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Four New Subspecies of *Acheilognathus* Bitterlings (Cyprinidae: Acheilognathinae) from Japan

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Abstract Four new bitterlings, *Acheilognathus tabira erythropterus* subsp. nov., *Acheilognathus tabira tohokuensis* subsp. nov., *Acheilognathus tabira jordani* subsp. nov. and *Acheilognathus tabira nakamurae* subsp. nov., were described on the basis of more than 600 specimens from 26 localities in Japan. *Acheilognathus tabira erythropterus*, *A. t. tohokuensis* and *A. t. jordani*, formerly all included in a single undescribed subspecies of *Acheilognathus tabira*, differ from other subspecies of *A. tabira* in having a red-edged anal fin in nuptial males. *Acheilognathus t. erythropterus*, distributed on the Pacific Ocean side of eastern Honshu, is distinguished from *A. t. tohokuensis* and *A. t. jordani* by having shorter ellipsoidal eggs (ratio of major axis to minor axis: 1.4–2.2 vs. 2.0–3.3 in *A. t. tohokuensis* and *A. t. jordani*). *Acheilognathus t. tohokuensis*, distributed on the Japan Sea side of eastern Honshu, is distinguished from *A. t. jordani* in lacking a black blotch on the dorsal fin in juveniles. *Acheilognathus t. jordani*, distributed on the Japan Sea side of western Honshu, is distinguished from *A. t. erythropterus* and *A. t. tohokuensis* by having a black blotch on the dorsal fin in juveniles. *Acheilognathus t. nakamurae*, distributed in the Kyushu area, differs from all other subspecies by the following combination of characters: edge of the dorsal fin in males red, anal fin in nuptial males edged with white, a conspicuous black blotch on the dorsal fin in both juveniles and small adult females, and long ellipsoidal eggs (ratio of major axis to minor axis: 2.3–2.9). *Acheilognathus t. tabira* Jordan and Thompson, 1914 differs from the 4 new subspecies by having more branched dorsal fin rays (10 vs. 9), the edge of the dorsal fin in males (grayish vs. red) and shorter ellipsoidal eggs (ratio of major axis to minor axis: 1.4–1.7 vs. 1.4–3.3). A key is provided for all Japanese species and subspecies of *Acheilognathus*.
Key words: Four new subspecies, *Acheilognathus tabira erythropterus*, *Acheilognathus tabira tohokuensis*, *Acheilognathus tabira jordani*, *Acheilognathus tabira nakamurae*, Cyprinidae, Japan.

The genus *Acheilognathus* includes about 28 species and subspecies, all being restricted to East Asia: 2 species are known from Russia (Bogutskaya and Naseka, 1996), 1 species from the Mongolian People's Republic (Sokolov *et al*., 1983), 4 species from Laos (Kottelat, 2001a), about 7 species from Vietnam (Mai, 1978; Kottelat, 2001b), about 18 species from China (Woo, 1964; Lin, 1998), 6 species from South Korea (Kim and Park, 2002) and 9 species and subspecies from Japan (Nakamura, 1969; Hagiwara, 2002).

Regarding *Acheilognathus* from Japan, Hosoya (1993) described 8 species and subspecies including *A. melanogaster* Bleeker, 1860, *A. cyanostigma* Jordan and Fowler, 1903, *A. rhombeus* (Temminck and Schlegel, 1846), *A. longipinnis* Regan, 1905, *A. typus* (Bleeker, 1863), *A. tabira tabira* Jordan and Thompson, 1914, *A. tabira* subsp. 1 and *A. tabira* subsp. 2. Hagiwara (2002) later reported an introduced bitterling, *A. macropterus* (Bleeker, 1871), which had become established in Lake Kasumigaura, Ibaraki Prefecture, eastern Honshu.

Acheilognathus tabira Jordan and Thompson, 1914 had earlier been divided into 3 subspecies by Nakamura (1969), with Japanese names for each, i.e., Shirohire-tabira for *A. tabira tabira*, Akahire-tabira for *A. tabira* subsp. (a) and Seboshi-tabira for *A. tabira* subsp. (b). Although the latter two subspecies have at no time formally described, biological information on them has been accumulated through various studies; interrelationships based on phenotypes and karyotypes (Arai, 1978, 1988), molecular phylogeny based on a mitochondrial gene (Okazaki *et al*., 2001), allozymes (Fujikawa *et al*., 1984), karyotypes (Ojima *et al*., 1973), sensory canal system (Arai and Kato, 2003), pharyngeal teeth and masticatory process of the basioccipital bone (Suzuki and Hibiya, 1985a), minute skin surface tubercles on larvae (Fukuhara *et al*., 1982; Suzuki and Hibiya, 1985b), development (Suzuki, 1985), and distribution (Nagata *et al*., 1981; Fujikawa, 1983; Suzuki, 1985; Saitoh *et al*., 1988; Watanabe, 1998). Predictably, however, the lack of formal designation has resulted in some difficulties in comparing the above studies.

Accordingly, morphological reexamination and formal taxonomic treatment of Nakamura's (1969) unnamed subspecies is necessary. Nakamura (1969) defined *Acheilognathus tabira* subspp. (a) and (b) on egg shape immediately after oviposition and presence or absence of a black blotch on the dorsal fin in juveniles and small adult females. According to Nakamura (1969), the egg shape of *A. t.* subsp. (a) was short ellipsoidal (Japanese 'keiran' type), similar to that of *A. t. tabira*, being distinguished from *A. t.* subsp. (b) by a lower ratio of major to minor axes (1.6–1.7 vs. 2.2–2.3 in *A. t.* subsp. (b)) (Nakamura, 1969). However, during the present study, eggs of *A. t.* subsp. (a) from the Japan Sea side of Honshu were found to be longer ellipsoid (ratio of major to minor axes, 2.0–3.3), similar to those of *A. t.* subsp. (b) (ratio of major to minor axes 2.3–2.9, present study). Furthermore, although Nakamura (1969) considered that both *A. t.* subsp. (a) and *A. t. tabira* lacked a black blotch on the dorsal fin, whereas it occurred in both juveniles and small adult females of *A. t.* subsp. (b), such were found in *A. t.* subsp. (a) juveniles from the Japan Sea side of western Honshu. Clearly, Nakamura's (1969) concept of *Acheilognathus tabira* subspecies was in need of revision. The present study showed that *A. t.* subsp. (b) and *A. t. tabira* (both Nakamura, 1969) differed from each other at the subspecific level, being consistent in their characteristics, whereas *A. t.* subsp. (a) comprised 3 hitherto unrecognized subspecies, identifiable by a combination of egg shape and presence or absence of a black blotch on the dorsal fin in juveniles. One subspecies had a black dorsal fin blotch in juveniles, previously considered an important diagnostic character of *A. t.* subsp. (b) by Nakamura (1969). The remaining 2 undescribed subspecies lacked a black dorsal fin blotch in juveniles, but could be distinguished from each other by ellipsoidal egg shape, barbel length, and vertebral number. Thus, a new classification of *Acheilognathus tabira*, which includes 4 new subspecies, is proposed below.

Materials and Methods

More than 1000 specimens in total, from 38 localities, were examined (Table 1, Fig. 1). The classification of genera of the subfamily Acheilognathinae follows Arai and Akai (1988), that of host mussels following Kondo (1982, 1998, 2006). Methods for counts and measurements follow Hubbs and Lagler (1958). Vertebrae and unpaired fin rays were counted from radiographs. Vertebral number includes the Weberian complex (as 4) and the terminal pleurostyle (1). The inserted position of the proximal segment of the first pterygiophore in the dorsal and anal fins, expressed as D-PTG-1 (Fig. 2) and A-PTG-1, respectively (see Arai *et al*., 1995), was examined from radiographs. D-PTG-1 was described in relation to the associated vertebra (vertebral number), suffix 'a' indicating insertion of the second dorsal pterygiophore into the succeeding intervertebral space (Fig. 2-left), suffix 'b' indicating no pterygiophore insertion into the succeeding intervertebral space (Fig. 2-right). Because proportional measurements of adults

Table 1. List of specimens examined in 5 subspecies of *Acheilognathus tabira*.

Loc. No.*	Cat. No.	No. of specimens	Subspecies	Locality	Date of collection
1	NSMT-P 74699	10	*A. t. tohokuensis*	Lake Kaikon-numa	28 Aug. 1978
2	OKU-P 114	42	*A. t. tohokuensis*	Lake Hachirogata	5 Aug. 1981
3	NSMT-P 74700	40	*A. t. tohokuensis*	Lake Ogata	5 Aug. 1981
4	NSMT-P 72657, 74701	66	*A. t. tohokuensis*	Lake Nishinuma	4 Aug. 1981
5	NSMT-P 27553	2	*A. t. tohokuensis*	Yasuda-machi	26 Oct. 1974
6	ZUMT 61513	1	*A. t. tohokuensis*	near Teradomari	21 Oct. 2005
7	NSMT-P 27043	2	*A. t. erythropterus*	Natori City	26 June 1975
8	ZUMT 61512	2	*A. t. erythropterus*	Nasu-machi	28 May 2005
9	NSMT-P 72656, 74702	50	*A. t. erythropterus*	Lake Kasumigaura	2 Apr. 1982
10	NSMT-P 74703	35	*A. t. erythropterus*	Seimeigawa River	1–2 Apr. 1982
11	NSMT-P 74704	38	*A. t. jordani*	Machinogawa River	16 Oct. 1981
12	NSMT-P 74705	3	*A. t. jordani*	Kawaradagawa River	16 Oct. 1981
13	NSMT-P 74706	41	*A. t. jordani*	Lake Akauragata	16 Oct. 1981
14	NSMT-P 72594	2	*A. t. jordani*	Himi City	29 May 2005
15	NSMT-P 74707	50	*A. t. jordani*	Takaoka City	7 Aug. 1981
16	NSMT-P 74708	5	*A. t. jordani*	Lake Ouchigata	17 Oct. 1981
17	NSMT-P 72658, 74709	7	*A. t. jordani*	Lake Kibagata	18 Oct. 1981
18	NSMT-P 74710	33	*A. t. jordani*	Lake Shibayamagata	18 Oct. 1981
19	NSMT-P 72595	2	*A. t. jordani*	Ono City	12 June 2005
20	OKU-P 110	34	*A. t. jordani*	Tanegaike Pond	27 June 1981
21	ZUMT 61511	12	*A. t. jordani*	Oharagawa River	4 July 2003
21	OKU-P 213	48	*A. t. jordani*	Oharagawa River	3 Aug. 1984
22	OKU-P 154	11	*A. t. nakamurae*	Hatahokogawa River	4 Apr. 1977
22	OKU-P 171	30	*A. t. nakamurae*	Hatahokogawa River	26 May 1982
22	NSMT-P 74711	57	*A. t. nakamurae*	Hatahokogawa River	28 July 1976
22	NSMT-P 11004	2	*A. t. nakamurae*	Hatahokogawa River	1 Sept. 1969
23	NSMT-P 72596	1	*A. t. nakamurae*	Tataragawa River	23 May 2005
24	NSMT-P 74712	47	*A. t. nakamurae*	Horikawayosui River	16 Apr. 1982
25	NSMT-P 72659, 74713	49	*A. t. nakamurae*	Futatsukawa River	15 Apr. 1982
26	NSMT-P 74714	13	*A. t. nakamurae*	Lake Shimoezuko	14–15 Apr. 1982
27	NSMT-P 72597	1	*A. t. tabira*	Kushidagawa River	10 June 2005
28	NSMT-P 74715	8	*A. t. tabira*	Lake Yogo	4 May 1982
29	NSMT-P 74716	49	*A. t. tabira*	Katayama, Lake Biwa	1 May 1982
30	NSMT-P 74717	50	*A. t. tabira*	Sugaura, Lake Biwa	4 May 1982
31	NSMT-P 74718	25	*A. t. tabira*	Setagawa River	21 Aug. 1981
32	NSMT-P 74719	36	*A. t. tabira*	Kanzakigawa River	27 Mar. 1982
33	NSMT-P 74720	40	*A. t. tabira*	Yodogawa River	10 Oct. 1980
34	OKU-P 170	29	*A. t. tabira*	Pond in Sanda City	18 May 1982
35	NSMT-P 74721	13	*A. t. tabira*	Mukogawa River	18 May 1982
36	NSMT-P 74722	33	*A. t. tabira*	Gion-yosui River	21 Mar. 1982
37	NSMT-P 74723	16	*A. t. tabira*	Nakajimaooike Pond	21 Mar. 1982
38	NSMT-P 74724	76	*A. t. tabira*	Ashimorigawa River	18 Apr. 1980

* Locality numbers correspond to those in Fig. 1.

differed from those of juveniles, only specimens longer than 40 mm in standard length (SL) were used in this study. Ripe eggs were obtained by pressing the belly of a mature female (identified by a characteristically long ovipositor) and placed on a mesh slide glass or transferred into a petri dish filled with distilled water for subsequent observation. Ripe eggs of bitterlings are non-spherical, the shape being indicated by the ratio of the major to minor axes (Coleman, 1991), following measurement of eggs fixed in 10% formalin. When eggs were not available for direct examination, measurements were taken from photographs. Eastern and western Honshu were defined as the areas east and west of the Fossa Magna (Shizuoka-Itoigawa Line), respectively.

