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Two new species of *Rhodeus* (Teleostei: Cyprinidae: Acheilognathinae) from the River Yangtze, China

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Abstract. *Rhodeus cyanorostris* sp. nov. and *R. nigrodorsalis* sp. nov. are described from two tributaries of the River Yangtze, in Sichuan and Jiangxi Provinces, China, respectively. Both species have a small number of branched dorsal-fin rays (both with a mode of 8) and anal-fin rays (mode of 7-8 and 8, respectively), which makes them easily distinguished from all congeners. *Rhodeus cyanorostris* sp. nov. differs from *R. nigrodorsalis* sp. nov. in having more predorsal scales (14-16 *vs.* 12-13), fewer pectoral-fin rays (10-11 *vs.* 12), a shorter major axis of the eggs (2.5-2.8 mm *vs.* mostly 3.3-3.5 mm), absence of two rows of light spots on the dorsal-fin rays (*vs.* presence), and absence of a black blotch on the dorsal fin in adult males (*vs.* presence). The breeding season in winter of the two new species is unique among the Acheilognathinae.

Key words: taxonomy, bitterling, lateral line, breeding season, egg size

Introduction

Bitterlings are small freshwater fishes characterized by compressed body and unique behaviour of depositing their eggs in the gills of living freshwater mussels (Bivalvia: Unionidae and Margaritiferidae) and clams (Bivalvia: Cyrenidae) using a long ovipositor (Smith et al. 2004, Nelson et al. 2016, Li et al. 2017). Bitterlings comprise the subfamily Acheilognathinae within the Cyprinidae, with approximately 72 species and six valid genera, viz. *Acheilognathus* Bleeker, 1860, *Paratanakia* Chang, Chen & Mayden, 2014, *Pseudorhodeus* Chang, Chen & Mayden, 2014, *Rhodeus* Agassiz, 1832, *Sinorhodeus* Li, Liao & Arai, 2017, and *Tanakia* Jordan & Thompson, 1914 (Arai & Akai 1988, Chang et al. 2014, Li et al. 2017). With the exception of three *Rhodeus* species distributed in Europe and the adjacent West Asian region, all others are restricted to East Asia (Arai et al. 2001, Bogutskaya & Komlev 2001, Bohlen et al. 2006, Li et al. 2017, Bartáková et al. 2019).

Although the definitions of some genera are unclear and controversial, the genus *Rhodeus* can be distinguished from the other genera by the absence of barbels, incomplete lateral line, two rows of light spots on the dorsal-fin rays, a pharyngeal teeth formula of 0,0,5-5,0,0, a black blotch on anterior part of the dorsal fin in juveniles (absent in *R. amarus* (Bloch, 1782), *R. meridionalis* Karaman, 1924, and *R. sericeus* (Pallas, 1776); based on personal observations by the

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first author), and wing-like yolk sac projections in the larvae (Arai & Akai 1988, Li et al. 2017).

Among the 19 valid species/subspecies of *Rhodeus*, five species have been reported from the River Yangtze basin, viz. *R. albomarginatus* Li & Arai, 2014, *R. ocellatus* (Kner, 1866), *R. sinensis* (Günther, 1868), *R. fangi* (Miao, 1934), and *R. shitaiensis* Li & Arai, 2011 (Kner 1867, Lin 1935, Woo 1964, Akai & Arai 1998, Lin 1998, Zhang et al. 2016). In the present study, we describe two new species of *Rhodeus* from the River Yangtze basin in China.

Material and Methods

Methods for measurements followed Hubbs & Lagler (2004). Counts of fin rays, vertebrae and scales followed Li et al. (2017). Transverse scale series were counted between dorsal and pelvic fin origins. The insertion of the proximal segment of the first pterygiophore in the dorsal and anal fins is expressed according to Arai et al. (1995, 2007). Vertebrae, unpaired fin rays and positions of the first dorsal- and anal-fin ray pterygiophore (D-PTG-1 and A-PTG-1, respectively) were examined from radiographs. When the proximal radial of D-PTG-1 is inserted between neural spines of the vertebral centra n^{th} and $(n + 1)^{th}$, the position of D-PTG-1 is expressed as D-PTG-1 = n. When the proximal radial of A-PTG-1 is inserted between haemal spines of the vertebral centra mth and $(m + 1)^{th}$, or in front of the first haemal spine supported by vertebral centrum (m + 1), the position of A-PTG-1 is expressed as A-PTG-1 = m.

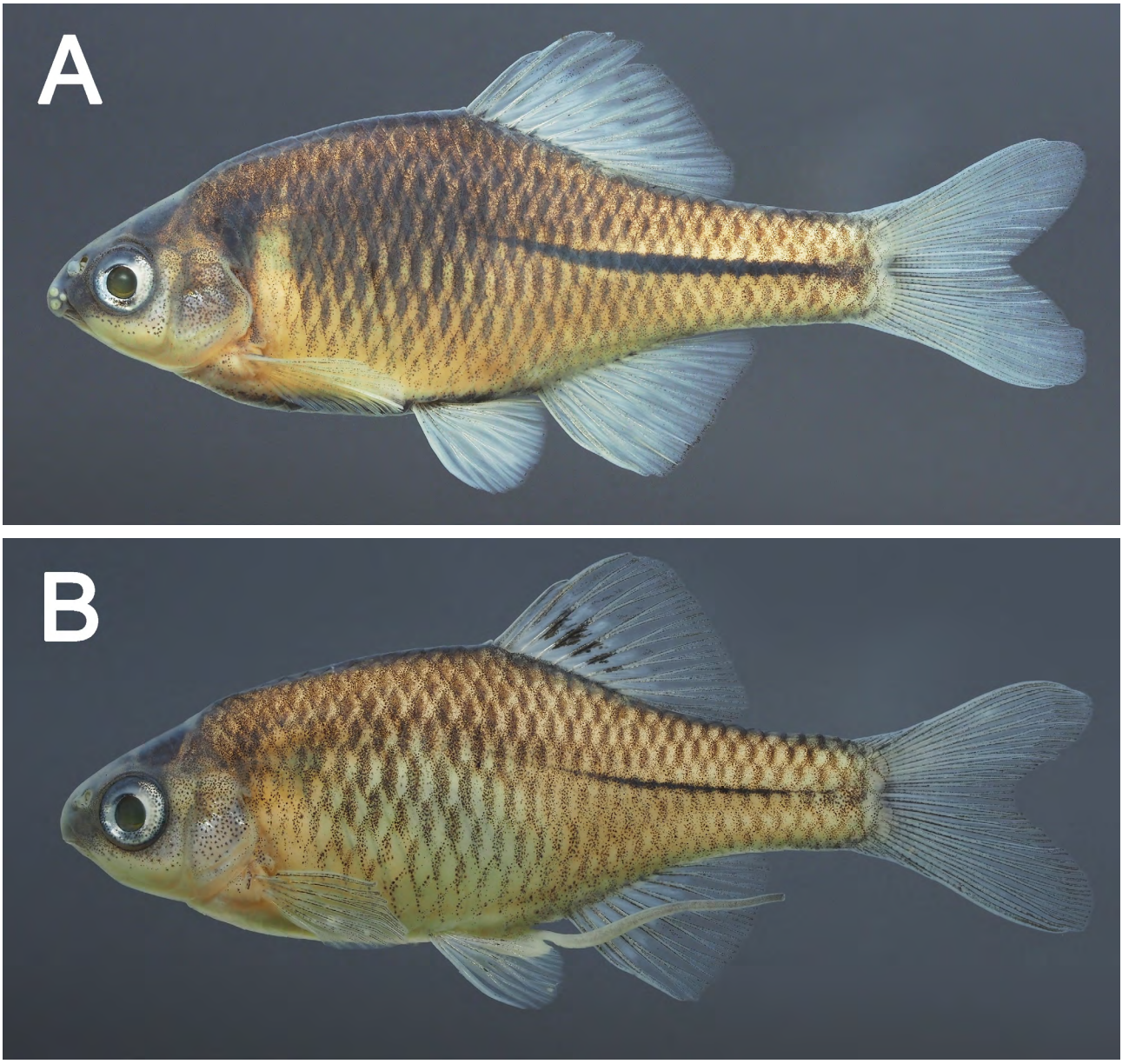

Fig. 1. *Rhodeus cyanorostris* sp. nov. A) SOU 1801001, holotype, ♂, 32.1 mm SL; B) SOU 1801004, paratype, ♀, 28.2 mm SL.

