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New Species of Grayling *Thymallus tugarinae* sp. nova (Thymallidae) from the Amur River Basin

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Abstract—Data on a new species, low Amur grayling *Thymallus tugarinae* sp. nova, inhabiting tributaries of the lower and middle current of the Amur River, are presented. This species has been earlier equated with the Amur grayling *T. grubii*, described by Dybowski (1869) from the rivers Onon and Ingoda (the Upper Amur Basin). The new species differs from other representatives of the genus in the body coloration, the pattern on the upper fin, and certain morphological characters. On most of the Amur Basin, the grayling from the Lower Amur is sympatric with *T. grubii* and in its tributary Bureya River, also with the Bureya grayling *T. burejensis.* Individuals with intermediate traits are unknown, pointing to reproductive isolation. These data are supported by the results of molecular-genetic analysis (Froufe et al., 2003, 2005; Knizhin et al., 2004).

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The history of the study of graylings in the Amur River Basin continues for more than two centuries. Georgi (1775) first noted graylings in small rivers off Nerchinsk (basin of the River Shilka) and identified it as *Salmo thymallus* Linnaeus, 1785. After almost one hundred years, graylings from the rivers Onon and Ingoda (the Upper Amur Basin) was described by Dybowski as a new species, Amur grayling *Thymallus grubii* (Dybowski, 1869). Berg (1916) and later Svetovidov (1936) analyzed the characteristics of 11 fish from different parts of Amur and identified the Amur grayling[1] as a subspecies of the arctic grayling *Thymallus arcticus gruber.*[2] Later, the opinions about the taxonomic status of this form disparted. Some investigators considered the Amur grayling a subspecies of *T. a. grubei* (Shatunovskii, 1983; Egorov, 1985; Karasev, 1987; Dorofeeva, 1998, 2002) whereas others, an independent species (Pivnička and Hensel, 1978; Tugarina and Khramtsova, 1980; Makoedov, 1987; Chereshnev, 1998; Safronov et al., 2001, 2003; Safronov and Nikiforov, 2003; Bogutskaya and Naseka, 2004; Knizhin et al., 2004). In the 1980s, it was determined that graylings from the upper and lower Amur River have significant morphological differences (Tugarina and Khramtsova, 1980, 1981; Shatunovskii, 1983; Skurikhina, 1984; Skurikhina et al., 1985).[3] Later, in addition to *T. grubii*, several other species were noted for the Amur River Basin: Bureya grayling *T. burejensis* Antonov, 2004, *Thymallus* sp. 1, lower Amur and *Thymallus* sp. 2, yellow-spotted grayling (Shed'ko, 2001; Bogutskaya and Naseka, 2004).

Currently, it seems obvious that four grayling forms live in the Amur River, three of which are sympatric in a part of their range but remain reproductively isolated (Antonov, 1995, 1999a, 1999b, 2001, 2004; Shed'ko, 2001; Bogutskaya and Naseka, 2004; Froufe et al., 2003, 2005; Knizhin et al., 2004). One of these forms is the Amur grayling *T. grubii* represented in the upper current of the river by a nominative subspecies *T. g. grubii*, noted in several studies as the "Upper Amur form" (Froufe et al., 2003; Antonov, 2004; Knizhin et al., 2004). The second is the yellow-spotted grayling *T. grubii flavomaculatus*, Knizhin, Antonov et Weiss, 2006 (Knizhin et al., 2006a), inhabiting the upper reaches of several large tributaries of the Lower Amur. The third form is the form earlier considered as a "large-scale form" (Antonov, 1999a, 1999b, 2001; Froufe et al., 2003, 2004; Knizhin et al., 2004) was later described as the species *T. burjensis* (Antonov, 2004). The fourth form, the "Lower Amur" grayling[4], differs morpholog-

[1] A mixed sample was used for the morphological analysis, including both lower Amur and upper Amur graylings and a specimen from the Ola River, inhabited, according to the current views, by the Eastern arctic grayling *T. arcticus pallasii* (Chereshnev, 1998; Chereshnev et al., 2002) as a subspecies of the arctic grayling Thymallus articus grubei.

[2] Berg (1900) changed the original name from *grubii* to *grubei.*

[3] The first complete description of morphological characters in the lower Amur grayling from the Khor River was conducted by Tugarina and Khramtsova (1980).

[4] Probably, this form was noted by Shed'ko (2001) as *Thymallus* sp. 1 and by Bogutskaya and Naseka (2004) under the same name, lower Amur grayling.

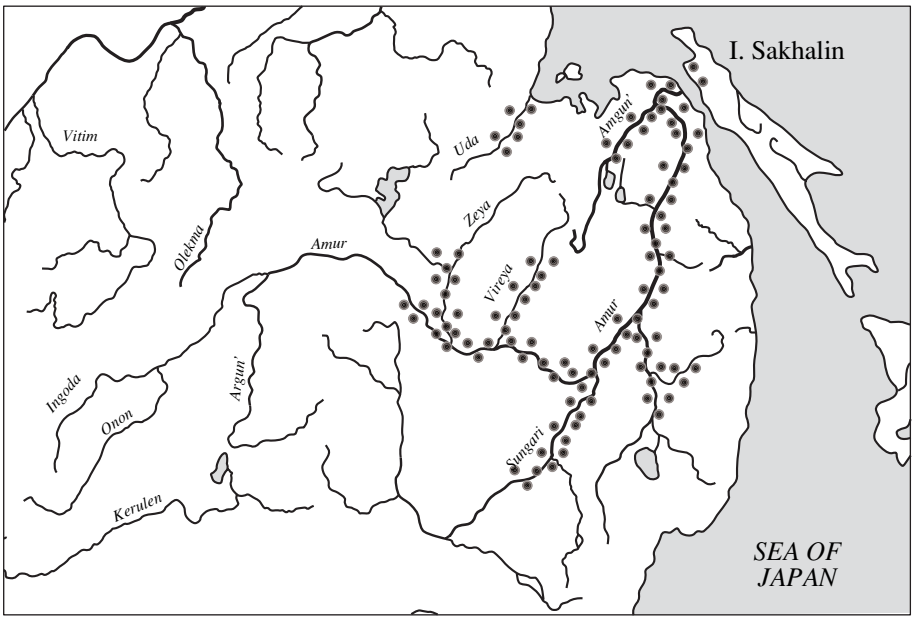

Fig. 1. The species range of the Lower Amur grayling *Thymallus tugarinae* sp. nova

ically and genetically from the abovementioned and other forms of the genus *Thymallus* and may be described as a species (Froufe et al., 2003, 2005; Knizhin et al., 2004), which was the aim of this study.

MATERIAL AND METHODS

The material was collected in the basin of the Amur River and in rivers of the northwestern margin of Sakhalin Island in 1989–2004 (Fig. 1). Graylings were caught with rods, dip nets, and gill nets with the mesh size 25–30 mm. Overall, 178 specimens were caught, from which were 57 fish from the Anyui River and 19 from the Khunmakta River (tributary of the Uanga River, Sakhalin) were subjected to complete morphological analysis following Pravdin (1966), taking account of the recommendations and modifications for graylings (Svetovidov, 1936; Tugarina and Khramtsova, 1980; Knizhin et al., 2004). To avoid errors, the traits were assessed by a single experienced operator. The statistical analysis and comparison with graylings from other water bodies were conducted using standard methods (Plokhinskii, 1970; Rokitskii, 1973) using the Statistica 5.5A software package (Borovikov and Borovikov, 1998) and SPSS 8.0. For the comparative analysis, in addition to the data published earlier (Svetovidov, 1936; Tugarina, 1972; Tugarina and Dashidorzhi, 1972; Zinov'ev, 1979; Tugarina and Khramtsova, 1980; Shatunovskii, 1983; Chereshnev et al., 2002; Safronov et al., 2003; Antonov, 2004; Knizhin et al., 2004, 2006a, 2006b), we used our materials on the morphology of graylings from other water bodies of Siberia. During the identification of the fish, we accounted for the body coloration, the shape and the pattern on the dorsal fin, which in graylings is an important diagnostic characteristic (Zinovyev and Bogdanov, 1976; Makoedov, 1987, 1999; Chereshnev, 1994; Chereshnev et al., 2002; Antonov, 2004; Knizhin et al., 2004, 2006a, 2006b, 2006c; Romanov, 2004a, 2004b, 2005).

For analysis of morphological traits using the principal components analysis, we used the variance–covariance matrix. The significance of the differences and their value were determined using the *t*-test with the significance level $p \le 0.001$ and using the *CD* coefficient (Mayr, 1971).

The composition of the food objects of the lower Amur grayling was analyzed following the recommendations in the *Methodical Guide…* (1974).

To ascertain the ranges of Amur graylings, we reviewed collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) and the Zoological Museum of Moscow State University (MSU, Moscow).

RESULTS AND DISCUSSION

Thymallus tugarinae Knizhin, Antonov, Safronov et Weiss sp. nova, lower *Amur grayling*

(Figs. 2, 3)

Thymallus grubei (non Dybowski, 1869) (sic.), Berg, 1906: 398 (the Amur system, part.); Berg, 1908: 67 (Amur, part.).

Thymallus (Thymalloides) grubei (non Dybowski, 1869) (sic.), Berg, 1909: 55 (mountain rivers of the Amur system, part.).