Principal component analyses (PCA) were carried out on 6 selected $\log_{10}$-transformed morpho-

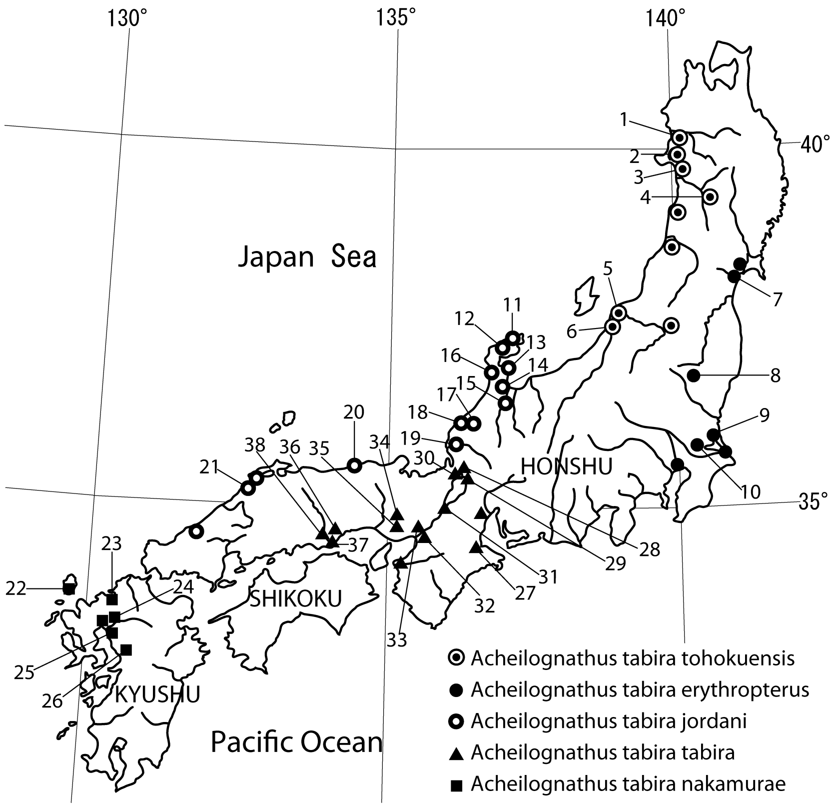

Fig. 1. Map showing distribution of 5 subspecies of *Acheilognathus tabira*. Numbered symbols, corresponding to locality numbers in Table 1, indicate collection localities of specimens examined; unnumbered symbols indicate collection locality of only eggs (Inabegawa River, new record) and literature records.

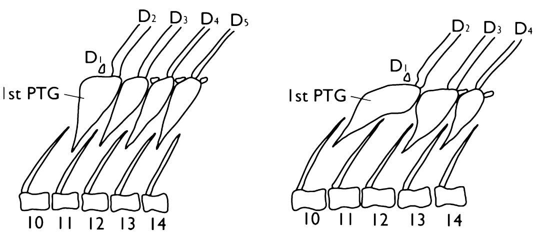

Fig. 2. Insertion of first pterygiophore in dorsal fin (D-PTG-1). Left, D-PTG-1=10th[a]; right, D-PTG-1=10th[b]. 1st PTG, first pterygiophore; D_{1-5}, first 5 dorsal fin rays; numbers, vertebrae.

metric characters (see 'Statistical analyses of morphometric and meristic characters') and 5 meristic characters in order to clarify which character was different among subspecies.

Institutional abbreviations are as follows: AKPM, Akita Prefectural Museum, Akita; FMNH, Field Museum of Natural History, Chicago; NSMT, National Museum of Nature and Science (formerly National Science Museum), Tokyo; OKU, Osaka Kyoiku University, Osaka; ZUMT, Department of Zoology, University Museum, University of Tokyo, Tokyo.

Acheilognathus tabira Jordan and Thompson, 1914

(Japanese name: Tabira)

(New English name: Tabira bitterling)

(Figs. 3–12)

Proportional measurements of specimens longer than 40 mm SL as % SL: body depth 29–38, head length (HL) 21–27, predorsal length 50–57, caudal peduncle depth 10–13; as % HL:

orbit diameter (OD) 27–40; as %OD: snout length 41–117 (relatively longer with growth) and barbel length 2–65. Dorsal rays, iii, 8–11; anal rays, iii, 8–10; number of dorsal rays minus number of anal rays, −1 to 2; first simple rays of dorsal and anal fins very small, hidden under skin; longest simple rays of dorsal and anal fins, soft; pectoral rays, i, 14–16; pelvic rays, i, 7; caudal rays, i+9/8+i; lateral line complete; lateral-line scales, 33–40; scales on proximal part of caudal fin, 1 or 2; transverse scales, 10–11; scales around caudal peduncle, 14; abdominal vertebrae, 17–20; caudal vertebrae, 17–20; total vertebrae, 35–38; first dorsal pterygiophore supporting first and second dorsal rays; insertion of first pterygiophore in dorsal fin (D-PTG-1), 10th to 13th; insertion of first pterygiophore in anal fin (A-PTG-1), 17th to 20th; pharyngeal teeth, 0.0.5–5.0.0; chewing area on pharyngeal teeth serrated; gill rakers on outer side of 1st gill arch, 9–11; a pair of maxillary barbels; pearl organs on snout and around nostrils in adult males; a round or elliptical black blotch immediately behind upper corner of gill opening; a short longitudinal stripe along mid-caudal peduncle to a point under middle of dorsal fin, not reaching caudal fin; edge of dorsal fin in males, red or grayish; nuptial coloration in males conspicuous during spawning season, distal anal fin margin being red or white (Figs. 3–4 and 7–11); female coloration unremarkable, an ovipositor obvious during February to August (spawning season); a black blotch absent or present on dorsal fin in juveniles and/or small adult females (Fig. 5); eggs ellipsoid immediately after oviposition, ratio of major axis to minor axis, 1.4–3.3 (Table 6, Fig. 6); diploid chromosome number, 44.

Remarks. *Acheilognathus tabira* differs from other Japanese *Acheilognathus* species by the following combination of characters: branched dorsal rays 8–11, branched anal rays 9–10, number of dorsal rays minus number of anal rays −1 to 2, and anal fin in nuptial males edged with red or white. This species comprises 5 subspecies (Tables 1–11). As shown in Tables 4 and 11, the number of total vertebrae is almost equal to that of lateral-line scales.

According to many previous studies (see synonymies for subspecies of *Acheilognathus tabira*) and the present survey, this species is endemic to Japan. Katayama (1941), Nakamura (1977) and the Research Group on Fishes and Shellfishes in Nagano Prefecture (1980: 68) reported *Acheilognathus tabira* from the Maruyama River, Hyogo Prefecture, from near Maizuru, Kyoto Prefecture, and from Lake Kizakiko, Nagano Prefecture, Japan, respectively. Because the specimens used by those authors were not available for the present study, they could not be identified to subspecific level.

This species has also been reported from Korea and China. Mori (1935: 566–567, 1 table) described *Paracheilognathus tabira* (=*Acheilognathus tabira*) from a single male specimen from Seoul, Korea. This Korean specimen, however, differed from *A. tabira* in Japan by having a longer longitudinal stripe on the body, i.e., reaching anteriorly beyond the dorsal fin origin (Mori, 1935), while it ends anteriorly below the middle of the dorsal fin in the latter (Jordan and Thompson, 1914), in that way being similar to *A. melanogaster*, although sharing with *A. tabira* a similar combination of dorsal and anal fin ray numbers (D. iii, 9; A. iii, 9). Additional specimens of *A. tabira* from Korea have not yet been reported. Woo (1964) reported *Acanthorhodeus tabiro* (=*Acheilognathus tabira*) from China, although this was later described as a new species, *Acheilognathus macromandibularis* Doi, Arai, and Liu, 1999.

Subspecies of *Acheilognathus tabira*

Acheilognathus tabira tabira Jordan and Thompson, 1914

(Japanese name: Shirohire-tabira)

(New English name: White tabira bitterling)

(Figs. 4C, 6 L–M, 7)

Acheilognathus tabira Jordan and Thompson, 1914: 220, pl. 25, fig. 1 (Lake Biwa); Aoyagi, 1957: 100 (in part).

Acheilognathus tabira tabira: Nakamura, 1963: 149, fig. 81; Nakamura, 1969: 36 and 378, pls. 2 A–A′, 14, 15,

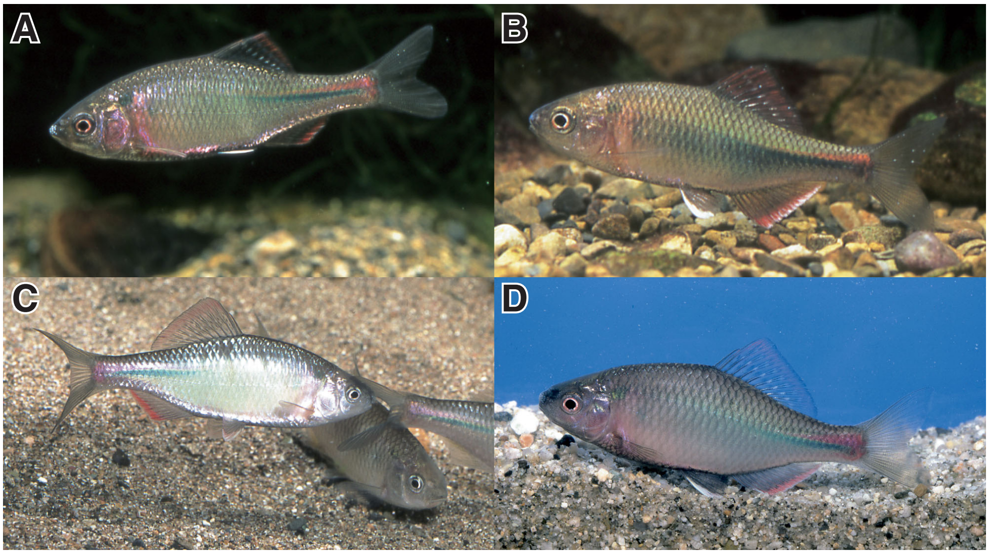

Fig. 3. Color in life of nuptial males of 2 subspecies of *Acheilognathus tabira*. A: *A. t. tohokuensis* subsp. nov., near Teradomari, collected by Nobuo Inoue, 21 Oct. 2005, photographed by Ryu Uchiyama, Oct. 2005 (after artificial induction of nuptial coloration). B–D: *A. t. erythropterus* subsp. nov.; B, Natori, Miyagi Prefecture, collected by Kenji Saitoh, 11 June 2005, photographed by Ryu Uchiyama, June 2005; C, Inashiki, Lake Kasumigaura, collected by Tomiji Hagiwara, 21 May 2005, photographed by Ryu Uchiyama, June 2005; D, Ichinosegawa River, Ibaraki Prefecture, collected and photographed by Yoshikazu Nagata, 2 Apr. 1986.

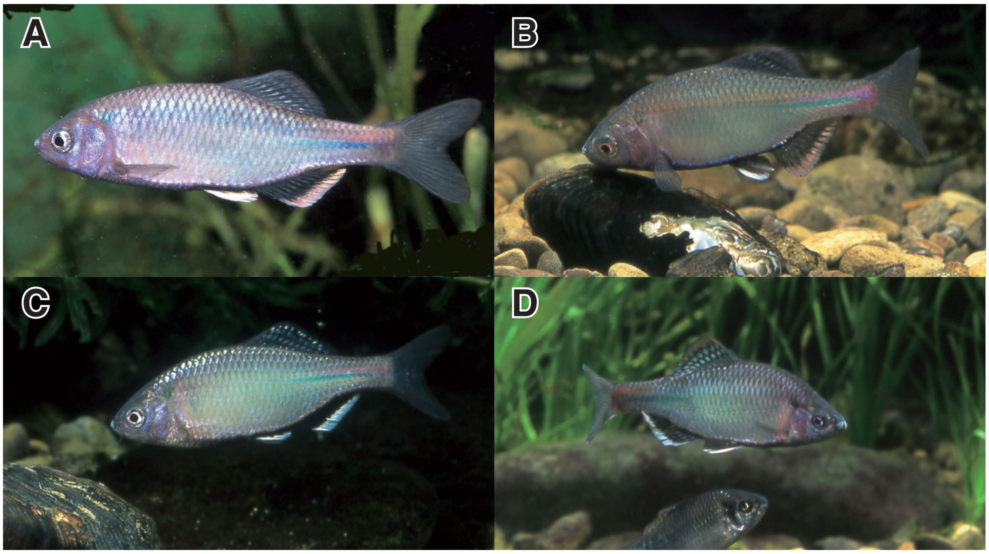

Fig. 4. Color in life of nuptial males of 3 subspecies of *Acheilognathus tabira*. A–B: *A. t. jordani* subsp. nov.; A, Himi, collected by Osamu Inamura, 2 Feb. 1992, photographed by Osamu Inamura, 20 May 1992; B, Ono, collected by Jun-ya Kitazima, 12 June 2005, photographed by Ryu Uchiyama, June 2005. C: *A. t. tabira*, Inabegawa River, Mie Prefecture, collected by Jun-ya Kitazima, 23 June 2004, photographed by Ryu Uchiyama, May 2005. D: *A. t. nakamurae* subsp. nov., Tataragawa River, collected by Jun Nakajima, 23 May 2005, photographed by Ryu Uchiyama, May 2005.

and 92 A–B; Ojima *et al*., 1973: 172, fig. 7 (Osaka and Okayama); Fukuhara *et al*., 1982: 233, fig. 2B (Okayama); Hosoya, 1982: 29 (Okayama); Sawada, 1984: 54, pl. 53 I–J; Fujikawa *et al*., 1984: 57 (Shiga, Osaka, Hyogo, and Okayama); Suzuki and Hibiya, 1985a: 184, fig. 5A (Shiga and Okayama); Suzuki and Hibiya, 1985b: 339, fig. 3A (Shiga); Suzuki, 1985: 64, figs. 2–3 (Okayama); Arai and Akai, 1988: 201; Nagata, 1989: 373, 3 figs.; Doi, 1992: 36 (Wakayama); Hosoya, 1993: 216; Watanabe, 1998: 262; Okazaki *et al*., 2001: 92, figs. 3–4 (Shiga); Arai and Kato, 2003: 3, table 1, fig. 6B (Shiga).

