, and in the three cleared and double stained (c&s) specimens (prepared following Taylor & Van Dyke, 1985). The fin rays of the other paratypes could not be counted reliably due to the folded, damaged and bent state of the fins. The number of vertebrae was taken from the three c&s specimens only. Alcohol and c&s specimens were photographed with a Zeiss Axiocam HRc digital camera attached to a Zeiss Discovery V20.

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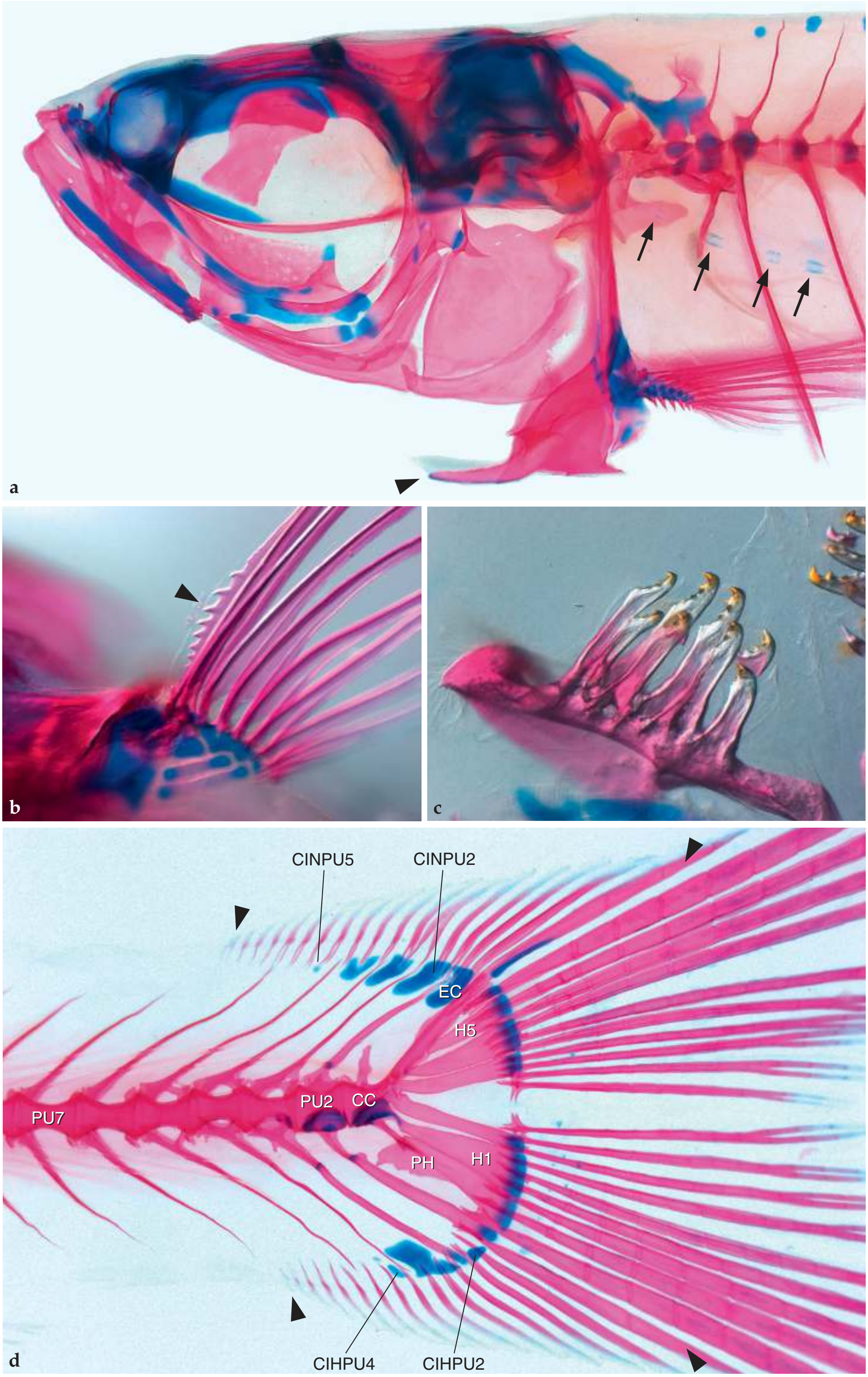
Fig. 1. *Fangfangia spinicleithralis*, MZB 17186, holotype, 16.5 mm SL; Indonesia: Borneo: Kalimantan Tengah: Sebangau drainage.