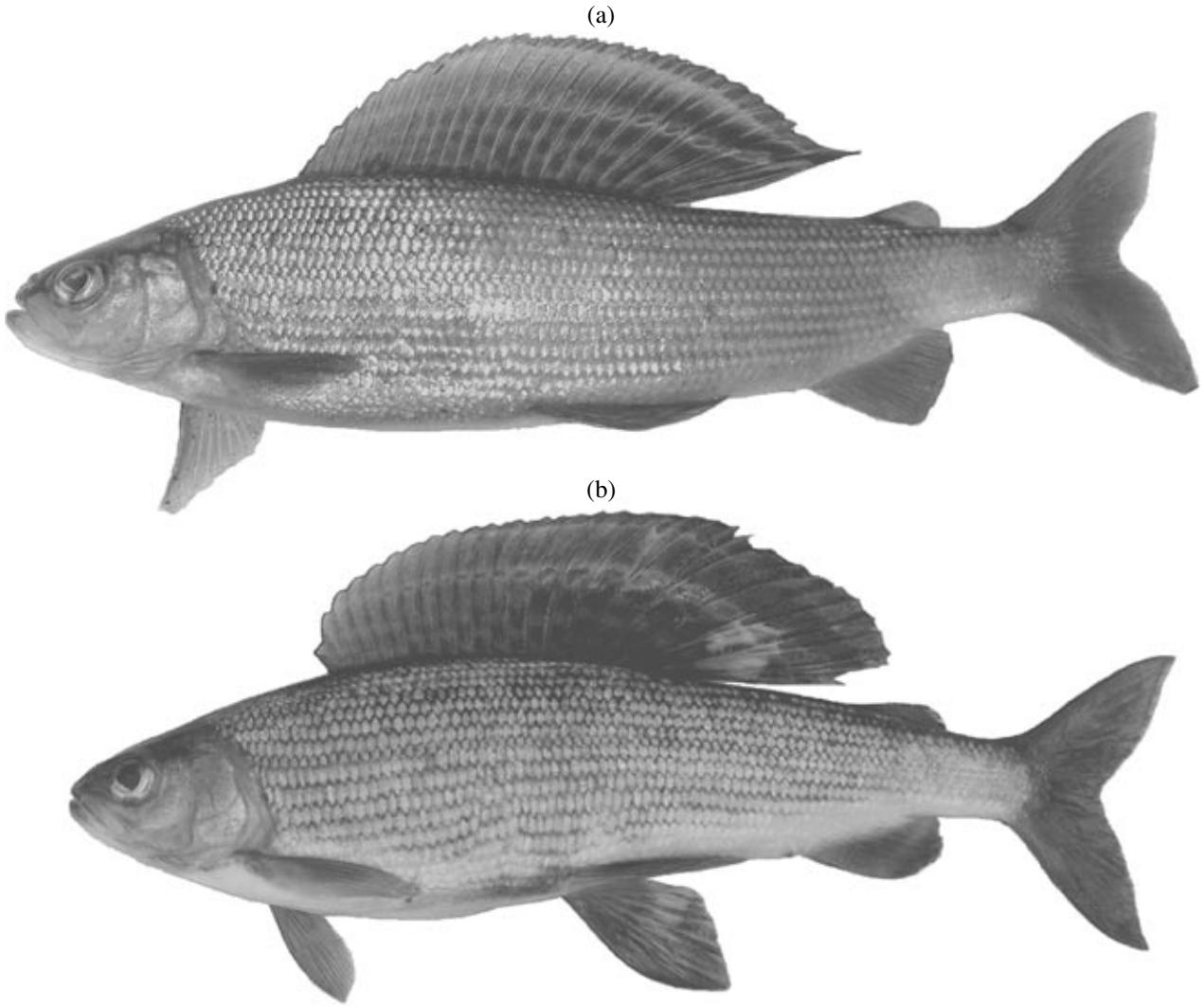

Fig. 2. The Lower Amur grayling *Thymallus tugarinae* sp. nova: a. the Anyui River (lower Amur), b. the Tengi River (Northwestern Sakhalin).

Thymallus arcticus grubei (non Dybowski, 1869) (sic.), Berg, 1916: 105 (River Amur, part.); Berg, 1923: 99 (Amur Basin, part.); Lindberg and Taranets, 1929: 231 (Sudzukhe River, The Sea of Japan Basin); Svetovidov, 1936: 209, table 4, fig. 8 (Kamra River, Lower Amur Basin); Taranets, 1936: 486 (Amur Basin, rivers of the Okhotsk coast and rivers flowing down from the eastern slopes of Sikhote-Alin on the south to the Sudzukhe River, part.); Berg, 1948: 430 (Amur Basin, rivers of the Sea of Okhotsk from Tugur and Uda to Gizhiga River, part.); Nikolsky, 1956: 83 (Amur Basin, from the lagoon to the upper reaches, part.); Samuilov and Svirskii, 1976: 87 (basin of Lake Khanka); Dorofeeva, 1998: 48 (Amur Basin, rivers of the eastern slope of Sikhote-Alin on the south to the Sudzukhe River, part.); Antonov, 1999b: 110 (basin of the upper reaches of the Bureya River); Dorofeeva, 2002: 164 (Amur Basin, rivers of the eastern slope of Sikhote-Alin on the south to the Sudzukhe River, part.); Zinovyev, 2005: 8 (Amur Basin, Uda, Primorye, part., Sakhalin).

Thymallus grubei (non Dybowski, 1969) (sic.), Pivnička and Hensel, 1978: 65 (Amur Basin, part.); Tugarina and Khramtsova, 1980: 590, Figs. 1, 2 (rivers Khor, Amgun); Tugarina and Khramtsova, 1981: 209; (rivers Im, Khor, Amgun); Makoedov, 1987: 906 (lower Amur from Khor River to the mouth); Makoedov, 1999: 68, Figs. 3.17, 8 (Amur Basin, part.).

Thymallus arcticus grubii (non Dybowski, 1869), Bogutskaya and Naseka, 1996: 14 (basin of Lake Khanka).

Thymallus sp. 1, Shed'ko, 2001: 237 (rivers of lower Amur Basin, Kievka River, The Sea of Japan Basin).

Thymallus grubii (non Dybowski, 1869), Safronov et al., 2001: 269 (rivers of the northwestern Sakhalin, Lower Amur Basin); Safronov and Nikiforov, 2003: 42

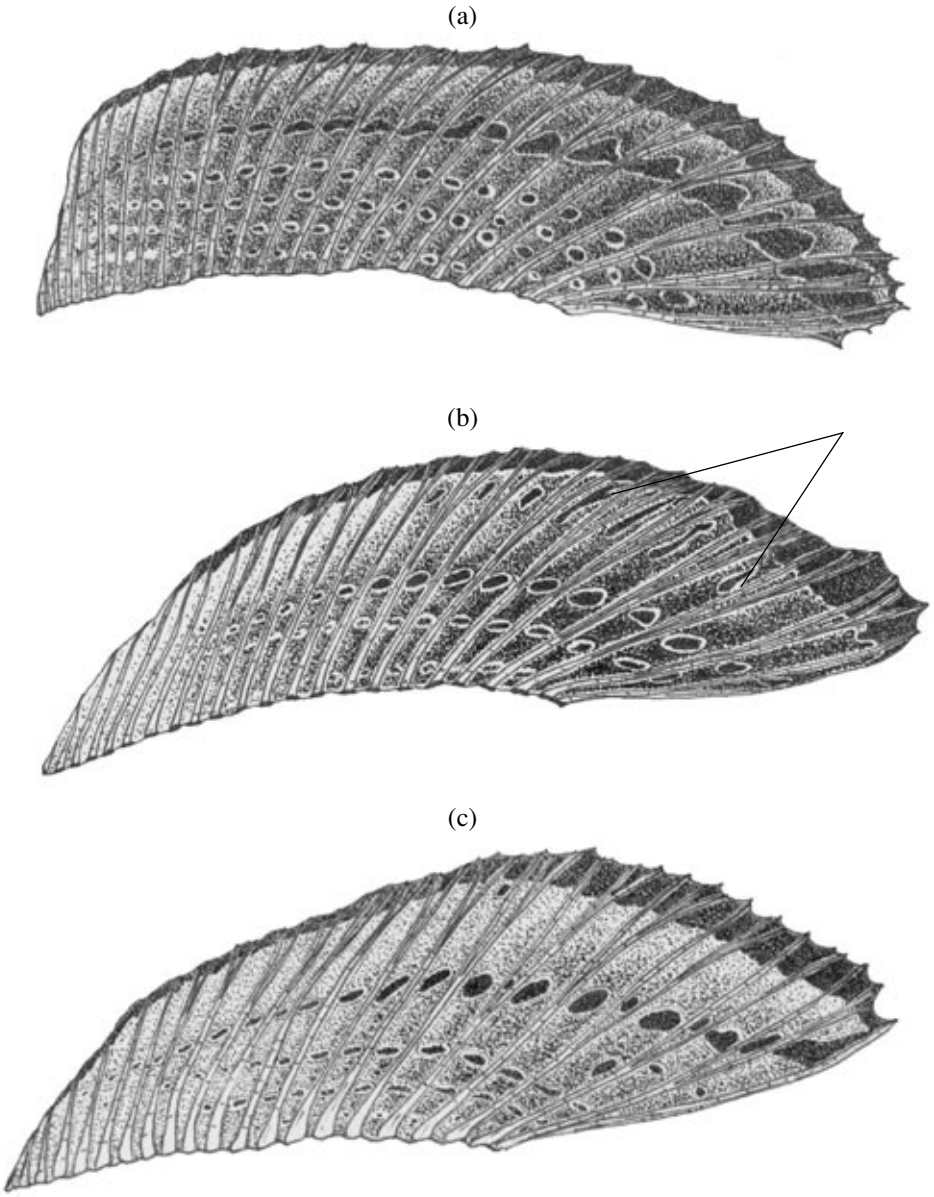

Fig. 3. Variants of the dorsal fin pattern in the Lower Amur grayling *Thymallus tugarinae* sp. nova: a, Anyui River, b, Bomboli River (arrows point to spots which occur only in some specimens), c, Chuken River.

(rivers of Northwestern Sakhalin, Lower Amur Basin); Safronov et al., 2003: 355 (rivers of northwestern Sakhalin, Lower Amur Basin).