Paracheilognathus tabira tabira: Tsubokawa, 1988: 4 (Okayama); Hosoya, 1988: 155.

Rhodeus (?) *tabira* tabira: Kawanabe, 1987: 26, 1 fig.

Acheilognathus lanceolata tabira: Niwa, 1967: 103 (Aichi and Gifu).

Acheilognathus limbata: Jordan and Fowler, 1903: 818 (in part: Shiga).

Material examined. FMNH 57071, holotype of *Acheilognathus tabira*, male, 68.0 mm SL, Lake Biwa; NSMT-P 74718 (ex OKU-P 101) (25 specimens: 5 males, 18 females, and 2 sex unknown), 26.3–75.8 mm SL, Setagawa River, Nango, Shiga Prefecture, 21 Aug. 1981; NSMT-P 74715 (ex OKU-P 167) (8: 3M+5F), 47.1–61.5 mm SL, Lake Yogo, Shiga Prefecture, 4 May 1982; NSMT-P 74716 (ex OKU-P 166) (49: 25M+24F), 41.1–70.8 mm SL, Katayama, Lake Biwa, Shiga Prefecture, 1 May 1982; NSMT-P 74717 (ex OKU-P 168) (50: 20M+28F+2 sex unknown), 31.8–79.3 mm SL, Sugaura, Lake Biwa, Shiga Prefecture, 4 May 1982; NSMT-P 74719 (ex OKU-P 158) (36: 11M+25F), 41.2–74.9 mm SL, Kanzakigawa River, Yodogawa River System, Osaka Prefecture, 27 Mar. 1982; NSMT-P 74720 (ex OKU-P 151) (40: 10M+30F), 26.1–64.8 mm SL, floodplain pools, Yodogawa River, Osaka Prefecture, 10 Oct. 1980; OKU-P 170 (29: 19M+10F: voucher specimens lost after examination but radiographs still available), 39.1–72.8 mm SL, pond in Sanda, Hyogo Prefecture, 18 May 1982; NSMT-P 74721 (ex OKU-P 169) (13: 2M+11F), 44.8–75.8 mm SL, Mukogawa River, Hyogo Prefecture, 18 May 1982; NSMT-P 74722 (ex OKU-P 155) (33: 15M+18F), 40.1–64.5 mm SL, Gion-yosui River, Okayama, Okayama

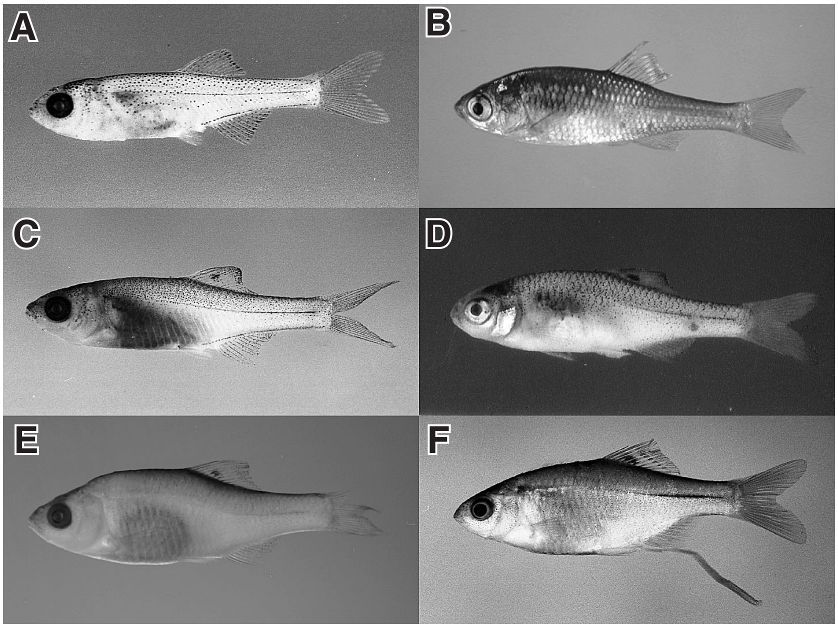

Fig. 5. Dorsal fin coloration in juveniles and adult females. A–B: Juvenile *A. t. tohokuensis* subsp. nov. (blotch absent); A, AKPM-P 436-1, paratype, 13.0 mm SL, Gojome-machi, Akita Prefecture, collected by Hideki Sugiyama, 27 June 2004; B, AKPM-P 438-2, paratype, 26.4 mm SL, Kisakata, Akita Prefecture, collected and photographed by Hideki Sugiyama, 4 June 2006. C–E: Juvenile *A. t. jordani* subsp. nov. (black blotch present); C, NSMT-PL 265-1, paratype, 19.5 mm SL, Lake Kibagata, collected by Kunihiko Yamamoto, 17 June 2005; D, 22.1 mm SL, Oharagawa River, collected 3 Aug. 1984 (from Saitoh et al., 1988); E, 31.0 mm SL, Oharagawa River, collected by Chika Oshiumi, Mar. 2003. F: Adult female of *A. t. nakamurae* subsp. nov. (black blotch present), NSMT-P 75167-6, paratype, 50.2 mm SL, Futatsukawa River, collected by Hiroshi Fujikawa, 3 Sep. 1980.

Prefecture, 21 Mar. 1982; NSMT-P 74723 (ex OKU-P 156) (16: 3M+13F), 40.5–72.1 mm SL, Nakajimaooike Pond, Okayama, Okayama Prefecture, 21 Mar. 1982; NSMT-P 74724 (ex OKU-P 148) (76: 21M+55F), 42.1–65.2 mm SL, Ashimorigawa River, Okayama Prefecture, 18 Apr. 1980; NSMT-P. 72597 (1M), 44.0 mm SL, Kushidagawa River, Mie Prefecture, 10 June 2005.

Diagnosis. Dorsal rays, iii, 9–11; anal rays, iii, 9–10; dorsal fin in males grayish; anal fin in nuptial males white; no black blotch on dorsal fin in juveniles; eggs short ellipsoid, ratio of major axis to minor axis, 1.4–1.7 (Table 11).

Description. Morphometric and meristic data are shown in Tables 2–4. Proportional measurements as % SL: body depth 30–38, head length 21–27, predorsal length 50–55, caudal peduncle depth 11–13; as % HL: orbit diameter 28–40; as % OD: snout length 41–106, barbel length, 12–51. Dorsal rays, iii, 9–11; anal rays, iii, 8–10; number of dorsal rays minus number of anal rays, 0–2; pectoral rays, i, 14–16; pelvic rays, i, 7; caudal rays, i+9/8+i; abdominal vertebrae, 17–20; caudal vertebrae, 17–20; total vertebrae, 35–38; insertion of first pterygiophore in dorsal fin (D-PTG-1), 10th to 13th (Table 5); insertion of first pterygiophore in anal fin (A-PTG-

Table 2. Averages of proportional measurements of body depth (BD), head length (HL), predorsal length (PredL), caudal peduncle depth (CPD), orbit diameter (OD), snout length (SnL), and barbel length (BarL) in specimens >40 mm SL in 5 subspecies of *Acheilognathus tabira*.

Loc. No.	Cat. No.	Locality (Prefecture)	No. of specimens	BD/SL (%)	HL/SL (%)	PredL/SL (%)	CPD/SL (%)	OD/HL (%)	SnL/OD (%)	BarL/OD (%)
A. t. tohokuensis										
1	NSMT-P 74699	Akita	7	32	25	55	11	30	82	22
2	OKU-P 114	Akita	42	32	24	53	12	31	87	11
3	NSMT-P 74700	Akita	40	32	25	54	11	30	76	22
4	NSMT-P 72657, 74701	Akita	54	31	25	54	11	29	90	23
A. t. erythropterus										
9	NSMT-P 72656, 74702	Ibaraki	49	32	24	53	11	30	81	36
10	NSMT-P 74703	Ibaraki	35	32	24	53	11	32	81	35
A. t. jordani										
11	NSMT-P 74704	Ishikawa	36	32	24	53	11	29	88	30
12	NSMT-P 74705	Ishikawa	2	32	24	53	11	31	72	14
13	NSMT-P 74706	Ishikawa	40	31	23	53	12	29	89	22
15	NSMT-P 74707	Toyama	41	31	24	54	11	31	82	17
16	NSMT-P 74708	Ishikawa	5	31	24	52	11	29	89	16
17	NSMT-P 72658, 74709	Ishikawa	7	30	25	53	11	31	78	18
18	NSMT-P 74710	Ishikawa	30	31	24	52	11	31	84	24
20	OKU-P 110	Tottori	34	32	24	53	12	32	87	27
21	OKU-P 213	Shimane	48	34	24	53	12	32	83	31
A. t. nakamurae										
22	OKU-P 154	Nagasaki	8	35	24	56	12	31	77	37
22	OKU-P 171	Nagasaki	30	35	23	53	12	30	81	34
24	NSMT-P 74712	Fukuoka	47	32	23	54	12	30	98	38
25	NSMT-P 72659, 74713	Fukuoka	49	32	24	54	12	32	85	38
26	NSMT-P 74714	Kumamoto	13	32	23	52	12	33	80	47
A. t. tabira										
28	NSMT-P 74715	Shiga	7	33	24	51	11	32	81	35
29	NSMT-P 74716	Shiga	49	34	24	52	11	33	85	35
30	NSMT-P 74717	Shiga	44	33	24	51	11	33	83	37
31	NSMT-P 74718	Shiga	21	35	23	52	12	35	75	26
32	NSMT-P 74719	Osaka	33	33	24	51	12	32	78	30
33	NSMT-P 74720	Osaka	21	33	24	54	11	33	75	33
34	OKU-P 170	Hyogo	27	34	24	54	12	31	84	22
35	NSMT-P 74721	Hyogo	13	35	22	53	12	32	80	34
36	NSMT-P 74722	Okayama	30	34	25	53	12	32	76	35
37	NSMT-P 74723	Okayama	12	35	24	53	12	37	57	32
38	NSMT-P 74724	Okayama	75	36	25	53	12	31	76	32

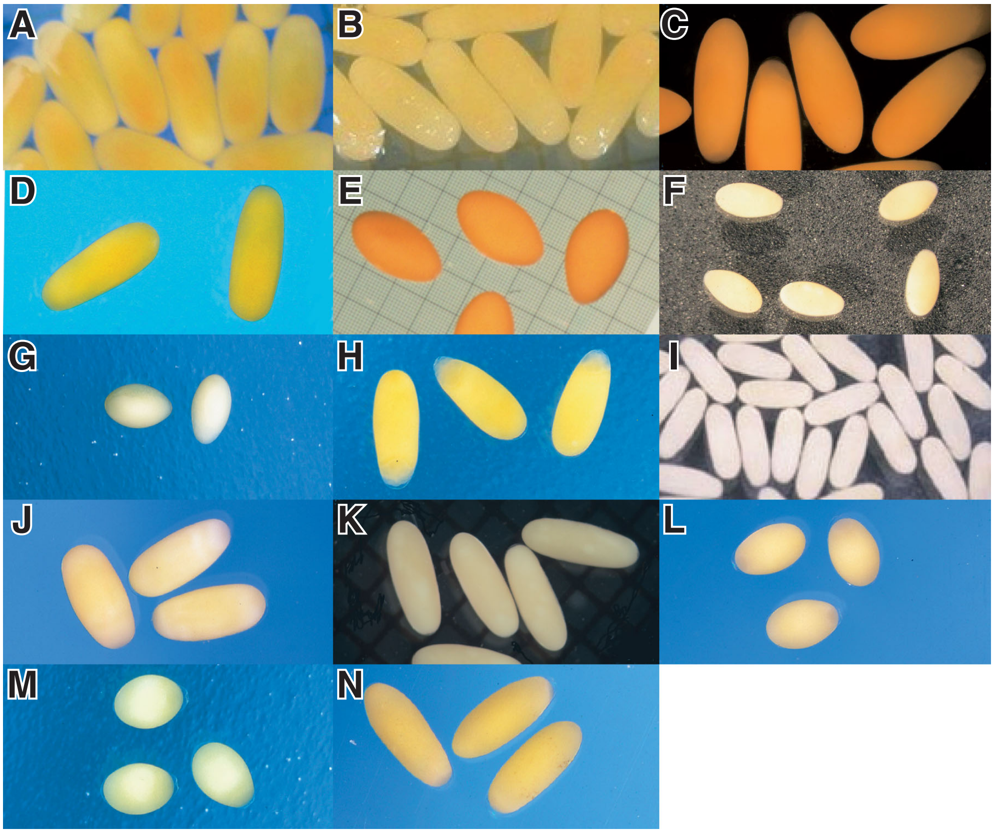

Fig. 6. Eggs of 5 subspecies of *Acheilognathus tabira*. A–D: *A. t. tohokuensis* subsp. nov.; A, Gojome-machi, photographed by Hideki Sugiyama, 29 Apr. 2006; B, Akita, Akita Prefecture, photographed by Hideki Sugiyama, 7 May 2006; C, Aizu area, Fukushima Prefecture, photographed by Makoto Kuraishi, 24 May 2006; D, near Teradomari, photographed by Ryu Uchiyama, 11 Dec. 2005 (after artificial induction of spawning). E–G: *A. t. erythropterus* subsp. nov.; E, Nasu-machi (A), photographed by Yoshikazu Nagata, 24 June 2006; F, Nasu-machi (B), photographed by Hitoshi Kubota, 15 June 2006; G, Lake Kasumigaura, photographed by Ryu Uchiyama, July 2005. H–K: *A. t. jordani* subsp. nov.; H, Himi, photographed by Ryu Uchiyama, June 2005; I, Lake Kibagata, photographed by Kunihiko Yamamoto, 31 May 2001; J, Ono, photographed by Ryu Uchiyama, May 2005; K, Oharagawa River, photographed by Chika Oshiumi, 7 Apr. 2003. L–M: *A. t. tabira*; L, Inabegawa River, photographed by Ryu Uchiyama, May 2005; M, Kushidagawa River, photographed by Ryu Uchiyama, June 2005; N, *A. t. nakamurae* subsp. nov., Tataragawa River, photographed by Ryu Uchiyama, May 2005.