Measurements were taken on the holotype and the paratypes of ZRC 52074 and CMK 20338 only with an ocular micrometer with an accuracy of 0.1 mm. Specimens used in this study are deposited in the following collections: BMNH, The Natural History Museum, London; CMK, personal collection of the second author; MZB, Museum Zoologicum Bogoriense, Bogor; ZRC, Zoological Reference Collection, The Raffles Museum of Biodiversity Research, Singapore.

To describe pigmentation in *Fangfangia* we have modified the colour pattern terminology by Britz & Kottelat (2008) developed for *Paedocypris*. For caudal radial cartilages the terminology of Fujita (1989) has been adopted.

Fig. 2. *Fangfangia spinicleithralis*, BMNH 2011.11.9.1, c&s paratype, 17.6 mm SL; **a,** lateral view of head region of right side (photograph reversed), gill arches, hyoid and left hyopalatine arch removed; note asymmetrically developed anterior cleithral spine (marked by arrowhead), small, pointed, posteriorly directed spine and tubular lateral line ossicles on body (marked by arrows); **b,** close-up of pectoral-fin base in ventral view; note serrated anterior base of dorsal hemitrich of first pectoral-fin ray (marked by arrowhead) and three pectoral radials; **c,** pharyngeal teeth on ceratobranchial 5 in anterodorsal view; note up to five cusps on tips of individual teeth; **d,** precaudal vertebrae and caudal fin in lateral view; note high number of procurrent caudal-fin rays (first and last dorsal and ventral procurrent rays marked by arrowheads) and associated caudal radial cartilages. CC, compound centrum; CIHPU, interhaemal spine cartilage; CINPU, interneural spine cartilage; EC, epural cartilage; H, hypural; PH, parhypural; PU, preural centrum. ▷



a
b
c
d
CINPU5
CINPU2
EC
H5
PU7
PU2
CC
PH
H1
CIHPU4
CIHPU2

Fangfangia, new genus

Type species. *Fangfangia spinicleithralis*, new species.

Diagnosis. *Fangfangia* is unique among cyprinids in having the anteroventral tip of the left cleithrum projecting into a strong anteriorly directed spine and a small, pointed, posteriorly directed spine at the posteroventral aspect of each cleithrum. In ventral view the anterior and the paired posterior spines form a Y-shaped structure with the anterior spine representing the stem and the posterior spines representing the arms of the Y. Other diagnostic features are: the base of the dorsal hemitrich of the first pectoral-fin ray with serrated margin, multicuspid pharyngeal teeth, ventrally directed lateral processes on vertebra 1, the high number of procurrent caudal-fin rays (14–18 dorsally, 11–15 ventrally), absence of scales with the exception of six or seven tubular lateral line ossicles, and the greatly elongated middle radials in the anal fin, which may reach half the length of proximal radials. The latter three characters are shared with *Sundadanio*, which has 9–12 dorsal and 8–11 ventral procurrent rays (Conway et al., 2011).

Etymology. The new genus is named after the late Fang Fang, a passionate and productive cypriniform researcher, who left us too early, honouring her contribution to danionine taxonomy and phylogeny. Gender feminine.

