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A New Subspecies of Anadromous Far Eastern Dace, *Tribolodon brandtii maruta* subsp. nov. (Teleostei, Cyprinidae) from Japan

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Abstract *Tribolodon brandtii maruta* subsp. nov. is described from the holotype and 29 paratypes. The subspecies differs from congeners and the other subspecies in the following combination of characters: preoperculo-mandibular canal of the cephalic lateral line system extended dorsally and connected with postocular commisure, dorsal profile of snout gently rounded, lateral line scales 73–87, scales above lateral line 12–17, scales below lateral line 9–14, predorsal scales 34–41. The new subspecies is distributed on the Pacific coast of Honshu Island from Tokyo Bay to Ohfunato Bay, Iwate Prefecture, Japan.

Key words: new subspecies, taxonomy, morphology, anadromy, cephalic lateral line system.

Introduction

The Far Eastern dace genus *Tribolodon* (Teleostei, Cyprinidae), well-known for exhibiting both freshwater and anadromous modes of life (Berg, 1949; Aoyagi, 1957; Nakamura, 1963, 1969; Kurawaka, 1977; Sakai, 1995), includes four species, two freshwater [*T. sachalinensis* (Nikolskii, 1889) recently resurrected by Shedko (2005) and a senior synonym of *T. ezoe* Okada and Ikeda, 1937, and *T. nakamurai* Doi and Shinzawa, 2000], one anadromous [*T. brandtii* (Dybowski, 1872)], and one anadromous and/or river resident [*T. hakonensis* (Günter, 1877); change of the original name "*hakuensis*" to "*hakonensis*" followed Hosoya (2002) and Eschmeyer (2014)].

Among them, *T. brandtii* from Japan has been suggested as including two forms, both anadromous; the Maruta form from Tokyo Bay and the Tone River (Fig. 1a) and the Jusan-ugui form from Lake Jusan, Aomori Prefecture (Fig. 1b), the former having fewer scales and being suggested to have a greater salinity tolerance than the latter (Nakamura, 1969). An allozyme allelic displacement with no hybridization trait between the Maruta form from Tokyo Bay and Ohfunato Bay, Iwate Prefecture and the Jusan-ugui form from Hokkaido, Yamagata and Niigata Prefectures (Sakai *et al.*, 2002), and a large mitochondrial genetic difference between the Maruta form from Fukushima Prefecture and the Jusan-ugui form from Yamagata Prefecture and Primorie, Russia (Sasaki *et al.*, 2007; Kartavtsev and Hanzawa, 2007; Imoto *et al.*, 2013) have also been reported. Recently, Amano and Sakai (2014) surveyed morphological characteristics of *T. brandtii* from the entire distribution range, and disclosed clear differences, especially in meristics, between the Maruta form on the pacific coast of the Honshu Island from Tokyo Bay to Ohfunato Bay, Iwate Prefecture, Japan, and the Jusan-ugui form in the other regions, from the Oirase River, Aomori Prefecture, to the Koyabe

Fig. 1. *Tribolodon brandtii maruta*, paratype, HUMZ 216755, 388.5 mm in standard length (SL), Tama River, Tokyo, Japan, 2 April 2012 (a), and *T. b. brandtii*, NSMT-P 112193, 415.3 mm SL, Koyabe River, Toyama Prefecture, Japan, 9 May 2012 (b). Photos were cited from Amano and Sakai (2014).

River, Toyama Prefecture on the Honshu Island, in addition to Hokkaido Island, Japan, the Sakhalin Island and Primorie, Russia, and Korea (Fig. 2). All of the information to hand suggests that the two forms are subspecifically distinct.

The type locality of *Tribolodon brandtii* (as *Telestes brandti*) was given as Lake Khanka, Russia (Dybowski, 1872), although the type specimen was later believed to have come from Vladivostok, Russia (Berg, 1949). All of the known synonyms of *T. brandtii* were described from within the distribution range of the Jusan-ugui form; *Leuciscus taczanowskii* Steindachner, 1881 from the Sea of Japan, *L. ledae* Warpachowski, 1892 from Vladivostok, *L. adele* Warpachowski, 1892 from Vladivostok, *L. warpachowskii* Schmidt, 1904 from Vladivostok, and *Akahara jusanensis* Jordan and Hubbs, 1925 from Lake Jusan, Aomori Prefecture, Japan (Eschmeyer, 2014), their morphological characteristics exhibiting typical traits of the Jusan-ugui form. The two forms being parapatrically distributed, the Maruta form is described herein as a new subspecies of *Tribolodon brandtii* and compared with the Jusan-ugui form *T. b. brandtii*.

