

# Redescription of *Icelus rastrinoides* Taranetz in Schmidt, 1935, a Senior Synonym of *Ricuzenius toyamensis* Matsubara and Iwai, 1951, with Notes on Geographic Variations (Teleostei: Cottidae)

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(Received 13 September 2022; Accepted 27 November 2022)

<https://zoobank.org/60FAB58F-E840-46D9-9055-BFC71AED89D8>

*Ricuzenius toyamensis* Matsubara and Iwai, 1951 was originally described on the basis of eight specimens collected from Toyama Bay, the Sea of Japan coast of central Honshu Island, Japan. The species has subsequently been considered as a valid species of the genus *Icelus* Krøyer, 1845, diagnosed by the following characters: supraocular and parietal spines absent; nuchal spine blunt and indistinct, covered with skin; uppermost preopercular spine unbranched; mid-sized scales scattered (not in rows) above and below lateral line; belly naked; minute ctenoid scales on upper part of maxillary; lateral line scales large, tubular, bearing spinules on dorsal and posterior margins; and lower jaw slightly protruding anteriorly. However, examination of the type specimens of *Icelus rastrinoides* Taranetz in Schmidt, 1935, a northern Sea of Japan species, showed them to be consistent with the holotype and paratypes of *I. toyamensis*. Accordingly, *I. rastrinoides* is regarded as a senior synonym of *I. toyamensis*, with the lectotype of the former being designated herein. The species is redescribed in detail on the basis of the types of both nominal species plus non-type specimens, with a note on geographic variations in dorsal- and anal-fin ray counts, which reflect Jordan's rule.

**Key Words:** Actinopterygii, Cottiformes, synonymy, Sea of Japan, Jordan's rule.

## Introduction

The cottid fish *Ricuzenius toyamensis* Matsubara and Iwai, 1951, known from the Japanese and Korean coasts of the Sea of Japan (Fukui to Yamagata Prefectures, Japan, and Gangwon-do and Gyeong-sanbuk-do, Korea), and originally included in the genus *Ricuzenius* Jordan and Starks, 1904 (Nakabo and Kai 2013; Fukuzawa et al. 2022), was transferred to *Icelus* Krøyer, 1845 by Nakabo (1993), due to sharing a blunt nuchal spine, tubed scales with serrated margins forming a distinct lateral line scale row, and enlarged platelike scales with serrated margins covering the body surface, with other members of that genus (see Nelson 1984; Mecklenburg et al. 2002; Tsuruoka et al. 2006). Molecular evidence presented by Fukuzawa et al. (2022) also supported inclusion within *Icelus*. Although Nelson (1984) did not recognize *I. toyamensis* as a member of *Icelus* in his revision of the genus, his description of *Icelus rastrinoides*

Taranetz in Schmidt, 1935 closely matched the holotype of the former, except for minute differences in the dorsal- and anal-fin ray counts (Nelson 1984; Nakabo 1993). *Icelus rastrinoides* first appeared in Schmidt (1935), a short description (herein regarded as the original description) being based on unpublished data of A. Y. Taranetz; Taranetz (1936) later described the species in detail on the basis of specimens collected from the northern Sea of Japan. Although Fukuzawa et al. (2022) regarded both *I. toyamensis* and *I. rastrinoides* as valid, a comparison (present study) of the type specimens of *I. rastrinoides* with those of *I. toyamensis*, as well as other non-type specimens widely collected from the Sea of Japan, showed that the two nominal species were conspecific, the minute morphological differences between the type specimens being attributable to geographic variations, which reflect Jordan's rule (Jordan 1891). *Icelus rastrinoides* is re-described herein, with comments on the geographic variations, and a lectotype designated for the species in order to avoid further taxonomic confusion.

## Materials and Methods

Methods for counts and measurements followed Fukuzawa et al. (2022). Terminology and abbreviations of the cephalic sensory system and head cirri followed Nelson (1984). Sex was determined by observation of the urogenital papilla and gonads. Standard length is abbreviated as SL. Counts and photos of specimens were taken from the right side if the left side was damaged. Institutional abbreviations follow Sabaj (2020). In order to determine significant differences of counts among the local populations, non-parametric Kruskal–Wallis tests followed by Dunn's multiple comparison tests were performed, using R software version 3.6.2 (R Core Team 2019). *P*-values were adjusted by Holm's method (Holm 1979).