Fangfangia spinicleithralis, new species
(Fig. 1)

Holotype. MZB17186, 16.5 mm SL; Indonesia: Borneo: Kalimantan Tengah: Sebangau drainage: Sebangau River, blackwater drainage canal, north side upstream from village, 2°17'44"S 113°52'17"E; M. Kottelat & Tan H. H., 6 March 2008.

Paratypes. ZRC 52074, 4; CMK 20388, 3; 13.7–15.6 mm SL; BMNH 2011.11.9.1, 1, c&s, 17.4 mm SL; same data as holotype. – MZB17187, 3; ZRC 52075, 11; BMNH 2011.11.9.2–4, 3; 15.4–21.2 mm SL; BMNH 2011.11.9.5–6, 2, c&s, 16.3–22.7 mm SL; Indonesia: Borneo: Kalimantan Tengah: Sebangau drainage; aquarium-fish trade; don. H. Tommy, 18 Sep 2007.

Diagnosis. As for genus.

Description. For general appearance see Figure 1. Morphometric data are provided in Table 1.

An elongate, laterally only slightly compressed cyprinid, almost circular to slightly oval in cross section, body depth 5–7 times in SL. Head large 3.4–3.8 times in SL. Eye large, 2.8–3.1 times in head length. Snout long and pointed, 3.9–4.5 times in head length. Mouth terminal, no barbels.

Pectoral-fin rays 9 (4) or 10 (7). Lateral margin of first (upper most) pectoral-fin ray with several fine serrae at base (Fig. 2b). Pelvic-fin with pelvic splint, and i + 5 rays (11). Dorsal-fin rays 8 (1), 9 (8) or 10 (2), with ii + 6 + i (8), ii + 5 + i (1) or iii + 6 + i (2). Anal-fin rays 9, with iii + 6 (11). Caudal fin forked, with 10 + 9 (11) principal caudal-fin rays and 14–18 dorsal and 11–15 ventral procurrent rays.

Head lateral-line system reduced, present as simple bone-enclosed canal on nasal, frontal, pterotic, circumorbitals, preopercular, anguloarticular and dentary. Body lateral line short, consisting of six or seven narrow tubular lateral line scales (Fig. 2a) extending in a ventrally arching line between shoulder girdle and rib of ninth vertebra slightly behind posterior pelvic-fin base. Body otherwise scaleless. Skull roof incomplete with two large fontanelles, one preepiphyseal and one postepiphyseal. Frontals approach each other on top of epiphyseal bar without actually meeting. Preethmoid, supraorbital, ectopterygoid, intercalar, extrascapular, posttemporal, postcleithrum and hypobranchials 1–3 absent (the latter present as cartilages only). Branchiostegal rays three, anteriormost ray not articulating with hyoid (Fig. 3a), free-floating in branchiostegal membrane. Pharyngeal teeth multicuspid (Fig. 2c), usually with five cusps, tooth formula 3,4–4,3. Three pectoral radials only (Fig. 2b); two lowermost radials developed as thin rods of perichondrally ossified cartilage. Cleithrum at its anterior and ventralmost tip asymmetrically developed, its left side with a strong, pointed, anteriorly directed spine (Figs. 1a, 2a); a small, pointed, posteriorly directed spine at posteroventral aspect of each cleithrum (Fig. 2a). Base of dorsal hemitrich of first pectoral-fin ray with serrated margin (Fig. 2b). Lateral process on first vertebra directed ventrally and connected to pharyngeal process of basioccipital process via ligament. Supraneural cartilages 5–9 present. Caudal fin (Fig. 2d) with six hypurals, one epural cartilage and four dorsal (CINPU2, 3, 4, 5) and three ventral radial cartilages (CIHPU2, 3, 4).

Vertebrae, based on three c&s specimens: 16 + 19 = 35 (2) or 16 + 18 = 34 (1).