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Table 1. Meristic and morphometric measurements of holotype and paratypes in *Rhodeus cyanorostris* sp. nov. Numbers in parentheses are number of specimens examined.

Sex	Holotype male	Paratypes	
		males	females
n	1	3	11
Standard length (mm)	32.1	30.1-33.2	23.6-28.9
Branched dorsal-fin rays (Br. D)	8	8 (3)	7 (1), 8 (10)
Branched anal-fin rays (Br. A)	7	7 (1), 8 (2)	7 (6), 8 (5)
Br. A minus Br. D	–1	–1 (1), 0 (2)	–1 (5), 0 (6)
Pectoral-fin rays	11	10 (1), 11 (2)	10 (3), 11 (8)
Pelvic-fin rays	7	7 (3)	7 (10), 8 (1)
Abdominal vertebrae	15	16 (3)	16 (11)
Caudal vertebrae	18	18 (2), 19 (1)	17 (4), 18 (7)
Total vertebrae	33	34 (2), 35 (1)	33 (4), 34 (7)
D-PTG-1	10	11 (3)	11 (11)
A-PTG-1	15	15 (1), 16 (2)	16 (10), 17 (1)
Scales in lateral series	34	33 (1), 35 (2)	32 (4), 33 (2), 34 (4), 35 (1)
Scales in transverse series	11	10 (2), 11 (1)	11 (10), 12 (1)
Pored lateral line scales	0	0 (3)	0 (11)
Circumpeduncular scales	14	12(2), 13 (1)	12(2), 13 (1), 14 (8)
Predorsal scales	15	15 (2), 16 (1)	14 (3), 15 (7), 16 (1)
Morphometry			
% standard length			
Head length	25.5	23.5-25.6	22.9-24.7
Body depth	33.1	30.0-37.6	34.4-36.7
Snout length	5.7	4.6-6.1	4.7-5.3
Orbit diameter	7.8	7.6-8.7	7.8-9.5
Predorsal length	51.0	51.9-55.4	50.6-57.1
Caudal peduncle length	26.1	24.2-25.3	22.7-26.4
Caudal peduncle depth	13.3	12.4-13.4	12.7-14.3

Pharyngeal teeth and gill rakers were observed by dissecting non-type specimens. Breeding season was confirmed based on field and aquarium observations. Ovipositors were measured and observed from living specimens. Measurements of eggs were taken from photographs.

Examined specimens in this study are deposited in the following collections: AMNH – American Museum of Natural History, New York; BMNH – The Natural History Museum, London; NMW – Naturhistorisches Museum, Wien; NSMT – National Museum of Nature and Science, Tokyo; DOS – Department of Oceanography, National Sun Yat-sen University, Kaohsiung; NTUM – National Taiwan University, Taipei; SMU – Sang Myung University, Seoul; SOU – Shanghai Ocean University, Shanghai; ZUMT – Department of Zoology, University Museum, University of Tokyo, Tokyo.

Results

Taxonomy

Rhodeus cyanorostris sp. nov. (Figs. 1-8, 15C; Table 1 and 3)

Type material: Holotype: SOU 1801001, ♂, 32.1 mm SL; the River Bai-Tiao, a tributary of the River Yangtze, in Pidu District, Chengdu City, Sichuan Province, China; 23 January 2018.

Paratypes: SOU 1801002, 1♂, 33.2 mm SL; SOU 1801003-1508009, 7♀♀, 23.6-28.9 mm SL; NSMT-P

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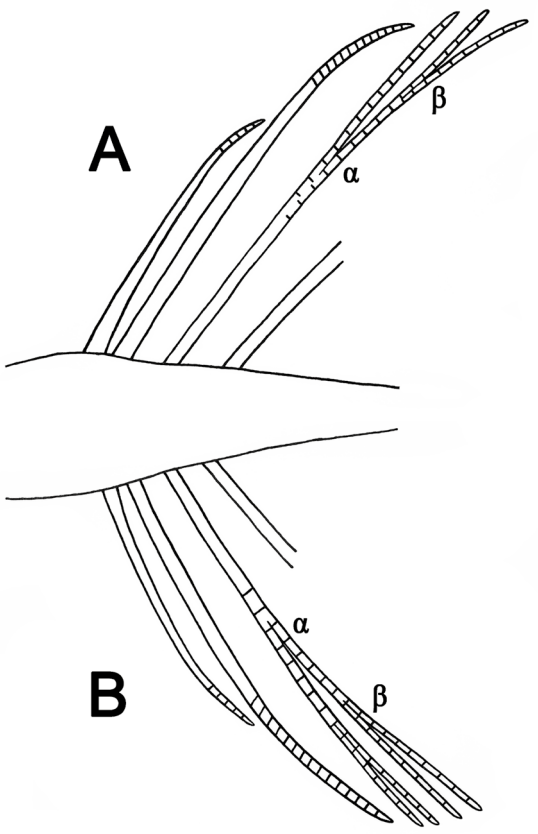

Fig. 2. Simple and first branched rays of dorsal A) and anal B) fins of *Rhodeus cyanorostris* sp. nov. (SOU 1801001, holotype, ♂, 32.1 mm SL). α and β for first and second branching points, respectively.

136898, 1♂, 33.1 mm SL; NSMT-P 136899, 1♀, 28.3 mm SL; same data as holotype. DOS 07306, 1♂, 30.1 mm SL; DOS 07307-07309, 3♀♀, 26.2-27.9 mm SL; same locality as holotype; 27 May 2018.

Non-type specimens: SOU 1805001-1805006, six specimens, 17.8-31.6 mm SL; same locality as holotype; 27 May 2018.

Diagnosis: Differs from all congeners by a combination of characters, including longitudinal scale series 32-35; pored scales absent; transverse scale series 11 (10-12); branched dorsal-fin rays 8 (rarely 7); branched anal-fin rays 7-8; vertebrae 33-34 (rarely 35); light spots on dorsal-fin rays absent; in males with nuptial colouration, snout blue, and iris, belly and all fins yellow.

Description: Morphometric and meristic data of holotype and paratypes as shown in Table 1. Body compressed. Mouth small and subterminal, corner of mouth not extending to vertical of anterior margin of orbit. Barbels absent. Two or three large pearl organs on each side of snout, absent in females. A long ovipositor present in mature females, maximum length approximately 8-13 mm, including a developed and rigid basal part approximately 2-3 mm in length.

Dorsal fin with 3 simple and 8 branched rays (rarely 7). Anal fin with 3 simple and 7-8 branched rays. First simple ray in dorsal and anal fins very small and hidden under the skin. Longest simple ray of dorsal fin thin and soft, width of basal portion equivalent to that of first branched ray; longest simple dorsal-fin ray segmented from area corresponding to second branching point of first branched ray (Fig. 2A). Longest simple ray of anal fin thin and soft, width of basal portion equivalent to that of first branched ray; longest simple anal-fin ray segmented from area corresponding to that between first and second branching points of first branched ray (Fig. 2B). Pectoral fin rays 10-11 rays, first and last one or two rays simple. Pelvic fin rays 7 (rarely 8), first and last (rarely last two)