*Icelus rastrinoides* Taranetz in Schmidt, 1935  
[Japanese name: Tomikajika]  
(Figs 1–3; Tables 1, 2)

*Icelus rastrinoides* Taranetz in Schmidt, 1935: 416 (original description, key to the species based on unpublished data of A. Y. Taranetz; type locality: the Sea of Japan at the Cape of Cave and the Cape of Olympiad and at 45°05'N, 138°06'E; type locality based on lectotype designated herein: 45.086°N, 138.100°E, 230–411 m depth); Taranetz 1936: 150 (description; Sea of Japan); Matsubara 1955: 1138 (key; northern Sea of Japan); Nelson 1984: 29 (description; off Fukui, Japan); Lindberg and Krasnyukova 1987: 193, fig. 119 (description, Sea of Japan); Parin et al. 2014: 255 (listed; Tatar Strait, Peter the Great Bay; northern Primorye, western Sakhalin Is., Russia); Fukuzawa et al. 2022: 6th page (comments; northern Sea of Japan).

*Ricuzenius toyamensis* Matsubara and Iwai, 1951: 86, fig. 1 (original description; type locality: Toyama Bay, Japan); Matsubara 1955: 1136 (key; Toyama Bay, Japan); Watanabe 1960: 22, pl. XVIII, fig. 1 (description; Toyama Bay and Yamagata, Japan); Lindberg and Krasnyukova 1987: 186, fig. 114 [description and figure after Watanabe (1960); Toyama Bay and Yamagata, Japan].

*Icelus toyamensis*: Nakabo 1993: 553, 1301, unnumbered fig. (new combination, key; Niigata southward to Ishikawa, Japan); Nakabo and Kai 2013: 1167, 2062, unnumbered fig. (key; Yamagata southward to Ishikawa, Japan); Fukuzawa et al. 2022: 6th page, fig. 4a–c (comparative materials; Yamagata southward to Fukui, Japan, and South Korea).

**Lectotype (designated here).** ZIN 21445, 90.9 mm SL, female, off Primorsky Krai, 45.086°N, 138.100°E, 230–411 m depth, coll. F. Derbek.

**Paralectotypes.** ZIN 56890–56891, 66.1–80.3 mm SL, 1 male and 1 female, same data as lectotype.

**Other materials.** Data of asterisked specimens from Fukuzawa et al. (2022). *Toyama Bay, Japan*: FAKU 13565, 72.6 mm SL, 1 male, off Uozu, Toyama, ca. 230 m depth; FAKU 14450\*, 130.0 mm SL, 1 female, holotype of *Ricuze-*

*nus toyamensis*, off Uozu, Toyama, ca. 230 m depth, coll. T. Iwai and H. Kinoshita, 15 October 1950; FAKU 14451\*, 14452\*, 14454, 145455–14457\*, 102.5–120.3 mm SL, 3 males and 3 females, paratypes of *Ricuzenius toyamensis*, same data as holotype; FAKU 14780–14782\*, 14784\*, 14785\*, 15418\*, 15419\*, 15421–15423\*, 15425\*, 70.4–121.3 mm SL, 8 males and 3 females, off Uozu, Toyama. *West of Noto Peninsula, Japan*: FAKU 99204, 76.0 mm SL, 1 female, 37.771°N, 136.394°E, 240 m depth, 17 June 2011; FAKU 132575–132580\*, 58.3–66.3 mm SL, 2 males and 4 females, 37.429°N, 136.206°E, 250 m depth, 16 June 2010; FAKU 145613–145615\*, 57.8–97.9 mm SL, 2 males and 1 female, 37.295°N, 136.170°E, 331 m depth, 22 June 2016; FAKU 147906\*, 94.8 mm SL, 1 female, 37.406°N, 136.321°E, 251 m depth, 18 June 2020; ZUMT 32015\*, 84.1 mm SL, 1 male, ZUMT 32022\*, 84.9 mm SL, 1 male, ZUMT 32025\*, 83.4 mm SL, 1 female, off Fukui, no further data. *Off Niigata to Yamagata, Japan*: FAKU 134922, 101.9 mm SL, 1 female, no further data; FAKU 140280–140282, 142243, 142244, 143214, 143215, 79.6–93.8 mm SL, 4 males and 3 females, 38.573°N, 138.412°E, 310 m depth, 23 July 2015; FAKU 142239, 83.5 mm SL, 1 female, 38.616°N, 138.409°E, 287 m depth, 23 July 2015; FAKU 145632, 2 males and 2 females, 71.7–83.5 mm SL, 38.584°N, 138.409°E, 311 m depth, 10 July 2016; FAKU 145680–145682, 145684, 145685, 65.1–101.9 mm SL, 2 males and 3 females, 38.619°N, 138.413°E, 291 m depth, 9 July 2016; FAKU 147842–147849\*, 147850, 68.1–84.0 mm SL, 3 males and 6 females, 39.147°N, 138.786°E, 345 m depth, 27 July 2020. *West of Hokkaido, Japan*: FAKU 200875–200879, 83.4–98.0 mm SL, 2 males and 3 females, 45.001°N, 140.439°E, 256 m depth, 20 May 2013; FAKU 201202–201208, 201210, 64.6–71.5 mm SL, 2 males and 6 females, 44.835°N, 140.517°E, 224 m depth, 19 May 2013. *East of Korean Peninsula*: FAKU 149086, 85.0–97.4 mm SL, 1 male and 3 females, 37.283°N, 132.250°E, 240 m depth; NIBR-P 16324\*, 90.4 mm SL, 1 male, off Gosong-gun, Gangwon-do, Korea; NIBR-P 4791\*, 1 male and 1 female, 79.2 and 117.5 mm SL, Uljin-gun, Gyeongsangbuk-do, Korea.