Colour in alcohol. Background whitish with pigment pattern consisting exclusively of melanophores as follows (Fig. 1): a narrow midlateral stripe following horizontal septum from shoulder girdle to end of caudal peduncle, extending as triangular patch of melanophores at tip of caudal peduncle. A ventrolateral row from anus along base of anal fin, behind which left and right row unit forming a midventral row extending to end of caudal peduncle; an anal-fin base row; a few scattered melanophores on ventrolateral abdominal area; numerous small densely set melanophores lining peritoneum and visible on ventrolateral area of abdominal cavity. A middorsal stripe consisting of a series of irregularly arranged larger melanophores with numerous smaller melanophores covering dorsolateral aspect of body reaching down to almost level of horizontal septum. Several large melanophores covering lateral aspect of otic capsule; large chromatophores on opercle; a number of melanophores following outline of branchiostegal rays, interopercle, and lower jaw. No pigment on isthmus or gular area. A series of melanophores following margin of anterior cleithral spine and continuing along ventral margin of cleithrum and converging with that of other side towards pelvic fin base. A number of densely set large melanophores covering occiput and optic tectum dorsally; a few melanophores covering telencephalon. A row above eye following margin of frontal; a number of preorbital melanophores peppering snout; a dense row of melanophores along upper margin of upper jaw. An infraorbital series following posterior and ventral margin of orbit. A few melanophores along pectoral- and dorsal-fin rays and principal caudal-fin rays, but not procurrent rays; a patch of densely aggregated melanophores on base of each upper and lower caudal-fin lobes, appearing as two irregular spots; a short line of melanophores along base of dorsal and ventral procurrent caudal-fin rays, continuous with midventral caudal peduncle row.

In life, body pale yellowish, translucent. No notable colour marks.

Distribution. *Fangfangia spinicleithralis* is presently known only from the type locality in Sebangau peat swamp forest, Kalimantan Tengah, Borneo, Indonesia.

Habitat. The natural habitat of the species is not known. It has been collected only in a deep drainage canal dug into the peat soil left exposed after the forest has been logged or burned. At the site of collection, the canal was more than 2 m deep, there was hardly any structure along the shore and in the water, there was a slow current, and there was no canopy cover (Fig. 4). Only very few fish (species and individuals) were obtained in

Table 1. Selected morphometric data for *Fangfangia spinicleithralis* holotype and 9 paratypes. Range includes holotype values.

	holotype	range	mean ± standard deviation
Standard length (SL) in mm	16.5	13.7–20.8	
In percent of standard length			
Head length (HL)	28.5	26.4–29.3	28.0 ± 0.9
Predorsal length	60.6	56.5–61.3	59.4 ± 1.3
Preanal length	63.0	62.5–65.5	63.7 ± 1.0
Prepelvic length	49.1	45.6–49.6	47.8 ± 1.3
Body depth at dorsal-fin origin	18.2	14.9–18.6	17.7 ± 1.3
In percent of head length			
Snout length	26	22–26	23.7 ± 1.2
Eye diameter	32	32–36	34.3 ± 1.2
Ratios			
Standard length/Head lenth		3.4–3.8 (3.5)	3.6 ± 1.1
Standard length/body depth at dorsal-fin origin		5.4–6.7 (5.5)	5.7 ± 0.5
Head length/snout length		3.9–4.5 (3.9)	4.2 ± 0.2
Head length/eye diameter		2.8–3.1 (3.1)	2.9 ± 0.1

