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RESEARCH ARTICLE

On the systematics of three eelpout species (Teleostei: Zoarcidae: *Lycodes*) endemic to the Sea of Okhotsk

К систематике трёх видов ликодов (Teleostei: Zoarcidae: *Lycodes*), эндемичных для Охотского моря

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Abstract. Three nominal species of eelpouts endemic to the Sea of Okhotsk, specifically *Lycodes ygreknotatus* Schmidt in Taranetz, 1937, *L. microlepidotus* Schmidt, 1950, and *L. fulvus* Toyoshima, 1985, are reinvestigated based on all type materials and additional specimens. The latter two species are recognised as junior synonyms of *L. ygreknotatus*, as no significant morphological differences were found among these taxa. *Lycodes ygreknotatus* is rediagnosed. It exhibits significant geographic variability in both the number of vertebrae and the density of scale cover. The observed variability can likely be attributed to differences in environmental temperatures across different parts of its extensive distribution range.

Резюме. Три номинальных вида ликодов, эндемичных для Охотского моря, *Lycodes ygreknotatus* Schmidt in Taranetz, 1937, *L. microlepidotus* Schmidt, 1950 и *L. fulvus* Toyoshima, 1985, заново исследованы на основе всех типовых материалов и дополнительных экземпляров. Два последних вида признаны младшими синонимами *L. ygreknotatus* в связи с отсутствием существенных морфологических различий между этими таксонами. Уточнен диагноз *L. ygreknotatus*. Для этого вида характерна существенная географическая изменчивость числа позвонков и плотности чешуйного покрова, которая может быть обусловлена температурными различиями в разных частях его широкого ареала.

Key words: Sea of Okhotsk, synonymy, redescription, distribution, eelpouts, *Lycodes*

Ключевые слова: Охотское море, синонимия, переописание, распространение, ликоды, *Lycodes*

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Introduction

Fishes of the eelpout genus *Lycodes* Reinhardt, 1831 (Teleostei: Zoarcidae) constitute an essential part of benthic marine fish communities in the Northern Hemisphere both in species diversity and population size (Andriashev, 1954; Borets, 1997; Møller et al., 2010). Currently, there are up to 64 recognised species within this genus (Froese & Pauly, 2023). The highest species diversity of these fishes is recorded in the northwestern part of the Pacific Ocean. These moderately elongated eel-like demersal fishes inhabit a range from littoral to bathyal zones, reaching depths of about three km (Møller & Gravlund, 2003; Møller et al., 2010; Mecklenburg et al., 2016). Their diet primarily consists of molluscs, crustaceans, and small fishes. While most species in the group are strictly marine, some Arctic species are also found in brackish waters (Andriashev, 1954). These eelpouts are intermediate in size, with certain individuals exceeding 80 cm in total length, while most of *Lycodes* species are notably smaller. Some species, like *L. soldatovi* Taranetz et Andriashev, 1935, can form numerous stocks (Balanov et al., 2004) which are targeted by the fisheries.

Taxonomically, *Lycodes* belongs to the zoarcid subfamily Lycodinae due to the presence of branchiostegal membranes attached to the isthmus, an L-shaped pattern of suborbital bones configuration, the absence of oral valves and dorsal-fin spines, a single epural, and not more than 12 caudal-fin rays (Anderson, 1994). *Lycodes* are distinguished from other zoarcids by the presence of so-called chin crests, which are the ventral ridge-like outgrowths of the lower jaw (Andriashev, 1954; Anderson, 1994). Additionally, the genus is characterised by the fused frontals with one unpaired dorsomedial opening and one to four paired dorsolateral openings (Nazarkin, 2010; Nazarkin et al., 2014).

Due to the high morphological plasticity and abundance of homoplastic characters, as well as the insufficient study of variability of characters and species distribution, a consistent phylogeny and dispersal history hypothesis for the genus has not yet been developed, and the natural groupings within *Lycodes* have not yet been established (Anderson, 1994; Møller & Gravlund, 2003; Mecklenburg et al., 2016). The elucidation of relationships among species of *Lycodes* is also significantly hindered by the fact that initial descriptions of some species were incomplete and inconsistent, and adequate comparisons with other species have not been conducted. Consequently, the species diversity of these fishes appears to be overestimated.

Thus, in the Sea of Okhotsk, *Lycodes* is considered one of the most taxonomically diverse genera, accounting for more than 20 species (Fedorov et al., 2003; Nazarkin & Shinohara, 2012; Nazarkin et al., 2014). Despite the long period of ichthyofauna studies in the Sea of Okhotsk, initiated by Schmidt (1904), the species composition and relationships of some *Lycodes* remain unclear, making their taxonomic status questionable. In this paper, we consider three species endemic to the Sea of Okhotsk: *L. ygreknotatus* Schmidt in Taranetz, 1937, *L. microlepidotus* Schmidt, 1950, and *L. fulvus* Toyoshima, 1985. These three species have the moderately elongated bodies (usually not exceeding 103 vertebrae), high and unfused chin crests, and similar counts and body proportions. In addition, their coloration is characterised by the presence of four to seven vertical light stripes on the dark background of the dorsal fin, which only slightly extend onto the dorsal body surface. Previously, close similarity of *L. ygreknotatus* and *L. fulvus* to *L. microlepidotus* was noted by Schmidt (1950) and Toyoshima (1985), respectively. However, there has been no comparison with *L. ygreknotatus* in the description of *L. fulvus* (see Toyoshima, 1985). Molecular comparison of these species has not been conducted due to a lack of fresh material on *L. ygreknotatus* and *L. fulvus*. Although Radchenko (2017) mentioned the latter species, the specimens considered in the study were misidentified and actually represented *L. jenseni* Taranetz et Andriashev, 1935, another endemic species from the Sea of Okhotsk (our observation during the preparation of this paper).