1), 17th to 20th. Eggs short ellipsoid, ratio of major axis to minor axis, 1.4–1.7 (Table 6, Figs. 6 L–M).

Color in life. Dorsal fin in males margined with gray (red in other subspecies). Nuptial coloration strikingly presented in sexually mature males during the spawning season: lateral surface of body bright greenish-blue, belly black; pelvic fin black proximally, margined with white along anterior edge; anal fin proximally black, margined with white (hence derivation of English name of subspecies). Females show no nuptial coloration, but develop an ovipositor to deposit eggs into host mussels. A black blotch on the dorsal fin is absent in juveniles.

Habitat. Widely distributed from the shore to 30–40 m depth in Lake Biwa, and numerous small nearby ponds continuous with the former. Also along rocky shores of rivers and irrigation creeks and in floodplain pools.

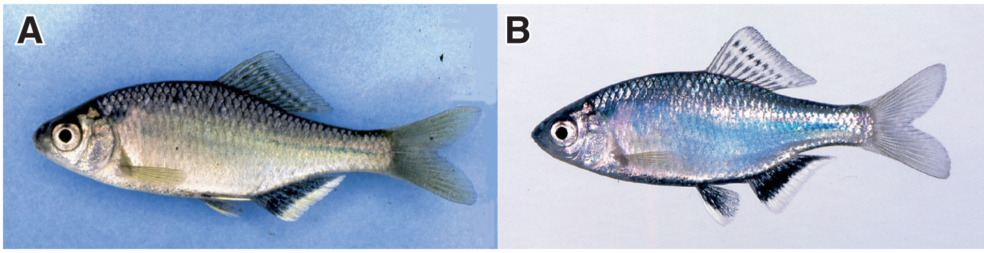

Fig. 7. *Acheilognathus tabira tabira*. A: NSMT-P 74718-9, male, 75.8 mm SL, Nango, Setagawa River, collected and photographed by Hiroshi Fujikawa, 21 Aug. 1981; B: NSMT-P 72597, male, 44.0 mm SL, Kushidagawa River, collected by Jyun-ichi Kitamura, 10 June 2005. Photographed by Ryu Uchiyama, 14 June 2005.

Spawning season. From late April to early August, with peak spawning in May and June.

Host mussels. Six species and subspecies of mussels have been reported as hosts for eggs of *A. tabira tabira*. *Obovalis omiensis* (Fukuhara *et al*., 1982), *Pronodularia japanensis* and *Anodonta woodiana* (Nakamura, 1963, 1969) are usually hosts for bitterling eggs. In Lake Biwa, *Unio douglasiae biwae*, *Inversiunio reinianus* and *A. calipygos* are hosts for bitterling eggs, there being no particular host selectivity evident. Selectivity of *O. omiensis* as host is unknown in Lake Biwa, however, because of the extremely low density of the former (Hirai, 1964). In a creek in Okayama City, *Obovalis omiensis* was clearly selected as host over *Unio douglasiae nipponensis*, in spite of the abundance of the latter (Kondo *et al*., 1984). No significant differences in mussel size preference by bitterlings were apparent in either Lake Biwa or the above creek (Hirai, 1964; Kondo *et al*., 1984).

Distribution. Western Honshu: Aichi, Gifu, Mie, Shiga, Kyoto, Osaka, Hyogo and Okayama Prefectures.

Remarks. *Acheilognathus t. tabira* is distinguished from the other 4 subspecies by the dorsal fin color in males (grayish vs. red in the other 4 subspecies) and more branched dorsal rays (9–11 vs. usually 9). Nakamura (1969, pl. 92B) showed that *A. t. tabira* lacked a black blotch on the dorsal fin in juveniles. The short ellipsoidal eggs of *A. t. tabira* were described by Nakamura (1969: 38) and Suzuki (1985), being the shortest among all subspecies of *Acheilognathus tabira* (ratio of major axis to minor axis: 1.4–1.7 vs. 1.4–3.3) (Table 6, Fig. 6).

Populations from Lake Biwa and adjacent areas (locality numbers 28–31, Fig. 1) were distinctive from those from the San-yo area (locality numbers 36–38) by the shorter predorsal length/SL on average (51–52 % vs. 53 % in San-yo populations), and a greater average of total vertebrae (36.4–36.9 vs. 35.9–36.1) (Tables 2 and 4). Twenty-five specimens (33% of 75 specimens) from the Ashimorigawa River had 11 branched dorsal rays. Twelve of 75 specimens had 9 branched anal rays (Table 3). The combination of 11 and 9 branched dorsal and anal rays, respectively, is similar to that in *Paracheilognathus pseudorhombeus* from Korea (Mori, 1935, table 1), which was synonymized with *Acheilognathus rhombeus* by Uchida (1939: 159–160). However, *A. t. tabira* from the Ashimorigawa River (75 specimens) differs from *P. pseudorhombeus* (9 specimens) by the dorsal fin (grayish vs. dark red in *P. pseudorhombeus*) and anal fin (white vs. pale red) color patterns in males, a shallower body (mean±SD and range of body depth/SL: 35.7±1.1, 33.3–38.0% vs. 40.4±1.6, 38.5–43.5%), shorter snout (mean±SD and range of snout length/HL: 23.5±2.1, 19.5–27.9% vs. 32.6±0.9, 31.3–34.5%) and larger orbit (mean±SD and range of OD/HL: 31.2±1.6, 27.5–35.0% vs. 26.7±1.2, 24.4–28.6%).

Acheilognathus tabira erythropterus subsp. nov.

(Japanese name: Akahire-tabira)

(New English name: Red tabira bitterling)

(Figs. 3 B–D, 6 E–G, 8)

Acheilognathus tabira: Okada and Ikeda, 1938: 102 (in part: Miyagi); Kuronuma, 1940: 235 (Chiba); Hubbs and Kuronuma, 1943: 184, figs.1–2 (Chiba).

Acheilognathus tabira subsp.: Nakamura, 1963: 149, fig. 82 (in part); Ojima *et al*., 1973: 172 (Ibaraki); Saito, 1979: 164, 1 fig. (Tochigi).

Acheilognathus tabira subsp. (a): Nakamura, 1969: 42 and 380, pl. 92C (in part); Fujikawa *et al*., 1984: 54 (in part: Ibaraki); Suzuki and Hibiya, 1985a: 184, fig. 5B (Ibaraki); Suzuki, 1985: 64, figs. 4–5 (Ibaraki); Arai

Fig. 8. *Acheilognathus tabira erythropterus* subsp. nov., ZUMT 61512, paratype, male, 64.6 mm SL, Nasu-machi, collected by Takayoshi Ueda, 28 May 2005. Photographed by Ryu Uchiyama, June 2005.

Table 3. Frequency distributions of branched dorsal fin rays/branched anal fin rays in 5 subspecies of *Acheilognathus tabira*.

Loc. No.	Cat. No.	Locality (Prefecture)	No. of specimens	8/8	8/9	9/8	9/9	9/10	10/8	10/9	10/10	11/9	11/10
A. t. tohokuensis													
1	NSMT-P 74699	Akita	10				10						
2	OKU-P 114	Akita	42		2		37	2			1		
3	NSMT-P 74700	Akita	40			2	34			3	1		
4	NSMT-P 72657, 74701	Akita	52	1		3	47	1					
5	NSMT-P 27553	Niigata	2				2						
A. t. erythropterus													
7	NSMT-P 27043	Miyagi	2				1	1					
9	NSMT-P 72656, 74702	Ibaraki	49		2	2	44						
10	NSMT-P 74703	Ibaraki	35		1	1	32	1					
A. t. jordani													
11	NSMT-P 74704	Ishikawa	38				21	2		10	5		
12	NSMT-P 74705	Ishikawa	3				3						
13	NSMT-P 74706	Ishikawa	39	1			37	1		1	1		
15	NSMT-P 74707	Toyama	49				35			13			
16	NSMT-P 74708	Ishikawa	5		1	1	3						
17	NSMT-P 72658, 74709	Ishikawa	7			3	4						
18	NSMT-P 74710	Ishikawa	32				22	1		8	1		
20	OKU-P 110	Tottori	33			5	28						
21	OKU-P 213	Shimane	48		1	2	45						
A. t. nakamurae													
22	OKU-P 154	Nagasaki	11	1			10						
22	OKU-P 171	Nagasaki	30		1	1	23			1	4		
22	NSMT-P 11004	Nagasaki	2				2						
24	NSMT-P 74712	Fukuoka	48				43	2		1	1		
25	NSMT-P 72659, 74713	Fukuoka	49			2	43	4					
26	NSMT-P 74714	Kumamoto	13				12	1					
A. t. tabira													
28	NSMT-P 74715	Shiga	8							8			
29	NSMT-P 74716	Shiga	49				3			39	5		2
30	NSMT-P 74717	Shiga	50				3			40	5	1	1
31	NSMT-P 74718	Shiga	25				3			20	2		
32	NSMT-P 74719	Osaka	36						2	28	4	1	1
33	NSMT-P 74720	Osaka	40							36	2	1	1
34	OKU-P 170	Hyogo	29			1			2	24	1	1	
35	NSMT-P 74721	Hyogo	13				3			10			
36	NSMT-P 74722	Okayama	34				2		2	26	1	2	1
37	NSMT-P 74723	Okayama	17			1				15			
38	NSMT-P 74724	Okayama	75			1	1			42	6	12	13

and Akai, 1988: 201 (in part); Okazaki *et al*., 2001: 92, figs. 3–4 (Ibaraki); Arai and Kato, 2003: 3, table 1, fig. 6C (Ibaraki).

Acheilognathus tabira subsp. 1: Sawada, 1984: 55, pl. 53 K–L (in part); Hosoya, 1993: 216 (in part); Watanabe, 1998: 262 (in part); Nagata and Fujikawa, 2000: 120, 1 fig. (in part); Ogawa, 2001: 35 (Tochigi).

Acheilognathus tabira subsp. R: Nagata, 1989: 374, 2 figs. (in part).

Paracheilognathus tabira subsp. 1: Hosoya, 1988: 155 (in part).

Holotype. NSMT-P 72656 (ex OKU-P 160-41), male, 49.5 mm SL, Lake Kasumigaura, Hama, Tamatsukuri, Ibaraki Prefecture, collected on 2 April 1982.

Paratypes. NSMT-P 74702 (ex OKU-P 160) (49: 29 males and 20 females), 41.4–62.8 mm SL, Lake Kasumigaura, Hama, Tamatsukuri, Ibaraki Prefecture, 2 Apr. 1982; NSMT-P 74703 (ex OKU-P 159) (35: 17M+18F), 40.5–56.8 mm SL, Seimeigawa River, Ami, Ibaraki Prefecture, 1–2 Apr. 1982; NSMT-P 27043 (2), 30.1 and 34.0 mm SL, Natori, Masudagawa River, Miyagi Prefecture, 26 June 1975; ZUMT 61512 (2: 1M+1F), 64.6 and 58.2 mm SL, Nasu-machi, Nakagawa River system, Tochigi Prefecture, 28 May, 2005.

Table 4. Frequency distributions and averages of numbers of vertebrae and avarages of lateral-line scales (LlSc) in 5 subspecies of *Acheilognathus tabira*.

Loc. No.	Cat. No.	Locality (Prefecture)	No. of specimens	Number of vertebrae					LlSc
				35	36	37	38	Average	Average
A. t. tohokuensis									
1	NSMT-P 74699	Akita	10		5	5		36.5	35.9
2	OKU-P 114	Akita	42		16	25	1	36.6	36.1
3	NSMT-P 74700	Akita	40		2	22	16	37.4	37.2
4	NSMT-P 72657, 74701	Akita	52		7	38	7	37.0	36.4
5	NSMT-P 27553	Niigata	2			2		37.0	
A. t. erythropterus									
7	NSMT-P 27043	Miyagi	2	1	1			35.5	
9	NSMT-P 72656, 74702	Ibaraki	49	5	37	7		36.0	35.5
10	NSMT-P 74703	Ibaraki	35	8	22	5		35.9	35.8
A. t. jordani									
11	NSMT-P 74704	Ishikawa	38		5	31	2	36.9	36.4
12	NSMT-P 74705	Ishikawa	3			3		37.0	36.5
13	NSMT-P 74706	Ishikawa	41		6	35		36.9	36.4
15	NSMT-P 74707	Toyama	48		7	32	9	37.0	36.3
16	NSMT-P 74708	Ishikawa	5		1	4		36.8	36.8
17	NSMT-P 72658, 74709	Ishikawa	7			6	1	37.1	36.3
18	NSMT-P 74710	Ishikawa	33	1	8	18	6	36.9	36.5
20	OKU-P 110	Tottori	33		24	9		36.3	36.1
21	OKU-P 213	Shimane	48	1	37	9	1	36.2	35.4
A. t. nakamurae									
22	OKU-P 154	Nagasaki	10	5	5			35.5	35.0
22	OKU-P 171	Nagasaki	27	12	15			35.6	35.3
22	NSMT-P 11004	Nagasaki	2	2				35.0	
24	NSMT-P 74712	Fukuoka	46		2	38	6	37.1	37.6
25	NSMT-P 72659, 74713	Fukuoka	49		8	36	5	36.9	36.8
26	NSMT-P 74714	Kumamoto	13		5	8		36.6	36.5
A. t. tabira									
28	NSMT-P 74715	Shiga	8		5	3		36.4	36.3
29	NSMT-P 74716	Shiga	49	1	13	30	5	36.8	36.8
30	NSMT-P 74717	Shiga	50		14	32	4	36.8	37.0
31	NSMT-P 74718	Shiga	24		6	14	4	36.9	36.7
32	NSMT-P 74719	Osaka	36	3	25	7	1	36.2	35.8
33	NSMT-P 74720	Osaka	38	9	23	6		35.9	35.5
34	OKU-P 170	Hyogo	29		17	11	1	36.4	36.1
35	NSMT-P 74721	Hyogo	13		4	9		36.7	36.1
36	NSMT-P 74722	Okayama	33	3	27	3		36.0	35.9
37	NSMT-P 74723	Okayama	16		14	2		36.1	35.9
38	NSMT-P 74724	Okayama	74	16	49	9		35.9	35.6

Diagnosis. Dorsal rays, usually iii 9; anal rays, usually iii 9; fewer total vertebrae than in all other subspecies, 36.0±0.6 (mean±SD); dorsal fin in males, red; anal fin in nuptial males, red; no black blotch on dorsal fin in juveniles; eggs ellipsoid, ratio of major axis to minor axis, 1.4–2.2 (Table 11).