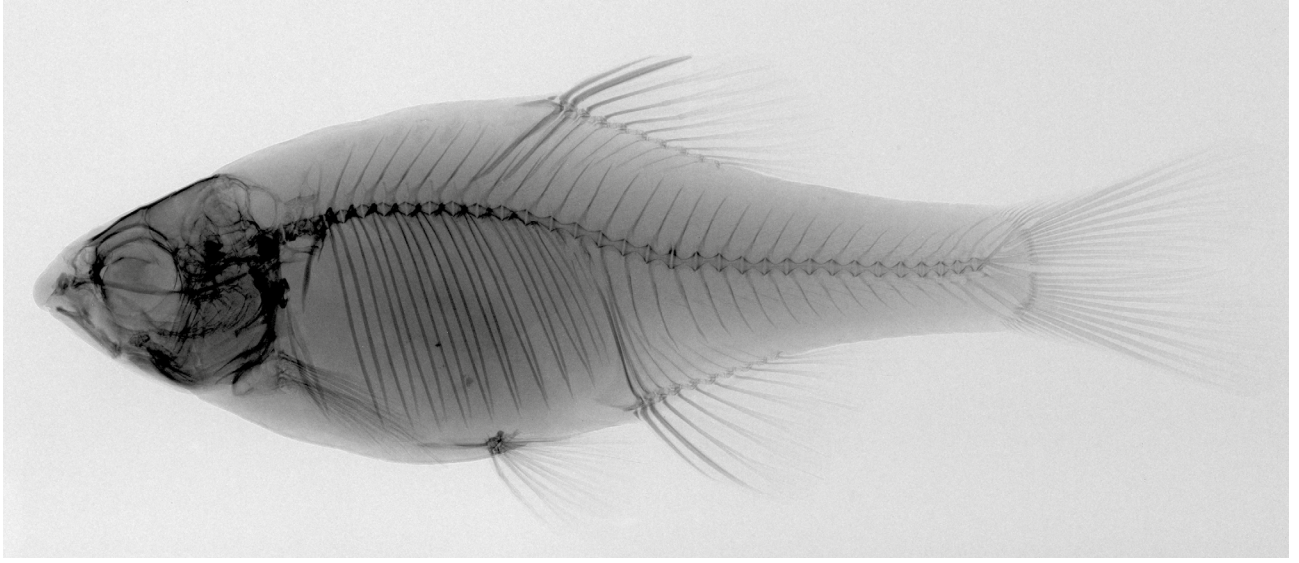

Fig. 3. Radiograph of *Rhodeus cyanorostris* sp. nov. (SOU 1801002, paratype, ♂, 33.2 mm SL).

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Fig. 4. Pharyngeal teeth of *Rhodeus cyanorostris* sp. nov. (SOU 1805001, ♀, 28.7 mm SL).

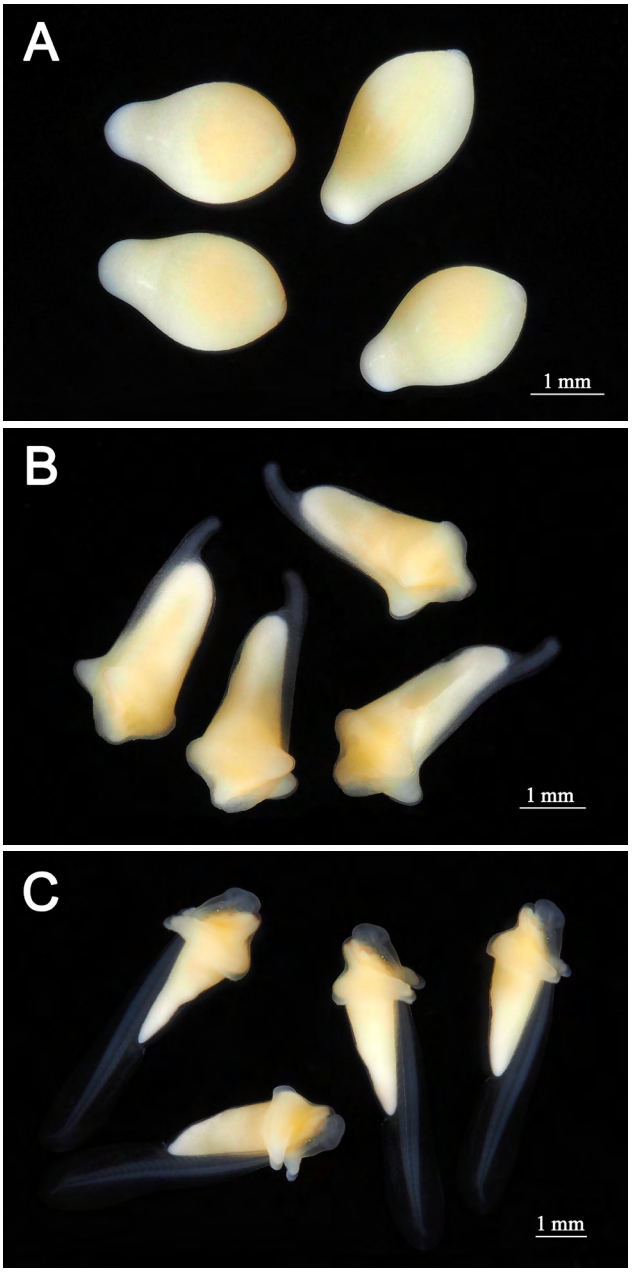

Fig. 5. Eggs and larva of *Rhodeus cyanorostris* sp. nov., incubated at a water temperature of 22 °C. A) ripe eggs just fertilized; B) newly-hatched larvae; C) larvae three days after hatching.

rays simple. Principal caudal rays 19, including branched rays 17 (9 + 8); dorsal procurrent rays 7-8, ventral procurrent rays 6-8.

Longitudinal scale series 32-35 (31-34 on body and 1-2 on caudal fin). Lateral line absent, pored scales 0. Transverse scale rows 11 (10-12). Predorsal scale rows 14-16. Circumpeduncular scales 12-14.

Abdominal vertebrae 16 (rarely 15); caudal vertebrae 17-18 (rarely 19); total vertebrae 33-34 (rarely 35). Position of first dorsal-fin ray pterygiophore (D-PTG-1) = 11 (between 11th and 12th vertebrae, denoted as 11; rarely 10). Position of first anal-fin ray pterygiophore (A-PTG-1) = 16 (range from 15 to 17) (Fig. 3). Pharyngeal teeth in one row, formula 0,0,5-5,0,0; tooth crowns serrated (Fig. 4). Gill rakers of first gill arch 8 (7-9).

Ripe eggs bulb-shaped, major axis approximately 2.5-2.8 mm (examined from six clutches of eggs from different females), ratio of major axis to minor axis 1.6-1.8 (Fig. 5A). Larvae with wing-like yolk sac projections (Figs. 5B, 5C).

Colouration in life: Nuptial colouration present in adult males in breeding season. Snout blue and enlarged. Iris and lower part of head yellow. Body colour mostly yellow, with blue sheen dorsally. Scales on side darker in central and dorsal regions with dark blue on anterior part. A light-yellow vertical band covering 2nd-3rd scales in lateral series. A blue longitudinal stripe running from below the dorsal fin and ending about two scales in front of caudal-fin base. All fins yellow, darker in pectoral, pelvic and anal fins (Fig. 6A). Nuptial colouration usually faded outside the breeding season.

In juveniles and adult females, a large black blotch is present on the anterior part of the dorsal fin (Figs. 6B, 7). Ovipositor of females mostly whitish and light yellow in rigid basal part.

Colour in preservative: Ground colour brownish, lighter towards belly. Vertical light band present on anterior of flank in males; absent in females. Broad longitudinal stripe on posterior of flank, broader in males than in females. Dorsal and anal fins without light spots on fin rays (Figs. 1A, 1B).

Distribution and ecology: Known only from the River Bai-Tiao, a tributary of the River Yangtze, in Pidu District, Chengdu City, Sichuan Province, China (Fig. 8). The type locality was a small river with

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Fig. 6. *Rhodeus cyanorostris* sp. nov. in breeding season, collected from its type locality. A) male; B) female just before spawning (with ovipositor in maximum length). Specimen not preserved.

mud and gravel mixed substrate. The water level varied from approximately 0.5 to 1.0 m depth.

Adult *R. cyanorostris* sp. nov. are small in size. The smallest female found with mature oocytes was 23.6 mm SL. The main spawning season is in winter, from January to March. Females spawn several times during the spawning period and usually releases clutches of 3-8 eggs when squeezed manually. Host mussels are not known.

Fig. 7. Juvenile of *Rhodeus cyanorostris* sp. nov., 13.2 mm SL. Specimen not preserved.

Etymology: The specific name, *cyanorostris*, is derived from the Latin terms *cyano* for blue and *rostris* for snout, a noun, alluding to the distinctive blue snout in nuptial males.