Methods

Counts and measurements generally followed Hubbs and Lagler (1958) and Nakamura (1969). Measurements were made with dial calipers to the nearest 0.1 mm. All the relative measurements except for standard length (SL) are given as percentage of SL or head length (HL). Vertebral counts and dorsal and anal fin ray counts were made from soft X-ray photos. Differences in relative measurements and counts were tested by analysis of co-variance (ANCOVA) and Mann-Whitney's *u*-test (M-W *u*-test), respectively. Institutional codes are as follows: HUMZ, Hokkaido University Museum, Hakodate; LBM, Lake Biwa Museum, Kusatsu; NSMT, National Museum of Nature and Science, Tsukuba (formerly National Science Museum, Tokyo).

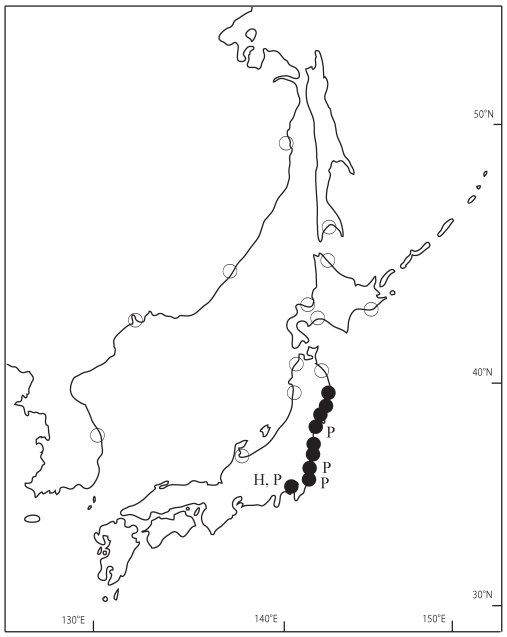

Fig. 2. Map showing distribution of *Tribolodon brandtii maruta* (closed circles) and *T. b. brandtii* (open circles) rearranged from Amano and Sakai (2014), with added localities as listed in the synonym list of *T. b. maruta*. Localities of the holotype and paratypes of *T. b. maruta* are indicated by letters "H" and "P", respectively.

Tribolodon brandtii maruta subsp. nov.

[Japanese name: Maruta]

(Figs. 1a, 3, 4a)

Tribolodon brandtii (*not of Dybowski, 1872*): Doi and Shinzawa, 2000: 246, fig. 3 (Karasu River, Tone River system, Gunma Prefecture, Japan); Sakai *et al.*, 2002: 1293, figs. 1–2 (in part, Tokyo Bay, Japan); Sasaki *et al.*, 2007: 331, figs. 1–5 (in part, Ukedo River, Fukushima Prefecture, Japan).

Tribolodon brandtii, maruta type: Sakai *et al.*, 2014: 64, fig. 1 (Pacific coast of Honshu Island from Tokyo to Ohfunato Bays, Japan); Amano and Sakai, 2014: table 1, figs. 4a, 5–10 (Pacific coast of Honshu Island from Tokyo to Ohfunato Bays, Japan).

Tribolodon brandtii, Pacific Ocean type: Imoto *et al.*, 2013: 115, figs. 2–6 (in part, Ukedo River, Fukushima Prefecture, Japan).

Tribolodon brandti (*not of Dybowski, 1872*): Zama, 1999: 52 (Mangoku-ura Bay, Miyagi Prefecture, Japan); Zama, 2001: 25 (Miyagi Prefecture, Japan); Kartavtsev and Hanzawa, 2007: fig. 1 (in part, Ukedo river, Fukushima Prefecture, Japan).

Tribolodon taczanowskii (*not of Steindachner, 1881*): Ikeda, 1938: 177 (in part, Matsushima Bay, Miyagi Prefecture, Japan); Nakamura, 1963: 128, fig. 54 (in part, Karasu River, Tone River system, Gunma Prefecture, Japan); Nakamura, 1969: 196, pls. 121–122 (in part, Karasu River, Tone River system, Gunma Prefecture, Edo and Ara Rivers, Tokyo, Japan); Nakamura, 1976a: 22, 124 photo D (Hirose-Natori River system, Miyagi Prefecture, Japan); Nakamura, 1976b: 60, 68 photo (Edo and Tama Rivers, Tokyo and Kanagawa Prefecture, Tone River, Chiba and Ibaraki Prefectures, Lake Hinuma, Ibaraki Prefecture, Japan); Kurawaka, 1977: 170–172 (in part, Kitakami and Abukuma Rivers, Miyagi Prefecture, Natsui River, Fukushima Prefecture, Edo River, Tokyo, Japan); Hanzawa and Taniguchi, 1982a: 26, 28, fig. 2 (Ukedo River, Fukushima Prefecture, Japan); Hanzawa and Taniguchi, 1982b: 51, figs. 1–2 (Ukedo River, Fukushima Prefecture, Japan).

Tribolodon hakonensis taczanowskii (*not of Steindachner, 1881*): Nakamura and Mochizuki, 1953: 12, figs. 1–2, pls. II–III (Naka River, Ibaraki Prefecture, Kabura River, Tone River system, Gunma Prefecture, Tama River, Tokyo Bay, Tokyo, Japan).