**Diagnosis.** A species of *Icelus* with the following combination of characters: supraocular and parietal spines absent; nuchal spine blunt, indistinct, covered with skin; uppermost preopercular spine unbranched; mid-sized scales scattered (not in rows) above and below lateral line; belly naked; minute ctenoid scales on upper part of maxillary; lateral line scales large, tubular, bearing spinules on dorsal and posterior margins; lower jaw slightly protruding anteriorly; spines of first dorsal fin 8 or 9; rays of second dorsal fin 18–22; anal-fin rays 16–20; pectoral-fin rays 17–20.

**Description.** Counts and measurements shown in Table 1. Data for lectotype presented first, followed by data of other materials in parentheses (if different). Body sub-cylindrical anteriorly and slightly compressed posteriorly; dorsal profile rounded below first dorsal fin, gradually sloping posteriorly (Fig. 1). Head robust, slightly depressed. Eye large, upper margin just below dorsal contour. Interorbital space almost flat or weakly depressed. Occipital region concave, rounded, without knob or ridge. Nasal spine short,

Table 1. Counts and measurements of *Icelus rastrinoides* (means in parentheses).

	<i>Icelus rastrinoides</i>			<i>Icelus toyamensis</i>
	Lectotype ZIN 21445	Paralectotypes n = 2	Other specimens n = 79	Holotype FAKU 14450
Standard length (SL)	90.9	66.1–80.3	57.8–121.3	130.0
In % of SL				
Head length	33.7	33.0–35.1 (34.1)	32.5–36.8 (34.8)	33.3
Snout length	9.5	8.1–9.4 (8.8)	7.1–10.0 (8.3)	7.7
Orbit diameter	12.1	11.0–12.4 (11.7)	10.4–14.4 (12.3)	11.3
Interorbital width	1.9	2.1*	1.6–2.6 (2.1)	2.0
Upper-jaw length	16.5	15.3–15.7 (15.5)	15.1–18.3 (16.8)	17.9
Body depth	20.9	19.4–22.0 (20.7)	14.6–22.8 (18.7)	21.5
Predorsal length	30.4	29.0–29.3 (29.2)	26.9–31.7 (29.2)	27.1
Caudal-peduncle depth	4.5	4.5–4.9 (4.7)	3.7–5.2 (4.5)	4.4
Pectoral-fin length	22.9	24.9–28.9 (26.9)	20.5–30.5 (24.6)	27.8
Pelvic-fin length	14.3	10.6–12.9 (11.8)	10.0–17.9 (14.9)	14.1
Caudal-fin length	—	19.5*	17.8–23.6 (21.0)	—
Counts				
Dorsal-fin spines	IX	IX	VIII–IX	VIII
Dorsal-fin rays	21	21–22	18–21	20
Anal-fin rays	19	19	16–20	17
Pectoral-fin rays	18	18–19	17–20	19
Lateral line scales	44	44	41–44	42

\* Damaged in one specimen.

sharp, directed posterodorsally. Anterior nostril with short tube level with lower margin of pupil; posterior nostril narrow, on anterior margin of orbit. Nuchal spine indistinct (indistinct or forming a blunt ridge), directed posterodorsally. Supraocular and parietal spines absent. Suborbital stay bearing a minute spine posteriorly or a blunt ridge. Maxilla extending to below posterior margin of pupil; lower jaw slightly protruding anteriorly. Small conical teeth on jaws, vomer and palatines, forming a narrow band. Four sharp unbranched preopercular spines; uppermost spine directed posterodorsally, second posteriorly, third and lowermost ventrally. Supraocular cirrus present in both sexes; parietal and nuchal cirri absent (present or absent). Branchiostegal membranes broadly united, forming a fold over isthmus. Gill rakers on first gill-arch short, round, covered with minute prickles; no rakers in angle between ceratobranchial and epibranchial.

Snout, interorbital space, opercle, and dorsolateral surface of head from suborbital stay covered with small scales with serrated margins. Minute ctenoid scales on upper portions of eye and maxillary. Ventral surface of head naked. Scales on lateral line large, tubular, bearing spinules on dorsal and posterior margins; lateral line scales extending past posterior edge of hypural plate. Mid-sized scales with spinules scattered above and below lateral line, not arranged in distinct rows on trunk, posteriorly forming a single indistinct row (1–3 indistinct rows) on caudal peduncle above and below lateral line; small scales scattered dorsally (Fig. 2A–C). Bases of first and second dorsal fins naked. Pectoral axilla with mid-sized scales (not in distinct rows) (Fig. 2D–F). Chin and belly without scales.

