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PAEDOCYPRIS CARBUNCULUS, A NEW SPECIES OF MINIATURE FISH FROM BORNEO (TELEOSTEI: CYPRINIFORMES: CYPRINIDAE)

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ABSTRACT. – Paedocypris carbunculus, new species, is described from Pangkalan Bun, Kalimantan Tengah on the island of Borneo, Indonesia. It differs from its congeners in the shape of its head blotches. It is readily distinguished further from *P. micromegethes* in having the middorsal stripe consisting of three rows of chromatophores, head kidney pigment, well developed opercular, subopercular, interopercular, and branchiostegal rows and isthmus and gular pigmentation, chest spots, a well developed chest blotch, and in the presence of a preanal larval fin fold in adult females. It differs also from *P. progenetica* in having the median row of the middorsal stripe formed by separated individual chromatophores, and sparsely-pigmented upper and lower lips.

KEY WORDS. - Miniature fishes, Paedocypris carbunculus, new species, sexual dimorphism, breeding behaviour.

INTRODUCTION

The genus *Paedocypris* was recently created for two miniature species of cyprinids collected from peat swamp forests in Sumatra and Borneo (Kottelat et al., 2006). With a recorded maximum size of 10.3 and 11.5 mm standard length, respectively, *P. progenetica* and *P. micromegethes* are among the smallest fish and vertebrate species, and *P. progenetica* is the smallest with females maturing at 7.9 mm (Kottelat et al., 2006). *Paedocypris* species can be easily distinguished from all other cyprinids, and even all other teleosts, by the uniquely modified pelvic fins in males, in which the first pelvic fin ray is greatly enlarged and supports keratinized pads of skin, termed "flange and hook" by Kottelat et al. (2006).

The anatomy of *Paedocypris* in general is highly modified and consists of a mixture of developmentally truncated characters that closely resemble larval stages of other cyprinids, and of highly derived, autapomorphic features of which many are unique among cyprinids (Kottelat et al., 2006).

This unusual mix of anatomical characters made it impossible to assign the new genus *Paedocypris* to any of the cyprinid subfamilies with confidence at the time of its description. A follow-up molecular study indicated, however, that

Paedocypris belongs to the Rasborinae clade A and its closest relative is Sundadanio, another miniature cyprinid from Southeast Asia (Rüber et al., 2007). This conclusion gained support from a detailed morphological study of Paedocypris sp. from Banka (Britz & Conway, submitted). Both, Sundadanio and Paedocypris are restricted to the highly fragmented peat swamp forest habitats in Southeast Asia and Rüber et al.'s (2007) molecular analysis indicated that four DNA samples of Paedocypris from different peat swamps show considerable genetic differences between localities.

When reviewing material of *Paedocypris* from a number of additional peat swamp forest areas across Sundaland, we realized that it contained several new species, one of which is described herein.

MATERIALS AND METHODS

Specimens of *Paedocypris* were studied and the number of fin rays counted under a Zeiss DRC stereomicroscope at magnifications of 10–80×. All photographs were taken with a Jenoptik ProgRes 12C digital camera attached to a Zeiss Tessovar. Measurements were taken 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, Cibinong; and ZRC, Zoological Reference Collection, Raffles Museum of Biodiversity Research, Singapore.

The different species of *Paedocypris* resemble each other very closely in fin ray counts and due to the absence of scales, no other external meristic characters are available. We found that colour pattern is species-specific and allows for a ready distinction of the different species. To describe the colour pattern more easily we developed a standardized terminology for its different components, which we explain here in detail and illustrate in Fig. 1:

Middorsal stripe: one or several rows of chromatophores along the dorsal midline from the posterior dorsal head blotch (see below for definition) to the end of the caudal peduncle. There may be just one row of single chromatophores, one row of several chromatophores, or several rows of chromatophores separated by narrow pigmentless spaces. The median row is expressed as an uninterrupted line in *Paedocypris progenetica*.

Midlateral row: a row of chromatophores along the horizontal septum from the shoulder girdle to the end of the caudal peduncle.