Leuciscus (*Tribolodon*) *brandti* (*not of Dybowski, 1872*): Takatori, 1993: 48 (Sendai, Miyagi Prefecture, Japan); Takatori, 1994: 71 (Minami-Sanriku region, Miyagi Prefecture, Japan).

"Maruta" (no designation of scientific name): Sendai City, 1978: 96, photo (Hirose River, Natori River system, Miyagi Prefecture, Japan).

Holotype. NSMT-P 112165: 424.0 mm SL, Tama River, Tokyo, Japan, 2 April 2012, coll. by S. Amano.

Paratypes. 29 specimens, 198.4–431.8 mm SL. HUMZ 216753–216755 (363.2–390.0 mm SL): 3 specimens, same date as holotype, coll. by S. Amano. LBM 1210054322 (418.9 mm SL), 1210054323 (431.8 mm SL): 2 specimens, same date as holotype, coll. by S. Amano. NSMT-P SK442-4–SK442-6 (212.4–289.8 mm SL): 3 specimens, same locality as holotype, 2 November 1952. NSMT-P SK8907-4 (252.5 mm SL): 1 specimen, Tone River, Ibaraki Prefecture, Japan, 18 December 1964. NSMT-P SK9147-5 (253.4 mm SL), SK9147-15 (226.5 mm SL): 2 specimens, Tone River, Ibaraki Prefecture, Japan, 5 January 1965. NSMT-P SK445-1–SK445-6 (198.4–296.0 mm SL): 6 specimens, Lake

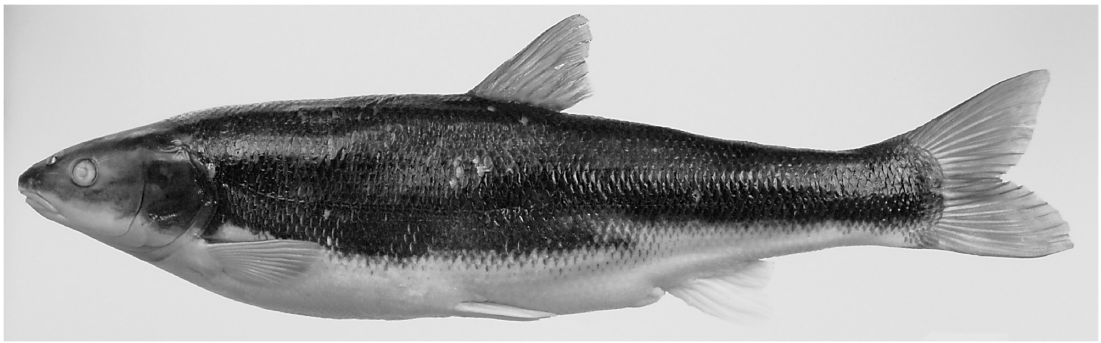

Fig. 3. Holotype of *Tribolodon brandtii maruta*, NSMT-P 112165, 424.0 mm SL, Tama River, Tokyo, Japan, 2 April 2012.

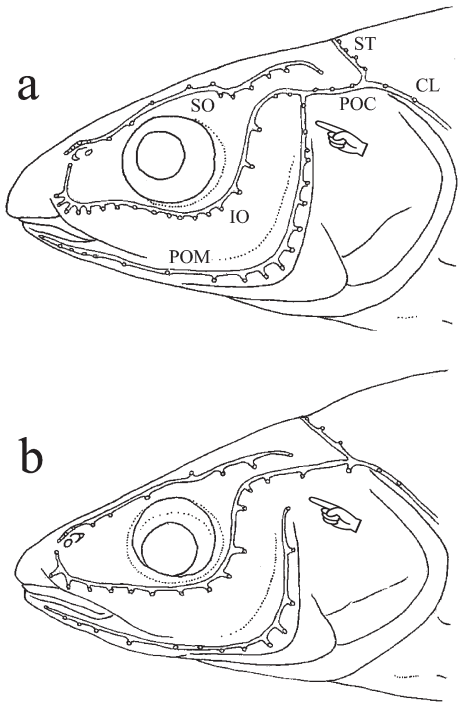

Fig. 4. Cephalic lateral-line systems of *Tribolodon brandtii maruta* and *T. b. brandtii* (a), and the states of the other species, *T. hakonensis, T. sachalinensis* and *T. nakamurai* (b). CL, cephalic lateralis; IO, infraorbital canal; POC, postocular commisure; POM, preoperculo-mandibular canal; SO, supraorbital canal; ST, supratemporal canal; the hands indicate the connection site between POC and POM in *T. b. marta* and *T. b. brandtii* (a), and the separate state of the other species (b).

Hinuma, Ibaraki Prefecture, Japan, 16 November 1952. NSMT-P SK2283-1–SK2283-7 (227.0–286.5 mm SL): 7 specimens, Natori River, Miyagi Prefecture, Japan, 4 May 1962. NSMT-P SK2287-2–SK2287-6 (202.2–325.0 mm SL): 5 specimens, Natori River, Miyagi Prefecture, Japan, 15 May 1962.

