Ichthyol. Explor. Freshwaters, Vol. 25, No. 4, pp. 289–298, 6 figs., 1 tab., March 2015 © 2015 by Verlag Dr. Friedrich Pfeil, München, Germany – ISSN 0936-9902

Pseudorasbora pugnax, a new species of minnow from Japan, and redescription of P. pumila (Teleostei: Cyprinidae)

Seigo Kawase*,** and Kazumi Hosoya*

Pseudorasbora pugnax, new species, is described from the Ise Bay area in central Honshu, Japan. It is distinguished from its Japanese congener *P. pumila* by the absence of a dark lateral stripe (vs. presence), 33–34 (vs. 34–35) vertebrae, a comparatively more developed infraorbital canal of the cephalic lateralis system with a rostral branch present (vs. absent), a nasal canal present (vs. absent) and mandibular canal complete (vs. incomplete). It is distinguished from the sympatric *P. parva*, by the longer head (27.5–31.9 % SL vs. 23.5–27.3), incomplete (vs. complete) lateral line, and incomplete (vs. complete) infraorbital, supraorbital and supratemporal canals of the cephalic lateralis. *Pseudorasbora pumila* is redescribed and a lectotype designated.

Introduction

Species of *Pseudorasbora* Bleeker, 1860 are small cyprinid fishes widely distributed in East Asia from south-eastern Russia and Japan to northern Vietnam (Hosoya, 2013). Of the fourteen nominal taxa, four species are recognized as valid in recent years: *P. parva* (Temminck & Schlegel, 1846), *P. pumila* Miyadi, 1930, *P. elongata* Wu, 1939 and *P. interrupta* Xiao, Lan & Chen, 2007. *Pseudorasbora parva* was originally distributed in East Asia from south-eastern Russia and west of Kanto region in Honshu, Japan to northern Vietnam and is an invasive pest in Europe and Australia (Bănărescu & Nalbant, 1973; Hosoya, 2013; Gozlan et al., 2010). *Pseudorasbora pumila* is endemic to Japan and was previously considered to comprise two subspecies, *P. p. pumila* and an undescribed subspecies (Nakamura, 1963, 1969). The two forms are allopatric in Honshu Island, being found north-east of the Fossa Magna (an important geographical barrier for Japanese freshwater fish fauna) and around the Ise Bay (the Tokai region of central Honshu) area, respectively.

Pseudorasbora pumila was originally described by Miyadi (1930), based on eight specimens from the Shinai-numa Pond, Miyagi Prefecture, Japan. It was believed at that time that this species was known only from northern Japan (north of the Fossa Magna). Later, Nakamura (1963) reported a population from the Ise Bay area, south-west of the Fossa Magna as "*P. pumila* subsp."; it shares

^{*} Graduate School of Agriculture, Kinki University, 3327-204, Nakamachi, Nara 631-8505, Japan.

^{**} Lake Biwa Museum, 1091, Oroshimo, Kusatsu, Shiga 525-0001, Japan. E-mail: kawauso0212@hotmail.co.jp, kawase@lbm.go.jp



Fig. 1. Pseudorasbora pugnax, KUN-P 43543, holotype, 59.7 mm SL, male; Japan: Gifu Prefecture: Mino.

the incomplete lateral line with *P. p. pumila*. This subspecies was distinguished from *P. p. pumila* by the absence of a dark lateral band (vs. presence). Since then, most Japanese ichthyologists have tentatively recognized *P. pumila* subsp. as a distinct, unnamed taxon (Nakamura, 1969; Kawanabe et al., 2001; Hosoya, 2013).

Biological information necessary for taxonomic evaluation of the two forms in *P. pumila* have been elucidated in previous studies, including differences in chromosome morphology (Matsuda, 1988), allozymes (Konishi et al., 2003), mitochondrial 16SrRNA (Watanabe et al., 2000) and cytochrome *b* (Watanabe & Mori, 2009) gene sequences, and on morphological characteristics (Uchiyama, 1987). In addition, both forms are geographically separated by the Fossa Magna. Taken together, these evidences indicate that the the two putative subspecies significantly differ biologically. We thus describe the unnamed subspecies of Japanese minnow as a new species, *P. pugnax*, and redescribe *P. pumila* in this study.