Ventrolateral row: postabdominal row of chromatophores running along the ventral margin of the hypaxial musculature from the end of the abdominal cavity to the end of the caudal peduncle, consisting of an anterior part at the dorsal (proximal) margin of the musculature of the anal fin and a posterior part along the base of the precaudal fin fold. Anteriorly at the level of the abdominal cavity it is contiguous with the swimbladder row (the pigment row that is formed by the chromatophores that cap the dorsal area of the anterior and posterior partitions of the swimbladder). The precaudal fin fold part is continuous with the anal fin base row that runs along the anal fin base.

Swimbladder row: the dorsolateral areas of the two swimbladder chambers are covered by numerous chromatophores, which, if observed in lateral view in the preserved specimens, are visible as a horizontal row of pigment spots at the level of and continuous with the ventrolateral body row. Anterior and posterior swimbladder rows may be connected by pigment.

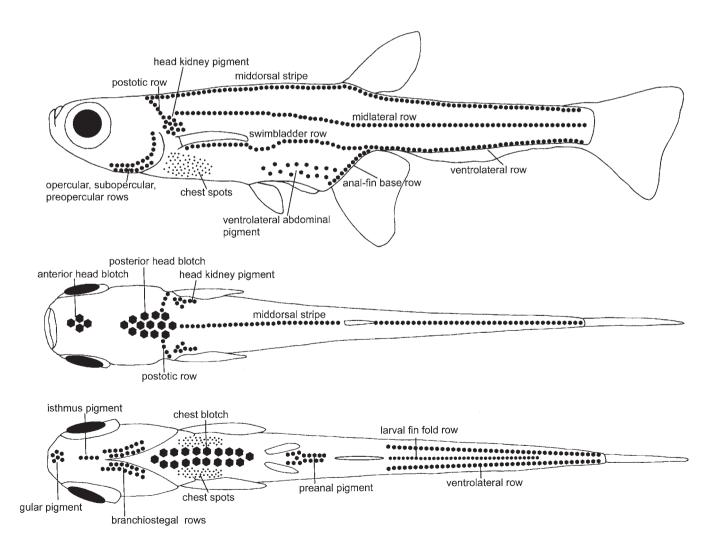


Fig. 1. Schematic representations of the pigment pattern terminology for *Paedocypris* in lateral (above), dorsal (middle) and ventral (below) views. Note that not all chromatophore patterns visible are actually depicted in each view.

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Anal-fin base row: extending from the base of the first anal-fin ray to the base of the last anal-fin ray where it meets the ventrolateral row.

Larval fin fold row: posterior continuation of anal-fin base row extending along the base of the precaudal larval fin fold to the caudal-fin base, running very close to ventrolateral body row, but more ventrally.

Ventrolateral abdominal pigment: a patch of pigment spots between the pelvic-fin base and the swimbladder chambers.

Preanal pigmentation: midventral area of pigment between the posterior base of the pelvic fins and the anus.

Chest blotch: numerous large chromatophores forming an elongate oval blotch of pigment in the ventral midline extending between the posterior end of the isthmus and the base of the pelvic fins.

Chest spots: numerous tiny chromatophores above the chest blotch.

Anterior head blotch: aggregation of pigment cells in the dorsal midline at the pre-epiphyseal area of the head, separated by the epiphyseal bar of the chondrocranium from the posterior head blotch.

Posterior head blotch: aggregation of pigment cells in the dorsal midline at the postepiphyseal area of the head forming a trapezoid blotch.

Opercular, subopercular, and pre-opercular rows: rows of pigment cells following the outline of the opercle, subopercle and preopercle, respectively; expressed as uninterrupted lines in *P. progenetica*.

Branchiostegal rows: rows of chromatophores following the curvature of the branchiostegal rays; expressed as uninterrupted lines in *P. progenetica*.

Isthmus and gular pigmentation: pigment spots in the isthmus area where the left and right hyoids meet in the ventral midline and in the gular area in front of the isthmus.