Together with *L. matsubarai* Toyoshima, 1985, inhabiting both the southern Sea of Okhotsk and the Sea of Japan (Nazarkin & Shinohara, 2012), the three species being examined belong to a group of Okhotsk-Sea *Lycodes*, that shared the ventromedial type of the trunk lateral line, along with striped bodies and pigmented body cavities. Two of the mentioned species, *L. microlepidotus* and *L. matsubarai*, have been recently redescribed in detail as valid species (Nazarkin, 2010; Nazarkin & Shinohara, 2012), while the taxonomic status of the other two species remains uncertain.

In this paper, we test the hypothesis that the nominal taxa *L. ygreknotatus*, *L. microlepidotus*, and *L. fulvus* actually represent the same species, and the diagnostic characters proposed for these nominal taxa simply reflect geographical variability.

Materials and methods

Morphometric counts and measurements were conducted following Anderson (1994), except for isthmus width, which was measured between the lower ends of the gill openings. Head sensory pores were stained with Methylene Blue. Head pores and pectoral-fin rays were counted on both sides of the body, and this was considered in the average value. The terminology for head pores follows Nazarkin (2010). Vertebrae and other osteological elements were examined using radiographs. Measurements were taken by a single operator with calipers to the nearest 0.1 mm. Head length (HL) and total length (TL) are the parameters used throughout. Specimens initially fixed with 4% formaldehyde and then transferred to ethanol are deposited in the Hokkaido Univer-

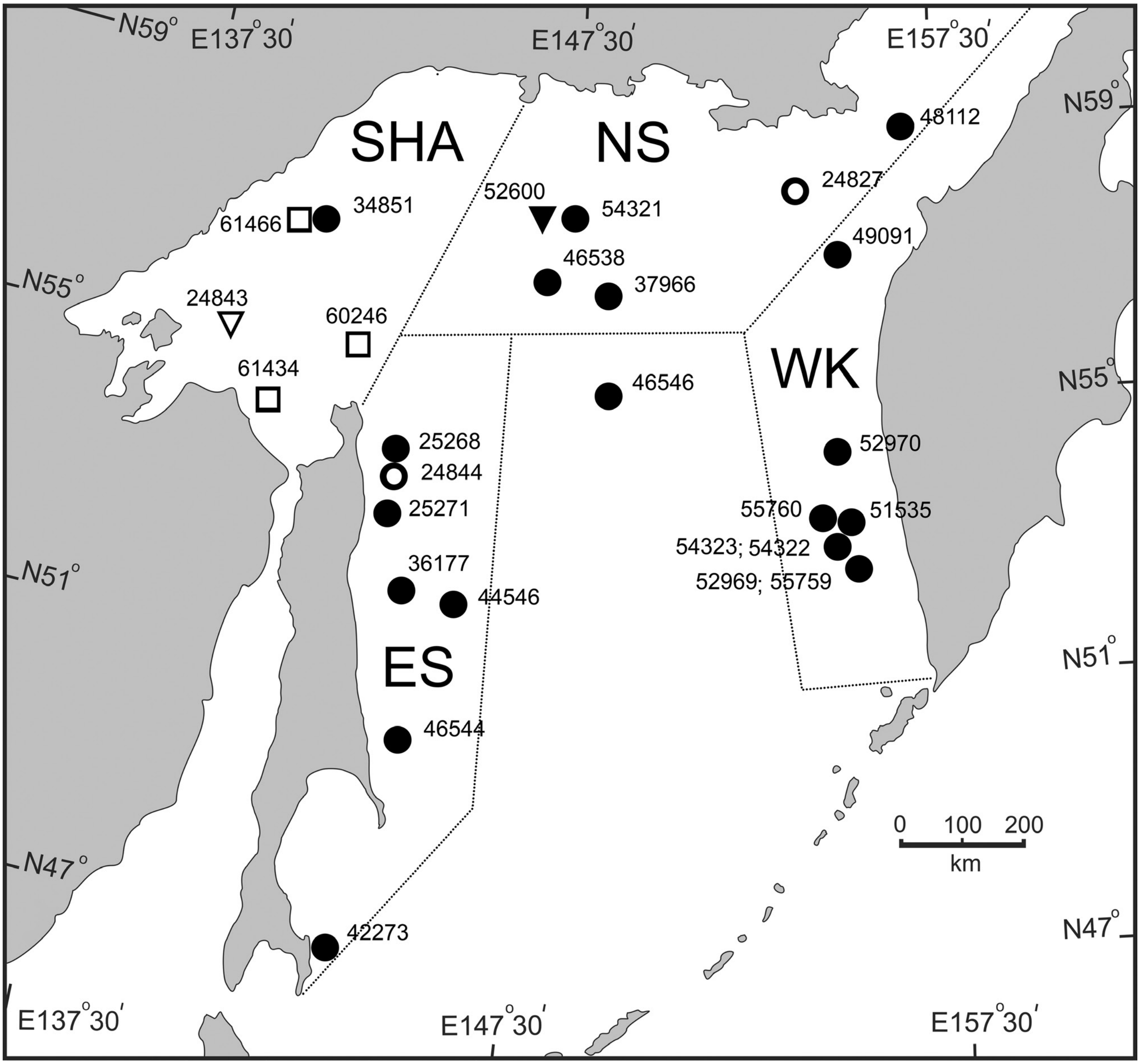

Fig. 1. Distribution map of three nominal taxa, *Lycodes ygreknotatus* Schmidt in Taranetz, 1937 (triangles), *L. microlepidotus* Schmidt, 1950, **syn. nov.** (circles), and *L. fulvus* Toyoshima, 1985, **syn. nov.** (squares) in the Sea of Okhotsk. Empty symbols indicate the localities of the type specimens. The lines delineate four regions within distribution range of the species. The numbers correspond to the collection numbers in HUMZ or ZIN. The exact locations for ZIN 52600 and 54321 are unknown; their placements on the map represent the centre of the research cruise area.

sity Museum, Hakodate, Japan (HUMZ), and the Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (ZIN). All specimens were collected in the Sea of Okhotsk. The known range of the species can be divided into four areas where some meristic characters of the specimens examined vary: Shantar area (SHA), northern shelf (NS), western Kamchatka (WK), and eastern Sakhalin (ES) (Fig. 1).