Rhodeus nigrodorsalis sp. nov. (Figs. 8-16; Table 2 and 3)

Type material: Holotype: SOU 1712001, ♂, 37.0 mm SL; the River Le-An, debouching into Lake Poyang in the River Yangtze basin, in Ziyang Town, Wuyuan County, Jiangxi Province, China; 3 December 2017.

Paratypes: SOU 1712002-1712006, 5♂♂, 30.2-38.4 mm SL; SOU 1712006-1712007, 2♀♀, 31.2-31.5 mm SL; DOS 07310, 1♂, 35.1 mm SL; DOS 07311, 1♀, 32.9 mm SL; NSMT-P 136901, 1♂, 35.2 mm SL; NSMT-P 136902, 1♀, 22.3 mm SL; same data as holotype.

Non-type specimens: SOU 1903001, 1♂, 47.1 mm SL; collected together with holotype, preserved after keeping in aquarium for 17 months. SOU 1910001-

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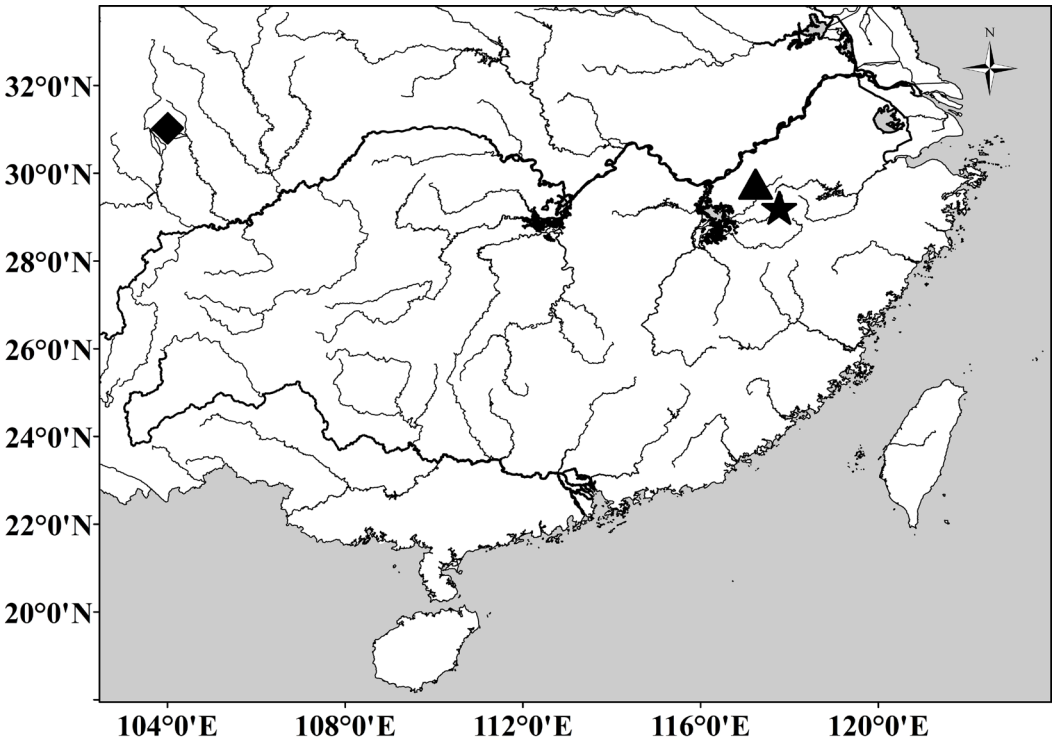

Fig. 8. Map of sampling localities. ◆ for type locality of *Rhodeus cyanorostris* sp. nov., China: Sichuan Province: Chengdu City: Pidu District; ★ for type locality of *R. nigrodorsalis* sp. nov., China: Jiangxi Province: Wuyuan County: Ziyang Town; ▲ for locality of *R. nigrodorsalis* sp. nov., China: Anhui Province: Qimen County: Rongkou Township.

1910005, 5♂♂, 38.1-42.3 mm SL; same locality as holotype; 10 October 2019. SOU 1609001, 1♂, 39.7 mm SL; SOU 1609002, 1♀, 30.8 mm SL; the River Lv, debouching into Lake Poyang, River Yangtze basin, in Rongkou Township, Qimen County, Anhui Province, China; 5 September 2016.

Diagnosis: Differs from all congeners by a combination of characters, including longitudinal scale series 33-35; pored scales 2-4 (rarely 0); transverse scale series 10 (rarely 11); branched dorsal-fin rays 8; branched anal-fin rays 8 (rarely 9); vertebrae 34-35 (rarely 33); iris yellowish, belly yellow, dorsal-fin membrane dark black, and a vertical band on the anterior of flank in nuptial males.

Description: Morphometric and meristic data of holotype and paratypes as shown in Table 2. Body compressed. Mouth small and subterminal, corner of mouth not extending to vertical of anterior margin of orbit. Barbels absent. Pearl organs on snout and area between nostril and eye in adult males, absent in females. Ovipositor present in mature females, maximum length approximately 7-11 mm, including a developed and rigid basal part of approximately 3-4 mm.

Dorsal fin with 3 simple and 8 branched rays. Anal fin with 3 simple and 8 branched rays (rarely 9). First simple ray in dorsal and anal fins very small and hidden under skin. Longest simple ray of dorsal fin thick and stiff, width of basal portion about two times wider than that of first branched ray; longest simple dorsal-fin ray segmented from area corresponding to that between second and third branching points of first branched ray (Fig. 10A). Longest simple ray of anal fin thin and soft, width of basal portion slightly wider than that of the first branched ray; longest simple anal-fin ray segmented from area corresponding to that between first and second branching points of first branched ray (Fig. 10B). Pectoral fin rays 12, first ray simple. Pelvic fin rays 8 (rarely 7), first and last rays simple. Principal caudal rays 19, including branched rays 17 (9 + 8); dorsal procurrent rays 7-8, ventral procurrent rays 6-8.

Longitudinal scale series 33-35 (32-34 on body and 1-2 on caudal fin). Pored scales 2-4 (rarely 0). Transverse scale rows 10 (rarely 11). Predorsal scale rows 13 (rarely 12). Circumpeduncular scales 14.

Abdominal vertebrae 15-16; caudal vertebrae 18-19 (rarely 17); total vertebrae 34-35 (rarely 33). Position of first dorsal-fin ray pterygiophore (D-PTG-1) = 10 (between 10^{th} and 11^{th} vertebrae, denoted as 10). Position of first anal-fin ray pterygiophore (A-PTG-1) = 15 or 16 (Fig. 11). Pharyngeal teeth in one row, formula 0,0,5-5,0,0; serration of tooth