Postotic row: line of pigment cells following the posterior margin of the otic capsule down towards the pectoral-fin base.

Head kidney pigment: pigmentation covering the bulging area that marks the head kidney.

TAXONOMY

Paedocypris carbunculus, new species (Figs. 2–4)

Material examined. - Holotype: MZB 10981, 9.7 mm SL, male,

Borneo: Kalimantan Tengah: Kotawaringin basin; Sungei Pasir Panjang, outskirts of Pangkalan Bun, along road leading to Kumai; 2°43.916′S 111°39.574′E, 21 m a.s.l.; O. Perrin, Jun.2005.

Paratypes: CMK 19658, 11, 6.4–10.8 mm SL, same data as holotype; ZRC 51381, 61; CMK 20313, 60; MZB 10982, 25; BMNH 2008.4.14.2–26, 25; 6.2–11.5 mm SL; Kalimantan Tengah: Kotawaringin basin; Sungei Pasir Panjang, outskirts of Pangkalan Bun, along road leading to Kumai; 02°43.916′S 111°39.574′E, 21 m a.s.l.; H. H. Tan, M. Kottelat & H. Tommy, 11 Mar.2008.

Diagnosis. – *Paedocypris carbunculus* differs from its congeners by the shape of the head blotches. It differs further from *P. micromegethes* (Fig. 5) in having the middorsal stripe comprising three rows of chromatophores (vs. a single row of chromatophores), head kidney pigment (vs. no head kidney pigment), well developed opercular, subopercular, preopercular, and branchiostegal rows, and isthmus and gular pigmentation (vs. opercular, subopercular, preopercular, and branchiostegal rows and isthmus and gular pigments consisting of only a few chromatophores or absent), chest spots (vs. no chest spots), chest blotch well developed (vs. poorly developed or absent), and in the presence of a preanal larval fin fold in adult females (vs. absence).

Paedocypris carbunculus differs further from P. progenetica (Fig. 6) in having the median row of the middorsal stripe formed by separated individual chromatophores (vs. chromatophores forming an uninterrupted line), sparsely pigmented upper and lower lips (vs. heavily pigmented lips appearing uniformly black).

Description. – For general body shape and pigmentation pattern see Figs. 1–4.

Miniature fishes, maximum length 11.3 mm in males and 11.5 mm in females. Body slender, laterally compressed. Head large and round, snout blunt, mouth strongly upturned, lower jaw vertical. Dorsal and ventral contour of abdominal region almost parallel, ventral contour curving ventrally in



Fig. 2. Live specimen of *Paedocypris carbunculus*, not preserved, male above, female below (Photos: Heok Hui Tan).

immediate preanal area, then curving dorsally again up to posterior end of anal-fin base. From there dorsal and ventral contours almost parallel again, only slightly converging towards each other as caudal peduncle tapers posteriorly. Body laterally compressed. In dorsal view lateral contour tapering continuously from widest region of head just behind eye to end of caudal peduncle. Lateral head contour parallel in opercular area, then tapering towards snout.

Both sexes with short dorsal precaudal larval fin fold and long ventral precaudal larval finfold. Males with prepelvic pad. Females with persisting preanal larval fin fold.

Morphometric information based on 10 adult specimens (incl. holotype; 2 males, one female of CMK 19658; 4 females, 3 males of BMNH 2008.4.14.2–26). Head length 20–23 % standard length (SL), head depth 14–16 % SL, predorsal length 55–58% SL, preanal length 50-54 % SL, prepelvic length 35–39 % SL, caudal peduncle length 36–39 % SL, caudal peduncle depth 6–8 % SL, body depth 17–21 % SL, dorsal-fin height 17–20 % SL, anal-fin height 14–17 % SL, caudal-fin length 18–21 % SL, pelvic-fin length 7–10 % SL,



Fig. 3. *Paedocypris carbunculus*, new species, holotype, male, MZB 10981, 9.7 mm, and paratype, female, CMK 19658, 10.8 mm; Indonesia: Kalimantan Tengah, Pangkalan Bun.

pectoral-fin length 14–18 % SL, eye diameter 8–10 % SL. Fin ray counts based on above 10 specimens: Dorsal fin ii, 4, i (10 specimens), anal fin iii, 7, i (5), iii, 6, ii (3) or iii, 6, i (1), or iii, 8, i (1). Pectoral fin 6 (1) or 7 (9). Pelvic fin 5 (10).