Description. Morphometric and meristic data are shown in Tables 2–4. Paratype data are given in parentheses. Proportional measurements as % SL: body depth 32 (30–34), head length 24 (23–26), predorsal length 53 (50–55), caudal peduncle depth 11 (10–13); as %HL: orbit diameter 30 (28–35); as % OD: snout length 103 (51–116), barbel length 31 (24–53). Dorsal rays, iii, 9 (iii, 8–9); anal rays, iii, 9 (iii, 8–9); number of dorsal rays minus number of anal rays, 0 (−1 to 1); pectoral rays, i, 14 (i, 14–15); pelvic rays, i, 7 (i, 7); caudal rays, i+9/8+i (i+9/8+i); abdominal vertebrae, 18 (17–19); caudal vertebrae, 18 (17–19); total vertebrae, 36 (35–37); insertion of first pterygiophore in dorsal fin (D-PTG-1), 11th (10th to 12th) (Table 5); insertion of first pterygiophore in anal fin (A-PTG-1), 18th (17th or 18th). Eggs ellipsoid, ratio of major axis to minor axis, 1.4–2.2 (Table 6, Figs. 6 E–G).

Color in life. Dorsal fin in males margined with red. Lateral body surface in males greenish in spawning season (similar to that of *A. t. jordani* and *A. t. tohokuensis*); pelvic fin black proximally, margined with white along anterior edge; edge of anal fin varying from red to pale red, but usually margined with red (hence deviation of English name of subspecies). Black blotch absent from dorsal fin in juveniles.

Habitat. Rivers, lakes and ponds in plains; creeks and rivers near coasts, and mouths of rivers draining into lagoons.

Spawning season. From April to June.

Host mussels. No information available.

Etymology. The subspecific name, *erythropterus*, is a Latin adjective referring to the nuptial color of males (*erythro*=red, *pterus*=fin).

Distribution. Pacific Ocean side of eastern Honshu: Miyagi, Tochigi, Ibaraki, Chiba Prefectures and Tokyo Metropolis.

Remarks. *Acheilognathus t. erythropterus* subsp. nov. differs from the other 4 subspecies by the following combination of characters: anal fin in nuptial males edged with red, no black blotch on the dorsal fin in juveniles, fewer total vertebrae, and eggs intermediate in shape between short and long ellipsoid. *Acheilognathus t. erythropterus* (85 specimens examined) differs from *A. t. tohokuensis* (127 specimens examined) by having fewer vertebrae (mean±SD and range: 36.0±0.6, 35–37 vs. 37.0±0.6, 36–38 in *A. t. tohokuensis*) and a longer barbel (mean±SD and range of BarL/OD: 35.8±6.5, 22–56% vs. 18.7±7.8, 2–39%) (Tables 2, 4, 8, and 11). Furthermore, eggs of the former are shorter than those of the latter (ratio of major axis to minor axis, 1.4–2.2 vs. 2.0–3.3, respectively). Eggs of tabira bitterlings from Natori City, Miyagi Prefecture were similar in shape to those from Nasu-machi, Tochigi Prefecture (Table 6, Fig. 6; Saitoh *et al*., 2007). Kuronuma (1940) and Hubbs and Kuronuma (1943) reported the shape and size of eggs of *A. t. erythropterus* from Chiba Prefecture, but those eggs were still within the ovipositor. Therefore, such data is not compatible here. Komakine (1976) reported that anal fin edge in males in populations from Lake Kasumigaura was red during the spawning season, becoming pale red at the spawning peak. Ogawa (2001) suggested *Margaritifera laevis* as a host mussel for eggs of *A. t. erythropterus* from Nasu-machi, Tochigi Prefecture. Saitoh *et al*. (2007) reported that juveniles of *A. t. erythropterus* from Natori basin, Miyagi Prefecture lacked a dark blotch on the dorsal fin.

Acheilognathus tabira tohokuensis subsp. nov.

(New Japanese name: Kitanoakahire-tabira)

(New English name: Northern red tabira bitterling)

(Figs. 3A, 5 A–B, 6 A–D, 9)

Acheilognathus tabira: Ikeda and Ide, 1937: 27 (Akita); Okada and Ikeda, 1938: 102 (in part: Akita and Yamagata); Aoyagi, 1957: 100 (in part); Fujita, 1990: 213, fig. 32 (Akita); Matsuura and Arai, 1993: 62 (in part); Sugiyama, 2000: 382, 1 fig. (Akita).

Acheilognathus tabira subsp.: Nakamura, 1963: 149 (in

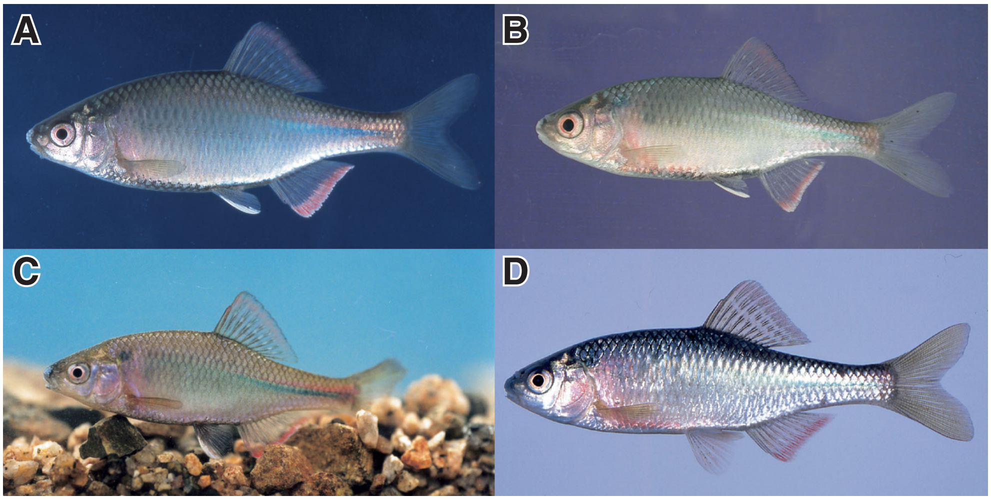

Fig. 9. *Acheilognathus tabira tohokuensis* subsp. nov. A: AKPM-P 435-2, paratype, male, 64.0 mm SL, Gojome-machi, collected and photographed by Hideki Sugiyama, 1 May 2004; B: AKPM-P 437-2, paratype, male, 48.2 mm SL, Kisakata, collected and photographed by Hideki Sugiyama, 4 June 2006; C: male, Aizu area, collected and photographed by Osamu Inaba, 13 May 2003; D: ZUMT 61513, paratype, male, 57.2 mm SL, near Teradomari, collected by Nobuo Inoue, 21 Oct. 2005, photographed by Ryu Uchiyama, 8 Nov. 2005 (after artificial induction of nuptial coloration).

part); Sugiyama, 1981: 20 (Akita); Sugiyama, 1985: 76, 2 figs. (Akita); Matsumoto *et al*., 1988: 73 (Niigata); Shimizu and Matsumoto, 1991: 287, fig. 6-9 (Niigata); Inaba, 2003: 51, fig. 3 (Fukushima).

Acheilognathus tabira subsp. (a): Nakamura, 1969: 42, pl. 92 D–E (in part: Akita, Niigata, and Fukushima).

Acheilognathus tabira subsp. 1: Nagata and Fujikawa, 2000: 120, 1 fig. (in part).

Rhodeus tabira: Sugihara, 1944: 12 (Yamagata).

Acheilognathus moriokae: Ikeda and Ide, 1937: 27 (Akita); Honma, 1952: 142 (Niigata); Kataoka, 1959: 8 (Akita); Matsumoto *et al*., 1988: 73 (Niigata).

Acheilognathus cyanostigma: Kataoka, 1959: 8 (Akita).

Holotype. NSMT-P 72657 (ex OKU-P 103-11), male, 59.0 mm SL, Lake Nishinuma, Yokote, Akita Prefecture, collected on 4 Aug. 1981.

Paratypes. NSMT-P 74701 (ex OKU-P 103) (65: 41 males and 24 females), 29.9–69.7 mm SL, Lake Nishinuma, Yokote, Akita Prefecture, 4 Aug. 1981; NSMT-P 74699 (ex OKU-P 109) (10: 5M+5F), 30.0–67.5 mm SL, Lake Kaikon-numa, Yamamoto-machi, Akita Prefecture, 28 Aug. 1978; NSMT-P 74700 (ex OKU-P 113) (40: 25M+15F), 42.9–62.9 mm SL, Lake Ogata, Kanaashi, Akita Prefecture, 5 Aug. 1981; AKPM-P 435 (5: 3M+2F), 61.8–72.6 mm SL, Gojome-machi, Akita Prefecture, 1 May, 2004; AKPM-P 436 (3 juveniles), 11.0–13.0 mm SL, Gojome-machi, Akita Prefecture, 27 June, 2004; AKPM-P 437 (5: 3M+2F), 39.8–53.3 mm SL, Kisakata, Nikaho, Akita Prefecture, 4 June, 2006; AKPM-P 438 (2 juveniles), 23.4–26.4 mm SL, Kisakata, Nikaho, Akita Prefecture, 4 June, 2006; NSMT-P 27553 (2), 57.2 and 61.0 mm SL, Yasuda-machi, Aganogawa River, Niigata Prefecture, 26 Oct. 1974; ZUMT 61513 (1M), 57.2 mm SL, near Teradomari, Niigata Prefecture, 21 Oct. 2005.

Non-type specimens. OKU-P 114 (42: 9M+33F: voucher specimens lost after examination but radiographs still available), 45.8–71.2 mm SL, Lake Hachirogata, Akita Prefecture, 5 Aug. 1981.

Diagnosis. Dorsal rays, usually iii 9; anal rays, usually iii 9; more total vertebrae than in all other subspecies, 37.0±0.6 (mean±SD); dorsal fin in males, red; anal fin in nuptial males, red; no black blotch on dorsal fin in juveniles; eggs long ellipsoid, ratio of major axis to minor axis, 2.0–3.3 (Table 11).

Description. Morphometric and meristic data are shown in Tables 2–4. Paratype and non-type data are given in parentheses. Proportional measurements as % SL: body depth 32 (29–34), head length 24 (23–26), predorsal length 53 (51–58), caudal peduncle depth 10 (10–13); as % HL: orbit diameter 31 (27–33); as % OD:

Table 5. Frequency distributions of insertion of first pterygiophore in dorsal fin (D-PTG-1) in 5 subspecies of *Acheilognathus tabira*.

Loc. No.	Cat. No.	Locality (Prefecture)	No. of specimens	10th[a]	10th[b]	11th[a]	11th[b]	12th[a]	12th[b]	13th[a]
A. t. tohokuensis										
1	NSMT-P 74699	Akita	10				6	3	1	
2	OKU-P 114	Akita	42			7	25	7	3	
3	NSMT-P 74700	Akita	40				9	19	11	1
4	NSMT-P 72657, 74701	Akita	52			1	15	26	10	
5	NSMT-P 27553	Niigata	2				1	1		
A. t. erythropterus										
7	NSMT-P 27043	Miyagi	2			2				
9	NSMT-P 72656, 74702	Ibaraki	49		1	15	21	11	1	
10	NSMT-P 74703	Ibaraki	35			5	21	9		
A. t. jordani										
11	NSMT-P 74704	Ishikawa	38			2	6	27	3	
12	NSMT-P 74705	Ishikawa	3			2		1		
13	NSMT-P 74706	Ishikawa	41			2	15	21	3	
15	NSMT-P 74707	Toyama	50			11	2	34	1	2
16	NSMT-P 74708	Ishikawa	5			5				
17	NSMT-P 72658, 74709	Ishikawa	7			2		5		
18	NSMT-P 74710	Ishikawa	33		1	11	9	11	1	
20	OKU-P 110	Tottori	33			9	17	7		
A. t. nakamurae										
22	OKU-P 154	Nagasaki	10			5	2	3		
22	OKU-P 171	Nagasaki	27			14	12	1		
22	NSMT-P 11004	Nagasaki	2				2			
24	NSMT-P 74712	Fukuoka	46				4	29	12	1
25	NSMT-P 72659, 74713	Fukuoka	49				3	35	11	
26	NSMT-P 74714	Kumamoto	13			2	5	5	1	
A. t. tabira										
28	NSMT-P 74715	Shiga	8		1	6	1			
29	NSMT-P 74716	Shiga	49	1	1	37	8	2		
30	NSMT-P 74717	Shiga	50	1	5	33	7	4		
31	NSMT-P 74718	Shiga	24		4	12	7	1		
32	NSMT-P 74719	Osaka	36	4	12	19	1			
33	NSMT-P 74720	Osaka	38	3	5	22	5	3		
34	OKU-P 170	Hyogo	29	1		18	8	2		
35	NSMT-P 74721	Hyogo	13			8	4	1		
36	NSMT-P 74722	Okayama	33	1	1	27	3	1		
37	NSMT-P 74723	Okayama	16		3	9	3	1		
38	NSMT-P 74724	Okayama	76	5	12	56	2	1		

snout length 86 (57–106), barbel length 20 (2–33). Dorsal rays, iii, 9 (iii, 8–9); anal rays, iii, 9 (iii, 8–9); number of dorsal rays minus number of anal rays, 0 (-1 to 1); pectoral rays, i, 14 (i, 14–15); pelvic rays, i, 7 (i, 7); caudal rays, i+9/8+i (i+9/8+i); abdominal vertebrae, 19 (18–19); caudal vertebrae, 18 (17–19); total vertebrae, 37 (36–38); insertion of first pterygiophore in dorsal fin (D-PTG-1), 12th (10th to 12th) (Table 5); insertion of first pterygiophore in anal fin (A-PTG-1), 19th (18th or 19th). Eggs long ellipsoid, ratio of major axis to minor axis, 2.0–3.3 (Table 6, Figs. 6 A–D).