Non-type specimens. 32 specimens, 108.7–423.2 mm SL. NSMT-P 112162–112164 (362.9–423.2 mm SL): 3 specimens, same locality as holotype, 3 June 1997, coll. by H. Kohno. NSMT-P SK8907-6, SK8907-9, SK8907-11, SK8907-12 (211.0–226.0 mm SL): 4 specimens, Tone River, Ibaraki Prefecture, Japan, 18 December 1964. NSMT-P SK9147-2–SK9147-4, SK9147-7, SK9147-9, SK9147-10, SK9147-14 (198.6–225.2 mm SL): 7 specimens, Tone River, Ibaraki Prefecture, Japan, 5 January 1965. NSMT-P SK2187 (108.7–178.5 mm SL): 10 specimens, Niita River, Fukushima Prefecture, Japan, 14 November 1961. NSMT-P SK2285-1 (226.0 mm SL): 1 specimen, Natori River, Miyagi Prefecture, Japan, 10 May 1962. NSMT-P 112155–112161 (232.0–268.8 mm SL): 7 specimens, Ohfunato Bay, Iwate Prefecture, Japan, 7 January 1998, coll. by A. Zama.

Diagnosis. *Tribolodon brandtii maruta* differs from congeners and the other subspecies in the following combination of the characters: preoperculo-mandibular canal (POM) of the cephalic lateral line system extended dorsally and connected with postocular commisure (POC)

Table 1. Morphometrics and counts of the holotype and paratypes of *Tribolodon brandtii maruta* (mean±standard deviation, range in parentheses), and comparisons between *T. b. maruta* (including types) and *T. b. brandtii* (analyses of covariance for morphometrics and Mann-Whitney's *u*-test for counts).

Characteristics	*T. b. maruta*		Comparison	
	Holotype	Paratypes ($n=29$)	*T. b. maruta* ($n=62$)	*T. b. brandtii* ($n=81$)
Standard length (mm)	424.0	198.4–431.8	108.7–431.8	108.6–422.6
In % of standard length				
Head length	25.0	25.2±0.7 (23.4–26.9)	25.1±0.8 (23.0–26.9)	27.2±1.0 (24.3–29.3)***
Body depth	24.4	22.3±2.3 (18.5–28.5)	21.9±1.9 (18.5–28.5)	22.8±1.7 (17.9–26.4)**
Body width	13.3	12.7±0.9 (11.1–14.6)	12.7±0.8 (11.1–14.6)	13.2±1.1 (10.4–15.9)**
Caudal peduncle length	21.2	21.1±1-1 (18.9–24.3)	20.8±1.4 (16.9–24.3)	21.1±1.3 (18.5–24.2)
Caudal peduncle depth	10.3	10.1±0.6 (9.0–11.4)	9.9±0.6 (8.1–11.4)	10.5±0.6 (8.8–11.6)***
Predorsal length	50.1	51.7±1.4 (49.0–55.3)	52±1.5 (48.2–56.6)	53.2±1.6 (49–56.9)***
Preanal length	72.8	72.0±1.6 (68.6–74.2)	72.1±1.8 (68.6–76.2)	72.6±1.9 (68.4–78.3)
Prepelvic length	50.6	50.3±1.4 (47.2–52.6)	50.1±1.3 (47.2–52.6)	51.9±1.7 (48.5–55.9)***
Dorsal fin base	10.4	9.7±0.7 (8.0–11.0)	9.6±0.7 (8.0–11.0)	9.6±0.6 (8.0–11.5)
Anal fin base	9.6	9.2±0.8 (7.8–11.0)	9.1±0.7 (7.6–11.0)	8.8±0.9 (6.8–11.1)*
Pectoral fin length	14.2	15.9±0.8 (13.7–17.7)	15.9±0.9 (13.7–17.7)	16.5±0.9 (14.6–18.5)***
Pelvic fin length	11.9	13.1±0.8 (11.0–15.0)	13.3±0.9 (11.0–15.1)	13.9±0.8 (11.4–15.7)***
In % of head length				
Snout length	35.3	33.7±1.3 (30.2–35.9)	33.2±1.4 (29.3–35.9)	33.4±1.6 (29.1–36.6)
Eye diameter	13.5	15.2±1.1 (13.5–17.3)	15.8±1.8 (13.0–21.3)	15.4±2.0 (12.0–21.6)
Interorbital width	38.3	34.7±1.4 (31.1–38.2)	34.7±1.6 (31.0–38.3)	32.2±1.9 (26.8–37.0)***
Upper jaw length	27.1	27.8±1.3 (25.4–30.1)	27.6±1.3 (24.4–30.1)	26.7±1.4 (23.7–30.4)***
Suborbital length	16.2	15.1±1.2 (12.9–17.4)	14.9±1.1 (12.2–17.4)	15.3±1.4 (10.9–18.0)
Branched dorsal fin rays	7	7	7.0±0.1 (7–8)	7.0±0.1 (6–7)
Branched anal fin rays	8	8.0±0.2 (7–8)	8.0±0.2 (7–9)	8.0±0.1 (7–8)
Lateral line scales	79	80.0±2.6 (75–86)	80.5±2.8 (73–87)	87.0±4.3 (78–98)***
Scales above lateral line	15	15.1±0.9 (14–17)	15.0±0.9 (12–17)	17.0±1.2 (15–20)***
Scales below lateral line	12	11.6±1.1 (10–14)	11.7±1.0 (9–14)	14.0±1.3 (11–18)***
Predorsal scales	36	37.5±1.6 (35–40)	37.3±1.6 (34–41)	43.1±2.3 (40–49)***
Sensory pores				
POC+IO	25	24.3±2.6 (19–31)	24.1±2.6 (19–31)	24.1±2.1 (18–30)
SO	15	14.5±1.4 (12–18)	14.5±1.4 (12–18)	14.3±1.3 (11–17)
POM	20	20.2±2.2 (17–26)	20.6±2.0 (17–26)	20.9±1.8 (16–26)
ST	10	9.3±1.1 (7–12)	9.3±1.2 (7–12)	9.0±1.2 (7–12)
Vertebrae	46	46.3±0.6 (45–48)	46.5±0.8 (45–48)	47.8±0.8 (46–50)***
Gill rakers	14	13.4±0.5 (13–14) (n=5)	13.3±0.6 (12–14) ($n=16$)	14.6±0.9 (13–16)*** ($n=17$)