Colouration. - In 70% ethanol (Figs. 3, 4): Entire body whitish, only coloration being numerous chromatophores in specific patterns. Head dorsally with anterior and posterior head blotches, both larger and more conspicuous in male; both blotches consisting of contiguous chromatophores with brown periphery and dark brown to black center. Anterior head blotch in male extending from horizontal at anterior limit of eyes posteriorly to epiphyseal bar, roughly oval in shape with small median indentation at posterior rim. Posterior blotch in male extending from posterior edge of epiphyseal bar to posterior end of tectum synoticum, broad posteriorly with convex outlines, abruptly narrowing at anterior third, where outlines concave. Anterior head blotch in female restricted to small oval area at horizontal through middle of eyes. Posterior head blotch in female restricted to area between ear capsules, but with an anterior narrow extension reaching posterior edge of epiphyseal bar. In both sexes, area limited medially by tapering anterior end of posterior head blotches, anterolaterally by eye, and posterolaterally by ear capsules with a number of separated large and interspersed tiny (a fifth of diameter of large ones) chromatophores. This area separated posterolaterally by a pigmentless parallel space from a streak of pigment following anterior edge of otic capsule. Small and large chromatophores between anterior head blotch and eye. Rostral to anterior head blotch with numerous, dense, tiny and fewer more distantly spaced chromatophores arranged in an area following the curvature of the ethmoid region. Postotic pigment row extending from posterior third of posterior head blotch laterally and ventrally following posterior rim of ear capsule down to pectoralfin base. Lateral head region with irregularly distributed chromatophores on ear capsule, behind eye, on lachrymal area, and upper and lower jaw. Rows of chromatophores following curvature of opercle, subopercle, preopercle, and branchiostegal rays, latter three continuing first ventrally

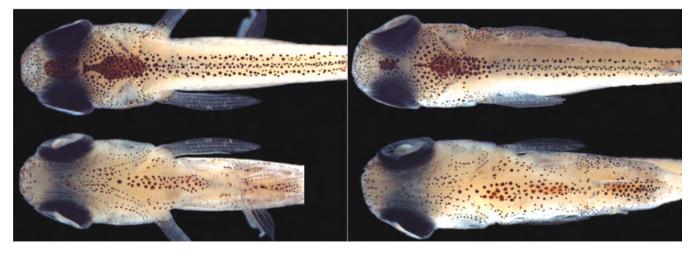


Fig. 4. *Paedocypris carbunculus*, new species, holotype (left), male, MZB 10981, 9.7 mm, and paratype (right), female, CMK 19658, 10.8 mm; head and anterior trunk in dorsal (above) and ventral view (below) to illustrate pigmentation pattern.

and then anteriorly. Ventral head region in addition with sparse chromatophores on hyoid and basihyal (= isthmus), and gular area.

Dorsally, posterior head blotch contiguous with middorsal stripe consisting of separated chromatophores arranged in three irregular, but recognizable rows with sparsely interspersed tiny chromatophores. Trunk with midlateral row of chromatophores from shoulder girdle to caudal-fin base. Head kidney pigment at angle formed by midlateral row and postotic row, extending down to pectoral-fin base. Swimbladder rows continuous and well developed confluent posteriorly with ventrolateral row. Anal-fin base row continuing posteriorly to caudal-fin base as larval fin fold row at base of fin fold, very close to but still slightly separated dorsally from ventrolateral row. Ventrolateral abdominal pigment well developed as numerous large and fewer tiny chromatophores. Chest blotch extending between cleithral symphysis and area slightly anterior to pelvic-fin base, developed as an elongate area of chromatophores of same kind as dorsal head blotches (irregular brownish periphery and dark brown to black centre) and a number of large chromatophores. Posterior and lateral to chest blotch with numerous tiny, but very few or no large chromatophores. Preanal pigmentation consisting of a number of large chromatophores forming an elongate blotch, separated from ventrolateral pigment by numerous tiny chromatophores. All fins transparent except for tiny chromatophores lining fin rays.