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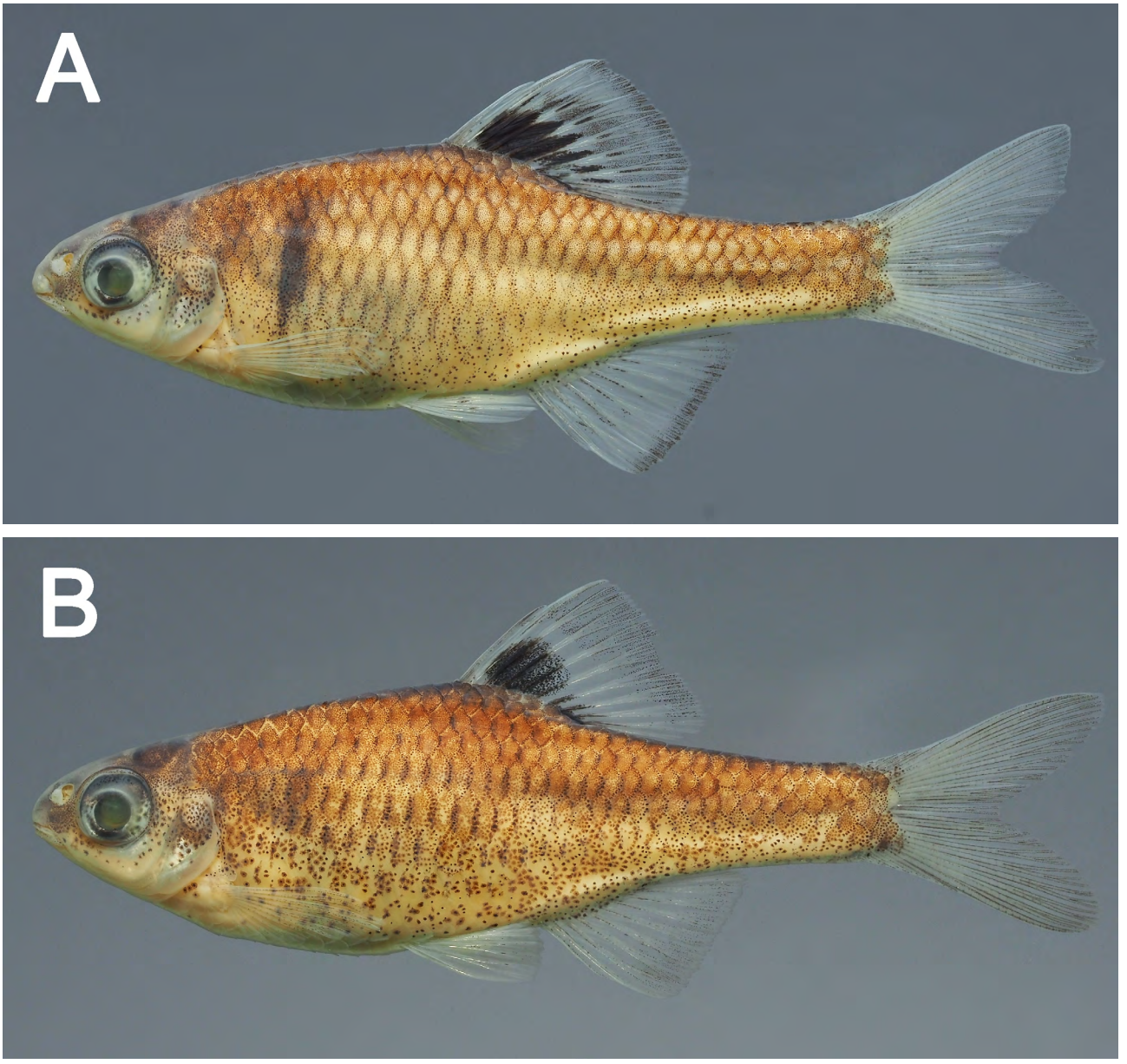

Fig. 9. *Rhodeus nigrodorsalis* sp. nov. A) SOU 1712001, holotype, ♂, 37.0 mm SL; B) SOU 1712007, paratype, ♀, 32.1 mm SL.

crowns varies in different body length, i.e. serrated in two males shorter than 40 mm SL, and smooth in two males longer than 40 mm SL (Fig. 12). Gill rakers of first gill arch 6-8.

Ripe eggs ellipsoid, major axis mostly 3.3-3.5 mm (varying widely from 3.0 to 3.9 mm; examined from eight clutches of eggs from different females), ratio of major axis to minor axis mostly 2.0-2.2 (vary from 1.9 to 2.3 mm) (Fig. 13A). Larvae with wing-like yolk sac projections (Figs. 13B, 13C).

Colouration in life: Adult males with light body colour. A bluish-black vertical band on 4th-5th scales in lateral series. Iris yellowish. Lower part of head, belly, and paired fins yellow. Dorsal and anal fins margined with black, lined proximally by a yellow stripe. Dorsal-fin membrane blackish with a black blotch on anterior base, and range of blotch extended posteriorly with age in males (Figs. 14A, 15A). The yellow colour indistinct outside the breeding season.

Females with brownish body colour, darker in dorsal. A large black blotch on anterior base of dorsal fin (Fig. 14B). Ovipositor mostly hyaline, posterior part slightly yellowish.

In juveniles, a large black blotch on anterior part of dorsal fin (Fig. 16A). Dorsal, anal and pelvic fins margin white (Fig. 16B).

Colour in preservative: Ground colour brownish, lighter towards belly. Dorsal-fin membrane blackish

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Table 2. Meristic and morphometric measurements of holotype and paratypes in *Rhodeus nigrodorsalis* sp. nov. Numbers in parentheses are number of specimens examined.

Sex	Holotype male	Paratypes	
		males	females
n	1	7	4
Standard length (mm)	37.0	30.2-38.4	32.1-32.9
Branched dorsal-fin rays (Br. D)	8	8 (7)	8 (4)
Branched anal-fin rays (Br. A)	8	8 (5), 9 (2)	8 (4)
Br. A minus Br. D	0	0 (6), 1 (2)	0 (4)
Pectoral-fin rays	12	12 (7)	12 (4)
Pelvic-fin rays	8	7 (1), 8 (6)	7 (1), 8 (3)
Abdominal vertebrae	15	15 (4), 16 (3)	15 (1), 16 (3)
Caudal vertebrae	19	17 (1), 18 (2), 19 (4)	18 (2), 19 (2)
Total vertebrae	34	33 (1), 34 (6)	34 (3), 35 (1)
D-PTG-1	10	10 (7)	10 (4)
A-PTG-1	15	15 (4), 16 (3)	15 (1), 16 (3)
Scales in lateral series	34	34 (4), 35 (3)	34 (2), 35 (2)
Scales in transverse series	10	10 (7)	10 (3), 11 (1)
Pored lateral line scales	3	0 (1), 2 (1), 3 (2), 4 (3)	2 (1), 3 (2), 4 (1)
Circumpeduncular scales	14	14 (7)	14 (4)
Predorsal scales	13	12 (1), 13 (6)	12 (1), 13 (3)
Morphometry			
% standard length			
Head length	23.3	22.9-24.1	22.5-23.8
Body depth	31.9	29.8-32.7	30.9-31.9
Snout length	6.0	5.2-6.1	5.4-6.0
Orbit diameter	8.3	8.3-9.0	8.8-9.5
Predorsal length	49.3	49.4-51.4	49.4-51.2
Caudal peduncle length	28.7	24.8-27.4	26.2-28.1
Caudal peduncle depth	11.7	11.8-12.5	11.4-11.9

with a black blotch on anterior base; two transverse rows of light spots on dorsal-fin rays, upper row narrower and usually indistinct. Dorsal and anal fin with black margin in males and a vertical band on the anterior of the flank in adult males, indistinct or absent in females (Figs. 9A, 9B, 15B).

Distribution and ecology: Known only from the River Le-An in Wuyuan County, Jiangxi Province (type locality) and the River Lv in Qimen County, Anhui Province both flowing into Lake Poyang in the River Yangtze basin (Fig. 8). The type locality is a large river where *R. nigrodorsalis* sp. nov. occurs mostly in shallow marginal areas with a substrate of mixed sand and mud.

Female *R. nigrodorsalis* sp. nov. starts spawning at just 30 mm SL, but with the maximum length of this species seen in a captive male kept in an aquarium for 17 months of 47.1 mm SL. The main spawning season is during winter, from January to March. Females spawn several times during the spawning period and usually release 2-7 eggs in a clutch when squeezed manually. Host mussels are not known.

Etymology: The specific name, *nigrodorsalis*, is derived from the Latin terms *nigro* for black and *dorsalis* for dorsal fin, a noun, alluding to the diagnostic black dorsal-fin membrane in adult males.