Material and methods

Specimens were fixed in 10 % formalin and preserved in 70 % ethanol. Material examined is in the following collections: FAKU, Department of Fisheries, Faculty of Agriculture, Kyoto University, Kyoto; FRLM, Fisheries Research Laboratory, Mie University, Mie; KUN-P, Kinki University, Nara (earlier FAK); NSMT-P SK, National Science Museum, Tokyo; RMNH, National Naturhistorisch Museum, Leiden. Counts and measurements follow Hubbs & Lagler (2004). As the lateral line in both species under study is incomplete, we included unpored scales in the total lateral-line scale count. Scales on the caudal fin were excluded from the lateral-line scale counts. The last two rays of the dorsal and anal fins were counted as one ray. Vertebral counts followed Hosoya (1983); they were counted on radiographs and included the first four vertebrae with the Weberian apparatus and one fused vertebra of the hypural complex. Observations of the cephalic lateral line systems followed Fujita & Hosoya (2005).

Pseudorasbora pugnax, new species (Figs. 1, 2, 3a)

- *Pseudorasbora pumila* subsp.: Nakamura, 1963: 125, pl. 52a-b; 1969: 181–185 (in part), pl. 53– 54, 117e-f; Kawamura & Hosoya, 1997: 57–60; Kawanabe et al., 2001: 294, 308–309; Hosoya, 2002: 266, 2013: 322.
- Pseudorasbora parva pumila: Niwa, 1967: 116-118.

Holotype. KUN-P 43543, 59.7 mm SL, male; Japan: Gifu: Mino: Ise Bay area, Nagara River system; K. Tsukahara; May 2011.

Paratypes. All from Ise Bay area, Japan. FRLM 16286, 1, 48.7 mm SL; Mie: Watarai: Miya River system; 25 Oct 1996. – GPM-Z 19302, 2, 43.1–50.1 mm SL; KUN-P 43544–43548, 5, 33.8–45.6 mm



Fig. 2. *Pseudorasbora pugnax;* **a**, KUN-P 43543, holotype, 59.7 mm SL, male; Japan: Gifu Prefecture: Mino (photograph by Toshihiko Morimune); **b**, about 35 mm TL, female; Japan: Gifu Prefecture: Ogaki; aquarium specimen, not preserved (photograph by Ryu Uchiyama).

SL; RMNH.PISC 37978, 1, 58.3 mm SL, male (fixed in 70 % ethanol); Gifu: Mino: Nagara River system; S. Kawase et al.; 20 June 2011 (fixed in 99.5 % ethanol). – GPM-Z 19303, 3, 26.0–27.3 mm SL; Gifu: Yoro: Yokoya, a pond on left bank of Tsuya River; K. Hosoya, 31 July 1984. – KUN-P 43553–43555, 3, 44.9–46.3 mm SL; Aichi: Tsushima: Tennou River; 16 June 1936. – KUN-P 44505, 1, 41.4 mm SL; MPM 1510–1511, 2, 40.9–46.0 mm SL; Mie: Ise; S. Mitani; 21 Nov 2013. – LBM 1210054972–1210054973, 2, 46.0–46.7 mm SL, male, Mie: Ise; S. Kawase and S. Mitani; 18 Nov 2013. – NSMT-P SK 662, 2, 33.8–45.1 mm SL, fe-

male and male; Gifu, Ogaki; M. Nakamura, preserved 22 April 1955. – NSMT-P SK 2605, 2, 32.4–49.0 mm SL, female and male; Gifu: Ogaki: irrigation canal; M. Nakamura.

Non-types. KUN-P 43556, 20, 4–30.3 mm SL; same data as GPM-Z 19303. – KUN-P 44095–44096, 2, 50.8–59.5 mm SL (cleared and stained). – NSMT-P SK 521, 1, 29.4 mm SL; Ogaki, Ezaki; M. Nakamura, 3 June 1949. – NSMT-P SK 25674, 5, 40.7–55.0 mm SL; artificially bred individuals; M. Nakamura, fixed during the period between August and November 1966. **Diagnosis.** *Pseudorasbora pugnax* is distinguishable from other Japanese congeners by following characters; a faint dark stripe on the flank which disappears in females (Fig. 2b); poorly-developed nuptial tubercles in adult males. From P. parva it is distinguished by the following features: longer head (27.5-31.9 % SL vs. 23.5-27.3), lateral line incomplete (vs. complete), infraorbital, supraorbital and supratemporal canals of the cephalic lateralis system incomplete (vs. complete; see Fig. 3). It is additionally distinguished from P. pumila by the following characters: 33-34 vertebrae (vs. 34-35), infraorbital canal of cephalic lateralis system developed (vs. undeveloped) with a rostral branch present (vs. absent), the nasal canal present (vs. absent) and mandibular canal complete (vs. incomplete).