In life (fig. 2): Individuals mostly transparent with a reddish tinge on body, caused by numerous red chromatophores. Mature males with a bright red body in ventral half of abdominal and caudal area and with anterior and posterior head blotches glowing red.

Etymology. – The species name is derived from the Latin *carbunculus*, meaning the gemstone ruby and alludes to the ruby in live colouration. A noun in apposition.

Habitat. – The type locality is a small stream, 3–6 m wide and 0.5 to 2 m deep; the substrate ranges from sand to detritus

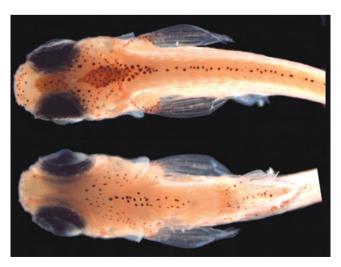


Fig. 5. *Paedocypris micromegethes*, holotype, male, ZRC 49869, 10.4 mm; head and anterior trunk in dorsal (above) and ventral view (below) to illustrate pigmentation pattern.

and peat, with flowing blackwater. Perrin & Beyer (2008a) reported that in June 2005, the water conductivity was 20 µS/cm at 29°C and the pH 4.1. *Paedocypris carbunculus* was observed in areas with slow current, near the surface, usually forming small shoals (estimated to up to 100–200 individuals), most abundant near or under overhanging structures or submerged vegetation near the surface (branches, leaves, etc.). The shore vegetation was abundant and dense (secondary forest or riparian corridor) and under there was very little light penetration. About 17 other species have been collected at the type locality, with *Hemirhamphodon phaiosoma* sharing about the same habitat as *P. carbunculus*; Perrin & Beyer (2008a) also mention the presence of *H. tengah*.

Biology. - Paedocypris carbunculus has been kept in the aquarium and bred over at least two generations (Perrin & Beyer, 2008a). The following account is based on Perrin & Beyer's (2008a) report, supplemented by information, photographs and video-clips provided by O. Perrin. Spawning starts in the early morning hours. Males flash their glowing red head blotches and attract females to the spawning site under leaves of water plants, where eggs are deposited. Once the male has been successful in attracting a female, the actual spawning act is extremely fast and impossible to observe in detail as it lasts less than one second. Photographs, however, reveal that both partners turn into an upside down position with their bellies directed towards the plant, then one or a few eggs are released and adhere to the leaf (Fig. 7). Before and between successful spawnings males can be seen remaining upside down and close to the leaf with their pelvic fins moving very fast back and forth over its surface. Among the pictures of the spawning act published by the authors is one that shows the male in an almost circular, close embrace with the female, which has its head, abdomen, and tail bent away from the leaf so that the genital opening is very close to the substrate (Fig. 7c). Other photographs illustrate both partners in a parallel upside down position under the leaf (Fig. 7b). Photographs of the male immediately before the actual spawning act also show its genital opening close to



Fig. 6. *Paedocypris progenetica*, paratype, male, ZRC 43199, 8.6 mm; head and anterior trunk in dorsal (above) and ventral view (below) to illustrate pigmentation pattern.

the substrate and its anterior anal-fin rays inclined strongly anteriorly. One photograph depicts a male with the prepelvic pad, the pelvic fins and the tip of the anal fin in close contact with previously laid eggs (Fig. 7d).

There is no parental care after egg deposition and eggs hatch after 36 hours. Hatched larvae remain attached and motionless until after a few hours the yolk sac is resorbed. For the next few weeks they swim very close to the water surface and their growth is surprisingly slow. In captivity, they require more than 6 months to reach maturity.

