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).


*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* subsp. (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 western Honshu were found to be longer ellipsoidal (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, whereas it occurred in both juveniles and small adult females 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 vertebrae (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...
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-

<table>
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<th>No. of specimens</th>
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<th>Locality</th>
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* Locality numbers correspond to those in Fig. 1.
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,

and 92 A–B; Ojima et al., 1973: 172, fig. 7 (Osaka and Okayama); Fukuharra 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; Arai and Kato, 2003: 3, table 1, fig. 6B (Shiga).


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


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, Nakajimaoike 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*.

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<th>HL/SL (%)</th>
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<th>CPD/SL (%)</th>
<th>OD/HL (%)</th>
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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.
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 japonensis 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%).

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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.
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

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

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| 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 |
| 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 | 1 | 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 |
| 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 |
| 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 | 3 | 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 | 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).


**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.

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**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, *erythroro*pterus, is a Latin adjective referring to the nuptial color of males (*eryth*ro=red, *pterus*=fin).

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

**Remarks.** *Acheilognathus t. erythroro*pterus 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. erythroro*pterus (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 (Saitoh et al., 2007). Kuronuma (1940) and Hubbs and Kuronuma (1943) reported the shape and size of eggs of *A. t. erythroro*pterus 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. erythroro*pterus from Nasu-machi, Tochigi Prefecture. Saitoh et al. (2007) reported that juveniles of *A. t. erythroro*pterus 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* subsp.: Nakamura, 1963: 149 (in
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. 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.


**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:
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 (H11002 1 to 1); pectoral rays, i, 14 (i, 14–15); pelvic rays, i, 7 (i, 7); caudal rays, i+9/8+1 (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-

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

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<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>34</td>
<td>OKU-P 170</td>
<td>Hyogo</td>
<td>29</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>35</td>
<td>NSMT-P 74721</td>
<td>Hyogo</td>
<td>13</td>
<td>8</td>
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<tr>
<td>36</td>
<td>NSMT-P 74722</td>
<td>Okayama</td>
<td>33</td>
<td>1</td>
<td>27</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>37</td>
<td>NSMT-P 74723</td>
<td>Okayama</td>
<td>16</td>
<td>3</td>
<td>9</td>
<td>3</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>38</td>
<td>NSMT-P 74724</td>
<td>Okayama</td>
<td>76</td>
<td>5</td>
<td>12</td>
<td>56</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 douglasi-an 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 japonensis* 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).

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

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>Locality</th>
<th>No. of eggs</th>
<th>Major axis (mm)</th>
<th>Minor axis (mm)</th>
<th>Ratio of major axis to minor axis</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. t. tabira</em></td>
<td>Lake Biwa</td>
<td>4</td>
<td>2.4–2.6</td>
<td>1.5</td>
<td>1.6–1.7</td>
<td>Nakamura 1969</td>
</tr>
<tr>
<td><em>A. t. tabira</em></td>
<td>Inabegawa River</td>
<td>3</td>
<td>1.8–2.1</td>
<td>1.2–1.3</td>
<td>1.4–1.7</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tabira</em></td>
<td>Kushidagawa River</td>
<td>38</td>
<td>2.3–2.8</td>
<td>1.3–1.7</td>
<td>1.4–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. erythropterus</em></td>
<td>Natori City</td>
<td>2</td>
<td>2.2–2.9</td>
<td>1.3–1.7</td>
<td>1.6–2.1</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. erythropterus</em></td>
<td>Nasu-machi (A)</td>
<td>79</td>
<td>1.8–2.2</td>
<td>1.1–1.4</td>
<td>1.5–1.7</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. erythropterus</em></td>
<td>Nasu-machi (B)</td>
<td>6</td>
<td>2.3–2.8</td>
<td>1.3–1.7</td>
<td>1.4–2.0</td>
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<tr>
<td><em>A. t. erythropterus</em></td>
<td>Lake Kasumigaura</td>
<td>unknown</td>
<td>2.0–2.5</td>
<td>1.2–1.4</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. erythropterus</em></td>
<td>Lake Kasumigaura</td>
<td>2</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. erythropterus</em></td>
<td>Goshikinuma</td>
<td>3</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Akita City</td>
<td>18</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Aizu area</td>
<td>5</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>near Teradomari</td>
<td>7</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Himi City</td>
<td>8</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Kichibata</td>
<td>2</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Ono City</td>
<td>9</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. tohokuensis</em></td>
<td>Ohara River</td>
<td>16</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. nakamurae</em></td>
<td>Tataragawa</td>
<td>19</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
<tr>
<td><em>A. t. nakamurae</em></td>
<td>Yanagawa City</td>
<td>20</td>
<td>2.0–2.5</td>
<td>1.1–1.2</td>
<td>1.5–2.0</td>
<td>present study</td>
</tr>
</tbody>
</table>

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


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


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:...
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. (b): Nakamura, 1969: 45 and 380, pls. 2 C–C’, 16, 17, and 93 (Fukuoka); Tomoda, 1970: 203 (Nagasaki); Fukuura *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.](image)
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. S: Nagata, 1989: 376, 4 figs.