Thymallus sp. 1 "lower Amur grayling," Bogutskaya and Naseka, 2004: 149 (rivers of the Lower Amur Basin, Kievka River, The Sea of Japan Basin).

Thymallus sp. "Lower Amur grayling," Knizhin et al., 2004: 59, 68, Figs. 3b, 4c (Northwestern part of Sakhalin Island, rivers of middle and lower Amur, part.; Zeya, Bureya, Anyui, Khor, Amgun and small tributaries below the Bureya River, as well as the Sungari with tributaries, upstream of the Amur to the Bolshoi Never River; rivers falling into the southern part of the Sea of Okhotsk and the Sea of Japan, Botchi, Tugur, Tumnin, Koppi).

Holotype. Zoological Museum of Irkutsk State University no. P-1, male L_{Sm} 238.0 mm, the Anyui River, October 2003, collector A.L. Antonov.

Paratypes. Zoological Museum of Irkutsk State University, no. P-2, one specimen, female L_{Sm} 244.0 mm, the Anyui River, October 2003, collector A.L. Antonov; no. P-5, 57 specimens, L_{Sm} 178.0–250.5 mm, the Anyui River, June 2001, collectors A.L. Antonov, I.B. Knizhin, S.J. Weiss; no. P-6, 19 specimens, L_{Sm} 178.3–255.0 mm, Khunmakta River,

Uanga River Basin, northwestern Sakhalin, August 2003, collector S.N. Safronov.

Accessory materials. Zoological Museum of Irkutsk State University, no. P-7, 10 specimens, collected with the paratypes, juveniles; Khunmakta River, Northwestern Sakhalin, August 2003; collector S.N. Safronov. Zoological Museum, Zoological Institute of the Russian Academy of Sciences, no. 13980, Kampa River; no. 16572, mouth of the Kiya River, a tributary of the Ussury River); no. 16628, mouth of the Khor River; no. 19600, Podkhorenok River (a tributary of the Ussury River); no. 19856, Mhy River (a lagoon of Amur); no. 19857, Pisui River (below Komsomolsk); no. 35334, Beshenaya River (below Komsomolsk); nos. 37358, 35368, Naleo River (lagoon of the Amur River); no. 41411, Khivanda River (below Komsomolsk). Zoological Museum of Moscow State University, no. P-6581, Khalzan River at Nizhnetambowskii, yearlings, *L* about 50 mm, 25 specimens; no P-8044, Iski River (north of the Amur Lagoon); no. P-8056, Khivanda River; no. P-8671, Amur River, Dzhalinda River, 2 specimens; no. P-20128, Komissarovka River (basin of Lake Khanka).

Description of the holotype. [5] Meristic traits: ll 76, sb 18, rb 10, D_1 10, D_2 17, P_2 14, V_2 10, A_1 5, A_2 9.

Oval black spot at the margin of cleithrum and subcleithrum below the beginning of the lateral line. There are broken bright orange stripes on the sides of the body between the scale rows. There is a fuzzy reddish-crimson spot above the pelvic fins shifting to the caudal peduncle at the abdominal part. Dorsal fin in the folded state almost reaches the fatty fin.

Morphometric traits, in% L_{Sm}: body length without the caudal fin (l) 93.4, the length to the tip of the scale cover (l_2) 76.7, anteanal distance (aA) 70.2, antedorsal distance (aD) 29.4, anteventral distance (aV) 45.8, postdorsal distance (pD) 36.5, pectoventral distance (PV) 29.0, ventroanal distance (VA) 26.6, the length of the pectoral fin (lP) 17.6, the length of the pelvic fin (lV) 19.9, the length of the dorsal fin base (lD) 28.7, its depth in the anterior part (hD_1) 13.7, its depth in the posterior part (hD_2) 21.6, the length of the anal fin base (lA) 10.1, its depth (hA) 14.3, the length of the caudal peduncle (lp) 16.5, the maximum body depth (H) 24.3, the minimum body depth (h) 7.5, head length (c) 18.8.

In% of the head length c: snout length (ao) 29.0, postorbital region (f) 49.3, eye diameter (o) 26.5, upper jaw length (lmx) 33.7, its width (i/lmx) 11.1, the length of the lower jaw (lmd) 53.3, forehead width (k) 28.1, head depth at the occiput (cH) 85.0, head depth at the eye (ch) 51.5.

Diagnosis. ll 75–91, D_1 8–12, D_2 13–17, D 23–26, vert. 49–55, pc 11–20.

A wide red to maroon edging with the width 5–6 mm is seen along the upper margin of the dorsal fin, broadening towards the posterior end of the fin (in large males it may be 10 mm in width and more). Below, in parallel with the edging, there are 4–5 rows (bands) of same-color spots. The upper row is slightly separated from the edging and the below bands and consists of the largest, slightly horizontally elongated oval spots. The lowest row of the spots, adjoining to the fin base, is weakly pronounced. There are bright orange sinuous stripes between the scale rows going along the body. The upper jaw overlaps with the anterior margin of the eye. The length of the dorsal fin base is from 25.3 to 33.3% L_{Sm}. Body significantly compressed laterally, its average depth is 22.9% L_{Sm}. Teeth on vomer absent.

Etymology. The species is named to honor a renowned investigator of graylings of Siberia and the Far East, Professor of Irkutsk State University, Polina Yakovlevna Tugarina (Dgebuadze et al., 2006).

Species description (composed from the type specimens of graylings from rivers Anyui and Khunmakta). Morphometric and meristic characteristics are presented in detail in Table 1. Most meristic traits are presented in the diagnosis.

There are from 12 to 16 branching rays in the pectoral fin (on average 14), their number in the pelvic fin is not less than 9 and not more than 11 (average 10). The number of nonbranched rays in the anal fin is 4–5 (most often, only 4) and 8–10 (most often 9) branched. There are usually about 80 scales in the lateral line. There are from 16 to 22 gill rakers (usually 18) on the first gill arch. Branchiostegal rays 8–11 (average 10). Body deep, up to 25.8% L_{Sm}, compressed laterally. Head small, 19.1% L_{Sm}, its depth at the occiput is on average 16.0% L_{Sm} and 83.6% c. Interorbital distance three times smaller than the head length. The length of the postorbital part is one half of the head length. Snout short, not more than 6.4% L_{Sm} or 30.7% c. Mouth subsuperior or terminal. Upper jaw overlaps with the anterior margin of the eye, its average length is 32.6% c. Lower jaw slightly protrudes in front of the lower jaw forming a kind of a scoop, its average length is equal to 52.5% c. Teeth on jaws small, on tongue and vomer absent. Posterior margin of the eye is at the middle of the head. Antedorsal distance ranges from 26.2 to 31.8% L_{Sm} (average 28.6%). Postdorsal distance approximately one quarter larger than antedorsal. Dorsal fin moderately deep and long, in mature fish usually reaches the fatty fin. Its posterior part deeper than anterior, the maximum depth 24.5% L_{Sm}. Average length of the dorsal fin base is equal to 28.5% L_{Sm}. Pectoral fins shorter than pelvic. The latter do not reach the anterior margin of anal fin, their length ranges from 14.3 to 23.9% L_{Sm}. Caudal peduncle short 17.1% L_{Sm} and wide, on average 7.4% L_{Sm}. Upper blade of the caudal fin slightly shorter than lower.

[5] Here and in the sequel, characters are designated as in Table 1.

Table 1. Morphometric and meristic characteristics of the Lower Amur grayling *Thymallus tugarinae* sp. nova