Color in life. Dorsal fin in males margined with red. Lateral body surface in males greenish in spawning season, similar to *A. t. erythropterus* and *A. t. jordani*; pelvic fin black proximally, margined with white along anterior edge; anal fin margined with white, lined proximally by a red band. Black blotch absent from dorsal fin in juveniles (Figs. 5 A–B).

Habitat. Rivers, lakes and ponds in plains; creeks and rivers near coasts, and mouths of rivers draining into lagoons. This subspecies co-

Table 6. Size and shape of eggs in 5 subspecies of *Acheilognathus tabira*.

Subspecies	Locality	No. of eggs	Major axis (mm)	Minor axis (mm)	Ratio of major axis to minor axis	Sources
A. t. tabira	Lake Biwa	4	2.4–2.6	1.5	1.6–1.7	Nakamura 1969
A. t. tabira	Inabegawa River	3	1.8–2.1	1.2–1.3	1.4–1.7	present study
A. t. tabira	Kushidagawa River	38	1.8–2.2	1.1–1.4	1.5–1.7	present study
A. t. erythropterus	Natori City	28	2.3–2.8	1.3–1.7	1.4–2.0	H. Sugiyama, pers. comm.
A. t. erythropterus	Nasu-machi (A)	79	2.2–2.9	1.3–1.7	1.6–2.1	present study
A. t. erythropterus	Nasu-machi (B)	6			1.8–2.2*	present study
A. t. erythropterus	Lake Kasumigaura	unknown	ca. 2.3	ca. 1.35	ca. 1.7	Nakamura 1969
A. t. erythropterus	Lake Kasumigaura	2	2.1–2.2	1.1–1.3	1.6–1.9	present study
A. t. tohokuensis	Gojome-machi	21	3.1–3.5	1.3–1.6	2.0–2.6	present study
A. t. tohokuensis	Akita City	18	3.2–3.8	1.1–1.4	2.5–3.3	present study
A. t. tohokuensis	Aizu area	5			2.5–2.8*	present study
A. t. tohokuensis	near Teradomari	7	2.8–3.0	1.0–1.1	2.6–3.0	present study
A. t. jordani	Himi City	8	2.4–2.9	1.0–1.3	2.2–2.5	present study
A. t. jordani	Lake Kibagata	19			2.4–2.8*	present study
A. t. jordani	Ono City	9	2.7–2.9	1.1–1.3	2.2–2.6	present study
A. t. jordani	Oharagawa River	16	3.3–4.0	1.5–1.6	2.2–2.6	C. Oshiumi, pers. comm.
A. t. nakamurae	Tataragawa River	19	2.5–2.7	1.0–1.1	2.3–2.9	present study
A. t. nakamurae	Yanagawa City	20	2.5–2.8	1.1–1.3	2.2–2.3**	Nakamura 1969

* Measurement based on photographs.
** Range of averages.

exists with a bitterling, *Tanakia lanceolata*, in large rivers such as the Omonogawa River, and with a cyprinid, *Pseudorasbora pumila pumila*, in small ponds or reservoirs, often man-made (so-called “tameike”) (Hideki Sugiyama, pers. comm.).

Spawning season. From May to July in Akita Prefecture (Sugiyama, 2000: 382). April and May in Fukushima Prefecture (Osamu Inaba, pers. comm.).

Host mussels. Two mussels, *Unio douglasiae nipponensis* and *Anodonta woodiana*, have been found to function as hosts for eggs of *A. t. tohokuensis* in Akita Prefecture (Hideki Sugiyama, pers. comm.). This bitterling subspecies also spawns eggs into *Anemina arcaeformis*, *Pronodularia japanensis* and *Inversiunio jokohamensis* in the Aizu area, Fukushima Prefecture (Osamu Inaba, pers. comm.).

Etymology. The subspecific name, *tohokuensis*, refers to the Tohoku area, where this subspecies is distributed.

Distribution. Japan Sea side of eastern Honshu: Akita, Yamagata, Fukushima (western area) and Niigata Prefectures.

Remarks. *Acheilognathus t. tohokuensis* subsp. nov. differs from the other 4 subspecies by the following combination of characters: anal fin in nuptial males edged with red, eggs long and ellipsoid, and a black blotch absent from the dorsal fin in juveniles. Nakamura (1969, pl. 92 D–E) reported 2 juveniles (21.5 mm and 36.5 mm in total length) from Lake Goshikinuma lacking a black blotch on the dorsal fin. Osamu Inaba (pers. comm.) also noted the absence of a black blotch on the dorsal fin in juveniles from the Aizu area, Aganogawa River and Lake Goshikinuma, western Fukushima Prefecture. *Acheilognathus t. tohokuensis* (127 specimens examined) differed from *A. t. erythropterus* (85 specimens examined) by the shorter barbel (mean±SD and range of barbel length/OD: 18.7±7.8, 2–39% vs. 35.8±6.5, 22–56 % in *A. t. erythropterus*) and more vertebrae (mean±SD and range: 37.0±0.6, 36–38 vs. 36.0±0.6, 35–37) (Tables 2, 4, 8, and 11). Furthermore, the eggs of the former were longer than those of the latter (Table 6, Fig. 6).

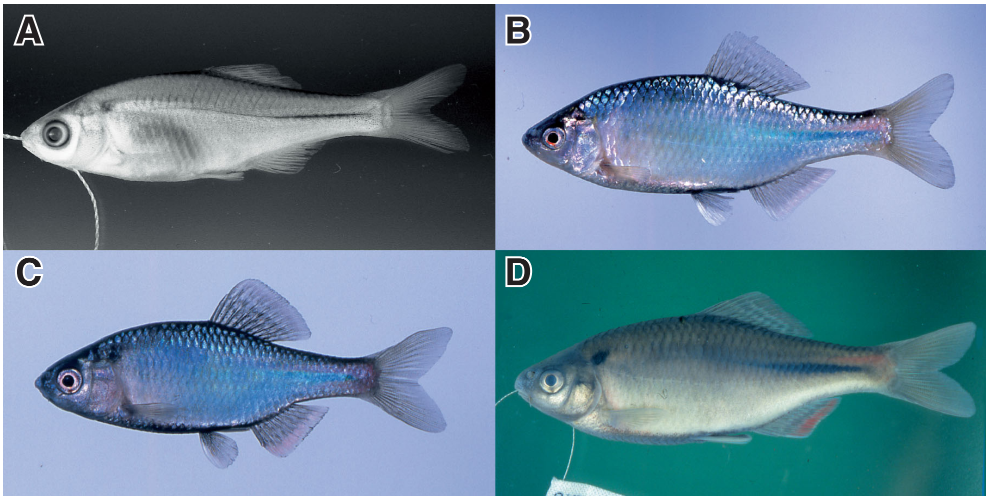

Fig. 10. *Acheilognathus tabira jordani* subsp. nov. A: NSMT-P 72658, holotype, male, 45.1 mm SL, Lake Kibagata, collected by Hiroshi Fujikawa, 18 Oct. 1981; B: NSMT-P 72594, paratype, male, 73.9 mm SL, Himi, collected by Osamu Inamura and Masaki Nishio, 29 May 2005, photographed by Ryu Uchiyama, May 2005; C: NSMT-P 72595, paratype, male, 53.1 mm SL, Ono, collected by Jun-ya Kitazima, May 2005, photographed by Ryu Uchiyama, 22 May 2005; D: OKU-P 212-1, male, 70.4 mm SL, Oharagawa River, collected and photographed by Yoshikazu Nagata, Mar. 1984.

Acheilognathus tabira jordani subsp. nov.

(New Japanese name: Minamiakahire-tabira)

(New English name: Southern red tabira bitterling)

(Figs. 4 A–B, 5 C–E, 6 H–K, 10)

Acheilognathus tabira: Aoyagi, 1957: 100 (in part); Matsuura and Arai, 1993: 72 (in part).

Acheilognathus tabira subsp.: Nakamura, 1963: 148 (in part); Nagata *et al*., 1981: 48 (Tottori); Yamaguchi, 1999: 12 (Shimane); Kawamura, 2003: 195 (Tottori and Shimane).

Acheilognathus tabira subsp. (a): Nakamura, 1969: 42 (in part); Fukuhara *et al*., 1982: 233, fig. 2C (Tottori); Fujikawa *et al*., 1984: 54 (in part: Toyama, Ishikawa, and Tottori); Saitoh *et al*., 1988: 59, fig. 2 (Shimane).

Acheilognathus tabira subsp. 1: Tanaka, 1989: 32, fig. 9 (Toyama); Watanabe, 1998: 262 (in part); Nagata and Fujikawa, 2000: 120, 1 fig. (in part).

Acheilognathus tabira subsp. R: Nagata, 1989: 374 (in part); Oshiumi, 2003 (Shimane).

Rhodeus tabira: Yanai, 1950: 18 (Shimane); Hirai, 1980: 22 (Ishikawa).

Paracheilognathus tabira: Mori, 1956: 8 (Shimane); Kato, 1985: 81, fig. 33, pl. III-13 (Fukui).

Holotype. NSMT-P 72658 (ex OKU-P 121-5), male, 45.1 mm SL, Lake Kibagata, Komatsu, Ishikawa Prefecture, collected on 18 Oct. 1981.

Paratypes. NSMT-P 74707 (ex OKU-P 116) (49: 33 males and 16 females), 39.4–63.3 mm SL, Takaoka, Toyama Prefecture, 7 Aug. 1981; NSMT-P 74705 (ex OKU-P 117) (3: 2M+1F), 66.0–70.3 mm SL, Suegawa River, Kawaradagawa River system, Mii, Wajima, Ishikawa Prefecture, 16 Oct. 1981; NSMT-P 74704 (ex OKU-P 118) (38: 26M+12F), 48.5–63.4 mm SL, Machinogawa River, Machino, Ishikawa Prefecture, 16 Oct. 1981; NSMT-P 74706 (ex OKU-P 119) (39: 19M+20F), 41.5–64.1 mm SL, Lake Akauragata, Nanao, Ishikawa Prefecture, 16 Oct. 1981; NSMT-P 74708 (ex OKU-P 120) (5: 4M+1F), 51.4–58.4 mm SL, Lake Ouchigata, Hakui, Ishikawa Prefecture, 17 Oct. 1981; NSMT-P 74709 (ex OKU-P 121) (6: 4M+2F), 40.8–49.9 mm SL, Lake Kibagata, Komatsu, Ishikawa Prefecture, 18 Oct. 1981; NSMT-PL 265 (ex OKU-P 254) (7 juveniles), 17.5–19.5 mm SL, Lake Kibagata, Komatsu, Ishikawa Prefecture, 17 June, 2005; NSMT-P 74710 (ex OKU-P 123) (33: 16M+17F), 36.7–79.0 mm SL, Lake Shibayamagata, Ishikawa Prefecture, 18 Oct. 1981; NSMT-P 72594 (2: 1M+1F), 73.9 and 58.5 mm SL, Himi, Toyama Prefecture, 29 May, 2005; NSMT-P 72595 (2: 1M+1F), 53.1 and 50.0 mm SL, Ono, Fukui Prefecture, 12 June, 2005; ZUMT 61511 (12: 7M+5F), 32.8–61.1 mm SL, Ohda, Oharagawa River, Shimane Prefecture, 4 July, 2003.

Non-type specimens. OKU-P 110 (34: 28M+6F: voucher specimens lost after examination but radiographs still available), 42.0–59.5 mm SL, Tanegaike Pond, Tottori, Tottori Prefecture, 27 June 1981; OKU-P 213 (48:

Table 7. Number of vertebrae (NV) and frequency distributions of insertion of first pterygiophore in dorsal fin in specimens characterised by 10/9 branched dorsal rays/branched anal rays in 2 subspecies of *Acheilognathus tabira*.

Loc. No.	Cat. No.	NV	No. of specimens	10th[a]	10th[b]	11th[a]	11th[b]	12th[a]	12th[b]	13th[a]
A. t. jordani										
11	NSMT-P 74704	38	1						1	
11	NSMT-P 74704	37	8					8		
11	NSMT-P 74704	36	1				1			
15	NSMT-P 74707	38	3					2		1
15	NSMT-P 74707	37	9			3		6		
15	NSMT-P 74707	36	1					1		
18	NSMT-P 74710	38	2				1	1		
18	NSMT-P 74710	37	3			2	1			
18	NSMT-P 74710	36	3			1	1	1		
A. t. tabira										
28	NSMT-P 74715	37	3			2	1			
28	NSMT-P 74715	36	5		1	4				
29	NSMT-P 74716	38	3			3				
29	NSMT-P 74716	37	25			20	4	1		
29	NSMT-P 74716	36	11	1	1	8	1			
31	NSMT-P 74718	38	4			2	2			
31	NSMT-P 74718	37	10		1	5	3	1		
31	NSMT-P 74718	36	6		3	3				

21M+27F: voucher specimens lost after examination), 42.4–66.7 mm SL, Ohda, Oharagawa River, Shimane Prefecture, 3 Aug. 1984.