Description. Morphometric data are shown in Table 1. Body small, elongate, rounded. Predorsal profile convex. Head large, depressed, relatively wide. Mouth superior, without barbels. Pharyngeal teeth in one row with dental formula 5-5. Snout long. Eye moderately large, medially or slightly dorsally positioned in head. Interorbital distance wide. Cheek broad. Lateral profile from chin to isthmus curved, imparting convex appearance to dorsal margin of head in lateral view. Opercle posteriorly curved. Body relatively deep and wide. Pectoral fin not reaching dorsal fin origin. Caudal fin forked; posterior tips of both lobes rounded. Trunk lateral line incomplete. Infraorbital canal of cephalic lateralis system incomplete, not connected to supraorbital and preopercle canals; rostral branch present; mandibular canal not connecting preopercular canal; supratemporal canal not reaching lateral margins of head (Fig. 3).

Dorsal fin with 3 simple and 7 branched rays. Anal fin with 3 simple and 6 branched rays. Pectoral fin with 1 simple and 12-14 branched rays. Pelvic fin with 2 simple and 7 branched rays. Caudal fin with 1 simple, 9+6-9 branched and 1 simple principal rays. Pored lateral-line scales 0-6, followed by 27-33 unpored scales (total lateral-line scales 31-33). Scale rows between lateral-line scales and dorsal-fin origin 5-7; between lateral-line scales and anal-fin origin 4-5. Abdominal vertebrae 18-19; caudal vertebrae 14-16; total vertebrae 33-34. Dorsal proximal pterygiophores (including a terminal stay) 10-11; anal proximal pterygiophores 19-20.

Table 1. Measurements of holotype (male) and selected paratypes (n=15) of *Pseudorasbora pugnax*, lectotype (male) and paralectotypes (n=5) of *P. pumila* and lectotype and paralectotype (n=1) of *P. parva*. SD, standard deviation. Values of holotype (H) and lectotype (L) included in ranges.

	P. pugnax				P. pumila				I	P. parva	
	Н	range	mean	SD	L	range	mean	SD	L	paralecto- type	
Standard length (mm)	59.7	32.4-59.7			63.0	37.8-63.0			83.7	52.8	
As percent of standard length											
Head length	28.2	27.5-31.9	29.2	1.1	28.2	26.5-29.2	27.8	1.0	23.5	24.7	
Body depth	27.9	25.3-31.5	28.1	2.0	31.3	27.5-32.0	30.0	1.8	27.0	28.6	
Body width	17.2	16.0-20.0	17.5	1.5	17.4	15.6-17.9	16.8	0.9	11.4	11.4	
Depth of caudal peduncle	14.3	11.2-15.3	13.4	1.1	15.1	12.2-15.9	14.3	1.4	12.5	12.9	
Length of caudal peduncle	20.8	18.5-23.5	20.8	1.5	23.1	20.0-23.1	20.7	1.2	24.1	21.0	
Preanal length	73.0	69.6-74.5	72.4	1.6	72.4	72.1-75.3	73.7	1.6	70.5	70.7	
Prepelvic length	49.5	35.3-52.4	49.5	4.1	50.7	50.7-54.0	52.3	1.3	46.8	48.8	
Height of dorsal fin	22.4	20.8-26.0	22.9	1.5	28.9	23.4-28.9	25.2	1.9	21.0	22.3	
Length of dorsal fin base	13.2	12.7-15.9	13.7	1.0	16.1	13.1-17.5	15.1	1.7	11.8	13.1	
Height of anal fin	15.3	11.4-17.5	15.4	1.6	17.9	15.9-20.1	17.2	1.6	15.4	13.9	
Length of anal fin base	9.4	7.3-11.5	9.0	1.1	7.5	7.5-11.3	9.2	1.3	7.4	8.7	
Pectoral fin length	18.4	15.2-21.3	17.5	1.6	18.3	13.2-18.3	16.0	2.2	17.8	17.8	
Percent of head lengh											
Head width	61	54-66	59.2	3.5	-	-	_	-	59	48	
Snout length	38	34-42	37.0	2.1	31	26-33	30.1	2.8	33	30	
Orbit diameter	22	21-30	25.0	2.9	24	23-27	25.5	1.5	26	27	
Interorbital width	47	32-49	41.7	4.3	48	40-49	44.5	4.1	43	40	