First dorsal fin originating above dorsal edge of gill slit; tips slightly protruding; first dorsal proximal pterygiophore

bearing first and second spines. First and second dorsal fins separated by short interspace. Second dorsal fin of similar height to first dorsal fin; tips free from membranes; rays unbranched. Anal fin originating slightly posterior to level of second dorsal-fin origin; rays unbranched. Caudal fin truncate. Pectoral fin large, upper half shallowly emarginate, 11th (11th or 12th) rays longest, extending beyond anal-fin origin; all rays unbranched. Pelvic fin with one spine and three rays, spine and outermost ray closely united; below first dorsal-fin origin. Male urogenital papilla distinct, cylindrical with large curved terminal appendage, located below posterior half of first dorsal fin.

*Cephalic sensory system* (based on FAKU 14450 and other non-type materials, Fig. 3). Supraorbital canal with anterior and posterior nasal pores (NA and NP), cluster of supplementary pores posteriorly NA; supraorbital pores SO1–5 present, SO5 forming a cluster of small pores; anterior and posterior coronal pores (CA and CP) present. Infraorbital canal with eight pores (IOP1–8); IOP1–2 large and oval, IOP 7–8 somewhat small, of similar size to supplementary pores along margins of infraorbital canal. Postorbital canal with four pores (T1–4); T1 without distinct canaliculus, T3 and T4 with long canaliculus. Occipital canal with anterior and posterior medial pores (OCA and OCP), and posterior lateral central pore (OCLP); anterior and posterior lateral pores (OLA and OLP), and anterior lateral central pore (OLA) present or absent. Preoperculo-mandibular canal with ten pores (PM1–10); PM1 on right and left sides separated.

*Coloration when fresh* (based on FAKU 99204, Fig. 1E). Head and body brown or yellowish-brown, lightening ventrally; body scales whitish, forming mottled markings. Anterior half of jaws black; indistinct black blotches below