Characters	Lower Amur			Sakhalin	
	paratypes Anyui River (n = 57)	Khor River (n = 100) (Tugarina and Khramtsova, 1980)	Duldi River (n = 50) (Safronov et al., 2003)	Langry (n = 100) (Safronov et al., 2003)	paratypes Khunmakta River (n = 19)
L_{Sm}, mm	212.0 178.0–250.5	230.0 200.0–265.0	215.0 197.0–252.0	263.8 220.0–350.0	219.9 178.3–255.0
			In % L_{Sm}		
l	94.7 ± 0.07 93.9–95.8	93.0 ± 0.13 89.1–95.1	93.3 ± 0.24 89.4–94.9	94.3 ± 0.12 89.8–99.2	94.1 ± 0.15 93.1–95.4
l_2	78.1 ± 0.23 75.7–81.9	74.3 ± 0.15 69.1–78.1	76.3 ± 0.31 70.6–78.9	79.6 ± 0.25 73.0–84.0	77.59 ± 0.28 75.2–80.0
ao	5.9 ± 0.05 5.3–6.3	5.0 ± 0.06 4.2–6.0	4.4 ± 0.08 3.3–5.1	4.7 ± 0.06 3.2–6.1	5.8 ± 0.08 4.8–6.2
o	5.2 ± 0.05 4.5–5.8	5.9 ± 0.05 4.7–7.2	5.0 ± 0.05 4.4–5.7	4.6 ± 0.06 3.7–6.8	4.8 ± 0.06 4.3–5.3
f	9.3 ± 0.06 8.6–9.9	9.6 ± 0.06 8.5–11.2	8.8 ± 0.07 7.8–9.6	8.6 ± 0.06 7.4–10.2	9.2 ± 0.07 8.7–9.7
c	19.1 ± 0.07 18.2–19.9	19.2 ± 0.08 16.5–20.5	17.6 ± 0.09 16.7–18.7	17.4 ± 0.08 15.1–19.6	18.6 ± 0.15 16.9–19.9
cH	15.9 ± 0.11 14.5–17.4	15.9 ± 0.09 13.5–18.5	14.7 ± 0.12 12.7–15.8	14.8 ± 0.1 12.6–17.5	15.8 ± 0.19 13.5–17.1
ch	11.1 ± 0.10 9.6–12.5	10.8 ± 0.05 9.5–13.5	–	–	10.6 ± 0.15 9.0–11.5
k	5.9 ± 0.05 5.3–6.7	5.6 ± 0.05 4.2–6.7	5.5 ± 0.07 4.9–6.4	4.9 ± 0.05 4.0–6.1	5.4 ± 0.07 4.8–6.3
lmx	6.1 ± 0.05 5.5–6.7	6.5 ± 0.05 5.2–7.2	7.2 ± 0.09 5.3–8.3	6.9 ± 0.7 5.2–8.1	6.1 ± 0.06 5.6–6.6
i/lmx	1.9 ± 0.03 1.6–2.4	1.9 ± 0.03 1.2–2.7	1.9 ± 0.21 1.4–2.3	1.6 ± 0.02 1.1–1.9	1.8 ± 0.03 1.6–2.2
lmd	10.0 ± 0.07 9.2–11.0	10.1 ± 0.13 8.5–11.2	8.7 ± 0.08 7.7–9.9	8.6 ± 0.06 7.3–9.7	9.7 ± 0.12 8.9–10.5
H	22.9 ± 0.22 19.7–25.8	20.59 ± 0.12 18.5–23.5	21.5 ± 0.28 18.8–26.2	23.4 ± 0.16 19.7–26.7	23.2 ± 0.22 21.3–24.8
h	7.5 ± 0.05 7.0–8.2	7.2 ± 0.06 5.5–8.5	6.8 ± 0.06 6.1–7.6	7.1 ± 0.06 5.8–9.7	7.3 ± 0.06 6.8–7.8
w	12.7 ± 0.15 10.6–14.1	–	–	–	12.4 ± 0.29 10.2–14.5
aD	28.7 ± 0.18 27.1–31.8	27.8 ± 0.14 24.1–30.1	27.9 ± 0.20 25.9–29.6	27.7 ± 0.14 22.5–30.0	27.3 ± 0.19 26.2–28.8
pD	40.4 ± 0.20 37.7–43.1	–	38.6 ± 0.27 35.7–41.8	38.7 ± 0.16 28.9–44.0	38.8 ± 0.23 37.3–40.8
aA	70.5 ± 0.19 67.9–73.0	69.2 ± 0.15 64.1–72.1	67.5 ± 0.41 63.8–72.7	70.1 ± 0.19 64.8–75.3	69.7 ± 0.25 67.2–71.5
aV	45.1 ± 0.19 42.5–46.9	44.7 ± 0.17 39.1–47.1	42.1 ± 0.33 38.8–45.2	45.6 ± 0.21 36.3–53.3	45.3 ± 0.20 43.2–46.7
lp	17.3 ± 0.13 15.7–19.0	15.5 ± 0.12 12.5–17.5	16.8 ± 0.24 13.6–19.8	16.1 ± 0.11 13.1–19.6	15.9 ± 0.14 14.8–17.3
PV	28.2 ± 0.16 26.2–30.3	28.5 ± 0.17 25.1–31.1	27.6 ± 0.31 22.9–30.7	29.5 ± 0.17 23.1–34.1	28.8 ± 0.23 26.9–30.8
VA	26.1 ± 0.23 22.6–29.1	26.5 ± 0.16 22.1–31.1	25.9 ± 0.27 23.8–29.4	24.9 ± 0.15 21.7–29.3	26.0 ± 0.21 24.4–27.5

Table 1. (Contd.)

Characters	Lower Amur			Sakhalin	
	paratypes Anyui River (n = 57)	Khor River (n = 100) (Tugarina and Khramtsova, 1980)	Duldi River (n = 50) (Safronov et al., 2003)	Langry (n = 100) (Safronov et al., 2003)	paratypes Khunmakta River (n = 19)
lD	28.4 ± 0.22 25.3–32.2	29.1 ± 0.14 25.2–32.5	28.9 ± 0.30 26.4–32.6	29.2 ± 0.15 25.2–32.6	29.8 ± 0.37 26.2–33.3
hD_1	11.6 ± 0.13 10.3–13.1	8.68 ± 0.19 7.5–10.5	–	–	11.4 ± 0.28 9.3–13.7
hD_2	16.6 ± 0.40 12.2–21.3	15.2 ± 0.26 11.0–24.0	15.2 ± 0.38 8.5–19.3	19.9 ± 0.27 13.8–26.9	20.5 ± 0.71 14.4–24.4
lA	9.4 ± 0.10 8.1–10.6	9.4 ± 0.15 6.5–14.5	9.9 ± 0.14 7.9–11.4	10.3 ± 0.8 8.9–12.6	10.4 ± 0.21 9.2–13.1
hA	13.1 ± 0.17 11.2–14.7	14.2 ± 0.12 10.5–16.5	14.4 ± 0.23 11.5–17.1	12.4 ± 0.14 8.6–15.5	13.0 ± 0.33 11.0–16.2
lP	16.6 ± 0.09 15.5–17.7	17.3 ± 0.08 16.0–20.0	15.7 ± 0.15 13.9–17.4	15.5 ± 0.1 12.7–19.1	16.4 ± 0.20 14.8–18.3
lV	17.1 ± 0.19 14.6–20.4	18.9 ± 0.14 16.0–21.5	16.1 ± 0.19 14.6–18.1	17.2 ± 0.14 13.9–20.9	19.2 ± 0.57 14.3–23.8
ll	81.6 ± 0.41 75–91	84.9 ± 0.36 78–94	88.9 ± 0.73 78–95	84.7 ± 0.43 63–96	85.3 ± 0.61 79–91
D_1	9.4 ± 0.12 8–11	9.5 ± 0.12 8–12	9.5 ± 0.15 8–11	9.8 ± 0.1 7–12	10.1 ± 0.20 8–12
D_2	15.5 ± 0.14 13–17	15.5 ± 0.09 14–17	14.1 ± 0.26 9–16	15.5 ± 0.14 12–19	14.3 ± 0.19 13–16
D	24.9 ± 0.10 23–26	25.1 ± 0.10 24–27	23.6 ± 0.20 20–25	25.2 ± 0.15 20–28	24.4 ± 0.23 23–26
P	14.2 ± 0.09 13–16	14.0 ± 0.05 13–16	13.4 ± 0.11 12–14	13.7 ± 0.08 12–16	13.6 ± 0.15 12–15
V	10.0 ± 0.05 9–11	9.6 ± 0.06 8–10	9.9 ± 0.09 9–11	9.9 ± 0.07 9–12	9.9 ± 0.07 9–10
A_1	4.2 ± 0.05 4–5	4.1 ± 0.04 3–5	3.6 ± 0.11 3–5	3.8 ± 0.07 3–5	4.2 ± 0.10 4–5
A_2	9.0 ± 0.06 8–10	9.2 ± 0.05 8–10	9.2 ± 0.12 8–11	9.8 ± 0.11 8–15	9.1 ± 0.11 8–10
sb	18.2 ± 0.15 17–22	18.1 ± 0.08 16–20	16.3 ± 0.27 13–20	17.9 ± 0.16 14–22	17.7 ± 0.21 16–20
rb	9.9 ± 0.09 8–11	10.1 ± 0.08 8–10	9.7 ± 0.12 9–11	10.4 ± 0.05 9–11	9.3 ± 0.11 9–10
vert.	53.3 ± 0.11 52–55	58.4 ± 0.12* 57–61	57.0 ± 0.19* 55–59	56.8 ± 0.16* 53–61	50.0 ± 0.14 49–51
pc	14.6 ± 0.20 12–18	14.3 ± 0.17 11–20	13.8 ± 0.48 9–20	16.5 ± 0.23 12–23	14.9 ± 0.50 11–20

Note: Designations of the characters in Tables 1–3: L_{Sm}—fork length; l—trunk length; l_2—the length to the tip of the scale cover; ao—snout length; o—horizontal eye diameter; f—the length of the postorbital region of the head; c—head length; cH—head depth at the occiput; ch—head depth at the eye; k—forehead width; lmx—upper jaw length; i/lmx—upper jaw width; lmd—lower jaw length; H—maximum body depth; h—minimum body depth; w—body thickness; aD—antedorsal distance; pD—postdorsal distance; aA—anteanal distance; aV—anteventral distance; lp—the length of the caudal peduncle; PV—pectoventral distance; VA—ventroanal distance; lD—the length of the dorsal fin base; hD_1—the length of the anterior part of the dorsal fin; hD_2—the length of the posterior part of the dorsal fin; lA—the length of the anal fin base; hA—the depth of the anal fin; lP—the length of the pectoral fin; lV—the length of the pelvic fin; ll—the number of perforated scales in the lateral line; D_1—the number of nonbranched rays in the dorsal fin; D—total number of rays in the dorsal fin; P—the number of branched rays in the pectoral fin; A_1—the number of unbranched rays in the anal fin; A_2—the number of branched rays in the anal fin; sb—the number of gill rakers; rb—the number of branchiostegal rays; vert—vertebral number without urostyle; pc—the number of pyloric caeca; mean and standard error over the line, range, under the line. * vertebral number with urostyle.

Coloration. Upper part of head dark gray. Gill cover silverish with green, rarely violet, shine. Lower jaw light gray, in the anterior part black. Tongue light. Back dark gray with greenish shine. Body sides light or dark gray, in large individuals (more than 250 mm) greenish nacreous, in dark individuals greenish violet. Thin broken stripes consisting of small bright orange spots go along the body between the scale rows. Certain individuals inhabiting small streams have black spots at the base of the dorsal fin. There is a large reddish maroon or crimson spot with fuzzy margin with the width up to 16 scales, continuing 3–4 rows above the lateral line. Caudal peduncle has the same color. In certain large individuals, the lower part of the body from pelvic to anal fins also has reddish maroon shine. There is an oval black spot at the border of the cleithrum and subcleithrum below the beginning of the lateral line. Belly white with two parallel yellowish brown stripes going from pectoral to pelvic fins.