Fig. 3. Cephalic lateral line system of Japanese species of *Pseudorasbora*. **a**, *P*. *pugnax*; **b**, *P*. *pumila*; **c**, *P*. *parva*. **IOC**, infraorbital canal; **LL**, lateral line; **POC**, preopercle canal; **MC**, mandibular canal; **NC**, nasal canal; **RB**, rostral branch; **SOC**, supraorbital canal; **ST**, supratemporal canal; **TC**, temporal canal.

Coloration. In life, body and head brownish in female, grayish in male with silvery tinge, dark dorsally and yellowish ventrally. Edge of each scale dark. Dorsal and caudal fin rays and membrane slightly brownish; other fin membranes almost clear. Lateral stripe absent or faint if present. In preservative, specimens grayish dorsally, pale yellowish and brown ventrally without silvery tinge. Grayish color provided by melanin on body and fins remains after fixation for a relatively long period.

Sexual dimorphism. Males develop secondary sexual characteristics in breeding season (Figs. 1, 2): body larger than that of female; nuptial tubercles sparsely developed on snout and lower jaw; dark grey nuptial color on all body surfaces. Anterior margin of anal fin straight in males, slightly concave in females.

Distribution and ecology. *Pseudorasbora pugnax* is known from Gifu, Aichi and Mie prefectures in central Japan (Fig. 4). Although the distribution of this species is restricted to the Ise Bay area, there is some geographical variation. Three genotypes have been recognized (Ohnaka et al., 1999). Morphologically, the Mie population is distinguished from the other populations of P. pugnax by having a sharp snout, imparting a pug-headed appearance, and extremely swollen humeral region (Kawamura & Hosoya, 1997; Tamaoki et al., 1999). The species inhabits deep irrigation canals and ponds (1-2 m depth) with emergent plant growth. The spawning season extends from late March to early July and eggs are preferentially laid under stones (<200 cm³ volume) in shallow water (<40 cm depth) (Kano et al., 2010).



Fig. 4. Distribution of *Pseudorasbora pumila* (green), *P. pugnax* (blue) and *P. parva* (grey). Type locality of *P. pugnax* indicated by a yellow star and of *P. pumila* by a red square.

Conservation. Most natural habitats of *P. pugnax* have been destroyed by human activities such as urbanization, erosion of the "satoyama" landscape (which is a traditional Japanese rural land-use system), and introduction of the alien invasive predators Micropterus salmoides and Lepomis microculus. Now wild populations are found in only approximately 10 irrigation ponds. Therefore, *P. pugnax* is currently categorized as critically endangered (IA) by the Ministry of the Environment, Japan. In addition, the species is listed as an endangered species by local governments and designated as a protected species under the Law for the Conservation of Endangered Species of Gifu, Aichi and Mie prefectures. To restore the native habitat of *P. pugnax*, conservationists have been attempting to improve the environment and re-introduce the minnow in the ponds (e.g. Mukai et al., 2011).

Etymology. The specific epithet, *pugnax*, is Latin for 'belligerent, aggressive, pugnacious'. Mature males protect their territory very aggressively during spawning season. Locally, this species is called 'Kenka-Moroko' (kenka means fighting in Japanese) (Niwa, 1967). Hence, the specific epithet well represents the behavioral characteristics of this species. **Remarks.** Pseudorasbora pugnax is easily distinguishable from *P. parva* in having an incomplete (vs. complete) lateral line. Two currently recognized species of Pseudorasbora have an incomplete lateral line: P. pumila and P. interrupta. Both P. pugnax and P. pumila differ from P. interrupta in the number of pored lateral line scales (0-6 vs. 7-15) (Xiao et al., 2007). It is more difficult to distinguish between P. pugnax and P. pumila, especially for individuals maintained in captivity for some time. However, in addition to the features mentioned in the diagnosis, P. pugnax differs from *P. pumila* in the following characteristics: dark lateral stripe absent (vs. present), number of vertebrae 33-34 (vs. 34-35), infraorbital canal of cephalic lateralis more developed, with longer supraorbital and infraorbital canals, rostral branch of the infraorbital canal present (vs. absent), the nasal canal present (vs. absent) and the mandibular canal complete (vs. incomplete).