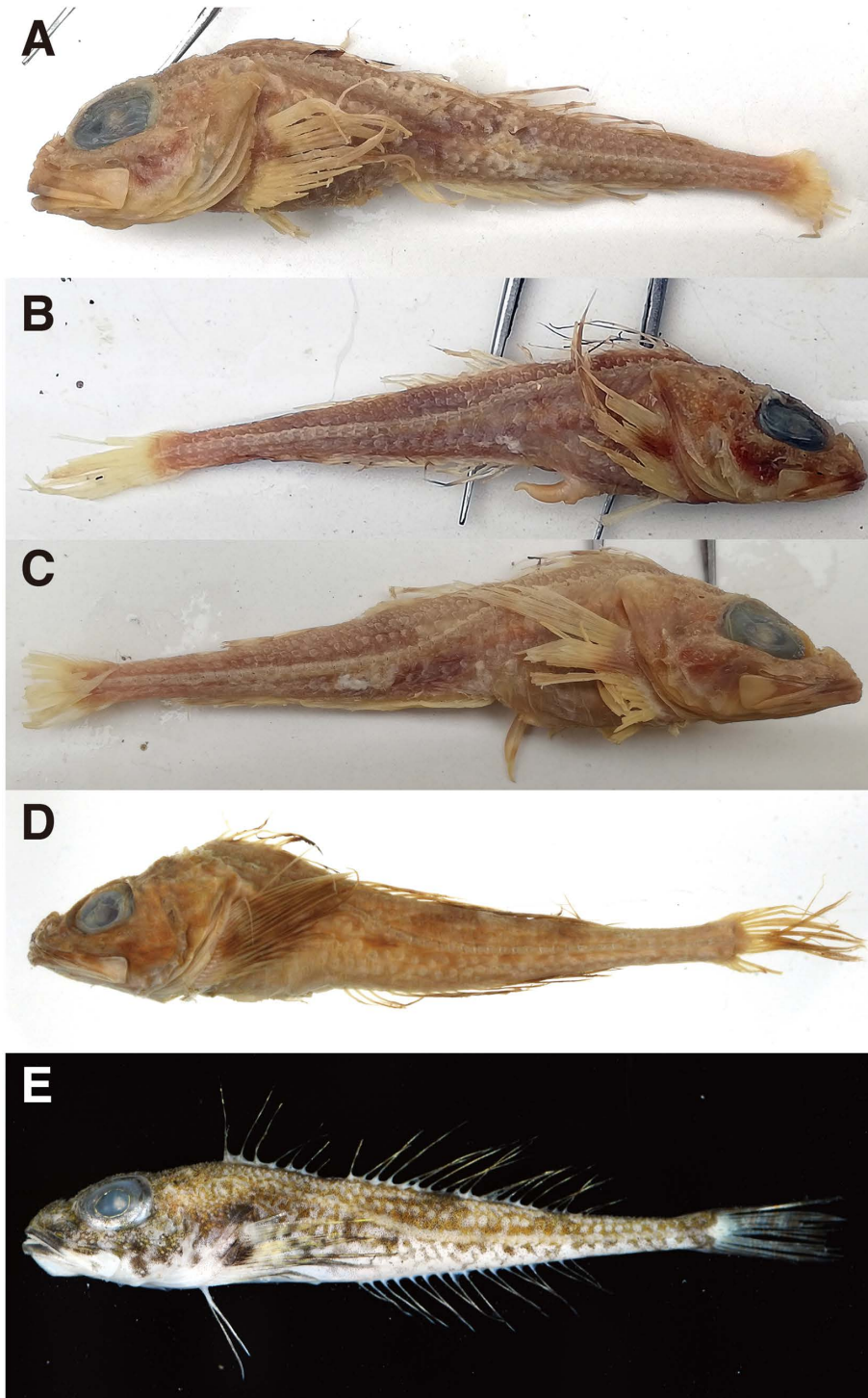


Fig. 1. *Icelus rastrinoides*. A, Lectotype, ZIN 21445, 90.9 mm SL; B, paralectotype, ZIN 56890, 66.1 mm SL; C, paralectotype, ZIN 56891, 80.3 mm SL; D, holotype of *Icelus toyamensis*, FAKU 14450, 130.0 mm SL; E, non-type specimen, FAKU 99204, 76.0 mm SL. A–D, in preservative; E, fresh condition.

eye; two faint dark brown saddles below second dorsal fin; caudal peduncle dark brown. Nostril tube brown; head cirri dark brown. First and second dorsal fins light brown with indistinct oblique dark brown bands; anal fin brown, distal part darker in males; caudal fin with faint pale brown vertical stripes; pectoral fin pale basally, a black blotch on base; pelvic fin whitish.

*Coloration in alcohol* (Fig. 1A–D). Head and body uni-

formly brown, becoming somewhat lighter ventrally (two faint dark brown saddles below second dorsal fin). Anterior half of jaws dark brown; indistinct black blotches below eye; caudal peduncle somewhat darker. Nostril tube brown; head cirri brown or light brown. First and second dorsal fins light brown with indistinct oblique dark brown bands; anal fin brown, distal part darker in males; caudal fin with faint pale brown vertical stripes; pectoral fin pale basally, a dark blotch