General coloration of the dorsal fin gray or dark gray. Wide dark red edging goes along the upper margin. Below, in parallel to the edging, there is a stripe consisting of relatively large spots with the same color (Fig. 3a). Some specimens have several additional spots not forming a stripe above the upper solid row. But such pattern occurs very rarely (Fig. 3b). There are from 3 to 5 (usually 4–5) rows of horizontally elongated oval spots from the base to the upper margin of the fin. The rows located lower may be incomplete, and the spots, from which they are formed, are always smaller. The row adjoining the dorsal fin base is less conspicuous. Pectoral fins gray, their tips yellowish. Pelvic fins yellowish gray with 3–5 red stripes going almost along the rays. Adipose fin small, cerise in color with turquoise shine. Anal and caudal fins dark maroon. The intensity of coloration may differ depending on the season and the conditions. Absolute length reaches 360 mm.

Comparative notes. Earlier work published different views on the species composition of the genus *Thymallus*, which, according to the opinion of Dorofeeva (1998, 2002) includes 3, and following Bogutskaya and Naseka (2004), 11 species. Such divergence in assessment is caused by the absence of reliable data on the morphological and genetic diversity of graylings and dissimilar methodologies used by different authors. Representatives of the genus *Thymallus* are especially difficult to identify because the variability ranges of many traits are overlapping (Svetovidov, 1936; Tugarina and Khramtsova, 1980; Chereshnev et al., 2002; Antonov, 2004; Knizhin et al., 2004, 2006c; Romanov, 2004a, 2004b, 2005). This is true also for the lower Amur grayling *T. tugarinae* sp. n. (Table 2).

Comparison of the lower Amur grayling with other species of the genus *Thymallus* by the *CD* coefficient (Mayr, 1971) indicated that the differences exceed the 1.28 threshold for many characters (Table 2). Based on our and published data (Tugarina and Khramtsova, 1980; Safronov et al., 2003; Antonov, 2004; Knizhin et al., 2004), we may conclude that the lower Amur grayling differs from the other Amur graylings by smaller number of scales in the lateral line (ll), and larger number of branched rays (D_2) and the total number of branched rays in the dorsal fin (D). In comparison with the Siberian *T. arcticus* and Amur *T. grubii* graylings, the lower Amur grayling *T. tugarinae* sp. n. and Bureya grayling *T. burejensis* are characterized by deeper body (H). With respect to the length of pelvic fins (lV), these species concede only to the Eastern Siberian subspecies of the arctic grayling *T. a. pallasii.* The lower Amur grayling has larger head depth at the occiput (cH) and at the eye (ch), the length of the dorsal fin base (lD), than in other taxa, whereas anterodorsal distance (aD) is smaller. The Lower Amur and Amur graylings concede with respect to the average length of both jaws (lmx and lmd) to only the Mongolian grayling.

Cluster analysis (UPGMA) of the species and subspecies of graylings inhabiting water bodies of Eurasia by 10 meristic traits[6] is presented in Fig. 4. Graylings from the Anyui River and Sakhalin, identified by us as the lower Amur grayling *T. tugarinae* sp. nova, are joined into a single branch. However, as seen from Fig. 4, it is not possible to judge the phylogenetic relationships between different taxa only on the basis of meristic and morphometric traits.

Analysis of publications (Tugarina and Khramtsova, 1980; Makoedov, 1987, 1999) and our data on the populations of graylings from more than 20 rivers of the Amur River Basin (Antonov, 1995; Safronov et al., 2003; Knizhin et al., 2004) point to the specificity and stability of the basic traits of the dorsal fin in the lower Amur grayling. When compared with other forms of graylings from Eurasia (Svetovidov, 1936; Berg, 1948; Tugarina and Dashidorzhi, 1972; Tugarina and Khramtsova, 1981; Makoedov, 1999; Makoedov and Korotaeva, 1999; Chereshnev et al., 2002; Antonov, 2004; Knizhin et al., 2004, 2006a, 2006b; Romanov, 2004b), its characteristic traits include the wide reddish maroon edging at the upper margin and 4–5 (rarely 3) rows of horizontally elongated oval spots. It should be noted that the dorsal fin pattern in the lower Amur grayling (*T. tugarinae* sp. n.) has much in common with that in the grayling (*Thymallus* sp.) inhabiting upper, middle, and partly lower current of the Lena River[7] (Makoedov, 1999; Makoedov and Korotaeva, 1999; Knizhin et al., 2004). Regardless of the general similarity of the pattern, in particular, the location and the shape of the spots, the Lena River grayling is different in the number of their rows (bands) going along the base of the fin: it usually has three (rarely four) such

[6] Because some investigators presented the number of vertebrae with the urostyle, whereas in others, without urostyle, this character was not included into the analysis. Total number of rays in the dorsal fin (D) was also excluded from the analysis.

[7] :The taxonomic status of the upper Lena form of grayling is currently discussed (Knizhin et al., 2006c, Weiss et al., 2006).

Table 2. Morphometric and meristic characters of different species and subspecies of graylings *Thymallus*

Characters	*T. tugarinae* (*n* = 76)	*T. grubii grubii* (*n* = 106)	*T. grubii flavomaculatus* (*n* = 48)	*T. burejensis* (*n* = 5)	*T. brevirostris* (*n* = 7)	*T. thymallus* (*n* = 64)	*Thymallus* sp. (*n* = 28)	*T. nikolskyi* (*n* = 39)	*T. arcticus baicalensis* (*n* = 45)	*T. arcticus baicalensis* (*n* = 50)	*T. arcticus nigrescens* (*n* = 35)	*T. arcticus pallasii* (*n* = 30)	*T. arcticus mertensii* (*n* = 117)
l	94.6 93.2–96.1	95.2 93.8–96.9	94.9 91.5–95.9	94.4 93.8–95.3	94.5 93.1–95.6	94.4 92.9–96.3	95.1 94.0–96.0	94.7 92.7–97.4	94.7 93.5–96.1	95.4 93.6–97.0	95.0 94.1–96.2	93.5 92.6–94.9	93.4 88.0–96.0
l_2	77.7 74.8–81.9	77.5 73.5–80.7	78.1 75.6–80.0	77.4 73.9–78.7	75.7 73.5–78.4	77.3 72.4–80.7	79.2 77.2–80.7	78.3 72.5–81.8	77.3 75.2–79.9	77.3 74.8–80.0	78.7 75.8–81.7	77.0 74.9–79.4	**74.8** **69.5–80.5**
ao	5.9 4.8–6.4	5.9 5.0–6.6	5.8 5.3–6.5	5.8 5.7–5.9	**6.9** **6.4–7.5**	**6.7** **5.9–7.7**	5.8 5.3–6.3	6.2 5.4–6.8	6.4 5.8–7.5	6.2 5.5–7.0	6.2 5.7–7.0	5.4 4.4–6.0	**4.8** **3.0–6.2**
o	5.2 4.4–6.0	5.1 4.3–6.0	4.8 4.3–5.7	4.5 3.9–5.4	**3.5** **3.2–3.7**	**4.2** **3.5–5.4**	**4.5** **3.9–4.8**	4.9 4.4–5.4	**4.6** **4.0–5.3**	**4.3** **3.8–4.8**	**3.9** **3.1–4.6**	**4.2** **3.4–5.1**	4.7 3.7–6.0
f	9.3 8.6–10.0	9.7 8.3–10.8	9.5 8.9–10.7	9.6 9.4–10.1	**12.4** **11.7–13.1**	9.1 8.5–10.2	9.0 8.6–9.7	9.5 8.7–10.5	9.6 9.0–10.2	**10.0** **9.2–11.2**	**10.5** **9.8–11.3**	9.8 9.1–10.4	**10.5** **9.0–12.5**
c	19.1 17.0–20.5	19.8 18.3–21.5	19.0 17.8–20.6	19.1 18.1–20.2	**22.0** **21.3–23.2**	19.0 17.4–20.6	18.7 17.9–19.9	19.3 17.5–20.6	19.9 18.8–20.9	19.6 18.3–21.3	19.6 18.5–21.2	18.6 17.5–19.5	19.2 16.5–21.0
cH	16.0 13.5–17.4	**14.7** **13.4–16.6**	14.8 13.2–16.5	14.7 13.01–15.87	14.9 13.9–18.0	**14.5** **13.2–16.7**	**13.8** **12.8–15.2**	15.5 14.1–16.6	**14.4** **13.4–16.5**	**14.1** **12.8–16.0**	**13.9** **12.5–17.0**	**14.0** **12.6–15.6**	14.8 13.0–16.9
ch	11.0 9.1–12.5	10.5 9.1–12.3	10.5 9.2–11.8	**9.8** **9.1–10.4**	**10.1** **9.5–11.0**	**9.8** **8.3–11.6**	**10.0** **8.9–11.3**	10.6 9.4–12.0	10.2 8.7–11.9	10.1 9.2–11.9	**9.7** **8.9–11.3**	**9.2** **7.9–10.5**	10.1 8.5–12.0
k	5.8 4.8–7.7	5.9 5.2–7.4	5.7 4.9–6.2	5.4 5.0–6.1	**7.0** **6.6–7.6**	5.4 4.5–6.1	6.0 5.6–6.6	6.1 5.5–6.7	6.2 5.4–7.0	6.1 5.2–6.8	6.0 5.5–7.8	**5.1** **4.7–6.1**	**4.9** **3.7–6.0**
lmx	6.2 5.5–7.1	6.2 5.3–7.1	5.7 5.0–6.5	5.6 5.1–6.1	**7.2** **6.7–7.9**	**5.3** **4.7–6.1**	**5.0** **4.6–5.4**	**5.6** **4.7–6.3**	5.5 4.8–6.4	**5.8** **5.3–6.7**	**5.5** **5.0–6.0**	**5.2** **4.5–5.7**	**5.4** **4.5–7.2**
i/lmx	1.9 1.6–2.5	1.8 1.4–2.2	1.9 1.6–2.2	1.9 1.8–2.1	**2.2** **2.0–2.5**	2.1 1.6–2.9	1.9 1.6–2.2	1.9 1.6–2.3	2.1 1.4–2.4	2.0 1.6–2.4	2.2 2.0–2.6	1.8 1.6–2.0	1.6 0.9–2.0
lmd	10.1 8.9–11.6	10.1 8.7–11.3	9.7 8.8–10.6	9.5 9.2–10.0	**12.2** **11.5–13.1**	**8.6** **7.5–9.6**	**9.0** **8.6–9.5**	9.6 8.2–10.6	9.9 9.0–10.9	9.9 8.9–11.1	9.9 9.2–10.7	**8.9** **7.8–9.8**	9.4 7.2–11.5
H	22.8 19.8–25.8	**19.3** **16.8–21.3**	20.9 18.3–25.5	23.1 21.4–25.6	–	22.5 19.3–26.8	**19.4** **17.7–21.3**	22.6 20.1–26.6	**19.6** **16.6–24.6**	**19.6** **17.1–22.1**	**18.2** **16.2–19.7**	20.6 18.1–23.2	20.9 17.1–25.1
h	7.4 6.8–8.3	6.5 6.0–7.3	7.0 6.2–7.6	7.5 6.9–8.0	–	7.5 6.6–8.2	6.6 6.1–7.1	7.6 7.1–8.4	**6.7** **6.1–7.8**	**6.3** **4.4–7.3**	**6.5** **6.0–7.2**	7.6 7.1–8.1	7.6 6.5–9.3
w	12.6 10.3–14.5	12.4 10.3–15.4	12.1 10.2–14.9	9.2 8.4–10.5	–	11.4 8.9–15.5	13.7 12.6–14.8	13.5 11.2–15.3	12.3 10.6–13.4	11.7 9.7–14.2	11.9 9.0–13.3	11.4 8.7–13.6	–