Rhodeus (?) *tabira* subsp. 2: Kawanabe, 1987: 20, 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 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); anal fin (A-PTG-1), 19th (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 japonensis*, *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*.

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>No. of specimens</th>
<th>Morphometrics</th>
<th>Meristics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SL (mm)</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>Mean±SD</td>
<td>Range</td>
</tr>
<tr>
<td><em>tabira</em></td>
<td>323</td>
<td>54.0±8.7</td>
<td>40.1–79.3</td>
</tr>
<tr>
<td><em>erythropterus</em></td>
<td>85</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>tohokuensis</em></td>
<td>127</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>jordani</em></td>
<td>249</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>nakamurae</em></td>
<td>144</td>
<td></td>
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</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Morphometrics</th>
<th>% SL</th>
<th>% Head length</th>
<th>% Orbit diameter</th>
<th>% Snout length</th>
<th>% Barbel length</th>
<th>Loadings</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>SL (mm)</td>
<td>54.0±8.7</td>
<td>40.1–79.3</td>
<td>48.1±3.9</td>
<td>40.5–62.8</td>
<td>53.7±6.4</td>
<td>42.9–71.2</td>
<td>51.6±6.2</td>
<td>40.1–71.2</td>
<td>55.0±7.9</td>
</tr>
<tr>
<td>Body depth</td>
<td>34.3±1.5</td>
<td>28.2–38.0</td>
<td>24.1±1.1</td>
<td>20.5–27.3</td>
<td>25.2±1.4</td>
<td>18.8–57.2</td>
<td>10.8±0.6</td>
<td>9.6–13.3</td>
<td>31.1±2.2</td>
</tr>
<tr>
<td>Head length</td>
<td>31.9±1.1</td>
<td>29.6–35.8</td>
<td>24.1±0.7</td>
<td>22.6–26.3</td>
<td>25.2±1.2</td>
<td>20.2–52.8</td>
<td>11.4±0.6</td>
<td>9.6–13.3</td>
<td>31.1±2.0</td>
</tr>
<tr>
<td>Predorsal length</td>
<td>11.8±0.6</td>
<td>9.6–13.3</td>
<td>24.1±0.7</td>
<td>22.6–26.3</td>
<td>25.2±1.2</td>
<td>20.2–52.8</td>
<td>11.4±0.6</td>
<td>9.6–13.3</td>
<td>31.1±2.0</td>
</tr>
<tr>
<td>Caudal peduncle depth</td>
<td>11.8±0.6</td>
<td>9.6–13.3</td>
<td>24.1±0.7</td>
<td>22.6–26.3</td>
<td>25.2±1.2</td>
<td>20.2–52.8</td>
<td>11.4±0.6</td>
<td>9.6–13.3</td>
<td>31.1±2.0</td>
</tr>
<tr>
<td>% Head length</td>
<td>30.2±1.7</td>
<td>27–34</td>
<td>17.8±1.1</td>
<td>9–60</td>
<td>18.1±0.8</td>
<td>9–60</td>
<td>17.6±1.0</td>
<td>33–39</td>
<td>16.6±1.2</td>
</tr>
<tr>
<td>% Orbit diameter</td>
<td>30.2±1.7</td>
<td>27–34</td>
<td>17.8±1.1</td>
<td>9–60</td>
<td>18.1±0.8</td>
<td>9–60</td>
<td>17.6±1.0</td>
<td>33–39</td>
<td>16.6±1.2</td>
</tr>
<tr>
<td>% Snout length</td>
<td>78.9±11.7</td>
<td>40–109</td>
<td>88.6±14.6</td>
<td>38–127</td>
<td>84.0±11.4</td>
<td>53–111</td>
<td>85.0±9.8</td>
<td>56–113</td>
<td>87.8±15.2</td>
</tr>
<tr>
<td>% Barbel length</td>
<td>32.1±8.4</td>
<td>9–60</td>
<td>35.8±6.5</td>
<td>22–56</td>
<td>18.7±7.8</td>
<td>2–39</td>
<td>24.3±8.6</td>
<td>8–65</td>
<td>38.1±8.4</td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion</td>
<td>84.641</td>
<td>8.365</td>
</tr>
<tr>
<td>Cumulative proportion</td>
<td>84.641</td>
<td>93.007</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Loadings</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body depth</td>
<td>0.429</td>
<td>−0.158</td>
<td>−0.27899</td>
</tr>
<tr>
<td>Head length</td>
<td>0.431</td>
<td>0.011</td>
<td>0.11462</td>
</tr>
<tr>
<td>Predorsal length</td>
<td>0.431</td>
<td>−0.013</td>
<td>−0.14441</td>
</tr>
<tr>
<td>Caudal peduncle depth</td>
<td>0.418</td>
<td>−0.123</td>
<td>−0.55569</td>
</tr>
<tr>
<td>Orbit diameter</td>
<td>0.388</td>
<td>−0.458</td>
<td>0.71983</td>
</tr>
<tr>
<td>Snout length</td>
<td>0.345</td>
<td>0.866</td>
<td>0.24744</td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion</td>
<td>30.803</td>
</tr>
<tr>
<td>Cumulative proportion</td>
<td>30.803</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Loadings</th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branched dorsal rays</td>
<td>−0.392</td>
<td>0.525</td>
</tr>
<tr>
<td>Branched anal rays</td>
<td>−0.250</td>
<td>0.606</td>
</tr>
<tr>
<td>Abdominal vertebrae</td>
<td>0.674</td>
<td>0.190</td>
</tr>
<tr>
<td>Caudal vertebrae</td>
<td>−0.129</td>
<td>0.302</td>
</tr>
<tr>
<td>Lateral-line scales</td>
<td>0.560</td>
<td>0.480</td>
</tr>
</tbody>
</table>
Etymology. The subspecific name, nakamurae, is named after Morizumi Nakamura, who contributed greatly to the systematics of Japanese bitterlings.