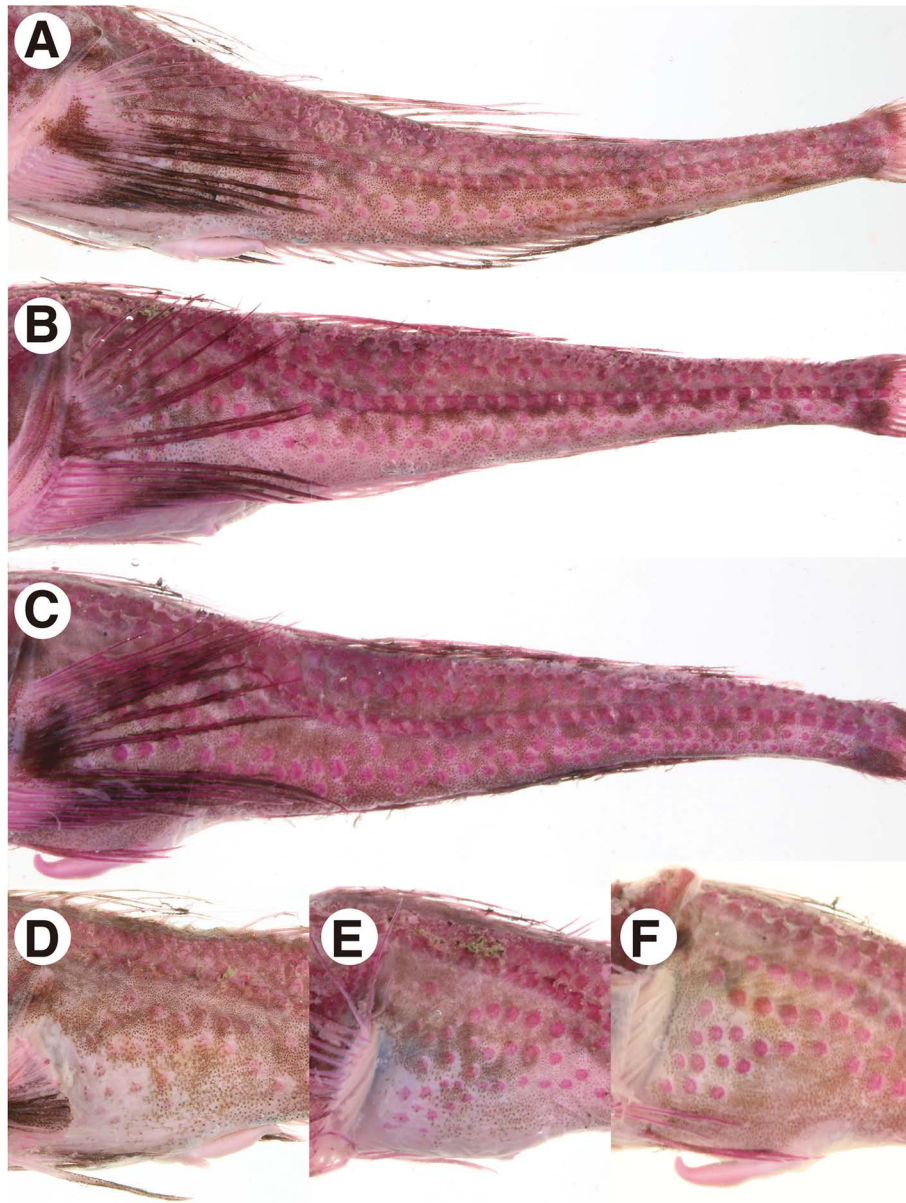


Fig. 2. Variations in squamation of *Icelus rastrinoides*. A–C, Scales on lateral surface of body, ranging from 1–3 rows; D–F, scales on pectoral axilla. A, D: FAKU 145680, 85.1 mm SL; B, E: FAKU 147843, 84.0 mm SL; C, F: FAKU 147842, 83.6 mm SL.

on its base; pelvic fin light brown.

**Distribution.** Known from the Sea of Japan, west of the Noto Peninsula northward to west of Hokkaido, Japan, and east of the Korean Peninsula northward to Primorsky Krai (Fukuzawa et al. 2022; this study).

**Geographic variations.** *Icelus rastrinoides* exhibits extensive geographic variations in dorsal- and anal-fin ray counts (Table 2). The specimens from the northern Sea of Japan off Primorsky Krai and Hokkaido, and east of the Korean Peninsula (Areas A–C in Fig. 4) had somewhat higher counts than those from the Sea of Japan coast of Honshu Is., Japan (Areas D–F in Fig. 4). Dorsal-fin ray counts differed significantly between the specimens from Areas B and E, C and D, and C and E, with those of the anal-fin rays being likewise between the specimens from Areas B and D, B and E, C and D, C and E ( $P < 0.01$ ). Along the Sea of Japan coast of Honshu Is., a north-south cline was apparent, the above

counts gradually increasing from south to north (Table 2). In addition, the dorsal-fin spine numbers differed slightly between the specimens from Areas B and F ( $P = 0.05$ ). However, counts of pectoral-fin rays and pored lateral line scales did not differ statistically among the above geographic areas ( $P > 0.01$ ).

## Discussion

**Type specimens of *Icelus rastrinoides*.** *Icelus rastrinoides* was first published by Schmidt (1935) in the form of a key to the species based on the unpublished data of A. Y. Taranetz. Although Taranetz (1936) later described the species in detail, such having been considered as the original description of *I. rastrinoides* by several authors (e.g., Lindberg and Krasnyukova 1987; Parin et al. 2014), Nelson (1984)