Discussion

Rhodeus cyanorostris sp. nov. and *R. nigrodorsalis* sp. nov. can be assigned to the genus *Rhodeus* by the absence of barbels, an incomplete lateral line, a pharyngeal teeth formula of 0,0,5-5,0,0, a black blotch

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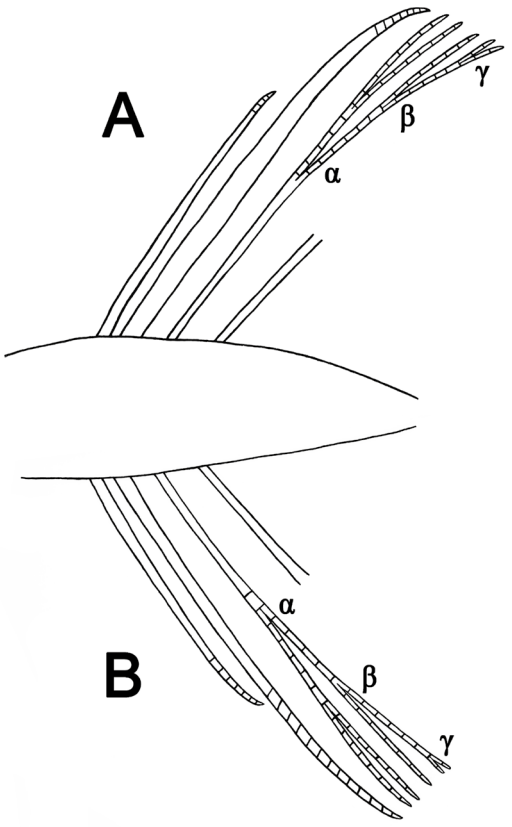

Fig. 10. Simple and first branched rays of dorsal A) and anal B) fins of *Rhodeus nigrodorsalis* sp. nov. (SOU 1712003, holotype, ♂, 38.4 mm SL). α, β and γ for first, second and third branching points, respectively.

on the anterior part of the dorsal fin in juveniles, and wing-like yolk sac projections in the larvae (Arai & Akai 1988, Arai et al. 2001, Li et al. 2017).

The two new species share a smaller number of branched dorsal- and anal-fin rays (both no more than 9), which make them distinguishable from all other *Rhodeus* species (all more than 8) (Pallas 1776, Bloch 1782, Tirant 1883, Jordan & Thompson 1914, Karaman 1924, Oshima 1926, Nichols 1929, Miao 1934, Arai et al. 1990, Akai & Arai 1998, Kottelat 1998, Arai et al. 2001, Li & Arai 2014) (Table 3). *Rhodeus cyanorostris* sp. nov. can be distinguished from *R. nigrodorsalis* sp. nov. by more predorsal scales (14-16 *vs.* 12-13), fewer pectoral-fin rays (10-11 *vs.* 12), greater D-PTG-1 (mode of 11 *vs.* 10), thicker longest simple ray of dorsal fin (width of basal portion equivalent to that of first branched ray *vs.* about two times wider), shorter major axis of eggs (2.5-2.8 mm *vs.* mostly 3.3-3.5 mm), and absence of a black blotch on dorsal fin in adult males (*vs.* presence).

In the Acheilognathinae, a complete lateral line is present in all species of the genera *Acheilognathus* (except *A. typus* (Bleeker, 1863)), *Tanakia*, and *Paratanakia*, while the lateral line is incomplete in *A. typus* and all species of *Rhodeus*, *Sinorhodeus*, and *Pseudorhodeus* (Tanaka 1909, Lin 1935, Woo 1964, Lin 1998, Hosoya 2002, Arai & Kato 2003, Kottelat & Freyhof 2007, Chang et al. 2014, Li et al. 2017). In most specimens of *R. ocellatus kurumeus* Jordan & Thompson, 1914, some specimens of *R. amarus* Bloch, 1782, *R. nigrodorsalis* sp. nov. and *R. sinensis*, a pored lateral line scale is absent (Kimura & Nagata 1992, Arai et al. 2001) while *R. cyanorostris* sp. nov. is unique among acheilognathines in its lack of pored scales (Table 3).

Furthermore, in the *Tanakia-Rhodeus* clade of the Acheilognathinae, two rows of light spots on the dorsal-fin rays are absent from the basal groups, viz. the genera *Paratanakia*, *Pseudorhodeus*,

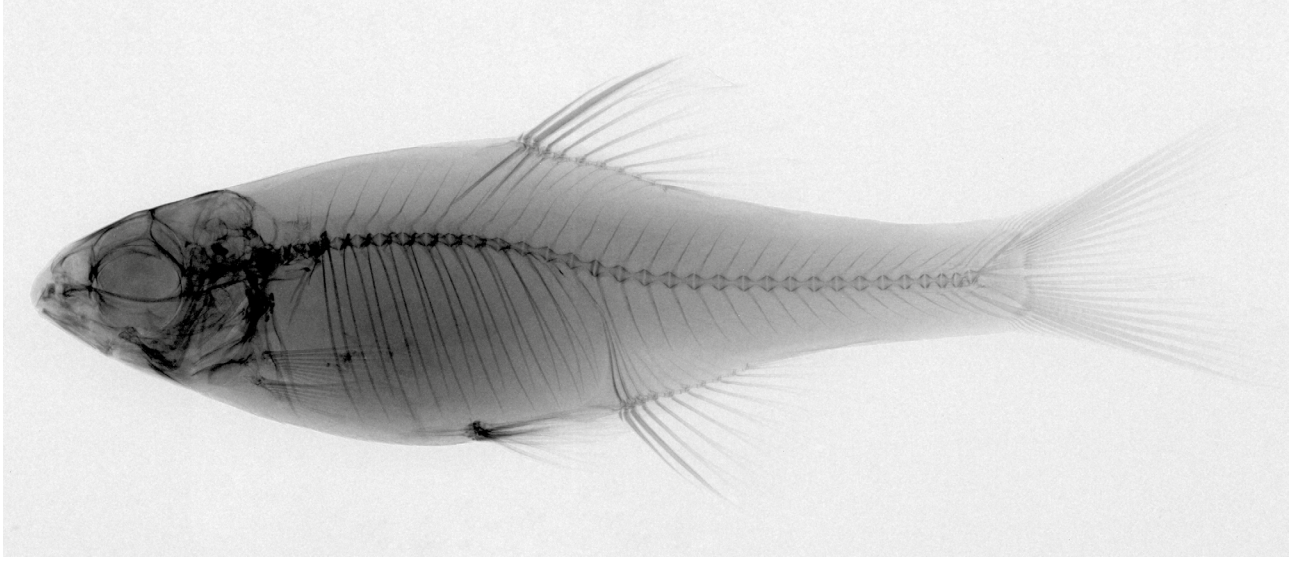

Fig. 11. Radiograph of *Rhodeus nigrodorsalis* sp. nov. (SOU 1712001, holotype, ♂, 37.0 mm SL).

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Fig. 12. Pharyngeal teeth of *Rhodeus nigrodorsalis* sp. nov. (SOU 1910001, ♂, 42.3 mm SL).

Sinorhodeus, and *Tanakia*, but present in the genus *Rhodeus* except for *R. cyanorostris* sp. nov. (Arai & Akai 1988, Chang et al. 2014, Li et al. 2017), a unique character that distinguishes it from all its congeners (Fig. 15C).

In adult males of *Rhodeus*, the dorsal-fin membrane of *R. amarus*, *R. meridionalis*, *R. shitaiensis*, *R. pseudosericeus* Arai, Jeon & Ueda, 2001, and *R. sericeus* is blackish (Arai et al. 2001, Li & Arai 2011; the colour of the dorsal-fin membrane of *R. meridionalis* was examined in this study) (Figs. 15D, 15E), but nearly hyaline in most of other species of *Rhodeus* (Figs. 15C, 15F). *Rhodeus nigrodorsalis* sp. nov. apparently has the highest intensity of melanophores on the dorsal-fin membrane among its congeners. Its black dorsal-fin membrane is distinctly darker than that of all known species of *Rhodeus* (Figs. 15A, 15B).

Rhodeus cyanorostris sp. nov. and *R. nigrodorsalis* sp. nov. are the only two bitterling species so far known to spawn primarily in winter, from January to March, with the lowest temperatures of the year in the River Yangtze basin at this time. In temperate regions, most bitterlings spawn in spring (from April to June in the River Yangtze basin). However, four *Acheilognathus* species (*A. barbatulus* Günther, 1873, *A. longipinnis* Regan, 1905, *A. rhombeus* (Temminck & Schlegel, 1846) and *A. typus*) spawn mainly in autumn (Kawamura et al. 2014), and *R. albomarginatus* and *A. macromandibularis* Doi, Arai & Liu, 1999 spawn in summer (Doi et al. 1999, Li & Arai 2014; the breeding season of *A. macromandibularis* was confirmed based on personal observations by the first author). Some species distributed in tropical regions may spawn all the year around. Kawamura et al. (2014) considered the shift of spawning seasons in the genus *Acheilognathus* as an adaptation to changed climatic conditions in the late Pliocene. As more species are found to spawn in summer and two species herein in winter, we speculate that the divergence of breeding seasons in the Acheilognathinae may potentially be a consequence of interspecific competition in utilizing host mussels.