Results

During our research, we had the opportunity to investigate all type and most of the known non-type specimens of the three mentioned species and compare them based on all available characters. We found that the three nominal species exhibit closely similar values in the characters examined. In instances where there are variations in the mean values, it is observed that their respective known ranges significantly overlap (Tables 1, 2). Based on the data provided below (see the section "Discussion"), we believe that *L. fulvus* and *L. microlepidotus* are not distinct species and should both be considered junior synonyms of *L. ygreknotatus*.

Family **Zoarcidae** Swainson, 1839

Subfamily **Lycodinae** Gill, 1861

Genus ***Lycodes*** Reinhardt, 1831

Lycodes ygreknotatus Schmidt in Taranetz, 1937.

Lycodes ygreknotatus Schmidt in Taranetz, 1937: 162.
Lycodes brevipes ochotensis Schmidt, 1950: 89.
Lycodes microlepidotus Schmidt, 1950: 91, pl. 6, fig. 1, **syn. nov.**
Lycodes fulvus Toyoshima, 1985: 216, fig. 52, **syn. nov.**

Type material examined. *Holotype* of *L. ygreknotatus*, ZIN 24843, 190.0 mm TL, female, north-western part of Sea of Okhotsk in Shantar Is. area, to north of Cape of Aleksander, depth 135 m, F/V "Ara", 28 Aug. 1932, st. 22, VII-t, coll. M.N. Krivobok. *Holotype* of *L. fulvus*, HUMZ 60246, 171.0 mm TL, female, north-western part of Sea of Okhotsk in Shantar Is. area, 55°19′N 142°34′E, depth 178 m, 23 Oct. 1976. *Paratypes* of *L. fulvus*: same data as for holotype: HUMZ 58291, 194.5 mm TL, female; HUMZ 58292, 159.0 mm TL, female; HUMZ 58293, 202.0 mm TL, male; HUMZ 60244, 207.0 mm TL, female; HUMZ 60248, 163.0 mm TL, female; HUMZ 60249, 219.5 mm TL, male; HUMZ 60250, 180.0 mm TL, female; HUMZ 60251, 163.5 mm TL, female; HUMZ 60252, 199.0 mm TL, male; HUMZ 60254, 169.0 mm TL, female; HUMZ 60255, 220.0 mm TL, male; HUMZ 60256, 205.0 mm TL, male; HUMZ 60257, 191.0 mm TL, female; HUMZ 60258, 222.0 mm TL, male; HUMZ 60278, 162.0mm TL, male; HUMZ 61434, 188.0 mm TL, female, north-western part of Sea of Okhotsk, 54°19′N 140°40′E, depth 68 m, 6 Sept. 1976; HUMZ 61466, 187.0 mm TL, sex unknown, north-western part of Sea of Okhotsk in Shantar Is. area, 56°55′N 140°36′E, depth 150 m, 8 Sept., 1976. *Syntypes* of *L. microlepidotus*: ZIN 24827, 178.0–219.0 mm TL, three males and female, Sea of Okhotsk off Kamchatka, depth 115 m, F/V "Plastun", 13 Aug. 1932, tr. 145, coll. I.A. Polutov; ZIN 24844, 290.0 mm TL, female, Sea of Okhotsk off Sakhalin, depth 168–201 m, F/V "Ara", 10 Sep. 1932, st. 29, III-t, coll. M.N. Krivobok. *Syntypes* of *L. brashnikovi*: ZIN 51535, 174.0–194.0 mm TL, two females, Sea of Okhotsk off Kamchatka, 53°17′N 154°47′E, cruiser "Komandor Bering", 5 Aug. 1907, coll. N.A. Smirnov & A.G. Begak (from ZIN 19167). *Holotype* of *L. brevipes ochotensis*, ZIN 25271, 281.0 mm TL, male, Sea of Okhotsk off Sakhalin, 53°17′N 144°10′E, depth 165 m, F/V "Gagara", tr. 233, 1932, coll. S.G. Generozova.