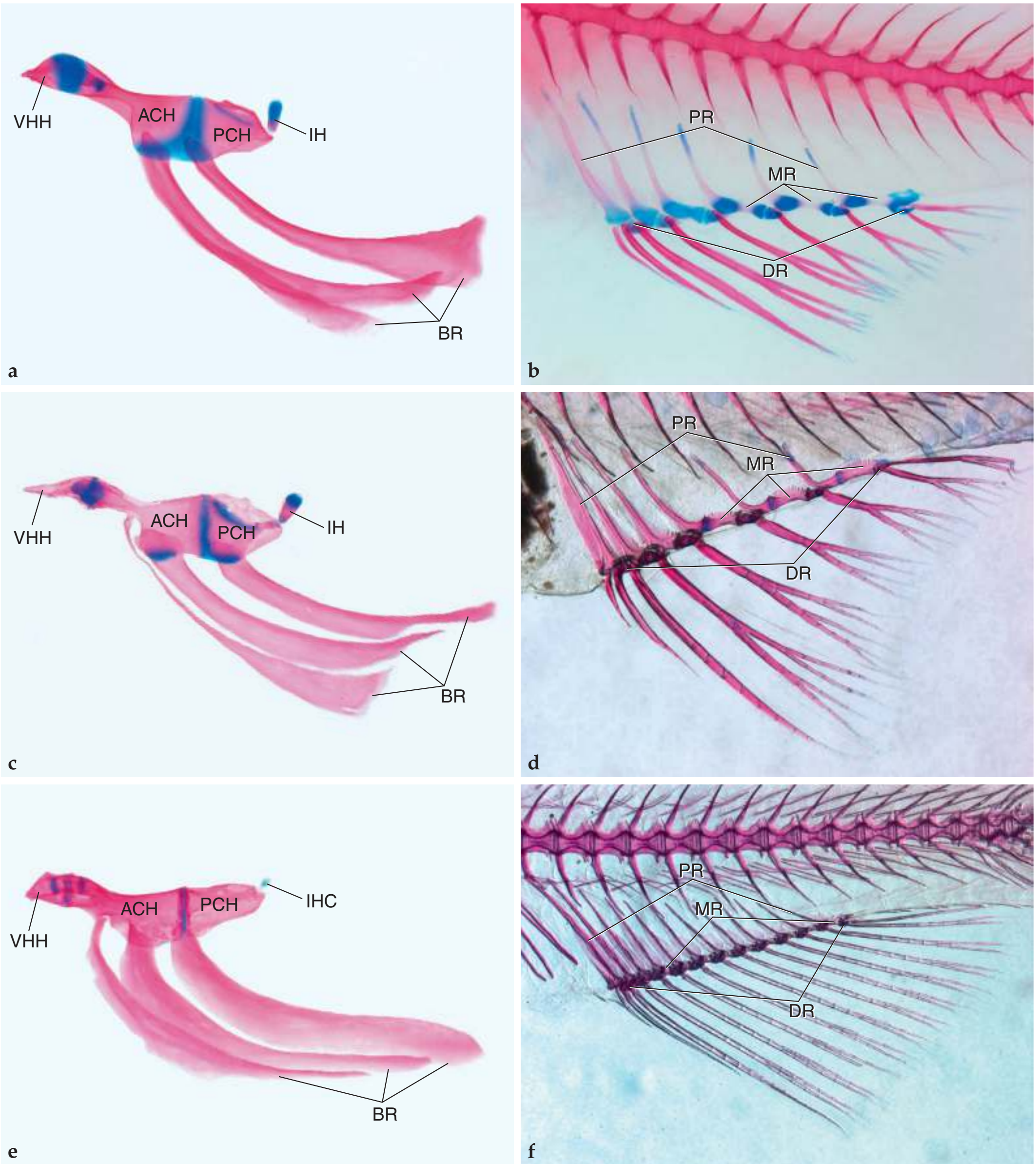


Fig. 3. Hyoid and anal-fin skeleton of: **a–b,** *Fangfangia spinicleithralis*, BMNH2011.11.9.1, paratype, 17.6 mm SL; **c–d,** *Sundadanio* sp., BMNH 2005.11.10.9–16; **e–f,** *Danio rerio*, BMNH 2001.3.12.76–92; note absence of articulation of first branchiostegal ray with anterior ceratohyal in **a**, greatly attenuated anterior part of first branchiostegal ray in **c**, and differences in segmentation and branching pattern of anal-fin rays between **b**, **d** and **f**. ACH, anterior ceratohyal; BR, branchiostegal rays; DR, distal radial; IH, interhyal; IHC, interhyal cartilage; MR, middle radials; PCH, posterior ceratohyal; PR proximal radials; VHH, ventral hypohyal.

the parts of the canal that could be fished (along the shores, with a 1-m steel-frame kicknet, from the surface down to about 2 m depth); more fish were present in the shallower water next to the confluence of the canal with Sebangau River, but still in low numbers, with only 14 species (one would reasonably expect 30–40 species in pristine conditions).