*: significant difference at 5% level; **: at 1% level; ***: at 0.1% level.

(Fig. 4a) (not connected in *T. hakonensis, T. nakamurai*, and *T. sachalinensis*, Fig. 4b); dorsal profile of snout gently rounded (Fig.1a) (relatively straight in *T. b. brandtii*, Fig. 1b); lateral line scales 73–87, scales above lateral line 12–17, scales below lateral line 9–14, predorsal scales 34–41 (78–98, 15–20, 11–18, 40–49, respectively, in *T. b. brandtii*).

Description. Measurements and counts of the holotype, paratypes, and non-type specimens are given in Table 1, together with those of *Tribolodon brandtii brandtii*. Frequency distributions of counts are shown in Table 2. Body elongated fusiform, somewhat compressed. Head pointed, dorsal profile of snout gently rounded. Mouth sub-terminal, slightly oblique. Lower jaw shorter than upper jaw. Maxillary not reaching to level with eye. Nostril closer to anterior margin of eye than tip of snout. Interorbital distance broad, slightly convex. Gill membrane connected to isthmus. Gill rakers large, like a rough teeth comb. Pectoral fins positioned ventrolaterally. Pelvic fins abdominal, at about center of trunk. Pelvic fin base with a single pointed axillary process. Insertion of pelvic fin slightly anterior to origin of dorsal fin. Pectoral fin longer than pel-

Table 2. Frequency distribution of meristic counts in *Tribolodon brandtii maruta* (*T. b. m.*) and *T. b. brandtii* (*T. b. b.*)

	Lateral line scales																								
	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
T. b. m.	1		2	1	3	6	11*	9	4	10	7	2	3	2	1											
T. b. b.						1	1	3	4	3	6	7	8	6	4	5	8	7	6	4	3	2	1		1	1

	Scales above lateral line									Scales below lateral line										Gill rakers				
	12	13	14	15	16	17	18	19	20	9	10	11	12	13	14	15	16	17	18	12	13	14	15	16
T. b. m.	1	1	12	30*	16	2				1	4	24	20*	11	2					1	9	6*		
T. b. b.				7	22	25	18	8	1			1	9	19	31	10	8	2	1		3	5	7	2

	Predorsal scales																Vertebrae					
	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	45	46	47	48	49	50
T. b. m.		1	6	15*	15	7	11	6	1									5	26*	26	5	
T. b. b.								11	10	14	15	8	12	1	8		2			3	27	39	11	1

*: including holotype.

vic fin. Dorsal and anal fins triangular. Outer margin of dorsal fin slightly concave. Outer margin of anal fin straight or slightly concave. Caudal fin forked. Body covered with small cycloid scales from nape and isthmus to caudal peduncle. Cephalic lateral line system (Fig. 4a) well developed, with supraorbital canal (SO), infraorbital canal (IO), postocular commisure (POC), preoperculo-mandibular canal (POM), and a transverse supratemporal canal (ST). IO, POC, and cephalic lateralis (CL) connected. ST connects POCs of both sides. POM extended dorsally, connected with POC. CL extended from shoulder, slowly down to midlateral trunk and straight to center of caudal fin base.