Additional material examined. **Sea of Okhotsk**: *north-western Sea of Okhotsk in Shantar Is. area (SHA)*: ZIN 34851, 175.0 mm TL, female, 57°02′N 141°46′E, depth 147 m, F/V "Ara", 5 Sep. 1932, coll. M.N. Krivobok; HUMZ 57870, 164.5 mm TL, male, same data as for holotype of *L. fulvus*; HUMZ 61462, 198.5 mm TL, female, same data as for holotype of *L. fulvus*; *northern shelf of the Sea of Okhotsk (NS)*: ZIN 37966, 224.0–227.0 mm TL, male and female, 56°24′N 148°45′E, depth 185 m, F/V "Seskar", 27 Aug. 1963, coll. V.P. Shuntov; ZIN 46538, 227.0–260.0 mm TL, three females, 56°30′N 147°00′E, depth 265 m, F/V "Equator", tr. 172, 23 Oct. 1982, coll. L.A. Borets; ZIN 46546, 330.0 mm TL, male, Deryugin Depression, 55°01′N 148°55′E, depth 520 m, F/V "Equator", tr. 148, 14 Aug. 1998; ZIN 48112, 226.0 mm TL, male, Shelikhov Gulf, 58°59′N 156°42′E, depth 386 m, F/V "Mys Babushkina", st. 1, dredge 41, 3 Aug. 1986, coll. L.A. Borets; ZIN 54321, 196.0–213.0 mm TL, three females, R/V "Zodiak", Aug. 2000, coll. V.A. Vyshegorodtsev & A.M. Panfilov [exact locality and depth are unknown; see comments to ZIN 52600]; ZIN 52600, 190.0 mm TL, female, R/V "Zodiak", Aug. 2000, coll. V.A. Vyshegorodtsev & A.M. Panfilov [exact locality and depth are unknown for the most materials collected in this research cruise which was conducted within the boundaries 56–61°N and 146–159°E in the depths of 41–433 m]; *eastern Sakhalin (ES)*: ZIN 25268, 136.0 mm TL, male, opposite to Okha City, depth 154–180 m, F/V "Ara", 10 Sept. 1932, st. 28 III-t, coll. M.N. Krivobok; ZIN 36177, 290.0–344.0 mm TL, two females, 53°17′N 144°10′E, depth 275 m, tr. 35, 19 Aug. 1959, coll. A.P. Nikolaev; ZIN 42273, 162.0–276.0 mm TL, five females, 46°49′N 143°50′E, depth 143-187 m, F/V "Toporok", st. 63–64, otter-trawl 24, 4 Sept. 1947; ZIN 44546, 238.0–304.0 mm TL, three male and female, 51°50′N 144°23′E, depth 240 m, F/V "Poseidon", st. III, tr. 4, 14 July 1978, coll. V.D. Tabunkov; ZIN 46544, 323.0 mm TL, female, 49°55′N 144°46′E, depth 230–212 m, R/V "Mys Yunony", tr. 56, 11 Oct. 1981, coll. A.I. Blagoderov; *western Kamchatka (WK)*: ZIN 49091, 288.0 mm TL, male, off Ust'-Khairyuzovo Vill., 57°10′N 154°32′E, depth 390–396 m, tr. 298, 12 Dec. 1986; ZIN 52969, 175.5 mm TL, unsexed, 52°32′N 155°02′E, depth 150 m, F/V "Sopochnoe", tr. 49, 23 Jul. 2002, coll. A.V. Vinnikov & K.A. Vinnikov; ZIN 52970, 159.0 mm TL, male, 54°21′N 154°28′E, depth 201 m, F/V "Sopochnoe", tr. 102, 1 Aug. 2002, coll. A.V. Vinnikov & K.A. Vinnikov; ZIN 54322, 227.0 mm TL, male, 52°52′N 154°35′E, depth 250–257 m, F/V "Kapitan Melamud", tr. 293, 10 Sep. 2006, coll. M.V. Nazarkin; ZIN 54323, 186.0 mm TL, male, 52°56′N 154°35′E, depth 250–254 m, F/V "Kapitan Melamud", tr. 298, shrimp trawl, 12 Sep. 2006, coll. M.V. Nazarkin; ZIN 56990, 194.0 mm TL, male, at 53°N, depth 180–240 m, F/V "Pacific Breeze", July–Aug. 1998, coll. P. Vasil'ev; ZIN 55759, 141.0 mm TL, male, 52°41′N 155°01′E, depth 148–151 m, R/V "Professor Kaganowsky", tr. 53, 12 July 2008, coll. M.V. Nazarkin; ZIN 55760, 206.0–238.0 mm TL, four females and two males, 53°71′N 154°12′E, depth 150 m, R/V "Professor Kaganowsky", tr. 69, 14 July 2008, coll. M.V. Nazarkin; *unknown exact locality*: ZIN 29091, 166.0–225.0 mm TL, five specimens, unsexed, 1932; ZIN 46545, 269.0 mm TL, male, F/V "Equator", 1982, coll. L.A. Borets.

Emended diagnosis. Ventromedial line of trunk neuromasts. Submental crests high and free anteriorly. Pelvic fin very short. Pectoral fin without notch, sometimes weakly emarginated. Dorsal fin with four to seven light, often Y-shaped stripes slightly descending to body sides. Branchial stripe sometimes present, usually interrupted. Orobranchial cavity speckled; peritoneum dusky, brownish. Body and abdomen scaled, occiput scaled or not. Total vertebrae 92–106, of them 19–22 abdominal.

Redescription. Body moderately elongated, with body depth at base of anal fin approximately 0.1 times as long as TL. Preanal distance about 40% of TL. Head of moderate size, with length of about one-fifth of TL. Bony interorbital width smaller than length of eye. Chin crests high, not fused anteriorly, with rectangular or, often, slightly pointed tips. Nostril short. Gill opening usually extending slightly ventral to base of pectoral fin. Teeth present on jaws, vomer, and palatines. Palatine with 6–22 teeth arranged in a single, uneven row; in third of specimens examined, from one to eight teeth forming another irregular outer row.

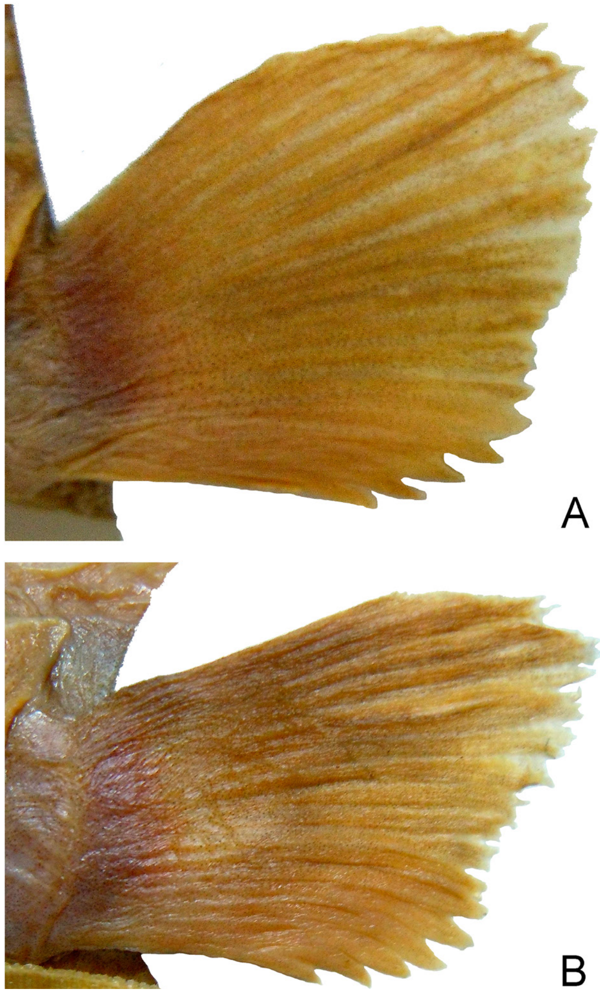

Fig. 2. Emarginated pectoral fins of paratypes of *Lycodes fulvus* Toyoshima, 1985, **syn. nov. A**, HUMZ 58293, male, 202.0 mm TL; **B**, HUMZ 60258, male, 222.0 mm TL.