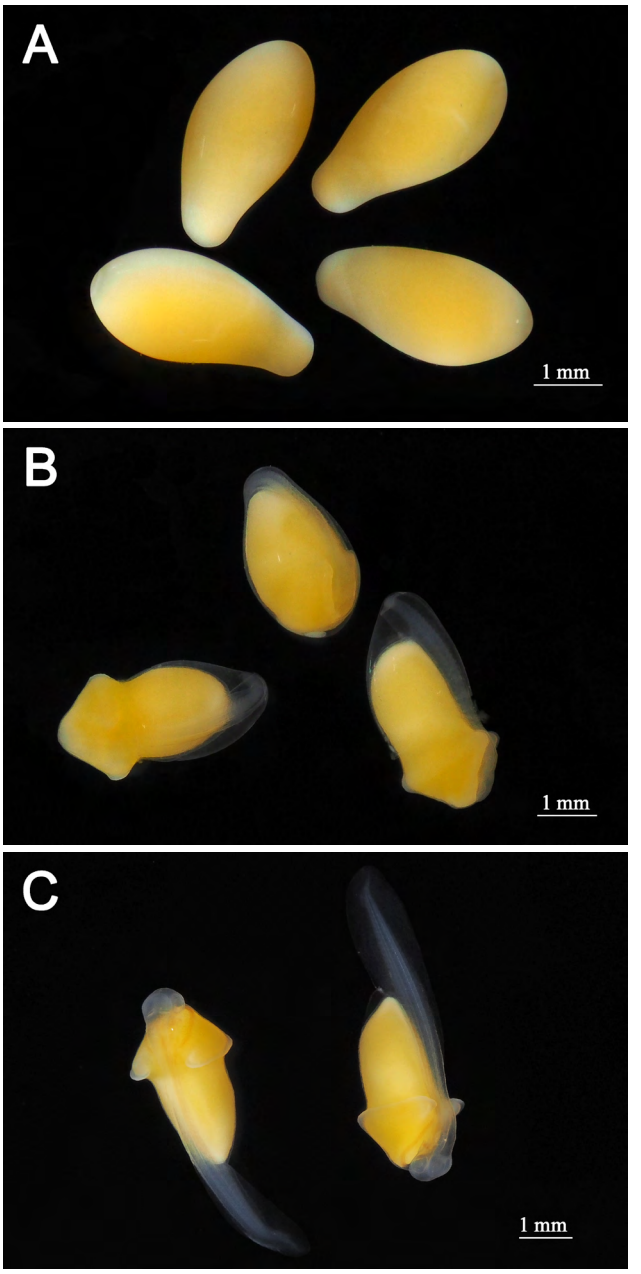

Fig. 13. Eggs and larva of *Rhodeus nigrodorsalis* sp. nov., incubated at a water temperature of 22 °C. A) ripe eggs just fertilized; B) newly-hatched larvae; C) larvae three days after hatching.

Comparative materials

Rhodeus albomarginatus: SOU 1306001, holotype, ♂, 53.4 mm SL; China: Anhui Province: Qimen County; 10 May 2013. SOU 1306002-1306005, 1♂ and 3♀♀, 43.3-53.6 mm SL; same data as holotype. SOU 1110001-1110013, 8♂♂ and 3♀♀, 39.8-58.4 mm SL; same locality as holotype; 3 October 2011.

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Fig. 14. *Rhodeus nigrodorsalis* sp. nov. in breeding season, collected from its type locality. A) male; B) female just before spawning (with ovipositor in maximum length). Specimen not preserved.

Rhodeus amarus: *SOU 200406501, 19 specimens, 35.2-57.5 mm SL; Germany: Oldenburg; 26 June 2004.

Rhodeus fangi: *SOU 200905501, 5♂♂ and 2♀♀, 31.4-34.5 mm SL; China: Jiangsu Province: Zhenjiang (Chinkiang) City; May 2009.

Rhodeus haradai: NTUM 7600, holotype, ♂, 54.6 mm SL; China: Hainan: Longtang; June 1942. NTUM 2203, eight specimens, 47.4-57.6 mm SL; same data as holotype.

Rhodeus notatus: AMNH 9654, holotype, ♂, 33.0 mm SL (X-ray); AMNH 10812, paratypes, 5♂♂ and 1♀, 24.3-29.2 mm SL; China: Shandong Province: Tsinan (Jinan); April-July 1924. *SOU 201805501; 1♂ and 8♀♀, 25.7-29.0 mm SL; China: Shandong Province: Tai'an City; May 2018. *SOU 201905501; 3♂♂ and 2♀♀, 29.8-37.0 mm SL; China: Shandong Province: Tai'an City; May 2019.

Rhodeus ocellatus ocellatus: NMW 10837, holotype, ♂, 51.6 mm SL (X-ray); China: Shanghai City. SOU 200705501, 10♂♂ and 7♀♀, 41.8-57.9 mm SL; China: Shanghai City; May 2007. SOU 200706501, 3♂♂ and 5♀♀, 36.8-56.3 mm SL; China: Zhejiang Province: Shengzhou City; 9 June 2007. SOU 200811501, 5♂♂ and 4♀♀, 44.7-55.6 mm SL; China: Anhui Province: Shitai County; November 2008. SOU 201005504, 1♂ and 2♀♀, 35.8-48.8 mm SL; China: Anhui Province: Xiuning County; 4 May 2010. SOU 201208501, 3♂♂ and 1♀, 39.1-56.6 mm SL; China: Liaoning Province: Zhuanghe City; 14 August 2014.

Rhodeus pseudosericeus: SMU 211, holotype, ♂, 45.5 mm SL; Korea: Gangwon-do: Hoengsong-gun: Gonggun-myon: Hakdam-ri; 16 October 1999. ZUMT 61149-61151, three paratypes, 1♂ and 2♀♀, 41.0-41.9 mm SL; same data as holotype.

Rhodeus rheinardti: *SOU 201708501, 26 specimens, 35.1-45.9 mm SL; Vietnam: Hue City; 27 August 2017.

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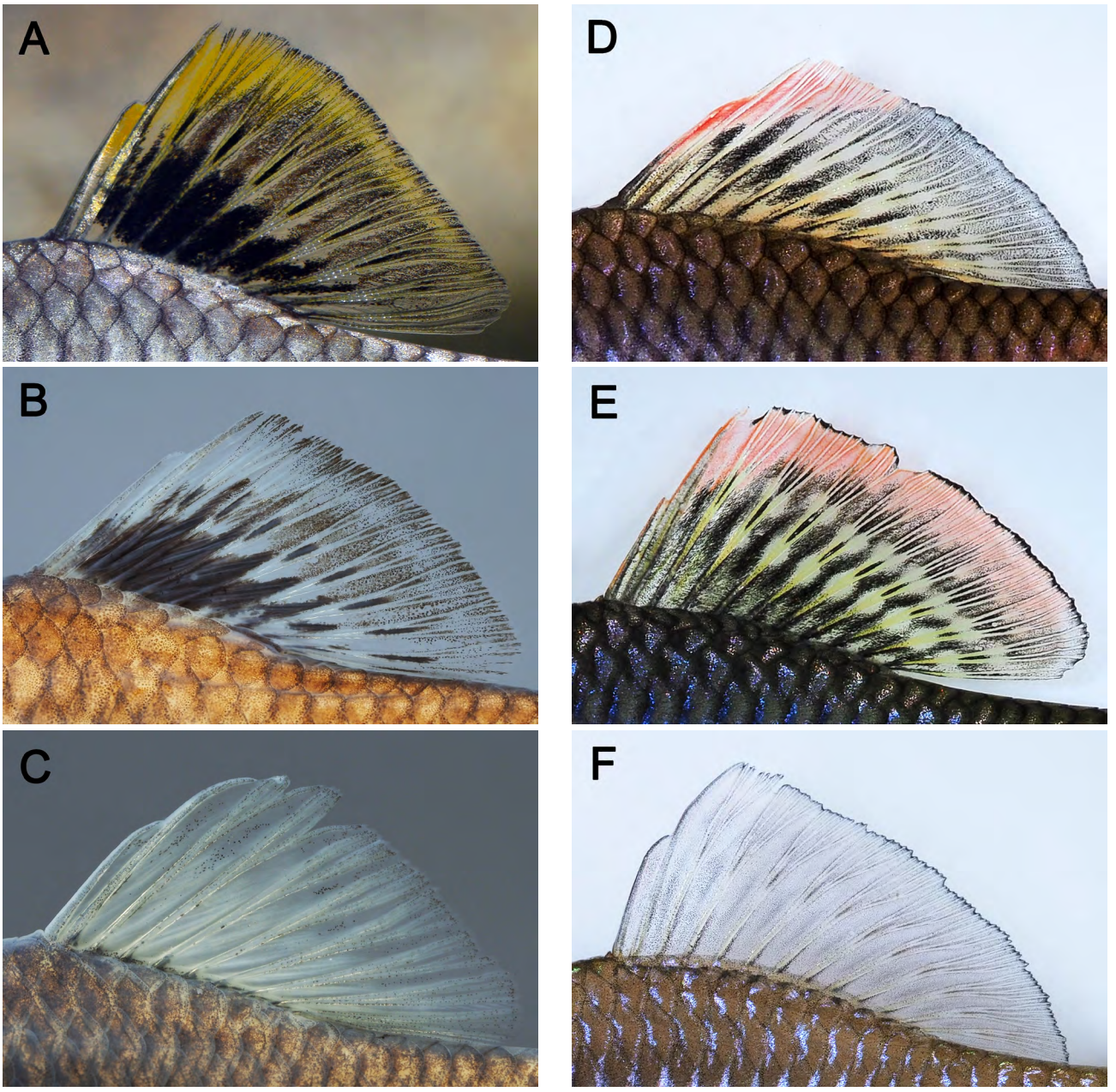