Diagnosis. Dorsal rays, iii, 9–10; anal rays, iii, 9; dorsal fin in males, red; anal fin in nuptial males, red; a black blotch on dorsal fin in juveniles; eggs long ellipsoid, ratio of major axis to minor axis, 2.2–2.8 (Table 11).

Description. Morphometric and meristic data are shown in Tables 2–4. Paratype and non-type data are given in parentheses. Proportional measurements as % SL: body depth 30 (29–37), head length 24 (23–26), predorsal length 51 (51–56), caudal peduncle depth 11 (11–13); as % HL: orbit diameter 33 (27–36); as % OD: snout length 72 (58–108), barbel length 14 (9–42). Dorsal rays iii, 9 (iii, 8–10); anal rays iii, 9 (iii, 8–10); number of dorsal rays minus number of anal rays, 0 (−1 to 1); pectoral rays, i, 14 (i, 14–15); pelvic rays, i, 7 (i, 7); caudal rays, i+9/8+i (i+9/8+i); abdominal vertebrae, 18 (17–20); caudal vertebrae, 19 (17–20); total vertebrae, 37 (35–38); insertion of first pterygiophore in dorsal fin (D-PTG-1), 11th (10th to 13th) (Table 5); insertion of first pterygiophore in anal fin (A-PTG-1), 18th (18th to 20th). Eggs long ellipsoid in populations from Himi (Toyama), Lake Kibagata (Ishikawa), Ono (Fukui) and the Oharagawa River (Shimane), ratio of major axis to minor axis, 2.2–2.8 (Table 6, Figs. 6 H–K).

Color in life. Dorsal fin in males margined with red. Lateral body surface in males more greenish in spawning season than in *A. tabira tabira*; pelvic fin black proximally, margined with white along anterior edge; anal fin generally margined with red, varying from red to pale red in nuptial males. Black blotch on the dorsal fin in juveniles from Lake Kibagata, Ishikawa Prefecture, and the Oharagawa River, Shimane Prefecture (Figs. 5 C–E), but not in adult females.

Habitat. Rivers, lakes and ponds in plains: creeks near coasts, and mouths of rivers draining into lagoons.

Spawning season. From April to June.

Host mussels. *Unio douglasiae nipponensis* was found to be a host mussel for eggs of this bitterling subspecies (Nagata *et al*., 1981).

Etymology. The subspecific name, *jordani*, is named after David Starr Jordan, who made a great contribution to Japanese ichthyology and was the first author of the original description of *Acheilognathus tabira*.

Distribution. Japan Sea side of western Honshu: Toyama, Ishikawa, Fukui, Tottori and Shimane Prefectures.

Remarks. *Acheilognathus t. jordani* subsp. nov. differs from the other 4 subspecies by the following combination of characters: anal fin in nuptial males edged with red, eggs long ellipsoid, a black blotch on the dorsal fin in juveniles, but lacking in adults. Although the whitish-edged anal fin of a nuptial male from Himi, Toyama Prefecture, is figured here (Fig. 4A), red-edged anal fins in males from Himi have also been reported (Tanaka, 1997: 240, fig. 1). Osamu Inamura (pers. comm.) noted that the edge of the anal fin in nuptial males from Himi changed from red to pale red. This subspecies is clearly separated from *A. t. erythropterus* and *A. t. tohokuensis* by the black blotch presentation on the dorsal fin in juveniles. Saitoh *et al*. (1988) reported short ellipsoidal eggs (Japanese 'keiran' type) of *A. t. jordani* from the Oharagawa River, but the eggs examined by them were still ovarian (not fully ripened). Oshiumi (2003) first reported that ripened eggs of bitterling from this area were, in fact, long ellipsoid. The number of total vertebrae of populations from the San-in area (locality numbers 20–21) was fewer than that of populations north of the Hokuriku area (Table 4). As shown in Table 3, 31 specimens (26% of 118 specimens examined) of *A. t. jordani* from 3 populations (locality numbers 11, 15 and 18) in the Hokuriku area had a combination of 10 branched dorsal rays and 9 branched anal rays, such being characteristic of *A. t. tabira*. The combination of characters such as total vertebral number, the D-PTG-1 (Table 7) and the whitish-edged anal fin in nuptial males from Toyama Prefecture, which is very similar to that of *A. t. tabira* (Nakamura, 1969: 43), suggests genetic introgression from *A. t. tabira* to *A. t. jordani* in the Hokuriku area (locality numbers 15 and 18) or vice versa. A boundary between the distributions of *A. t. jordani* and *A. t. tohokuensis* corresponds to the Fossa Magna, considered important for speciation of Japanese freshwater fishes (Watanabe, 1998; Watanabe *et al*., 2006). Molecular analyses of lactate and malate dehydrogenase isozymes in *Acheilognathus tabira* by Fujikawa *et al*. (1984) indicated that among the presently-recognized subspecies, *A. t. jordani* is more closely related to *A. t. erythropterus* than to *A. t. nakamurae*.

Acheilognathus tabira nakamurae subsp. nov.

(Japanese name: Seboshi-tabira)

(New English name: Blotched tabira bitterling)

(Figs. 4D, 5F, 6N, 11)

Acheilognathus tabira: Aoyagi, 1957: 100 (in part).

Acheilognathus tabira subsp.: Nakamura, 1963: 149, fig. 83; Ojima *et al*., 1973: 172 (Fukuoka); Kimura, 2003: 150.

Acheilognathus tabira subsp. (b): Nakamura, 1969: 45 and 380, pls. 2 C–C′, 16, 17, and 93 (Fukuoka); Tomoda, 1970: 203 (Nagasaki); Fukuhara *et al*., 1982: 233, fig. 2D (Fukuoka); Fujikawa *et al*., 1984: 54 (Fukuoka

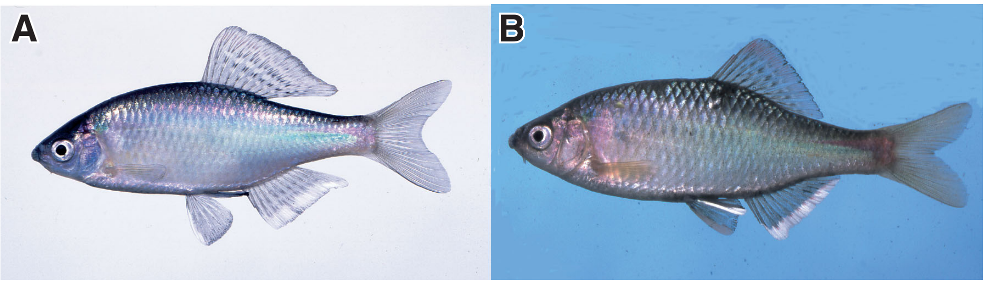

Fig. 11. *Acheilognathus tabira nakamurae* subsp. nov. A: male, 94 mm total length, Futatsukawa River, collected and photographed by Ryu Uchiyama, June 1995; B: OKU-P 171-21, male, 59.8 mm SL, Hatahokogawa River, collected by Hiroshi Fujikawa, 26 May 1982, photographed by Hiroshi Fujikawa, 27 May 1982.

and Nagasaki); Suzuki and Hibiya, 1985a: 184, fig. 5C (Fukuoka); Suzuki and Hibiya, 1985b: 339, fig. 3B (Fukuoka); Suzuki, 1985: 64, figs. 6–7 (Fukuoka); Arai and Akai, 1988: 201; Okazaki *et al*., 2001: 92, figs. 3–4 (Fukuoka); Arai and Kato, 2003: 3, table 1 (Fukuoka).

Acheilognathus tabira subsp. 2: Sawada, 1984: 55, pl. 53 M–N; Hosoya, 1993: 216; Watanabe, 1998: 262; Tashima, 1999: 9 (Fukuoka); Imasaka, 1999: 23 (Fukuoka); Nagata and Yokoyama, 2000: 122.

Acheilognathus tabira subsp. S: Nagata, 1989: 376, 4 figs.

Paracheilognathus tabira subsp. 2: Hosoya, 1988: 155.

Rhodeus (?) *tabira*: Azuma *et al*., 1977: 317 (Nagasaki).

Rhodeus (?) *tabira* subsp. 2: Kawanabe, 1987: 27, 3 figs.

Holotype. NSMT-P 72659 (ex OKU-P 163-36), male, 54.0 mm SL, Futatsukawa River, Yanagawa, Fukuoka Prefecture, collected on 15 Apr. 1982.

Paratypes. NSMT-P 74713 (ex OKU-P 163) (48: 30 males and 18 females), 40.3–64.9 mm SL, Futatsukawa River, Yanagawa, Fukuoka Prefecture, 16 Apr. 1982; NSMT-P 75167 (ex OKU-P 138) (11: 3M+8F), 47.2–59.7 mm SL, Futatsukawa River, Yanagawa, Fukuoka Prefecture, 3 Sep. 1980; NSMT-P 74712 (ex OKU-P 165) (48: 10M+38F), 45.9–74.0 mm SL, Horikawayosui River, Asakura, Fukuoka Prefecture, 16 Apr. 1982; NSMT-P 74714 (ex OKU-P 162) (13: 5M+8F), 47.8–64.6 mm SL, Lake Shimoezuko, Kumamoto Prefecture, 14–15, Apr. 1982; NSMT-P 74711 (ex OKU-P 253) (57), 50.8–68.8 mm SL, Hatahokogawa River, Iki Islands, Nagasaki Prefecture, 28 July 1976; NSMT-P 11004 (2), 68.8 and 73.5 mm SL, Hatahokogawa River, Iki Islands, Nagasaki Prefecture, 1 Sep. 1969; NSMT-P 72596 (1M), 76.4 mm SL, Tataragawa River, Fukuoka Prefecture, 23 May 2005.

Non-type specimens. OKU-P 154 (11: 5M+5F+1 sex unknown: voucher specimens lost after examination but radiographs still available), 16.1–72.4 mm SL, Hatahokogawa River, Iki Islands, Nagasaki Prefecture, 4 Aug. 1977; OKU-P 171 (30: 8M+22F: voucher specimens lost after examination but radiographs still available), 42.2–73.5 mm SL, Hatahokogawa River, Iki Islands, Nagasaki Prefecture, 26 May 1982.

Diagnosis. Dorsal rays, iii 9; anal rays, iii 9; dorsal fin in males, red; anal fin in nuptial males, white; a black blotch on dorsal fin in juveniles and small adult females; eggs long ellipsoid, ratio of major axis to minor axis, 2.3–2.9 (Table 11).

Description. Morphometric and meristic data are shown in Tables 2–4. Paratype and non-type data are given in parentheses. Proportional measurements as % SL: body depth 32 (30–37), head length 24 (22–25), predorsal length 55 (51–57), caudal peduncle depth 12 (11–13); as % HL: orbit diameter 34 (27–36); as % OD: snout length 74 (63–117), barbel length 37 (18–59). Dorsal rays, iii, 9 (iii, 9–10); anal rays, iii, 9 (iii, 8–10); number of dorsal rays minus number of anal rays, 0 (−1 to 1); pectoral rays, i, 14 (i, 14–15); pelvic rays, i, 7 (i, 7); caudal rays, i+9/8+i (i+9/8+i); abdominal vertebrae, 19 (18–20); caudal vertebrae, 18 (17–19); total vertebrae, 37 (35–38); insertion of first pterygiophore in dorsal fin (D-PTG-1), 12th (11th to 13th) (Table 5); insertion of first pterygiophore in anal fin (A-PTG-1), 19th (18th or 19th). Eggs long ellipsoid, ratio of major axis to minor axis, 2.3–2.9 (Table 6, Fig. 6N).

Color in life. Dorsal fin in males margined with red. In spawning males, lateral body surface brightly greenish-blue; anal fin margined with white; pelvic fin black proximally, margined with white along anterior edge. A black blotch on the dorsal fin (from which the English name was derived) was observed in an adult female (50.2 mm SL) from Fukuoka Prefecture (Fig. 5F), and in a juvenile (16.1 mm SL) and 2 small adult females (37.2 and 39.9 mm SL) from the Iki Islands, Nagasaki Prefecture.

Habitat. Rivers and creeks in plains.

Spawning season. From February to August, peaking from April to June in the Futatsukawa River, Yabegawa River system, Yanagawa, Kyushu (Nagata and Nakata, 1988). This subspecies starts spawning earlier than all other subspecies of *A. tabira*.

Host mussels. Four mussel species, *Obovalis omiensis*, *Pronodularia japanensis*, *Anodonta woodiana* and *Corbicula leana* have been reported as hosts for eggs of this subspecies, *O. omiensis* being the primary host, in spite of its low density (4% of all mussels), in the Futatsukawa River, where coexisting *C. leana* was rarely utilized (Matsushima, 1980). *Obovalis omiensis* has also been reported as a primary host in other creeks. It is interesting that *Acheilognathus t. nakamurae* has not been collected at stations where *O. omiensis* was not found (Fukuhara *et*

Table 8. Morphometrics and meristics of specimens >40 mm SL in 5 subspecies of *Acheilognathus tabira*.