Dorsal and anal fins low, usually not exceeding half of body depth at anal fin origin. Pectoral fin consisting of 18–21 rays, shorter than head. Posterior margin of pectoral fin without deep notch, but in 52% of specimens examined, it shallowly emarginated from one or both sides of body (Fig. 2). Pelvic fin very short, sometimes nub-like, never reaching base of pectoral fin, 21.3–61.1% (40.1% on average) of eye length. Pelvic fin base

Fig. 3. General appearance of live specimens of *Lycodes microlepidotus* Schmidt, 1950, **syn. nov.** from western Kamchatka. **A**, **B**, ZIN 55759, male, 141.0 mm TL; **C**, **D**, ZIN 55760, female, 211.0 mm TL (C) and male, 216.0 mm TL (D); **E**, male, 238.0 mm TL.

on isthmus or slightly anterior to line connecting ventral ends of gill openings.

Usually no more than 103 vertebrae, of which 19–22 in abdominal region (Table 2). Only one specimen (ZIN 42273, 194.5 mm TL) from eastern Sakhalin area (Fig. 1) with 106 total vertebrae. Centrae of abdominal vertebrae slightly asymmetrical in 79% of cases; in other cases, symmetrical or almost symmetrical. Anteriormost pterygiophore of dorsal fin associated with vertebrae 4 or 5, very rarely 6.

Sensory head pores not reduced in number (Table 2); their openings small, but not microscopic, without tubes or skin collars. Anterior infraorbital pore just posterior to nostril. Interorbital pore present in 78% of specimens. Main line of trunk neuromasts ventromedial. From 30 to 42 neuromasts located between posterior postorbital pore and bend of line above bases of anal-fin rays 2–6.

Body and vertical fins scaled. On body sides dorsal to pectoral fins, scale cover extending anterior of dorsal-fin origin. Usually, scale cover not

Fig. 4. General appearance of preserved specimens. **A**, ZIN 24843, holotype of *Lycodes ygreknotatus* Schmidt in Taranetz, 1937, female, 190.0 mm TL; **B**, HUMZ 60244, paratype of *L. fulvus* Toyoshima, 1985, **syn. nov.**, female, 207.0 mm TL.

reaching pectoral-fin base to a distance of half-length of eye. However, in five specimens, it extending this base, and some sparse scales located on bases of pectoral rays from inner side of fin. Scales absent from nape in holotype of *L. ygreknotatus* and in most paratypes of *L. fulvus*, **syn. nov.**, whereas several transverse scale rows present anterior to beginning of dorsal fin in all examined specimens of *L. microlepidotus*, **syn. nov.** and three paratypes of *L. fulvus*. Belly scaled to base of pelvic or pectoral fin, but specimen HUMZ 60255 with narrow scaleless area along abdomen.

Life body coloration light brown, belly and underside of head light grey or whitish (Fig. 3). Pectoral fin yellowish brown, with whitish lower rays. Dorsal and anal fins with blackish margins becoming narrower in larger specimens. Usually four to six, in one case seven, light stripes on dorsal fin, slightly extending to dorsal sides of body. Stripes expanded dorsally and usually with a dark area inside making them Y-shaped. In 20% of specimens examined, branchial stripe connecting upper ends of gill openings, usually interrupted in middle (Fig. 3B). Sometimes a light spot located at base of anterior dorsal-fin rays. Colouring of younger specimens more prominent and contrast; in larger fishes, light stripes becoming hardly discernible. Preserved specimens greyish brown, with faded stripes (Fig. 4). Orobranchial cavity and peritoneum pigmented in all specimens examined in same manner as described here for type series of *L. fulvus*.

Distribition. Endemic to the Sea of Okhotsk (Fig. 1).

Notes on morphology. The original descriptions of the three species are often controversial and require clarification. Contrary to Schmidt (1950: 92) stating that the orobranchial cavity and intestine are unpigmented, we found that they are pigmented in all specimens of *L. microlepidotus*, **syn. nov.**, including the syntypes. The dorsum anterior to the dorsal fin lacks scales in the holotype of *L. ygreknotatus*, in contrast to Schmidt's (1950: 93) assertion of scaling on the dorsum anterior to the base of the dorsal fin.

The coloration of the body cavities of *L. fulvus*, **syn. nov.** was not mentioned in the original description (Toyoshima, 1985). Upon examination of all type specimens, it was noted that the orobranchial cavity is weakly pigmented with small and sparse pigment dots, whereas the pigmentation of the peritoneum is heavier and consists of large and closely spaced spots. The section "Description" (p. 217) and the identification key (p. 187) specify that "dorsum before dorsal fin scaleless", while the diagnosis (p. 216) indicates that "dorsum before dorsal fin scaled to occipital region" (Toyoshima, 1985). Our investigation reveals that the dorsum anterior to the base of the dorsal fin lacks scales in most paratypes of *L. fulvus*. The condition of this character in the holotype is uncertain due to the skin damage in this area. Three paratypes have some scales on the nape: HUMZ 60256 and HUMZ 58293 with two and four rows of sparse

Table 1. Selected proportional measurements of *L. ygreknotatus*, *L. fulvus*, **syn. nov.**, and *L. microlepidotus*, **syn. nov.** Average values are specified under line.