Pseudorasbora pumila Miyadi, 1930 (Figs. 3b, 5, 6)

Pseudorasbora pumila: Miyadi, 1930: 445–448. Pseudorasbora parva pumila: Okada, 1960: 461–463. Pseudorasbora pumila pumila: Nakamura, 1963: 126,

plate 51a-b; 1969: 181–185 (in part), plate 117 (A–D); Bănărescu & Nalbant, 1973: 26–28 (in part); Kawanabe et al., 2001: 306–307; Hosoya, 2002: 266, 2013: 322.

Lectotype. FAKU-P 0178a, 63.0 mm SL, male; Japan: Miyagi: Shita: Shinai-Numa pond; 1916; D. Miyadi.

Paralectotypes. FAKU-P 0178b-f, 5, 37.8-51.3 mm SL; same data as lectotype.

Non-types. All from Japan. FAKU 51853–51856, 4, 44.1–58.5 mm SL; Yamagata, Sakata, Mogami River system, Yadare River; K. Hosoya. – FAKU 51857, 51859, 2, 56.2–71.3 mm SL, male; Akita, Yamamoto; Y. Kimizuka, 7 May 1978. – FAKU 116478–116480, 3, 43.5–47.4 mm SL; Nagano, Murayama; K. Hosoya, 24 April 1997. – KUN-P 43557–43561, 5, 39.4–42.3 mm SL; Nagano, Shinonoi; K. Hosoya, 24 April 1997.

Diagnosis. *Pseudorasbora pumila* is distinguished from the other of *Pseudorasbora* by the following combination of characters: head length 26.5-31.6 % SL, lateral line incomplete, dark lateral stripe present in adults, 34–35 vertebrae and ce-



Fig. 5. Pseudorasbora pumila, FAKU-P 178-a, lectotype, 63.0 mm SL, male; Japan: Miyagi Prefecture: Shinai-numa pond.



Fig. 6. *Pseudorasbora pumila*; Japan: Niigata Prefecture: Tokamachi; not preserved; **a**, male (spawning season), about 50 mm TL; **b**, female, about 30 mm TL (photograph by Ryu Uchiyama).

phalic lateral line systems undeveloped: infraorbital canal incomplete, rostral branch almost absent, nasal canal (anteriormost part of supraorbital canal) absent and mandibular canal incomplete.

Description. Morphometric data are shown in Table 1. Body small, elongate, rather rounded. Predorsal profile straight. Head longer, depressed, relatively wide. Mouth superior; no barbels. Pharyngeal teeth in one row, 5-5. Snout somewhat long. Eye moderately large, medially or slightly high dorsally positioned in head. Interorbital space wide. Cheek somewhat broad. Lateral profile from chin to isthmus curved, imparting convex appearance to dorsal margin of head. Opercle posteriorly curved. Body relatively deep, and relatively wide. Dorsal-fin origin located midway along SL. Pectoral fin not reaching dorsal-fin origin. Pelvic-fin origin slightly anterior to dorsal-fin origin. Posterior margin of caudal fin forked; posterior tips of both lobes of caudal fin rounded. Infraorbital canal of cephalic lateralis system incomplete, not connecting supraorbital and preopercle canal; rostral branch absent; mandibular canal incomplete, not connecting preopercular canal; supratemporal canal not reaching lateral margins of head (Fig. 3).

Dorsal fin with 3 simple and 7 branched rays. Anal fin with 3 simple and 6 branched rays. Pectoral fin with 1 simple and 10–13 branched rays. Pelvic fin with 2 simple and 7 branched rays. Caudal fin with 1 simple, 9+8 branched and 1 simple principal rays. Pored lateral-line scales 3-4, followed by 29–32 unpored scales (total lateral-line scales 34–35). Scale rows between lateral-line scales and dorsal-fin origin 5–7; between lateral-line scales and anal-fin origin 4–6. Abdominal vertebrae 20–22; caudal vertebrae 13–15; total vertebrae 34–35. Dorsal proximal pterygiophores (including terminal stay) 11–12; anal proximal pterygiophores 20–21.