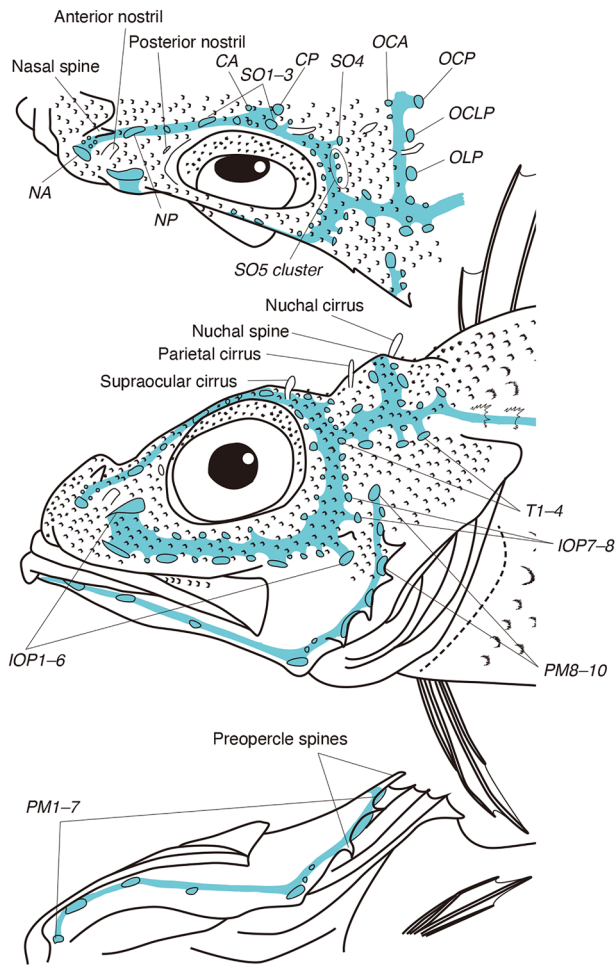


Fig. 3. Schematic drawing of head spines, cirri, and cephalic sensory system of *Icelus rastrinoides* based on FAKU 14450, 130.0 mm SL, holotype of *I. toyamensis* (upper: dorsal; middle: lateral; lower: ventral views). Blue lines indicate sensory canals. NA, anterior nasal pore; NP, posterior nasal pore; SO, supraorbital pores; T, postorbital pores; IOP, posterior infraorbital pores; OCA, anterior medial pore of occipital canal; OCP, posterior medial pore of occipital canal; OCLP, posterior lateral central pore of occipital canal; OLP, posterior lateral pore of occipital canal; PM, preoperculo-mandibular pores.

and Fukuzawa et al. (2022) considered that the key to *I. rastrinoides* in Schmidt (1935) included distinguishing features of the species and was therefore available as the original description [Article 13.1.1 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999)]. Neither Taranetz in Schmidt (1935) nor Taranetz (1936) provided registration numbers of the type specimens, although the latter noted that the description was made on the basis of eight specimens collected from “the Sea of Japan at the Cape of Cave and the Cape of Olympiad and at 45°05′N, 138°06′E (depths 230–411 m)”. Three specimens held in the Zoological Museum of the Russian Academy of Sciences, ZIN 21445 (3 specimens), collected from 45°05′N, 138°06′E, and registered as the syntypes of *I. rastrinoides* (see also Fricke et al. 2022), were apparently part of the original series on which the key to *I. rastrinoides* provided in Schmidt (1935) was based. To

avoid further taxonomic confusion, one of those syntypes is designated here as the lectotype, the other two specimens (reregistered as ZIN 56890 and ZIN 56891) becoming paralectotypes.

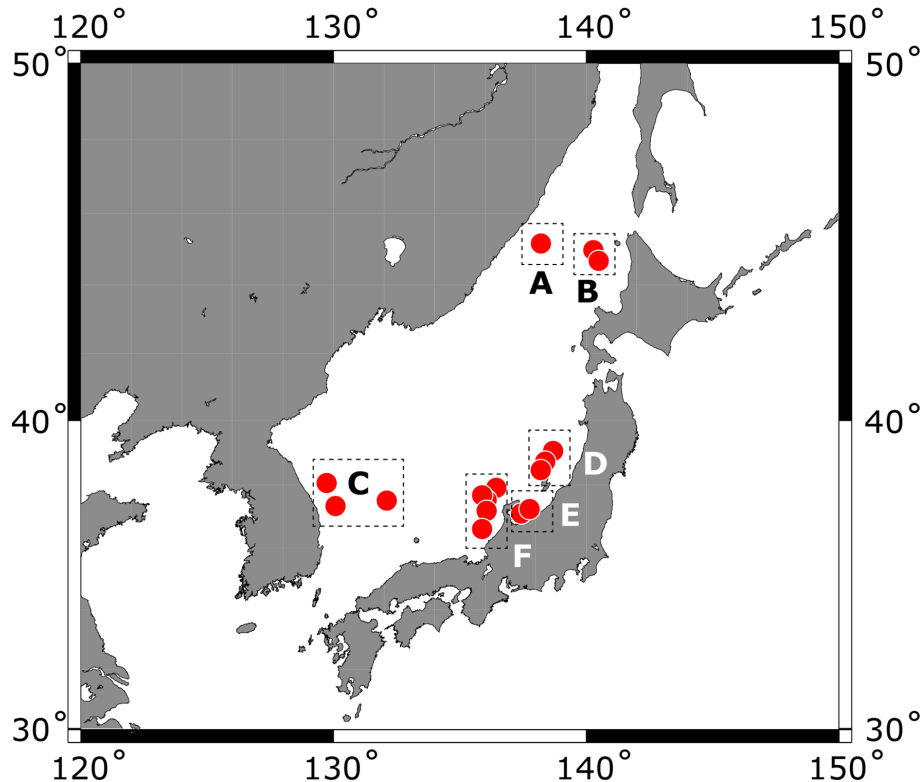
**Type specimens of *Icelus toyamensis*.** *Icelus toyamensis* was originally described as *Ricuzenius (Alloricuzenius) toyamensis* by Matsubara and Iwai (1951), and subsequently transferred to *Icelus* by Nakabo (1993) (see Introduction). The holotype (FAKU 14450) and paratypes (FAKU 14451, 14452, 14554–14457) agreed well with the lectotype and paralectotypes of *I. rastrinoides* in head spine features, arrangement of body scales, and having the lower jaw slightly protruding anteriorly. Matsubara (1955) placed the species under *Ricuzenius*, distinguished from *Icelus* by having small scales entirely covering both the head and body. However, the type specimens of *I. toyamensis* lacked scales on the chin and belly, as often seen in other species of *Icelus* (see Nelson 1984; Fukuzawa et al. 2022). Fukuzawa et al. (2022) regarded both *I. rastrinoides* and *I. toyamensis* as valid, due to the former having scales between the lateral line and anal-fin base forming a single row, clearly differing from the latter (having scales not in distinct rows). However, the number of scale rows between the lateral line and anal-fin base varied considerably among the present specimens examined, ranging from 1–3 rows (Fig. 2A–C), including the type specimens of *I. toyamensis*.