	L. ygreknotatus		*L. fulvus*			*L. microlepidotus*	
	holotype	nontype (n = 1)	holotype	paratypes (n = 17)	nontypes (n = 2)	syntypes (n = 5)	nontypes (n = 41)
TL (mm)	190.0	190.0	171.0	159.0–222.0 190.1	164.5–198.5 181.5	179.0–290.0 220.2	136.0–345.0 226.1
In % of TL							
Predorsal length	23.2	23.5	23.5	21.7–25.1 23.6	24.2–25.4 24.8	21.8–24.2 23.2	20.2–26.3 23.1
Preanal length	42.1	40.6	40.1	38.3–42.1 40.3	39.4–39.8 39.6	36.3–41.2 38.8	37.2–43.3 39.2
Prepectoral length	19.4	21.5	19.1	17.8–20.5 19.3	19.6–20.7 20.2	17.9–23.0 19.8	17.6–22.3 19.6
Preventral length	16.7	19.1	15.7	13.2–16.5 15.1	15.1–15.6 15.4	14.6–20.2 16.5	14.3–19.6 15.9
Pectoral fin length	13.2	12.7	10.2	10.1–13.0 11.5	12.2–12.7 12.5	11.7–12.9 12.2	9.8–14.6 11.7
Pelvic fin length	1.6	1.9	0.9	1.0–1.8 1.4	1.7–1.8 1.7	1.4–1.9 1.6	0.8–2.4 1.6
Pectoral-fin base height	5.7	5.8	4.3	4.5–5.8 5.0	4.7–5.2 4.9	4.7–5.1 4.9	4.0–6.2 4.9
Gill opening height	7.1	7.0	6.7	5.9–7.7 6.7	6.8–6.9 6.9	5.7–7.3 6.6	5.5–7.8 6.7
Isthmus width	5.1	6.6	4.2	3.9–6.2 4.9	4.3–5.3 4.8	4.4–5.8 4.9	3.8–7.0 4.8
Dorsal fin height	4.9	4.5	–	4.0–5.3 4.6	5.5–5.7 5.6	4.4–6.1 5.3	3.4–5.3 4.5
Anal fin height	4.5	4.3	–	3.6–4.4 4.1	4.1–5.3 4.7	3.4–4.6 4.2	2.8–4.9 3.7
Caudal fin length	2.5	3.1	–	1.9–3.1 2.5	2.6–2.7 2.6	1.4–2.1 1.7	1.5–3.3 2.2
Body depth at anal origin	10.0	9.9	10.6	9.2–12.0 10.5	10.2–10.4 10.3	9.1–10.2 9.7	8.4–11.8 9.9
Head length	19.0	19.8	18.7	18.1–20.7 19.1	19.0 - 20.1 19.5	17.6–21.0 19.0	16.9–21.4 19.0
In % of head length							
Snout length	28.5	27.9	31.9	25.5–33.9 29.6	26.5–30.0 28.3	28.4–33.2 31.2	24.6–34.2 28.6
Eye diameter	19.9	21.5	19.4	15.2–21.6 18.5	18.2–19.4 18.8	17.3–23.1 20.2	16.8–30.1 21.1
Skiny interorbital width	16.6	16.7	–	12.4–18.1 14.9	10.6–14.6 12.6	10.4–13.0 11.7	8.7–18.2 13.6
Bony interorbital width	4.2	3.7	3.8	2.5–4.7 4.0	4.2–4.8 4.5	3.7–4.7 4.1	2.8–4.9 3.8
Upper jaw length	37.5	38.7	35.3	33.1–43.8 38.4	34.8–38.2 36.5	32.1–44.6 39.4	37.0–50.9 41.6

Table 2. Selected counts of *L. ygreknotatus*, *L. fulvus*, **syn. nov.**, *and L. microlepidotus*, **syn. nov.** Average values specified under line.

	L. ygreknotatus		*L. fulvus*			*L. microlepidotus*	
	holotype	nontype (n = 1)	holotype	paratypes (n = 17)	nontypes (n = 2)	syntypes (n = 5)	nontypes (n = 46)
Abdominal vertebrae	20	20	21	19–21 20.1	19–20 19.5	20–21 20.6	19–22 20.4
Caudal vertebrae	75	75	74	72–77 74.4	75–76 75.5	76–80 78.5	73–84 78.8
Total vertebrae	95	95	95	92–96 94.5	95–95 95.0	96–101 99.0	93–106 99.1
Dorsal fin rays	88	88	89	86–90 88.1	88–89 88.5	89–95 92.8	87–99 92.5
Anal fin rays	76	76	76	73–77 74.6	76–76 76.0	76–81 79.0	73–85 79.0
Pectoral fin rays	21	21	19-20	19–21 20.4	20–20 20.0	19–20 19.6	18–21 19.4
Dorsal fin origin associated with vertebrae	5	4	4	4–5 4.8	5–5 5.0	5–5 5.0	4–6 4.9
Nasal pores	3	3	3	2–3 2.8	2–3 2.5	2–3 2.7	2–3 2.7
Suborbital pores	9	10	10	9–10 9.9	10–10 10.0	10–11 10.1	9–11 10.1
Interorbital pores	0	1	?	1–1 1.0	1–1 1.0	0–1 0.5	0–1 0.7
Postorbital pores	3	3	3	3–3 3.0	3–3 3.0	3–3 3.0	2–5 3.0
Preoperculomandibular pores	8	8	8	8–8 8.0	8–8 8.0	8–8 8.0	8–8 8.0
Occipital pores	3	3	3?	2–3 2.9	3–3 3.0	3–3 3.0	2–4 3.0
Scales rows on nape	0	0	?	0–5 0.3	0–0 0	15–20 16.8	4–25 15.1
Scales rows at anal fin origin	21	21	20	18–25 22.5	21–22 21.5	23–29 26.6	19–33 25.5
Light stripes on body	5	6	?	0–5 3.7	4–4 4.0	1–4 2.3	0–7 4.0
Branchial stripe	1	1	?	0–1 0.2	0	0	0–1 0.3

scales, respectively, which are separated from the scaled area of the body sides, while HUMZ 60258 has five continuous scale rows that are connected to the scaled lateral body areas.