Fig. 15. Dorsal fin of adult males of five *Rhodeus* species. A) *R. nigrodorsalis* sp. nov. in life, SOU 1903001, 47.1 mm SL; B) *R. nigrodorsalis* sp. nov. in preservative, SOU 1712002, 37.9 mm SL; C) *R. cyanorostris* sp. nov. in preservative, SOU 1801001, holotype, 32.1 mm SL; D) *R. amarus* in life, 59.8 mm SL (specimen not preserved), collected from Ballica, Turkey; E) *R. shitaiensis* in life, 56.1 mm SL (specimen not preserved), collected from Shitai County, Anhui Province, China; F) *R. rheinardti* in life, 49.3 mm SL (specimen not preserved), collected from Hue City, Vietnam.

Rhodeus sericeus: *SOU 201208504, 11♂♂ and 4♀♀, 34.9-66.5 mm SL; China: Heilongjiang Province: Mishan City; August 2012.

Rhodeus shitaiensis: SOU 0811001, holotype, ♂, 59.9 mm SL; China: Anhui Province: Shitai County; November 2008. SOU 0811002-0811004, 4♂, 48.4-53.9 mm SL; same data as holotype. SOU 0905001-0905010, 4♂♂ and 6♀♀, 41.7-61.5 mm SL; same locality as holotype; May 2009.

Rhodeus sinensis: BMNH 1868.10.19-150, lectotype, ♂, 51.6 mm SL; China: Chikiang (Zhejiang); 19 October 1868. *SOU 201005504, 4♂♂ and 1♀, 35.2-58.2 mm SL; China: Anhui Province: Xiuning County; 4 May 2010. *SOU 201107501, 10 specimens, 25.5-52.0 mm SL; China: Shanghai City; July 2011. *SOU 201804501, 7♂♂ and 11♀♀, 31.2-45.1 mm SL; China: Jiangxi Province: Wuyuan County; 25 April 2018.

Rhodeus spinalis: NSMT-P 31906, neotype, ♂, 49.7 mm SL; Hainan: Dingan; 27 March 1966. SOU 201312501, 14 specimens, 34.1-51.8 mm SL; China: Hainan Province: Haikou City; 21 December 2013. SOU 201810501, three specimens, 33.2-41.5 mm SL; China: Hainan Province: Danzhou City; 13 October 2018.

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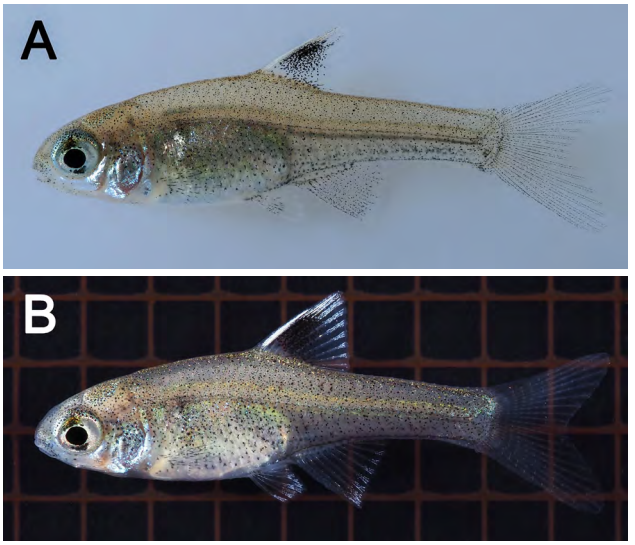

Fig. 16. Juvenile of *Rhodeus nigrodorsalis* sp. nov., 13.5 mm SL. A) with white background; B) with black background. Specimen not preserved.

Acknowledgements

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Table 3. Comparison of pored scales, branched dorsal-fin rays (Br. D), and branched anal-fin rays (Br. A) among all valid *Rhodeus* species. Numbers in parentheses are modal number.

Species	n	Pored scales	Br. D	Br. A	Br. A minus Br. D	Source[a]
R. cyanorostris sp. nov.	15	0	7-8 (8)	7-8	–1-0	this study
R. nigrodorsalis sp. nov.	12	0-4	8	8-9 (8)	0-1	this study
R. albomarginatus	20	4-7	10	10-11	0-1	Li & Arai 2014
R. amarus	19	0-6[b]	9-10 (9)	8-10 (9)[c]	–1-0	this study
R. atremius	2	4	10	9-10	–1-0	Jordan & Thompson 1914
R. colchicus	na	3-9	9-10 (9)	8-10 (9)[d]	unknown	Bogutskaya & Komlev 2001
R. fangi	7	4-6	10-11	10-11	0-1	this study
R. haradai	13	5-8	12-13	12-14	0-2	Arai et al. 1990
R. laoensis	na	6-8	11	13	2	Kottelat 1998
R. meridionalis	5	5-7	9-10 (9)	9-10 (9)	–1-1	this study
R. notatus	14	2-6	9-10	8-10[e]	–1-0	this study
R. ocellatus ocellatus	37	3-7	10-12	10-12	–1-1	Li & Arai 2011
R. o. kurumeus	12	0-2	9-11	9-11	unknown	Kimura & Nagata 1992
R. pseudosericeus	24	2-7	9-10	9-11	0-2	Arai et al. 2001
R. rheinardti	16	4-9	11-12	13-16	2-5	this study
R. sericeus	15	5-8	9-10 (9)	9-10 (9)	0-1	this study
R. shitaiensis	21	6-12	9-10 (9)	9-10 (9)	–1-1	Li & Arai 2011
R. sinensis	33	2-5	8-10 (9)[f]	8-10[g]	0-1	this study
R. smithii	1	3	11	11	0	Kimura & Nagata 1992
R. spinalis	39	5-8	10-13	13-17	2-4	Arai et al. 2001
R. suigensis	1	4	10	10	0	Mori 1935

[a]Data for 'this study' from specimens listed in comparative materials with symbol *, except data for *R. meridionalis* which derive from examination of five live specimens from the River Vardar in Greece.
[b]Zero only found in one specimen among a total of 19 specimens.
[c]Eight only found in two specimens among a total of 19 specimens.
[d]Eight only found in three specimens among a total of 35 specimens.
[e]Eight only found in one specimen among a total of 14 specimens.
[f]Eight only found in one specimen among a total of 33 specimens.
[g]Eight only found in one specimen among a total of 33 specimens.

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