Table 2. (Contd.)

Characters	*T. tugarinae* (*n* = 76)	*T. grubii grubii* (*n* = 106)	*T. grubii flavomaculatus* (*n* = 48)	*T. burejensis* (*n* = 5)	*T. brevirostris* (*n* = 7)	*T. thymallus* (*n* = 64)	*Thymallus* sp. (*n* = 28)	*T. nikolskyi* (*n* = 39)	*T. arcticus baicalensis* (*n* = 45)	*T. arcticus baicalensis* (*n* = 50)	*T. arcticus nigrescens* (*n* = 35)	*T. arcticus pallasii* (*n* = 30)	*T. arcticus mertensii* (*n* = 117)
aD	28.6 26.2–31.8	**31.7** **27.7–38.3**	29.3 27.6–30.8	**31.9** **30.9–32.8**	–	**33.8** **31.2–37.1**	**33.2** **31.7–34.7**	**33.6** **30.8–35.7**	**34.8** **33.0–37.0**	**34.9** **33.2–36.9**	**34.1** **31.5–36.3**	29.4 28.2–30.9	**31.5** **28.1–38.1**
pD	40.1 37.3–43.7	**42.9** **39.4–46.9**	**43.4** **39.4–48.2**	42.1 39.6–44.2	–	41.2 38.3–45.4	42.2 39.1–45.0	40.9 36.6–44.2	42.0 36.5–44.8	41.9 39.2–45.1	**44.8** **42.4–48.0**	39.3 36.8–40.9	–
aA	70.2 67.2–73.0	69.8 66.0–73.1	69.3 66.5–72.4	68.9 67.6–70.4	–	70.6 65.9–74.1	70.3 67.9–73.1	69.8 64.1–72.2	69.8 67.4–72.9	71.7 69.1–74.5	70.8 68.6–75.1	69.8 66.4–72.4	68.5 62.1–76.1
aV	45.1 42.5–47.3	45.6 42.4–48.0	44.6 41.7–47.2	45.1 42.3–47.9	–	46.2 42.0–49.9	45.1 42.5–47.8	45.7 42.2–48.3	45.6 43.5–48.2	**47.8** **45.1–50.3**	46.0 43.5–48.3	45.0 43.4–46.5	45.2 39.1–49.1
lp	17.1 14.0–19.5	17.5 15.7–19.6	18.1 15.6–19.7	16.5 15.3–17.4	–	16.1 14.2–19.0	16.8 15.3–18.1	17.1 14.9–19.0	18.0 15.6–19.9	17.0 14.5–19.0	17.4 15.5–19.2	15.8 14.6–17.4	**14.9** **12.5–17.0**
PV	28.1 24.8–33.3	27.0 23.0–30.6	27.6 25.4–30.9	28.2 27.6–28.9	–	29.2 25.0–33.3	27.9 25.4–30.0	29.3 25.8–32.5	27.4 24.4–30.2	29.7 25.9–32.0	27.4 25.3–30.3	29.1 27.3–31.7	28.8 24.5–33.0
VA	26.0 22.6–29.1	25.3 21.8–28.4	25.3 22.7–27.3	23.8 20.6–25.7	–	24.7 20.6–27.5	26.9 25.4–28.9	25.2 22.6–27.7	25.2 23.5–27.1	25.3 22.7–28.7	25.3 22.5–27.8	25.5 23.2–28.6	24.4 21.5–28.5
lD	28.5 24.3–33.3	**22.0** **18.2–25.5**	**24.6** **21.2–28.2**	26.0 23.2–27.1	–	**22.4** **18.3–25.6**	**21.9** **19.3–24.8**	**23.4** **20.6–25.9**	19.9 16.8–23.5	19.4 16.6–21.6	18.8 16.2–22.2	26.7 23.0–29.8	**22.9** **19.0–28.5**
hD_1	11.6 9.4–13.8	11.2 8.9–16.2	10.4 7.8–12.0	11.0 9.5–12.1	–	11.8 9.1–13.5	10.0 8.6–11.5	11.8 9.0–13.9	11.6 8.9–14.2	11.4 9.8–13.9	11.4 9.7–13.5	10.4 8.1–13.4	**7.97** **5.0–12.5**
hD_2	16.8 11.3–24.5	10.5 6.7–21.0	13.0 8.3–20.1	15.0 12.8–17.4	–	**13.6** **8.1–23.1**	12.4 8.6–17.7	9.2 6.9–15.3	11.1 7.4–22.9	10.9 7.8–16.7	**9.4** **6.9–12.2**	**26.5** **15.4–37.0**	21.4 12.5–26.5
lA	9.5 7.5–13.1	9.3 7.9–11.0	9.3 7.6–12.2	9.3 8.0–9.9	–	9.4 7.6–11.4	9.6 8.7–10.8	8.9 7.4–15.4	9.0 7.6–10.7	8.3 7.5–9.6	8.8 7.2–9.9	9.9 8.4–11.6	9.2 6.5–11.5
hA	13.1 11.1–16.2	12.2 9.6–16.1	11.9 9.6–13.9	13.0 11.1–14.2	–	11.6 9.8–13.7	11.9 9.7–14.6	11.7 8.8–13.5	11.8 10.3–14.1	**10.7** **9.1–13.3**	**10.8** **7.5–12.9**	12.0 9.4–13.8	**10.3** **8.0–14.0**
lP	16.5 14.9–18.3	**15.2** **13.9–17.1**	15.6 13.6–17.5	17.0 14.8–18.9	–	**14.8** **12.0–17.3**	**14.7** **13.0–15.6**	16.2 14.3–17.6	**15.2** **14.1–17.0**	16.0 14.7–17.6	15.6 13.6–16.9	17.3 14.6–19.6	15.3 12.5–18.0
lV	17.3 14.3–23.9	15.0 12.9–19.0	15.8 12.4–19.4	17.4 16.3–18.2	–	14.6 10.8–17.5	**14.7** **13.5–16.0**	15.1 13.2–17.1	14.7 12.8–17.7	**14.5** **12.7–16.6**	14.7 12.6–16.3	22.2 15.2–30.4	15.8 12.5–18.5
ll	82.6 75–91	**90.6** **82–102**	**90.5** **82–101**	83.6 80–91	80.7 77–84	86.3 80–94	**91.8** **86–103**	81.3 76–91	**97.4** **89–104**	**99.5** **88–110**	**94.2** **87–100**	**93.3** **87–110**	**75.3** **69–86**

Table 2. (Contd.)