Comparative notes. Among the species with the ventro-medial lateral line, *L. ygreknotatus* is more similar to *L. marsubarai* Toyoshima, 1985 in the body proportions, small pelvic fin, striped body coloration, and pigmentation of body cavities (Nazarkin & Shinohara, 2012). Most of the characters of these two species broadly overlap. However, the latter species can be distinguished from *L. ygreknotatus* by a greater number of vertebrae (99–107, usually more than 100 *vs.* 92–106, usually less than 100), a greater number of vertical body stripes (1–10, usually more than 6 *vs.* 0–7, usually no more than 5), and longer body stripes (usually reaching the midbody and bounding rectangular dark spots on its sides [Nazarkin & Shinohara, 2012: figs. 2 and 3] *vs.* just slightly descending to the upper body). As currently known, the ranges of both species, although close to each other, are still separated, and therefore these species are allopatric. *Lycodes marsubarai* is mainly distributed in the Sea of Japan, while in the Sea of Okhotsk, it inhabits only its southernmost part off Hokkaido. The morphological differences mentioned above, coupled with the allopatric distribution of these taxa, offer compelling evidence that they are distinct species. The great similarity of these species suggests that they are descendants of a common ancestor and had acquired their distinctive features as a result of isolation during the Pleistocene glaciations when the Japan and Okhotsk sea basins were separated by a marine regression (Nishimura, 1974). It is also possible that these two taxa are currently so-called "young species", the divergence of which is not yet clearly expressed in morphology. Apparently, future molecular investigations can help clarify their relationships.

Discussion

Our investigation did not reveal significant morphological differences between the type specimens of *L. fulvus*, **syn. nov.** and *L. ygreknotatus*. The proportional measurements, meristic counts, scales distribution, and colour pattern of the body and its cavities of the holotype of *L. ygreknotatus* (Fig. 4A) fall well within the range of variability of the type series of *L. fulvus* (Tables 1, 2). Additionally, the type specimens of both species were collected in the same area of the Shantar Islands (Fig. 1). Therefore, we conclude that these nominal taxa belong to the same species, and that *Lycodes fulvus* Toyoshima, 1985 should be considered a junior synonym of *L. ygreknotatus* Schmidt in Taranetz, 1937.

Toyoshima (1985) found that *L. fulvus* is very similar to *L. microlepidotus*, **syn. nov.** in coloration, meristic counts, lateral-line pattern, and many proportional measurements, but can be easily distinguished from the latter by the absence of scales on the dorsum anterior to the base of the dorsal fin. We found up to five rows of scales on the nape in some paratypes of *L. fulvus*. This finding bridges the gap between the completely scaleless occiput thought to be diagnostic for both *L. ygreknotatus* and *L. fulvus*, and the scaled nape in *L. microlepidotus*. According to our data, the minimum number of scale rows on the nape in the latter species is four in the specimen ZIN 55760 (male, 216 mm TL) collected off Western Kamchatka. The highest number of scale rows on the occiput, equaling 25, was found in the specimen ZIN 46546 collected from the center of the sea, in the Deryugin Trough at a depth of 520 m. According to Toyoshima (1985), *L. fulvus* also differs from *L. microlepidotus* by the greater interorbital width (15.7–24.6% of the head length *vs.* 4.9–5.8% in *L. microlepidotus*), smaller eye (14.4–22.0% of the head length *vs.* 20.3–23.7%), and shorter pectoral fin (10.2–13.1% TL *vs.* 11.3–13.2%). Our data do not confirm the proportional differences between the type specimens of these nominal taxa (Table 1). Apparently, in the case of the interorbital space, Toyoshima compared the skiny width for *L. fulvus* with the bony width for *L. microlepidotus*.

In the original description of *L. microlepidotus*, Schmidt (1950) pointed out a similarity in body proportions and meristic counts between this new species and *L. ygreknotatus*, which he had previously described. Schmidt (1950) did not exclude the possibility that the former species might be a subspecies of the latter. As morphological features that distinguish *L. ygreknotatus*, he indicated larger and sparser scales, a slightly different head shape, a higher dorsal fin, and a colour pattern with whitish stripes in the shape of the letter Y (Schmidt, 1950). Later, it was shown that the body proportions of *L. ygreknotatus* fall within the range of those of *L. microlepidotus*, and the number and arrangement of scales on the body of both species are very similar, except for the area anterior to the dorsal fin: the nape lacks scales in the former and is scaled in the latter species (Nazarkin, 2010). It was also shown that some specimens of *L. microlepidotus* possess light stripes descending from the dorsal fin in the shape of the letters Y or V, which is typical for *L. ygreknotatus*. The data