Coloration. In life, body silvery brown in female, greyish in male, darker dorsally and yellowish ventrally, with a black lateral stripe. Edge of each scale dark. Dorsal and caudal-fin rays and membranes slightly brownish, other fin membranes almost clear. In preservative, specimens grayish dorsally, pale yellowish and brown ventrally, without silvery tinge. Remaining after fixation, a black lateral stripe gradually disappearing by

depigmentation because of long-term preservation, as in lectotype.

Sexual dimorphism. Males develop secondary sexual characteristics in breeding season: body larger than that of female; nuptial tubercles developing on snout and lower jaws; dark grey nuptial color on all body surfaces. Lateral stripe disappearing in males during the spawning season.

Distribution and ecology. *Pseudorasbora pumila* is distributed in the Honshu Island, north-east of the Fossa Magna from Nagano to Aomori prefectures (Fig. 4). It shows significant genetic differentiation between populations of the Ohu Mountain range on the Sea of Japan slope and the Pacific slope (Hanzawa, pers. comm.). It inhabits irrigation canals and ponds with muddy or sandy/muddy bottoms. The spawning season extends from April to July.

Conservation. Wild populations of *P. pumila* are facing extinction by hybridization with domestic invasive *P. parva* and predation by alien species such as *M. salmoides*. Now, *P. pumila* is listed as an endangered species by the Ministry of the Environment, Japan and many local governments. In addition, *P. pumila* is designated as a protected species by Nagano Prefecture and by Aomori City (Matahachinuma-pond).

Remarks. Miyadi (1930) briefly described *P. pumila* on the basis of eight specimens without designating a holotype. Among them, six syntypes are deposited in FAKU. The other two syntypes are probably lost. We designate FAKU 0178a as lectotype; it is the largest male and presents the characteristics of the species.

Pseudorasbora pumila uchidai is known from the Ise Bay area. Its range partially overlaps with that of *P. pugnax. Pseudorasbora pumila uchidai* was originally described as *Pseudorasbora parva uchidai* by Okada & Kubota (1957) based on specimens collected in Mie Prefecture, Japan. Subsequently, *P. parva uchidai* was treated as a subspecies of *P. pumila* by Nakamura (1963; 1969) because they share an incomplete lateral line. Although Bănărescu & Nalbant (1973) agreed with Nakamura's opinion, they suggested that *P. pumila pumila* and *P. pumila uchidai* may have originated independently from distinct populations of *P. par-* *va* because *P. pumila uchidai* has more pored lateral line scales (at least 15 vs. 0–6) and a more slender body (depth 19.3–21.9 % SL vs. 27.5–32.0) than *P. pumila pumila*. Hosoya (2013) treated *P. parva uchidai* as a geographic variant of *P. parva* because individuals of *P. parva* with an incomplete lateral line are occasionally encountered and because there are many geographic variants of *P. parva*.

Comparative materials. All from Japan. *Pseudorasbora parva*: RMNH 2634, 1, lectotype, 83.7 mm SL; RMNH 2638, 1, paralectotype, 52.8 mm SL. – FAK 15260, 15263, 15265, 3, 51.3–60.4 mm SL, female and males; Osaka: Hattori River. – KUN-P 41740, 1, 66.4 mm SL, male; Fukuoka: Yanagawa: Futatsu River. – KUN-P 41756–41757, 2, 59.1–63.3 mm SL, male; Saga: Ogi. – KUN-P 43793, 1, 61.4 mm SL, female; Kyoto: Koga Irrigation. – KUN-P 43795–43798, 4, 37.4–52.1 mm SL; Kyoto: Koga irrigation. – KUN-P 43800–43802, 3, 63.7–75.9 mm SL; Mara: Tawaramoto. – KUN-P 43817, 1, 66.2 mm SL, male; Osaka: Akagawa wando-pool of Yodo River. – KUN-P 43820–43823, 1, 50.5 mm SL, male; Kyoto: Seika: Kizu River.