DISCUSSION

With the description of *Paedocypris carbunculus*, three species are known in this recently described genus. Their minute size, almost transparent body, reductive anatomical structure, and close similarity in meristic characters make them difficult to study and to distinguish without the use of a microscope. Even then, differentiating external characters are quite limited, and the elements of the colour pattern proved the most useful and reliable. Of the three species, *P. micromegethes* has the sparsest and therefore lightest pigmentation, with each row consisting only of few widely separated individual chromatophores. It can be easily distinguished from its congeners by its single middorsal row of chromatophores, and the lack of the head kidney

pigment and the tiny chest spots. Of the other two species *P. progenetica* has the denser and more extensive pigmentation with the upper lips entirely covered with pigment cells giving the impression of uniformly dark lips.

The lack of the pre-anal larval fin fold in adult females also characterizes *P. micromegethes*; this finfold is, however, present in juvenile females. Its retention in adults of the other two species, *P. progenetica* and *P. carbunculus*, might indicate their more developmentally truncated nature. The greatly reduced size and even occasional absence of pelvic fins in females of the smallest species *P. progenetica* are clearly additional developmental truncations unique to that species.

The size and shape of the dorsal head blotches seem to be species-specific and they most likely play an important visual cue during courtship, as indicated by the repeatedly successful breeding of *P. carbunculus* (Perrin & Beyer, 2008a). The blotches are much more obvious in males than in females, and in the very dark blackwater habitat under forest cover they would certainly facilitate male-female recognition. Apparently the blotches are displayed prominently when the reproductively active male is upside down under a leaf, as evidenced by Perrin & Beyer's (2003a) pictures. This may represent a signal to a ripe female that the displaying male is waiting at a suitable spawning site and ready to mate. We also note that on all photographs, in which the male is

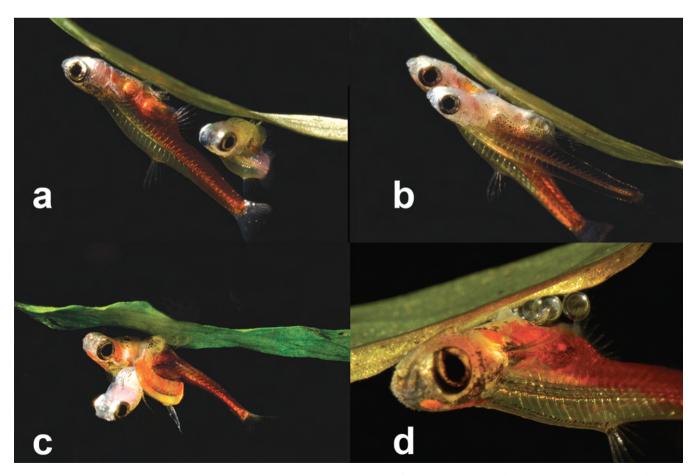


Fig. 7. Paedocypris carbunculus, spawning behaviour: a, male has attracted a female; b, male and female in parallel posture during egg deposition; c, both in spawning embrace; d, male in contact with eggs via pelvic fins and keratinized pad (Photos: Oliver Perrin).

against a leaf, it keeps a position with the head turned away from the leaf; this may help in keeping a closer contact of the genital area with the leaf, but also in displaying the blotches better.

Perrin & Beyer (2008b) discussed the possible function of the modified pelvic fins of the male. They noted that the fins are moved at a high frequency shortly before spawning when the male is in close contact with the leaf as if it were 'scratching' its surface while the female is in the closer vicinity. They rejected the hypothesis that these movements could be linked to the preparation of the spawning site (e.g., cleaning, deposition of an adhesive substance on which eggs are laid, deposition of sperm, etc.) because this 'scratching' behaviour often occurs at sites on the leaf where subsequently no eggs are deposited. Their SEM studies of the surface of such leaves at the sites of the 'scratching' movements also did not reveal any sperm or other substances. They rather hypothesized that these movements may produce sound to attract the female or keep it nearby. We do not think that such movements could actually produce sound, but rather suggest that the vibrations caused by the rapid movements of the pelvic fins may be perceived by the female.