Color in life. Sides silver with brown dorsum in marine environment. During the spawning season in brackish to fresh water, dorsum blackish-brown. A broad black midlateral band from head to caudal fin base. A red or orange band also appeared just below the lateral black band from mouth to caudal peduncle (Fig. 1a). Under sides of head and body whitish. A pair of red or orange spots just above gill openings. Lower side of eye and bases of dorsal, anal, pelvic, and caudal fins also tinted red or orange. Both sexes exhibit similar nuptial coloration but paler in female than male.

Color in alcohol. Dorsal sides of head and body dark brown, under side lighter brown. Dorsal, caudal, and upper side of pectoral fins dark. Pelvic, anal, and under side of pectoral fins lighter brown.

Distribution. Pacific coast of Honshu Island from Tokyo Bay to Ohfunato Bay, Iwate Prefecture, Japan (Fig. 2), found in both lower reaches of large rivers and coastal marine waters.

Etymology. The subspecific name "*maruta*" refers to the Japanese name "Maruta", a traditional local name for the subspecies in the Kanto District, Japan.

Comparative note. Nakamura (1969) first pointed out the differences in the scale numbers, salinity tolerance (only suggested), and head shape between *Tribolodon brandtii maruta* (as Maruta form) and *T. b. brandtii* (as Jusan-ugui form). Subsequently, an allozyme allelic displacement with no hybridization trait in *Gpi-1** between the two subspecies from Japan was revealed by Sakai *et al.* (2002). A large mitochondrial genetic difference, on the other hand, has been demonstrated between *T. b. maruta* and *T. b. brandtii* from both Japanese and continental localities, the genetic distance between the two subspecies corresponding to those between each and *T. nakamurai* (Sasaki *et al.*, 2007; Kartavtsev and Hanzawa, 2007; Imoto *et al.*, 2013).

Morphological differences revealed by Amano

and Sakai (2014) were confirmed here (Table 1), *T. b. maruta* having a significantly larger head (also see Fig. 5), deeper and wider body, deeper caudal peduncle, longer predorsal, preanal and prepelvic lengths, shorter anal fin base, longer pectoral and pelvic fins, shorter interorbital (Fig. 5) and upper jaw lengths, and fewer scales (see also Fig. 6), vertebrae (Fig. 6) and gill rakers than *T. b. brandtii*. Relative lengths in smaller specimens especially less than 100 mm SL, however, are quite different from those in larger specimens and, therefore, unavailable for diagnostic characters between the two subspecies (Amano and Sakai, 2014).

All of the known synonyms of *T. brandtii* were described from within the distribution range of *T. b. brandtii*, and differs from *T. b. maruta* morphologically, exhibiting typical traits of *T. b. brandtii* as follows: *Telestes brandti* from Vladivostok has more than 52 predorsal scales (Dybowski, 1872) (34–41 in *T. b. maruta*, 38–49 in *T. b. brandtii*, see Table 1 and Fig. 6 in the present study); interorbital width of *Leuciscus taczanowskii* from the Sea of Japan is 29–33% of