Characters	*T. tugarinae* (*n* = 76)	*T. grubii grubii* (*n* = 106)	*T. grubii flavomaculatus* (*n* = 48)	*T. burejensis* (*n* = 5)	*T. brevirostris* (*n* = 7)	*T. thymallus* (*n* = 64)	*Thymallus* sp. (*n* = 28)	*T. nikolskyi* (*n* = 39)	*T. arcticus baicalensis*		*T. arcticus nigrescens* (*n* = 35)	*T. arcticus pallasii* (*n* = 30)	*T. arcticus mertensii* (*n* = 117)
									(*n* = 45)	(*n* = 50)			
D_1	9.6 8–12	8.2 7–11	10.4 9–15	9.8 9–10	**7.4** **7–8**	**7.7** **7–9**	**7.8** **7–9**	**8.0** **6–10**	**7.2** **6–8**	**7.8** **7–10**	**7.9** **7–9**	10.2 9–12	10.3 7–15
D_2	15.2 13–17	**12.6** **10–16**	**13.3** **10–15**	14.6 14–15	**12.1** **12–13**	14.4 12–16	**12.5** **11–14**	15.3 14–18	**13.1** **11–15**	**12.5** **11–15**	**11.3** **10–13**	14.0 12–16	**12.2** **10–16**
D	24.9 23–26	**20.8** **19–23**	**23.7** **21–25**	24.4 23–25	**19.5** **19–20**	22.1 20–24	**20.4** **19–22**	23.3 21–25	**20.3** **19–23**	**20.4** **19–22**	**19.3** **18–22**	24.1 22–26	**22.7** **20–25**
P	14.1 12–16	14.0 12–16	14.4 13–16	14.8 14–16	14.1 14–15	14.2 12–16	14.1 13–15	15.1 14–17	14.3 13–16	14.7 13–16	14.5 13–16	14.6 13–16	14.0 9–15
V	10.0 9–11	**9.1** **8–10**	9.3 8–11	9.8 9–10	10.0 –	**9.0** **8–10**	**8.9** **8–9**	9.9 9–11	9.9 9–11	9.8 9–11	9.5 9–11	9.3 9–10	**8.9** **6–14**
A_1	4.2 4–5	4.1 3–5	4.4 4–6	4.4 4–5	4.3 4–5	4.1 3–5	3.8 3–4	4.2 4–5	4.2 3–5	4.5 4–5	4.7 4–6	4.0 3–5	4.2 2–6
A_2	9.1 8–10	9.0 7–11	9.3 8–10	9.8 9–11	**8** **7–9**	9.8 9–11	9.3 9–10	9.4 8–10	9.2 8–10	8.9 8–11	8.9 8–11	9.4 8–10	8.8 7–10
sb	18.1 16–22	17.8 15–21	18.3 16–22	**20.0** **19–21**	18.6 18–19	23.9 21–28	18.6 17–20	19.4 17–21	18.2 16–21	**20.7** **17–23**	**25.9** **21–30**	18.7 16–21	17.3 15–20
rb	9.8 8–11	9.8 8–12	9.5 9–11	9 –	10.1 10–11	9.5 8–11	9.1 8–11	9.3 9–10	10.1 9–12	9.3 8–10	9.3 8–10	9.1 8–10	8.6 8–10
vert.	52.5 49–55	**55.3** **53–57**	**55.0** **53–57**	53.2 53–54	**56.4** **56–57**	52.3 51–55	**55.3** **54–57**	52.6 51–55	56.1 54–58	55.9 52–59	55.2 54–57	53.0 51–55	59.5* 57–64
pc	14.8 11–20	15.1 10–22	17.3 14–24	**18.0** **15–21**	**25.6** **20–29**	**20.0** **15–32**	15.9 12–19	**20.4** **17–27**	16.2 12–20	15.8 10–21	**23.6** **16–29**	**19.9** **14–29**	**18.9** **15–23**

Note: *T. tugarinae*, the rivers Anyui (basin of the lower current of Amur), Khunmakta (Northwestern Sakhalin); *T. grubii grubii*, the rivers Ingoda and Onon (basin of the upper current of Amur); *T. grubii flavomaculatus*, the rivers Anyui, Merek (basin of the lower current of Amur), Buta, Bochi (Tatar Strait); *T. burjensis*, the Levaya Bureya river; *T. brevirostrus*, Khokh Nur Lake (Central Asian Basin, Mongolia); *T. thymallus*, the rivers Obr, Gurk, Socha (basins of the Black Sea and the Adriatic Sea); *Thymallus* sp., Kutima River (basin of the upper current of the Lena River); *T. nikolskyi*, the rivers Biya, Bashkaus (basin of the upper current of the Ob River); *T. arcticus baicalensis*: (*n* = 45), Nizhnyaya Tunguska River (basin of the middle current of Enisei), (*n* = 50) Lake Baikal (black grayling); *T. arcticus nigrecens*, Lake Hubsugul (Mongolia); *T. arcticus pallasii*, the rivers Indigirka, Kolyma (basins of the East Siberian Sea and the Lptev Sea), morphometric traits were analyzed in 24 specimens; *T. arcticus mertensii*, Kamchatka River (data of Tugarina, 1972). The emphasis denotes the traits which showed the *CD* differences exceeding 1.28 when compared with the lower Amur grayling. *T. a. mertensii* was not compared with the Kamchatka grayling. * Vertebral number with urostyle.

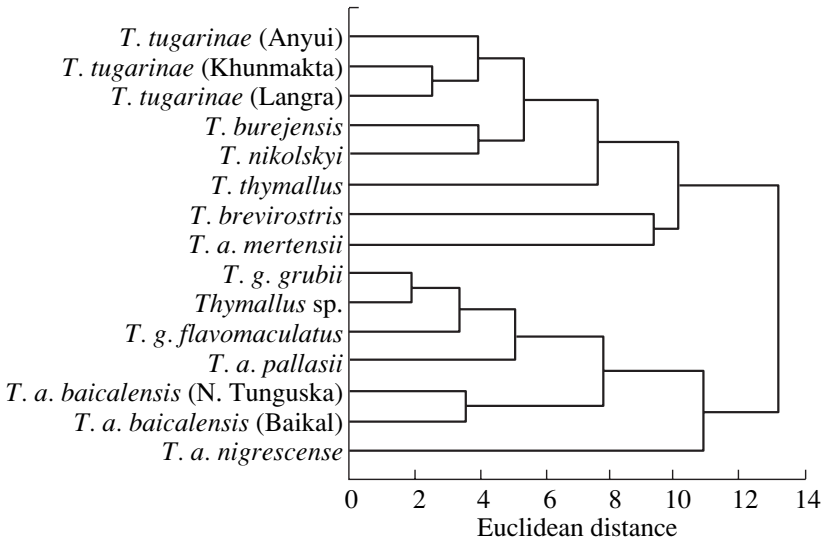

Fig. 4. Dendrogram of the similarities of *Thymallus* grayling species and subspecies by 10 meristic traits built using the UPGMA (only total number of rays in the dorsal fin D was counted). Legend: *T. tugarinae* sp. nova, Lower Amur grayling (the Anyui River, the Khunmakta River), *T. burjensis,* Bureya grayling (the Levaya Bureya River), *T. nikolskyi,* Nikolsky's grayling (the Upper Ob Basin, rivers Biya and Bashkaus), *T. thymallus,* European grayling (basins of the Black and Adriatic Seas, the rivers Obr, Gurk, Socha), *T. brevirostris,* Mongolian grayling (Central Asian Basin, Khokh Nur Lake), *T. a. mertensii,* Kamchatka grayling (Kamchatka River; Tugarina, 1972), *T. g. grubii,* Upper Amur grayling (the Upper Amur, the rivers Ingoda, Onon), *Thymallus* sp., Upper Lena grayling (the Upper Lena River Basin, Kutima River), *T. g. flavomaculatus,* yellow-spotted grayling (the Lower Amur, rivers of the Tatar Strait coast), *T. a. pallasii,* Eastern arctic grayling (the Indigirka, the Kolyma rivers), *T. a. baicalensis,* black Baikal grayling (northern Baikal, the Tompuda River), *T. a. nigrescens,* Kosogol grayling (Khubsugul Lake).

bands. In addition, the width of the edging on the fin of the Lena grayling is 2–3 times smaller and represents only a few millimeters, whereas, in the lower Amur, it may reach 2 cm. In addition to the pattern on the dorsal fin, the forms compared differ by color of the broken bands going between the rows of scales (they are orange-yellow in the Lower Amur grayling, whereas, in the Lena River grayling, black), and the total number of rays in the dorsal fin (in the lower Amur grayling (24.9), their number is 5 times greater than the Lena River grayling (20.4)). Why the dorsal fin patterns are similar in these two species is not quite clear. It is possible that there is merely a parallelism in these traits. Definitely, there is a significant genetic and morphological divergence between these fish (Knizhin et al., 2000, 2002, 2004; Koskinen et al., 2002; Froufe et al., 2003, 2005; Table 2). With respect to the grayling inhabiting rivers of the northwestern part of Sakhalin, it was shown that it is very close in many respects to the Lower Amur grayling of the Khor River (Safronov et al., 2003). They have the same body shape and coloration, identical dorsal fin pattern and biological traits (Safronov et al., 2003; Knizhin et al., 2004). This made it possible to suppose that graylings of Sakhalin and the Lower Amur grayling are really the same species. With this purpose, we analyzed fish from the Khunmakta River (Northwestern Sakhalin) and from the Amur River by 10 meristic traits. The first two principal components accounted for 81.3% of the total variance. The loadings of the eigenvectors on the first and the second principal components are given in Table 3. The scatterplot (Fig. 5) of the first two principal components revealed an overlap between all Amur River forms. Nonetheless, there is some divergence between the groups compared.

Our studies of lower Amur and Sakhalin graylings revealed a hiatus in the number of vertebrae: respectively 52–55 and 49–51 (Table 1). In contrast, Safronov et al. (2003) did not note such in the continental and island populations of this form, pointing to significant population variability of the lower Amur graylings in this trait.