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 log10-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 *Acheilognathus tabira* are detailed in Table 11.

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

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

We would like to thank Ryu Uchiyama (Shirahama-machi, Wakayama Prefecture), Hideki Sugiyama (Akita Prefectural Institute of Fisheries, Oga), Osamu Inamura (Uozu City Board of Education, Uozu), Jyun-ichi Kitamura (Department of Zoology, Kyoto University, Kyoto), Osamu Inaba (Minamisoma City Museum, Minamisoma), Makoto Kuraishi (Marine Science Museum, Fukushima Prefecture, Iwaki), Hitoshi Kubota (Tochigi Prefectural Fisheries Experimental Station, Ohtawara), Kunihiko Yamamoto (Ishikawa Zoo, Komatsu) and Chika Oshiumi (Japan Corbicula Research Institute, Matsue) for specimens and photographs of adults, juveniles and/or eggs of tabira bitterlings, and Mikio Azuma (Shizukuishi-machi, Iwate Prefecture), Tomiji Hagiwara (Global Environmental Forum, Tsukuba), Nobuo Inoue (Biodiversity Network

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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 .......................................................

2a. Branched dorsal rays 12–13 ............................................................
   *A. rhombeus* (western Japan*) .......................................................

2b. Branched dorsal rays more than 13 .......................................................

2c. Branched dorsal rays less than 12 .......................................................

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 .......................................................

5a. Branched dorsal rays 8 .......................................................
   *A. cyanostigma* (western Japan) .......................................................

5b. Branched dorsal rays usually 9 .......................................................

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 .......................................................

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 .......................................................

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. .......................................................

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.
Niigata, Niigata), Jun-ya Kitazima (Gifu University, Gifu), Jun Nakajima (Fisheries Research Laboratory, Kyushu University, Fukuoka), Masaki Nishio (Himi City Board of Education, Himi), Kenji Saitoh (Tohoku National Fisheries Research Institute, Sendai), Takayoshi Ueda (Utsunomiya University, Utsunomiya) and Katsuhide Yamaguchi (Hoshizaki Green Foundation, Hirata) for gifts of tabira bitterlings. We are also much obliged to M. A. Rogers (FMNH, Chicago) and Gento Shinohara (NSMT, Tokyo) for gifts of tabira bitterlings. We are also much obliged to M. A. Rogers (FMNH, Chicago) and Gento Shinohara (NSMT, Tokyo) for gifts of tabira bitterlings. We are also much obliged to M. A. Rogers (FMNH, Chicago) and Gento Shinohara (NSMT, Tokyo) for gifts of tabira bitterlings. We are also much obliged to M. A. Rogers (FMNH, Chicago) and Gento Shinohara (NSMT, Tokyo) for gifts of tabira bitterlings. We are also much obliged to M. A. Rogers (FMNH, Chicago) and Gento Shinohara (NSMT, Tokyo) for gifts of tabira bitterlings.

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