Acknowledgments

We greatly appreciate Takahiko Mukai (Gifu University), Koji Tsukahara, Yoshiaki Miwa (Gifu Mino Ecological Research Group), Shinya Mitani (Toba Aquarium) and Jun-ichi Kitamura (Mie Prefectural Museum) for collecting the specimens of *P. pugnax*, Kiyotaka Takahashi (Conservation Society of Shinaimotsugo) and Kouichi Kawamura (Mie University) for their help and advice, and Naoto Hanzawa (Yamagata University) for providing helpful genetic information. We sincerely thank Tetsuji Nakabo (FAKU), M. J. P. Van Oijen, R. de Ruiter (RMNH), Keiichi Matsuura, Gento Shinohara (NSMT) and Masanari Matsuda (LBM) for observations or loan of material under their care, Ryu Uchiyama (nature photographer) and Toshihiko Morimune (KUN) for photographs of live specimens. Part of this study was financially supported by a Grant-in-Aid for JSPS Fellows (no. 24-4703 for S. Kawase).

Literature cited

- Bănărescu, P. & T. T. Nalbant. 1973. Pisces, Teleostei, Cyprinidae (Gobioninae). Das Tierreich, 93: i-vii, 1-304.
- Bleeker, P. 1860. Ichthyologiae archipelagi indici prodromus. Vol. II. Cyprini. Lange, Batavia, xiv+492 pp.
- Fujita T. & K. Hosoya. 2005. Cephalic lateral line systems in the Far Eastern species of the genus *Phoxinus* (Cyprinidae). Ichthyological Research, 52: 336–342.

297

- Gozlan, E. R., D. Andreou, T. Asaeda, K. Beyer, R. Bouhadad, D. Burnard, N. Caiola, P. Vakic, V. Djikanovic, H. R. Esmaeili, I. Falka, D. Golicher, A. Harka, G. Jeney, V. Kovac, J. Musil, A. Nocita, M. Povz, N. Poulet, T. Virbickas, C. Wolter, A. S. Tarkan, E. Tricarico, T. Trichkova, H. Verreycken, A. Witkowki, C. G. Zhang, I. Zweimueller & J. R. Britton. 2010. Pan-continental invasion of *Pseudorasbora parva*: towards a better understanding of freshwater fish invasions. Fish and Fisheries, 11: 315–340.
- Hosoya, K. 1983. Geographic variation of number of vertebrae in *Squalidus*. The Freshwater Fishes, 9: 43–48. [In Japanese].
- 2002. Cyprinidae. Pp. 253–272 in: T. Nakabo (ed.), Fishes of Japan with pictoral keys to the species. English edition. Tokai University Press, Tokyo.
- 2013. Cyprinidae. Pp. 308–327, 1813–1819 in: T. Nakabo (ed.), Fishes of Japan with pictoral keys to the species, third edition. Tokai University Press, Tokyo. [In Japanese].
- Hubbs, C. L. & K. F. Lagler. 2004. Fishes of the Great Lakes region. Revised edition. University of Michigan Press, Bloomfield Hills, xxxii+276 pp.
- Kano, Y., J. Kitamura & K. Kawamura. 2010. [Spawning ecology and schemes for the conservation of an endangered cyprinid, *Psudorasbora pumila* subsp. sensu Nakamura (1969), including comparisons with a related species, *Pseudorasbora parva*]. Japanese Journal of Ichthyology, 57: 43–57. [In Japanese].
- Kawamura, K. & K. Hosoya. 1997. [Discovery of an endangered cyprinid, *Pseudorasbora pumila* subsp. sensu Nakamura (1969), from the Miya River System, Mie]. Japanese Journal of Ichthyology, 44: 57–60. [In Japanese, English abstract].
- Kawanabe, H., N. Mizuno & K. Hosoya. 2001. [Freshwater fishes of Japan]. Yama-Kei, Tokyo, 719 pp. [In Japanese].
- Konishi, M., K. Hosoya & K. Takata. 2003. Natural hybridization between endangered and introduced species of *Pseudorasbora*, with their genetic relationships and characteristics inferred from allozyme analyses. Journal of Fish Biology, 63: 213–231.
- Matsuda, M. 1988. [Chromosome of *Pseudorasbora pumila* subsp.]. The annual reports of the Biwako Bunkakan, 6: 31–33. [In Japanese].
- Miyadi, D. 1930. Notes on a new cyprinoid fish, *Pseudorasbora pumila*, sp. nov. from Sinai-numa, prov. Rikuzen. The Zoological Society of Japan, 12: 445– 448.
- Mukai, T., K. Tsukahara & Y. Miwa. 2011. The re-introduction of the Ushimotsugo minnow in Gifu Prefecture, Japan. Pp. 54–58 in: P. S. Soorae (ed.), Global re-introduction perspectives: 2011. More case studies from around the globe. IUCN/SSC Re-introduction Specialist Group, Gland & Environment Agency, Abu Dhabi.