Fig. 4. Type locality of *Fangfangia spinicleithralis*. Canal in recently cleared peatswamp forest. Water depth over 2 m. (Photograph Tan Heok Hui).

Interestingly, *Fangfangia spinicleithralis* was collected only in the canal. It was caught in the deepest pulls of the net or in a small area with slow countercurrent. It cannot be guessed whether this reflects the natural habitat of the species; some species of *Sundadanio* have also been collected at similar depths (MK, pers. obs.).

Forest was still visible at some distance from the collecting site but could not be reached (not enough water to reach it by boat and impossible to walk). The type locality is at the edge of Sebangau National Park, where it is expected that suitable habitat remains. It is possible that this tiny species prefers deeper channels, a habitat type poorly sampled within the peat swamp forest ecology.

Etymology. The species name *spinicleithralis*, an adjective, is derived from the Latin words *spina*, thorn, and *cleithralis*, belonging to the cleithrum (the main element of the dermal shoulder girdle). It refers to the unique pointed anterior and posterior spines on the cleithrum of this species.

Discussion

The peat swamp forests of Southeast Asia is one of the most endangered freshwater habitats in the world. They harbour an amazing diversity of stenotopic, and largely endemic, fish species adapted to the highly acidic blackwaters. Kottelat et al. (2006) and Rüber et al. (2007) pointed out that an unusually high percentage of miniature (as defined by Weitzman & Vari, 1988) Southeast Asian freshwater fishes have evolved in peat swamp forests, which may, as Kottelat et al. (2006) argue, correlate with the greatly spatially restricted water depth in the swamp forests during the dry season. *Fangfangia* is an additional example of a miniature species apparently restricted to the blackwaters of peat swamp forests. Hanken (1993) and Hanken & Wake (1993) pointed out that miniaturisation is often linked to the evolution of morphological novelties, an idea further developed by Rüber et al. (2007) and Britz & Conway (2009), Britz et al. (2009), and Britz (2009) for miniature cypriniforms. The latter three papers provided examples in which miniaturization via developmental truncation has lead to spectacular cases of evolutionary morphological novelties in *Paedocypris*, *Danionella*, and *Sundadanio*. *Fangfangia spinicleithralis* is another example of a miniature fish with unique morphological novelties that can be added here. It is the only cypriniform with a cleithral spine, which, in addition, is asymmetrically developed (Fig. 2a). Most likely unique among cypriniforms is also the evolution of a serrated base on the dorsal hemitrich of the uppermost, or first, pectoral-fin ray (Fig. 2b). *Sundadanio*, another Southeast Asian miniature, peat swamp restricted cyprinid genus, shows serrations on its pectoral fin, but they are present on the fifth ray rather than the first (Conway & Britz, 2007). *Sundadanio* shows additional striking morphological novelties, modifications of the vertebral skeleton and its associated musculature, which are sexually dimorphic and related to the production of sound (see Conway & Britz, 2007). Hanken & Wake (1993) also noted that miniaturized taxa are often difficult to place phylogenetically due to the reduction of informative characters as a result of body size reduction. Britz & Conway (2009) provided an example how this difficulty could be overcome in the case of *Paedocypris*.