Subspecies No. of specimens	*tabira* 323		*erythropterus* 85		*tohokuensis* 127		*jordani* 249		*nakamurae* 144	
	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range	Mean±SD	Range
SL (mm)	54.0±8.7	40.1–79.3	48.1±3.9	40.5–62.8	53.7±6.4	42.9–71.2	51.6±6.2	40.1–71.2	55.0±7.9	40.3–74.0
Morphometrics										
% SL										
Body depth	34.3±1.5	28.2–38.0	31.9±1.1	29.6–35.8	31.9±1.2	28.9–35.6	31.9±1.6	28.0–37.3	33.1±1.5	29.6–37.2
Head length	24.1±1.1	20.5–27.3	24.1±0.7	22.6–26.3	24.6±0.8	22.9–26.9	23.9±0.8	21.4–26.9	23.4±1.0	20.8–26.2
Predorsal length	52.5±1.4	48.8–57.2	52.8±1.2	50.2–55.8	54.0±1.3	51.2–57.9	53.1±1.2	49.7–59.1	53.8±1.4	50.6–57.3
Caudal peduncle depth	11.8±0.6	9.6–13.3	11.4±0.6	10.2–13.0	11.2±0.7	8.9–13.0	11.7±0.7	9.9–14.2	12.0±0.6	10.0–13.6
% Head length										
Orbit diameter	32.2±2.2	28–40	31.1±2.0	27–35	30.2±1.7	27–34	30.6±1.9	27–36	31.1±2.1	25–37
% Orbit diameter										
Snout length	78.9±11.7	40–109	88.6±14.6	38–127	84.0±11.4	53–111	85.0±9.8	56–113	87.8±15.5	49–139
Barbel length	32.1±8.4	9–60	35.8±6.5	22–56	18.7±7.8	2–39	24.3±8.6	8–65	38.1±8.4	18–58
Meristics										
Branched dorsal rays	10.1±0.4	9–11	9.0±0.2	8–10	9.0±0.2	9–10	9.1±0.4	8–10	9.0±0.2	8–10
Branched anal rays	9.1±0.4	8–10	9.0±0.3	7–10	9.0±0.3	8–10	9.0±0.3	8–10	9.0±0.3	8–10
Abdominal vertebrae	18.2±0.6	17–20	17.9±0.4	17–19	18.8±0.5	18–20	18.5±0.5	17–20	18.6±0.5	18–20
Caudal vertebrae	18.2±0.6	17–20	18.1±0.5	17–19	18.2±0.6	17–19	18.2±0.6	17–20	18.0±0.6	17–20
Lateral-line scales	36.2±1.0	34–39	35.7±0.8	33–38	36.6±0.9	33–39	36.2±1.0	33–39	36.6±1.2	33–40

Table 9. Loadings of the log-transformed measurements on the first 3 principal components of *Acheilognathus tabira tabira* (323 specimens), *A. t. erythropterus* (85), *A. t. tohokuensis* (127), *A. t. jordani* (249) and *A. t. nakamurae* (144) .

	PC 1	PC 2	PC 3
Proportion	84.641	8.365	3.7706
Cumulative proportion	84.641	93.007	96.7771
Loadings			
Body depth	0.429	−0.158	−0.27899
Head length	0.431	0.011	0.11462
Predorsal length	0.431	−0.013	−0.14441
Caudal peduncle depth	0.418	−0.123	−0.55569
Orbit diameter	0.388	−0.458	0.71983
Snout length	0.345	0.866	0.24744

Table 10. Loadings of the meristics on the first 2 principal components of *Acheilognathus tabira tabira* (323 specimens), *A. t. erythropterus* (85), *A. t. tohokuensis* (127), *A. t. jordani* (249) and *A. t. nakamurae* (144).

	PC 1	PC 2
Proportion	30.803	25.677
Cumulative proportion	30.803	56.480
Loadings		
Branched dorsal rays	−0.392	0.525
Branched anal rays	−0.250	0.606
Abdominal vertebrae	0.674	0.190
Caudal vertebrae	−0.129	0.302
Lateral-line scales	0.560	0.480

al., 1998).

Etymology. The subspecific name, *nakamurae*, is named after Morizumi Nakamura, who contributed greatly to the systematics of Japanese bitterlings.

Distribution. Kyushu area: Fukuoka, Saga and Kumamoto Prefectures, and Iki Islands in Nagasaki Prefecture.

Remarks. *Acheilognathus t. nakamurae* subsp. nov. differs from the other 4 subspecies by the following combination of characters: edge of the dorsal fin in males red, anal fin in nuptial males edged with white, and a black blotch on the dorsal fin in juveniles and small adult females (Nakamura, 1969, pl. 93 B and D). Nakamura (1969: 37) reported that the anal fin in nuptial males was rarely reddish-white. Nakamura (1969: 46), Suzuki (1985) and Hosoya (1988, 1993) all described eggs of this subspecies as being usually long ellipsoid, but short ellipsoidal eggs have been infrequently observed. Nobuhiro Suzuki (pers. comm.) suggested that such short ellipsoidal eggs may not have been fully ripe. Populations from the Iki Islands (locality number 22) differed from those on the Kyushu mainland (locality numbers 24–26) by having deeper body, fewer total vertebrae and different insertion of the first pterygiophore in the dorsal fin (D-PTG-1) (Tables 2, 4, and 5).

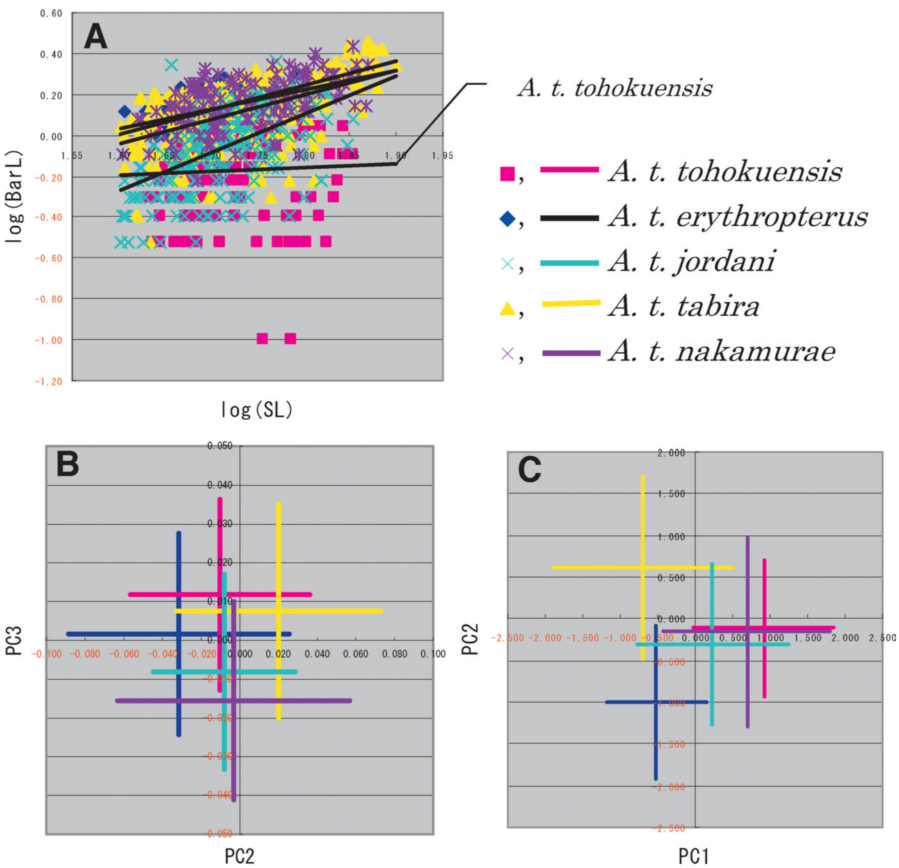

Fig. 12. Statistical analyses of morphometric and meristic characters in 5 subspecies of *Acheilognathus tabira*. A: Relationship between $\log_{10}$ standard length (SL) and $\log_{10}$ barbel length (BarL); B: average and standard deviation of scores on PC2 and PC3 of 6 morphometric characters; C: average and standard deviation of scores on PC1 and PC2 of 5 meristic characters.

Statistical Analyses of Morphometric and Meristic Characters

Statistical analyses of 7 morphometric and 5 meristic characters were carried out (Table 8). Although the barbel length tended to be shorter in large specimens of *A. t. tohokuensis* than in the other 4 subspecies (Fig. 12A), the large variance in barbel length in *A. t. tohokuensis* and large overlap among the subspecies (Fig. 12A) precluded the treatment of that character as diagnostic for *A. t. tohokuensis*.

In a principal component analysis (PCA) on the 6 remaining $\log_{10}$-transformed morphometric characters, the loadings of the variables on the first principal component (PC1) were all positive and of similar magnitude (0.345–0.431) (Table 9), indicating that the axis can be interpreted as a proxy for general size. The PC2 and PC3 scores largely overlapped among the subspecies (Fig. 12B), indicating the absence of diagnostic characters.

PCA on the 5 meristic characters showed *A. t. erythropterus* to overlap less with *A. t. tohokuensis* on the PC1 (Fig. 12C). The loadings of abdominal vertebral and lateral-line scale numbers were high on PC1 (Table 10), indicating that those characters were useful for separating *A. t. erythropterus* from *A. t. tohokuensis*. In fact, raw data of the number of lateral-line scales separated *A. t. erythropterus* from *A. t. tohokuensis* (Table 4). The PC2 of meristic characters showed *A. t. tabira* to be largely separated from *A. t. erythropterus* (Fig. 12C). Loadings of branched anal ray and branched dorsal ray numbers were high on this principal axis (Table 10). However, raw data for the number of branched dorsal rays separated *A. t. tabira* from all of the other 4 subspecies (Table 3).

The diagnostic characters and distribution of 5 subspecies of *Acheilignathus tabira* are detailed in Table 11.

Table 11. Diagnostic characters (*) and distribution of 5 subspecies of *Acheilognathus tabira*.

Subspecies	*tabira*	*nakamurae*	*erythropterus*	*tohokuensis*	*jordani*
Egg shape (Ratio of major axis to minor axis)	short ellipsoid (1.4 to 1.7)	long ellipsoid (2.3 to 2.9)	middle ellipsoid (1.4 to 2.2)	long ellipsoid (2.0 to 3.3)	long ellipsoid (2.2 to 2.8)
Black blotch on dorsal fin in juveniles	absent	present	absent	absent	present
Black blotch on dorsal fin in small adult females	absent	present	absent	absent	absent
Color of dorsal fin in males	grayish	red	red	red	red
Color of anal fin in nuptial males	white	white	red	red	red
Spawning season	April to August	February to August	April to June	May to July	April to June
Barbel length (BarL/OD)	long (32.1±8.4%)	long (38.1±8.4%)	long (35.8±6.5%)	short (18.7±7.8%)	long (24.3±8.6%)
Branched dorsal rays	10.1±0.4	9.0±0.2	9.0±0.2	9.0±0.2	9.1±0.4
Number of dorsal rays minus number of anal rays	0.96±0.43	−0.01±0.29	0.01±0.36	0.01±0.29	0.16±0.41
Insertion of 1st pterygiophore in dorsal fin	10th to 12th	11th to 13th	10th to 12th	11th to 13th	10th to 13th
Total vertebrae	more (36.4±0.7)	more (36.6±0.8)	fewer (36.0±0.6)	more (37.0±0.6)	more (36.7±0.6)
Lateral-line scales	36.2±1.0	36.6±1.2	35.7±0.8	36.6±0.9	36.2±1.0
Distribution	Western Honshu	Kyushu	Pacific Ocean side of eastern Honshu	Japan Sea side of eastern Honshu	Japan Sea side of western Honshu

*Proportional measurements of barbel length and meristic characters taken from specimens >40 mm SL.

Key to 11 Species and Subspecies of *Acheilognathus* from Japan

1a. Scales in lateral series more than 55 ....*A. typus* (eastern Honshu)
1b. Scales in lateral series less than 41 2

2a. Branched dorsal rays 12–13 ....*A. rhombeus* (western Japan*)
2b. Branched dorsal rays more than 13...3
2c. Branched dorsal rays less than 12...4

3a. Number of dorsal rays minus number of anal rays 3–6 ....
....*A. macropterus* (Lake Kasumigaura)
3b. Number of dorsal rays minus number of anal rays 0–2 .....*A. longipinnis* (Kinki and Chubu area)

4a. Branched dorsal rays usually 10; edge of dorsal fin in males grayish; edge of anal fin in males white during spawning season ....*A. tabira tabira* (western Honshu)
4b. Branched dorsal rays less than 10..5

5a. Branched dorsal rays 8...*A. cyanostigma* (western Japan)
5b. Branched dorsal rays usually 9 6

6a. Branched anal rays 8; edge of dorsal fin in males black ....*A. melanogaster* (eastern Honshu)
6b. Branched anal rays usually 9, edge of dorsal fin in males red...7

7a. Edge of anal fin in males white during spawning season; a black blotch on dorsal fin in small adult females ....***A. tabira nakamurae*** subsp. nov. (Kyushu)
7b. Edge of anal fin in males red during spawning season; no black blotch on dorsal fin in small adult females... 8

8a. A black blotch on dorsal fin in juveniles ....
....***A. tabira jordani*** subsp. nov. (Japan Sea side of western Honshu)
8b. No black blotch on dorsal fin in juveniles. 9

9a. Ellipsoidal eggs short, 1.4–2.2 in ratio of major axis to minor axis; total vertebrae fewer in number, 36.0±0.6 (mean±SD) ....
.................................***A. tabira erythropterus*** subsp. nov. (Pacific Ocean side of eastern Honshu)
9b. Ellipsoidal eggs long, 2.0–3.3 in ratio of major axis to minor axis; total vertebrae more numerous, 37.0±0.6 (mean±SD)..
....***A. tabira tohokuensis*** subsp. nov. (Japan Sea side of eastern Honshu)

*Distribution expanded to eastern Honshu by artificial transplantation.

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