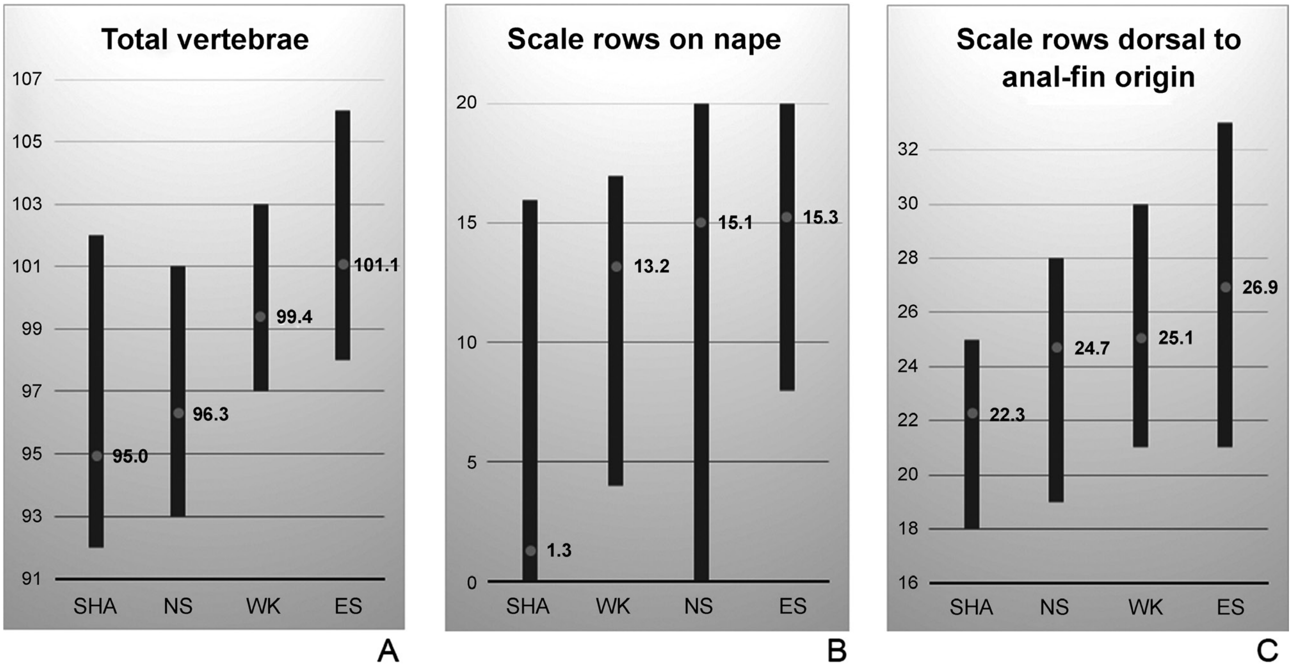

Fig. 5. Graph showing the ranges and mean values distribution of the total number of vertebrae (A), the number of scale rows on the nape (B), and the number of scale rows dorsal to the anal-fin origin (C) in the four regions of the range of *Lycodes ygreknotatus* Schmidt in Taranetz, 1937.

gathered in this research support the conclusions of Nazarkin (2010) and bridge the gap between the presence and absence of scales on the nape, which was the only remaining feature suitable for distinguishing between these species. We also confirm that the Y- or V-shaped light marks on the dorsal fin, previously believed to be specific to *L. ygreknotatus* (Taranetz, 1937; Lindberg & Krasykova, 1975; Toyoshima, 1985; Hatooka, 2002), are often present in the specimens attributed to *L. fulvus* or *L. microlepidotus* based on other characters (Figs 3 and 4B).

The intermediate numbers of scale rows on the nape (i.e., between zero and ten) in some specimens might indicate potential hybridisation between *L. microlepidotus* and *L. ygreknotatus*. In this case, it would also be reasonable to expect intermediate counts for other metameric structures, such as vertebrae and rays in the vertical fins, in these specimens (Hubbs, 1955). However, these specimens have meristic counts that align more closely with the average values for their respective regions rather than falling within the range of values that are intermediate between the species (Fig. 5A). The total number of vertebrae varies among specimens from different regions: 92–94 in three specimens from SHA (2–5 scale rows on the nape), 100 in two specimens from WK (4–7 rows), 95 in the specimen from NS (9 rows), and 102 in the specimen from ES (8 rows). In contrast, hybrid individuals were expected to have a vertebral count ranging between 94.5 and 99.0. Therefore, the likelihood of the listed specimens having a hybrid origin is currently deemed low. In cases of backcrosses, the range of meristics can significantly differ between F1 hybrids and the parental species, influenced by the number of backcrossing generations and the genetic basis of meristic phenotypes (Garrett et al., 2007). Subsequent genetic studies hold the potential to provide further insights into this matter.

Our data reveal significant variability in the number of vertebrae and scale rows in *L. ygreknotatus* from different parts of its distributional range (Fig. 5; Table 3), with the lowest mean values of these characters found in the Shantar Islands region (Fig. 5). The highest mean values are observed in the eastern Sakhalin and, to a lesser degree, western Kamchatka regions. This pattern of mean values distribution can be tentatively in-

Table 3. Regional variations of selected counts in *Lycodes ygreknotatus*.

Variations of total number of vertebrae

Region	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106
SHA	1		8	9	3						1				
NS		1	1	4	2	2		2		1					
WK						1	4	3	4	2		1			
ES							1	3	1	4	4	1			1

Variations of the number of scale rows dorsal to the base of anal fin

Region	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
SHA	2		2	5	2	2	6	3								
NS		1		1		3	1	1	1	3	2					
WK				1	1	2	1	3	3	1	1		1			
ES				2	1	1	1			1	2	3	1			2

Variations of the number of scale rows on the nape

Region	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
SHA	17		1		1	1											1				
NS	1									1					1	3	1	1	2	1	2
WK					1			1					3	1	2	2	1	2			
ES									1				1	2	2	1	3	1	2	1	1

terpreted as a north-south clinal variation. The observed geographic cline in the number of vertebrae and scale density contradicts Jordan's rule (Jordan, 1891) but aligns with the observations of Andriashev (1954, footnote on p. 269), who pointed out that in species of *Lycodes*, scale cover is more pronounced in the southern populations of the same species compared to the northern ones.

Embryogenesis of fish is influenced by a number of environmental factors. Experiments by Schmidt (1920) showed that an increase in salinity and temperature during the prenatal period positively affects the increase in the average number of vertebrae in offspring in populations of the European eel *Zoarces viviparus* (Linnaeus, 1758). Since the precise timing, depth, temperature, oxygen levels, and other details of the reproduction of *Lycodes* species are unknown, we cannot definitively attribute the clinal variability in *L. ygreknotatus* to specific environmental factors. However, the population of *L. ygreknotatus* with the lowest number of vertebrae and lowest scale density occurs in the region of Shantar Islands. This region is characterised by extremely cold temperatures year-round and long ice periods, averaging 260 days (Glukhovsky et al., 1998). Prolonged exposure to low temperatures is likely to significantly impact the early development and growth of poikilotherms, leading to substantial delays in organ and system formation. Therefore, the decrease in the number of vertebrae and scales in the Shantar Islands population of this species may be a consequence of the extremely cold conditions in this part of its range.

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