The actual sequence of events during the spawning act is still unclear due to the high speed with which they happen. A single photograph (Fig. 7d) shows the pelvic fins apparently in close contact with an egg on a leaf, with the pad in front of it in contact with the leaf. Kottelat et al. (2006) already hypothesized that the modified pelvic fin could be used to manipulate the spawned eggs. Actually, the modified first pelvic-fin ray may have different functions at different phases of the spawning phase.

Elusive also remain the precise function or functions of the pad of keratinized skin in front of the pelvic fins. Perrin & Beyer (2008b) commented that the pad is not present in 'normally swimming' males and they suggested that it is only developed in males shortly before courting and spawning (Fig. 7). They hypothesized that the pad were produced by a gland or would represent an organ with a glandular function. Their first interpretation would have to assume that the pad is non-cellular, which is easily contradicted by our SEM investigation of that region in *P. micromegethes* clearly showing the cellular structure of the pad. While we doubt that tissue of the pad has a glandular function, we note that this hypothesis can only be tested through histological studies of that area.

One last structure, the function of which is not yet clear, is the hypertrophied genital papilla of the male *Paedocypris*, which has the form of a small bag surrounding and including the anterior 2 or 3 anal-fin rays, and which is confluent posteriorly with the membrane of the anal fin. This baglike papilla was confused by Perrin & Beyer (2008b) with the preanal fin fold, which is present only in females. They also misidentified the genital opening as the anus and vice versa. The enlarged genital papilla could act as a temporary

receptacle for sperm, which could then be released onto the eggs in a more controlled way. The quantity of sperm produced by such a small fish is probably very limited and this would be a mechanism to 'concentrate' it and direct it more precisely towards the eggs.

Even with the successful spawning of *P. carbunculus*, the majority of the original questions about the role of the modified pelvic fins and the prepelvic pad of male *Paedocypris* still remain unanswered and will need to be readdressed with high-speed cinematography of the spawning behaviour, as well as a histological studies of the pad. If the additional sexually dimorphic characters of the skeleton of *Paedocypris* described by Britz & Conway (submitted) also play a role during reproduction will need to be analysed in this context.

Comparative material. – Paedocypris progenetica: MZB 5998, holotype, male, 8.6 mm SL; Sumatra: Jambi Province: peat swamp, 15 km from Muara Sabak on road to Jambi; 1°14'17.8"S 103°35'56.8"E. MZB 5999, 12 ex., paratypes; ZRC 43199, 54 ex., paratypes; 10 males, 8.0–9.6 mm SL, 56 females, 5.8–8.3 mm; same data as holotype. ZRC 43130, 6 ex., paratypes, 7.9–9.4 mm SL; Sumatra: Jambi Province: Bayou Rantau Panjang; 1°23'03.1"S 103°55'10.7"E. CMK 11260, 28 ex., paratypes, 7.8–10.3 mm SL; Sumatra: Jambi Province: swamp near Pematang Lumut, 40 km before Kuala Tungkal on road to Jambi (95 km) and Simpangtuan (36 km).

Paedocypris micromegethes: ZRC 49869, holotype male, 10.4 mm SL; Borneo: Sarawak: Sungai Gayao, ca 40 km from Mukah (128 km from Sibu) on road Mukah Sibu; 2°54'29"N 112°19'32"E. ZRC 49870, 166 ex., paratypes; SM uncat., paratypes, 20 ex.; BMNH 2004.11.16.1–40, paratypes , 40 ex.; CMK 10942, 160 ex., paratypes; total 386 ex, 6.5–11.6 mm; same data as holotype. BMNH 2004.11.16.41–60, 20 ex., paratypes cleared and double stained, 8.7–11.1 mm; same data as holotype. ZRC39852, 19 ex., paratypes, 7.3–10.4 mm; Borneo: Sarawak: Batu Kawa-Matang, Taman Koperkasa, ca. 10 km from Kuching; 1°34'42.0"N 110°16"24.7"E.

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