**Intraspecific variations in dorsal- and anal-fin ray numbers.** Although the type specimens of *I. toyamensis* had lower numbers of dorsal- and anal-fin rays (19–20 and 18–19, respectively) than those of *I. rastrinoides* (21–22 and 19–20, respectively), we considered such differences to be attributable to intraspecific geographic variations, as stated above. In fact, the collection localities of the type specimens of the two nominal species are located near the northern and southern limits of the distributional area of *I. rastrinoides* as recognized here, with the fin ray counts of the type specimens being included within the ranges determined for non-type specimens.

While Nelson (1984) did not mention “*Ricuzenius toyamensis*” in his review of *Icelus*, probably due to its generic status at that time, he included comments on fin ray number variations in his treatment of *I. rastrinoides*. Specimens collected from Fukui, Japan (Area F of Fig. 4) had higher numbers of dorsal- and anal-fin rays than the type specimens collected from Primorsky Krai (Area A of Fig. 4). Such geographic variations, shown in Table 2, can be explained by the temperature-dependent development of fins (i.e., higher counts in lower temperatures) (e.g., Ha and Iguchi 2021). Although the early-life history of *Icelus* is largely unknown, an unidentified example of the genus was recorded from 50 m depth in April (Kojima 2014). Because the shallow area of the Sea of Japan coast of Japan is dominated by the Tsushima Warm Current, flowing from south to north, and those of Russia and Korea by the cold Liman Current, the fish faunas of western and eastern Sea of Japan regions are strikingly different (Kai and Motomura 2022; Tashiro 2022). In fact, Tashiro (2022) showed that cold-water species dominate the Eastern Korea, Primorsky Krai, Tatar, and Hok-

Table 2. Regional variations in selected counts for *Icelus rastrinoides*.

Area	Dorsal-fin spines		Dorsal-fin rays					Anal-fin rays					Pectoral-fin rays			
	8	9	18	19	20	21	22	16	17	18	19	20	17	18	19	20
A	0	3	0	0	0	2	1	0	0	0	3	0	0	2	1	0
B	1	12	0	0	5	8	0	0	0	6	6	1	0	8	4	1
C	1	6	0	0	0	7	0	0	0	2	5	0	0	4	3	0
D	9	18	1	2	17	6	0	1	9	16	1	0	2	9	16	0
E	9	10	1	9	8	1	0	2	7	10	0	0	0	7	11	1
F	9	5	0	5	7	2	0	0	7	5	2	0	2	7	4	1

Fig. 4. Collection localities of *Icelus rastrinoides* examined in this study. Areas A–F were established for statistical analysis.

kaido areas of the Sea of Japan. It should be noted that the *I. rastrinoides* specimens examined here from Areas A–C have higher numbers of dorsal- and anal-fin rays than those from Areas D–F. In addition, a north-south cline was apparent among the specimens from Areas D–F (Table 2), reflecting Jordan's rule (Jordan 1891; Ha and Iguchi 2021).

In conclusion, the morphological differences between the nominal species *I. rastrinoides* and *I. toyamensis* recognized in previous studies can be attributed to the intraspecific variations as described above. Accordingly, *I. rastrinoides* is considered to be conspecific with and a senior synonym of *I. toyamensis*.

### Acknowledgments

We are grateful to A. Yoshikawa (Japan Fisheries Research and Education Agency), the crews of T/V *Tanshu-maru* (Kasumi High School), T/V *Tenyo-maru* (Japan Fisheries

Research and Education Agency), R/V *Kaiyo-maru* No. 5 (Kaiyo Engineering Co. LTD.), A. Tohkairin and R. Misawa (formerly FAKU) for their help in collecting specimens. G. S. Hardy (Ngunguru, New Zealand) critically reviewed the manuscript. This work was partly supported by the Russian Government research theme No. 122031100285-3 and by the Fisheries Agency of Japan under the projects of 'Assessment of Fisheries Stocks in the Waters around Japan.'

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