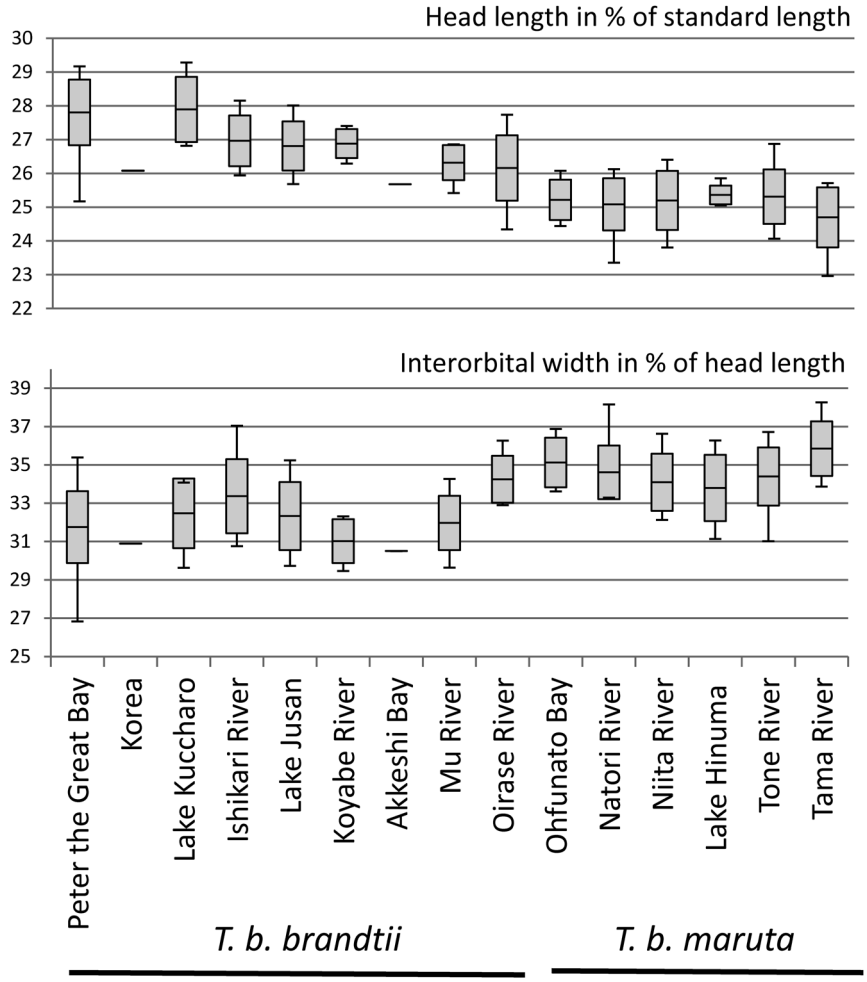

Fig. 5. Box plots indicating average, standard deviation and range of two measuring characteristics different between *Tribolodon brandtii maruta* and *T. b. brandtii*, rearranged from Amano and Sakai (2014); head length (% of standard length) and interorbital width (% of head length) in six populations of *T. b. maruta* and nine populations of *T. b. brandtii*.

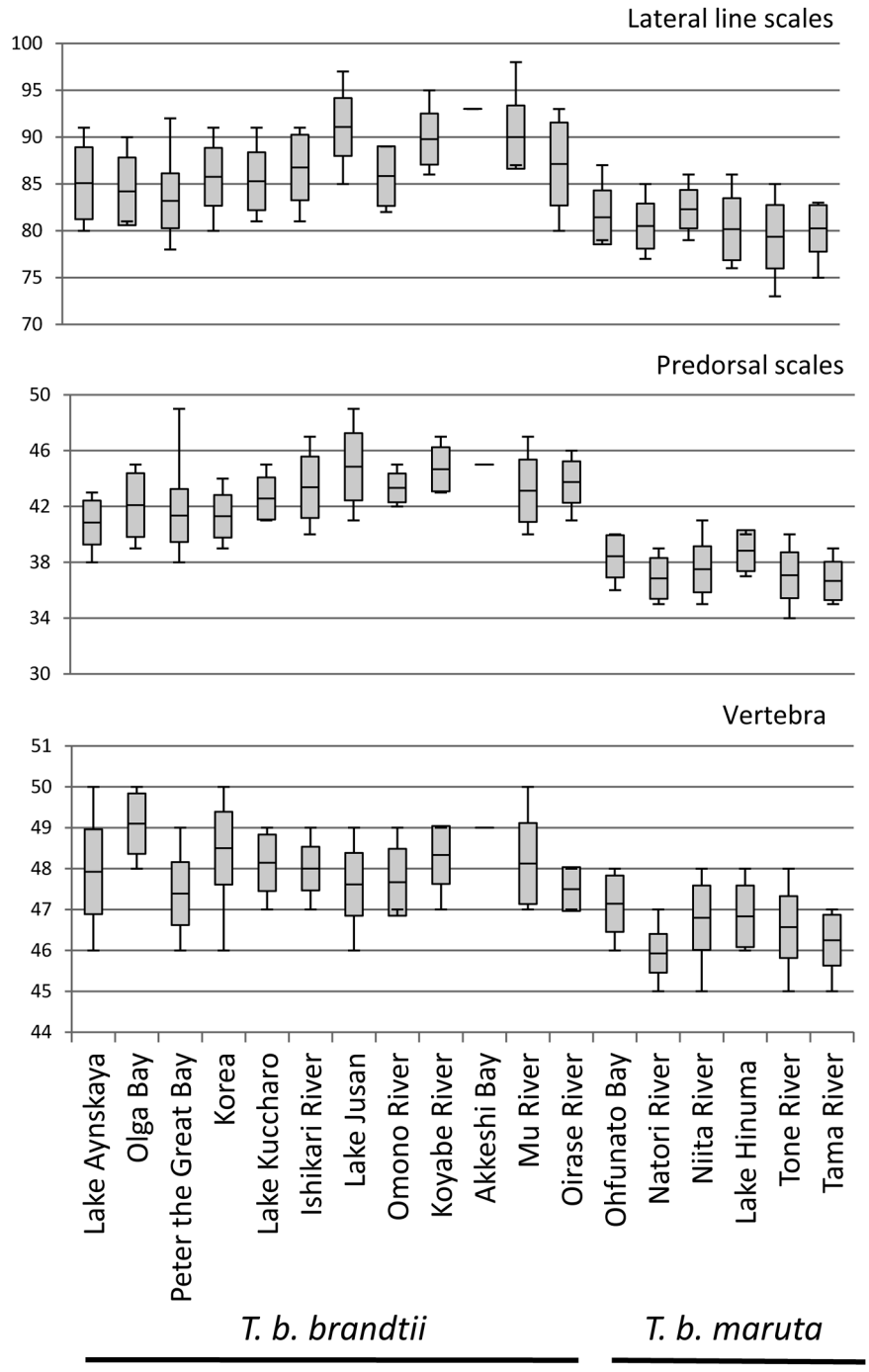

Fig. 6. Box plots indicating average, standard deviation and range of lateral line and predorsal scales and vertebral count, quite different between *Tribolodon brandtii maruta* (six populations) and *T. b. brandtii* (12 populations), rearranged from Amano and Sakai (2014).