Based on its derived characters, the phylogenetic relationships of *Fangfangia* seem to lie with *Sundadanio*. It shares with *Sundadanio* a number of putative synapomorphies. (1) The middle radials of the anal fin are greatly elongated and may reach up to 50 % the length of the proximal radials (Fig. 3b,d). (2) The segmentation and branching pattern of the anal-fin rays is very similar. Commonly in cyprinids there are a number of segments between the long basal segment and the segment that includes the first dichotomous branching (4–6 in *Danio rerio*; Fig. 3f). In *Fangfangia* and *Sundadanio* there is only one segment between the long basal element and the branching segment (Fig. 3b,d). (3) The lateral process of the first centrum, which is, as the name implies, directed laterally in other cyprinids, if present, is directed ventrally and connected to the pharyngeal process of the basioccipital process in *Fangfangia* and *Sundadanio*.

An additional potential synapomorphy of the two taxa is the presence of a high number of procurrent caudal-fin rays, which is supported by caudal radial cartilages (Fig. 2d). Comprehensive information on the number of procurrent rays in a large number of cyprinids is missing, but Fujita (1990) illustrated and described 13 species of this family and Conway (2011) six species. The number of procurrent rays ranges in cyprinids from 3–4 dorsally and 2–3 ventrally in *Danionella dracula* (Britz et al. 2009) to 16 dorsally and 16 ventrally in *Zacco platypus* (Fujita, 1990: 219). With the exception of *Sundadanio* the number of procurrent rays seems to be under 10 among Danioninae (RB pers. obs.) and appears to be highest in *Luciosoma setigerum* (BMNH 2001.3.13.109–121) with up to 9 dorsally and 8 ventrally. The count of 14–18 dorsal and 11–15 ventral procurrent rays in *Fangfangia* (Fig. 2d) is thus exceptionally high among cyprinids and unique, as far as we know, among danionines, and only matched by *Sundadanio* with 9–12 dorsal and 8–11 ventral procurrent rays (Conway et al., 2011). Outside of cyprinids, a high number of procurrent caudal fin rays is present in loaches among cypriniforms (e.g. 20 dorsal and 17 ventral procurrent rays in *Syncrossus berdmorei* according to Conway, 2011) and catfishes (14–19 dorsal and ventral procurrent rays in diplomystids according to Arratia, 2003). Comparative data are mostly missing regarding the presence and number of caudal radial cartilages in cyprinids, but Fujita (1990: 214–225) illustrated 2 large dorsal and 1 ventral radial cartilages in the acheilognathine *Tanakia tanago*. *Fangfangia* possesses 4 dorsal and 3 ventral caudal radial cartilages (Fig. 2d) possibly associated with the high number of procurrent rays.

Another probably unique feature of *Fangfangia* among cyprinids is the absence of an articulation between the first branchiostegal ray and the hyoid arch effected by an anterior shortening of the ray (Fig. 3a). Commonly, the first branchiostegal ray articulates with the anterior half of the anterior ceratohyal, as in *Danio rerio*

(Fig. 3e), even if its anterior portion is greatly attenuated as in *Sundadanio* (Fig. 3c).

The most conspicuous character of *Fangfangia* is, however, the anteriorly directed and asymmetrically developed strong cleithral spine. This spine is found in all specimens of the type series, which includes males and females and is thus not sexually dimorphic. The biological role of this spine is unknown; all specimens collected at the type locality have this spine exposed externally. This is probably an artifact, as it is covered by a thin layer of skin that can easily get damaged and leads to the spine getting caught up in the net during collection. This is supported by the fact that all specimens of *Fangfangia* from the aquarium trade have the spine still covered by skin. Similarly unclear is the role of the serrations on the first pectoral-fin ray. We found these serrations in various degrees of development in all except six specimens of *Fangfangia*. As far as we can tell, their presence as such does not seem to be sexually dimorphic. Clearly, behavioural information is needed to resolve the function of the cleithral spine and pectoral-fin serrations.

Fangfangia shows thus a remarkable collection of unusual or unique skeletal characters. All the similarities between *Fangfangia* and *Sundadanio* point presently to a close relationship of the two genera, which is a hypothesis that will need to be further analyzed and tested.

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