- Nakamura, M. 1963. [Keys to the freshwater fishes of Japan fully illustrated in colors]. Hokuryukan, Tokyo, 258 pp. [In Japanese].
- 1969. [Cyprinid fishes of Japan]. Research Institute for Natural Resources, Tokyo, viii+iv+455 pp., 149 pls. [In Japanese].
- Niwa, H. 1967. [Fish of Kiso River]. Taishushobou, Gifu, 293 pp. [In Japanese].
- Ohnaka, T., H. Sasaki, K. Nagai & K. Numachi. 1999. [Marked monomorphism at the D-loop region of mtDNA in an endangered species *Pseudorasbora pumila* subsp. sensu Nakaamura (1963)]. Nippon Suisan Gakkaishi, 65: 1005–1009. [In Japanese].
- Okada, Y. 1960. Studies on the freshwater fishes of Japan. Journal of Faculty for Fisheries Prefectural University of Mie, 4: 267–890.
- Okada, Y. & S. S. Kubota. 1957. A new cyprinoid fish, *Pseudorasbora parva uchidai*, sub-sp. nov. found in Japan. Journal of the Faculty of Science, Hokkaido University, Series 6, Zoology, 13 (1–4): 99–100.
- Tamaoki, F., S. Mitani, G. Kamioka, M. Furuta & K. Kawamura. 1999. [Discovery of an endangered cyprinid, *Pseudorasbora pumila* subsp. sensu Nakamura (1969) from Ise (Isuzu River system)]. Annual Report of Toba Aquarium, 10: 33–39. [In Japanese, English abstract].
- Temminck, C. J. & H. Schlegel. 1842–1850. Pisces. In: Fauna japonica, sive descriptio animalium quae in itinere per Japoniam suscepto annis 1823–30 collegit, notis observationibus et adumbrationibus il-

lustravit P. F. de Siebold conjunctis studiis C. J. Temminck et H. Schlegel pro vertebratis atque W. de Haan pro invertebratis elaborata. Lugdunum Batavorum [Leiden], 324 pp., 161 pls.

- Uchiyama, R. 1987. [Morphology and ecology of *Pseudorasbora pumila* subsp.]. Freshwater Fish, 13: 74–84. [In Japanese].
- Watanabe, K. 1998. Parsimony analysis of the distribution pattern of Japanese primary freshwater fishes, and its application to the distribution of the bagrid catfishes. Ichthyological Research, 45: 259–270.
- 2012. Faunal structure of Japanese freshwater fishes and its artificial disturbance. Environmental Biology of Fishes, 94: 533–547.
- Watanabe, K., K. Iguchi, K. Hosoya & M. Nishida. 2000. Phylogenetic relationships of the Japanese minnows, *Pseudorasbora* (Cyprinidae), as inferred from mitochondrial 16SrRNA gene sequences. Ichthyological Research, 47: 43–50.
- Watanabe, K & S. Mori. 2009. Comparison of genetic population structure between two cyprinids, *Hemigrammocypris rasborella* and *Pseudorasbora pumila* subsp., in the Ise Bay basin, central Honshu, Japan. Ichthyological Research, 55: 309–320.
- Wu, H.W. 1939. On the fishes of Li-Kiang. Sinensia, 10: 92–142.
- Xiao, Z., Z. H. Lan & X. L. Chen. 2007. A new species of the genus *Pseudorasbora* from Guangdong province, China (Cypriniformes, Cyprinidae). Acta Zootaxonomica Sinica, 32: 977–980.

Received 21 October 2013 Revised 28 September 2014 Accepted 15 February 2015