Discussing the taxonomic status of the Lower Amur grayling, we must note the work by Mori (1928), describing the Korean subspecies *T. a. yaluensis.* Unfortunately, his description does not allow us to determine whether he used fixed or recently caught specimens. In the opinion of the author, graylings from the Yalu River are close to the Amur grayling. Its characteristic traits, in contrast to the latter, are shorter snout, larger eyes, and wider forehead. The values provided by Mori basically lay within the variability ranges of the Lower Amur *T. tugarinae* sp. n. and Amur *T. grubii.* The only exception was the number of gill rakers on the first gill arch, which in the fish from the river Yalu is equal to 13. Such number of rakers was noted by Safronov et al. (2003) in the Lower Amur grayling from the Duldi River, and Antonov (2001)[8] in the yellow-fin grayling from the Lower Amur tributar-

[8] Possibly, it was the result of uncounted underdeveloped rakers on the first gill arch.

ies. We did not find this limit in the lower Amur grayling. The eye diameter index in the Korean subspecies from the Yalu River is smaller than in the Amur forms known to us (3.75% of the body length) and the other taxa of the genus. It is possible that the eye diameter in the description of the Korean subspecies was given not by its ratio to the fork length but by the ratio to the total body length to the end of the caudal fin rays. Mori noted five bands on the dorsal fin, but the spots were not maroon-red as in the Amur River forms but black-blue. No mention was given to the maroon-red edging along the upper margin of the fin. On the contrary, it is said that the margin of the fin is black. The author mentions only two stripes going along the pelvic fin rays, whereas in the Amur, lower Amur, and Bureya graylings their number is not less than three. There are also discrepancies in the descriptions of the anal fin coloration, dorsal part of the body as well as the color of the stripes going along the scale rows, which are brownish gray rather than orange-brown as in the lower Amur grayling. It is known that such stripes are absent in the Amur grayling *T. grubii* from the Ingoda and Onon (Knizhin et al., 2004). Given these data, we cannot agree with the conclusion of Mori (1928) on the relatedness of graylings from the Yalu River and Amur *T. grubii* or the Lower Amur *T. tugarinae* sp. n. No mention was made in the description to the traits pointing to common coloration patterns in *T. a. yaluensis* and the Bureya grayling *T. burejensis.* Thus, the questions concerning the phylogenetic relationships of grayling *T. a. yaluensis* and its taxonomic status remain open and require additional studies.

Reproductive isolation of the lower Amur grayling *T. tugarinae* sp. nova and the sympatric Bureya *T. burjensis* and both forms of the Amur grayling *T. grubii*, as well as its significant divergence from all known species of the genus *Thymallus* were supported by molecular-genetic studies (Froufe et al., 2003, 2005; Knizhin et al., 2004).

A complex of diagnostic traits differentiating the new species *T. tugarinae* sp. n. from all known representatives of the genus *Thymallus* include the following: the pattern on the dorsal fin, the length of its base, the number of branched rays, broken bright orange stripes on the sides of the body, antedorsal distance, head depth at the occiput and eye, bucket-like shape of the mouth, the position of the posterior margin of the upper jaw with respect to the middle of the eye.

Based on some of these characteristics, we prepared a key to the identification of graylings of the Amur River Basin, presented below.

1(2) Red-maroon edging along the upper margin of the dorsal fin present; short and long stripes parallel to the rays on the interray membrane in its posterior part…..... ***T. burejensis* Bureya grayling**

2(1) Red-maroon edging along the upper margin of the dorsal fin present; there are no short and long stripes parallel to the rays on the interray membrane in its posterior part; instead of stripes, there are spots with other shape.

3(5) Sinuous bright orange stripes are between the rows of scales; small black spots on the sides in adult individuals absent, and if present, in small quantity and only at the head.

4(6) Edging along the upper margin of the dorsal fin wide (up to 1 cm and more), red-maroon in color.

Table 3. Loadings of eigenvectors on the first two principal components for 10 meristic traits

Character	Principal Components	
	1	2
ll	0.996	0.027
D	−0.567	0.397
P	−0.025	0.237
V	−0.515	0.082
A_1	−0.052	0.149
A_2	0.068	0.160
sb	−0.041	0.251
rb	−0.169	−0.111
vert.	0.525	−0.182
pc	0.103	0.938

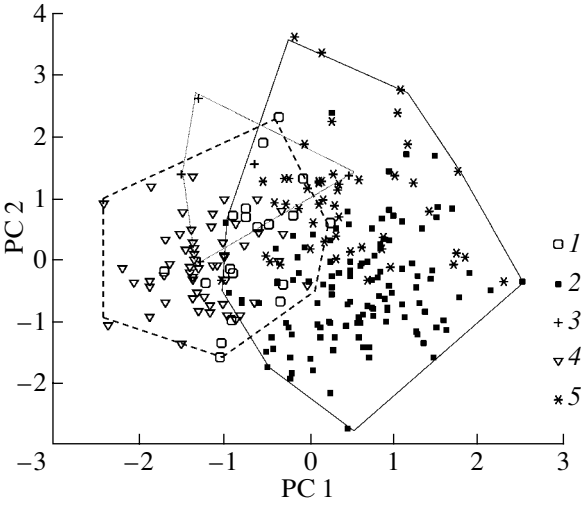

Fig. 5. Scatterplots of different forms of *Thymallus* graylings in the first two principal components space by 10 meristic traits (only the total number of rays in the dorsal fin D was included into the analysis): *1*, Lower Amur grayling *T. tugarinae* sp. nova (Sakhalin Island); *2*, Upper Amur grayling *T. g. grubii* (the rivers Ingoda, Onon); *3*, Bureya grayling *T. burjensis* (Levaya Bureya River); *4*, Lower Amur grayling *T. tugarinae* sp. nova (Anyui River); *5*, yellow-spotted grayling *T. g. flavomaculatus* (the rivers Anyui, Merek, Buta).

The upper row of spots and the rows below are parallel to the fin base. The lower part of the fin consists of spots, which may be positioned in a chessboard pattern. The yellow-orange spot on the last interray membranes absent. Body deep, significantly compressed laterally. Mouth bucket-like. Absolute length up to 36 cm.....
....***T. tugarinae*** **sp. nova, Lower Amur grayling (Tugarina grayling)**

5(3) No bright orange stripes along the scale rows; there are numerous black spots instead.....
.....***T. grubii grubii*** **Upper Amur grayling**

6(4) The edging along the margin of the dorsal fin narrow, bright red. There are no less than five rows of spots under the edging. The upper row has an ascending pattern, and the rows located below are parallel to the base of the fin. The lower part of the fin consists of spots with broad matted edging. There is a well distinguishable spot on the last interray membranes. Body oblong. Mouth terminal. Absolute length up to 45 cm.....
.....***T. grubii flavomaculatus*** **Yellow-spotted grayling**

Thus, the results of this study defined the taxonomic composition of graylings inhabiting the Amur River Basin, several rivers of the southern coast of the Sea of Okhotsk and the Sea of Japan and Sakhalin, including the following species and subspecies:

(1) *Thymallus grubii* Dybowski, 1869, Amur grayling; *T. g. grubii* Dybowski, 1869, upper Amur grayling; *T. g. flavomaculatus* Knizhin, Antonov et Weiss, 2006, yellow-spotted grayling.

Table 4. Food composition of the lower Amur grayling *Thymallus tugarinae* sp. n. (the Anyui River, July)

Components	Weight proportion, %	Frequency of occurrence
Trichoptera	37.1	69.7
Ephemeroptera	17.4	93.0
Plecoptera	9.1	48.8
Musci	1.7	34.8
Simulidae	3.9	53.4
Blepharoceridae	5.89	67.4
Coleoptera	6.11	79.0
Formicidae	2.62	39.5
Hymenoptera	8.61	44.1
Pisces	0.01	2.3
Fish eggs	0.02	4.6
Plant fragments	1.11	13.9
Other organisms	6.43	–
Number of fish	43	

(2) *Thymallus burjensis* Antonov, 2004, Bureya grayling.

(3) *Thymallus tugarinae* sp. nova Knizhin, Antonov, Safronov et Weiss, 2006, lower Amur grayling (Tugarina's grayling).

Because of the high adaptive capacities of graylings, we cannot exclude that their new forms may be discovered in less easily accessible areas of the Amur River Basin. Their study will widen our understanding of the microevolution processes and the paleo-hydrological history of the region.

Distribution. The lower Amur grayling inhabits most of the lower Amur River Basin, partly its middle and the upper current up to the Never River, possibly even further to the upper reaches. This species inhabits certain rivers falling into the southern part of the Sea of Okhotsk (the rivers Tugur and Uda: M.B. Skopets and E. Machino, personal communication; the Mukhtel River, I. Olkhovskii, personal communication) and the Sea of Japan (Shed'ko, 2001), as well as in rivers of the Amur lagoon and on the south to the Psyu River (inclusive) and the northwestern extremity of Sakhalin Island: the Bolshaya, Bolshoi Vagis, Bolshaya Nelma, Bolshoi Nyavan, Volchanka, Glukharevka, Irkyr, Komulan, Langry, Pilvo, Pyrki, Sladkaya, Tengi, Uangi (Safronov and Nikiforov, 2003; Safronov et al., 2003). Its southern border in the Amur Basin is the tributaries of the rivers Ussuri and probably the Sungari. At the north, the range of the Lower Amur grayling is limited by the rivers Tugur and Uda (see Fig. 1). Unlike graylings of Siberia, it is absent in mountain lakes. This species is sympatric with the nominative subspecies of the Amur grayling *T. grubii grubii* in the basin of the Middle and partly the Upper Amur, in upper reaches of all its large tributaries (the Amgun, Anyui, Bikin, Gur, Kur, Khor), as well as in rivers Tugur and Uda (M.E. Skopets and E. Machino, personal communication). It is sympatric with the yellow-spotted grayling *T. g. flavomaculatus* and in the Bureya River, with the Bureya grayling *T. burjensis* (Antonov, 2004; Knizhin et al., 2004). In the sympatric zones with the above-mentioned species, the Lower Amur grayling usually inhabits lower and middle areas of the rivers and usually does not occur in the upper reaches. It penetrates upstream up to the absolute altitude about 700 m.

Some biological and ecological characteristics. The Lower Amur grayling spawns in rivers of the Amur Basin from the middle to the end of May, 7–10 days before the yellow-spotted grayling *T. g. flavomaculatus.* The autumn downstream migration in tributaries of the lower Amur takes place from September to October.

The range of the food components of the Lower Amur grayling in the Anyui River in July is represented by various zoo benthos organisms. The most weight part in the food boluses of fish older than the age 3+ is represented by mayfly and stonefly larvae, imago caddis and bugs. The composition and the frequency of occurrence of different organisms in the food boluses of

the Lower Amur grayling are presented in Table 4. A comparison of the feeding spectra in the Lower Amur and yellow-spotted graylings caught in the same stations did not reveal any significant differences in the diversity of the food components.

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