head length (Steindachner, 1881) (31.0–38.3% in *T. b. maruta*, 26.8–37.0% in *T. b. brandtii*, Table 1 and Fig. 5); *L. ledae* from Vladivostok has 88–90 lateral line scales (Warpachowski, 1892) (73–87 in *T. b. maruta*, 78–98 in *T. b. brandtii*, Table 1 and Fig. 6); *L. adele* from Vladivostok has 87 lateral line scales (Warpachowski, 1892) (73–87 in *T. b. maruta*, 78–98 in *T. b. brandtii*, Table 1 and Fig. 6); *L. warpachowskii* from Vladivostok has 86 lateral line scales (Schmidt, 1904) (73–87 in *T. b. maruta*, 78–98 in *T. b. brandtii*, Table 1 and Fig. 6). Specimens from Lake Jusan, Aomori Prefecture, Japan, from where *Akahara jusanensis* had described by Jordan and Hubbs (1925) are identified as *T. b. brandtii* in the present study. *Tribolodon b. maruta*, therefore, is obviously endemic to Japan.

Several Japanese name "candidates" for *T. b. brandtii* have been presented to date, namely, "Jusan-ugui" for *T. jusanensis* (Ikeda and Ide, 1937), "Oku-ugui" for *T. taczanowskii* (Okada and Ikeda, 1938), "Siberia-ugui" for *Leuciscus brandti* (Miyadi, 1940), "Yusan-ugui (Maruta)" for *T. hakonensis taczanowskii* including both subspecies (Matsubara, 1955), "Maruta-ugui" for *T. taczanowskii* including both subspecies (Miyadi *et al.*, 1963), and "Maruta" for *T. taczanowskii* including both subspecies (Nakamura, 1963). Among them, "Maruta" is applied to *T. b. maruta* in the present study, being a traditional local name (see above) (Nakamura and Mochizuki, 1953). We propose that *T. b. brandtii* continue to be named "Jusan-ugui", the oldest Japanese name for the subspecies.

Comparative materials. *Tribolodon brandtii brandtii*. 81 specimens, 108.6–422.6 mm SL. HUMZ 103221 (125.4 mm SL): 1 specimen, Daesu River, Korea, 1 August 1984, coll. by S.-R. Jeon. HUMZ 216704, 216706, 216707, 216709–216715, 216717, 216719–216723, 216725, 216726, 216728, 216729, 216731, 216738, 216739, 216741, 216743, 216744 (108.6–236.0 mm SL): 26 specimens, Peter the Great Bay, Russia, 9 September 1995, coll. by H. Sakai. NSMT-P 112185–112193 (346.9–422.6 mm SL): 9 specimens, Koyabe River, Toyama Prefecture, Japan, 9 May 2012, coll. by T. Nakai. NSMT-P SK937-1–SK937-4 (218.0–305.0 mm SL): 4 specimens, Lake Jusan, Aomori Prefecture, Japan, 1 October 1957. HUMZ 74697–74073 (168.0–243.6 mm SL): 7 specimens, Lake Jusan, Aomori Prefecture, Japan, 21 July 1976. NSMT-P SK965-1 (181.5 mm SL), SK965-2 (161.4 mm SL): 2 specimens, Sanbon River, Aomori Prefecture, Japan, 13 October 1957. NSMT-P SK479-1 (372.0 mm SL), SK479-2 (341.0 mm SL): 2 specimens, Oirase River, Aomori Prefecture, Japan, 17 June 1953. NSMT-P SK475-1–SK475-3, SK475-5 (225.0–297.5 mm SL): 4 specimens, Lake Ogawara, Aomori Prefecture, Japan, 22 May 1953. HUMZ 74695 (262.5 mm SL), 74696 (251.3 mm SL): 2 specimens, Lake Ogawara, Aomori Prefecture, Japan, 25 May 1976. HUMZ 216745–216752 (292.0–378.0 mm SL): 8 specimens, Mu River, Hokkaido, Japan, 28 May 1981, coll. by H. Sakai. NSMT-P SK2536-2, SK2536-4, SK2536-5, SK2536-7–SK2536-11 (195.0–266.0 mm SL): 8 specimens, Ishikari River, Hokkaido, Japan, 18 July 1962. HUMZ 80889 (343.5 mm SL): 1 specimen, Akkeshi Bay, Hokkaido, Japan, 22 June 1978. NSMT-P SK2446 (138.3–251.7 mm SL): 7 specimens, Lake Kuccharo, Hokkaido, Japan, 30 June 1962.

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