ISSN 0032-9452, Journal of Ichthyology, 2006, Vol. 46, No. 3, pp. 234–246. © Pleiades Publishing, Inc., 2006.
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On the Diversity and Taxonomic Status of Graylings (*Thymallus* Thymallidae) from the Lena River

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Received February 10, 2004

Abstract—Two forms of graylings were distinguished in the Lena River, which differ in body coloration, the shape and pattern of the dorsal fin, and biological characteristics. With respect to these traits, the forms are divided between the upper and lower Lena. The first inhabits most of the basin, from the upper courses to the lower reaches, whereas the second inhabits the Lena delta and the adjacent arctic rivers and their tributaries. Comparative analysis of meristic traits revealed their low appropriateness for diagnosing Lena lineages as well as grayling populations inhabiting other northern rivers of Siberia. The body and fin coloration in the upper Lena form significantly differ from that found in forms and subspecies of graylings from the basins of the other rivers in the ranges of Eastern Siberian, Kamchatka, and Alaska. The lower Lena form should be classified with the Eastern Siberian subspecies *T. arcticus pallasii* and is closer to the populations of graylings from the rivers Anabar and Yana, and the rivers of the Chukot Peninsula and Alaska, and the upper courses of the Missouri. These results are supported by analysis of the mitochondrial DNA of graylings throughout the Paleoarctic. Further studies of these lineages and phylogenetic relationships between Arctic lineages are necessary for the final determination of the taxonomic status of the upper Lena form.

DOI: 10.1134/S0032945206030039

According to the prevailing opinion, the Lena is inhabited by a subspecies of the Arctic grayling *Thymallus arcticus*, *T. a. pallasii* (Borisov, 1928; Sych-Averintseva, 1932; Svetovidov, 1936; Berg, 1948; Karantonis et al., 1956; Kirillov, 1972; Kalashnikov, 1978; Egorov, 1985). Its range stretches from the lower reaches of the Yenisei to rivers of the coast of the Sea of Okhotsk and the Bering Sea (Berg, 1948; Novikov, 1966; Kirillov, 1972; Tyaptirgyanov, 1980; Romanov, 1988, 1990, 2002; Chereshnev, 1990, 1996; Skopets, 1993; Romanov and Brus'yanina, 1996; Dorofeeva, 1998, 2002; Volobuev and Rogatnykh, 1999; Makoedov, 1999; Makoedov and Korotaeva, 1999; Pavlov and Savvaitova, 1999; Chereshnev et al., 2001, 2002).

The first data on the Lena grayling is found in works of Maak (cit. in Borisov, 1928). Borisov (1928) noted the presence of grayling from the upper courses of the river to the delta and presented the morphological characteristics of seven individuals from the lower reaches of Lena. Fragmentary data on grayling morphology from the lower Lena may be found in the work of Sych-Averintseva (1932). Svetovidov (1936) analyzed several individuals from the upper and lower Lena, 23 individuals of the Kolyma river as well as specimens from Lake Essei (basin of the Khatanga River) and the Yana River from the collections of the Zoological Institute, Academy of Sciences of the USSR. Because of the small number of specimens, the morphological diagnosis of East Arctic grayling is very general and does not reflect the variability of the populations inhabiting the great territory of Siberia from the Khatanga to the Kolyma. In addition, the description of the fish could not be absolutely correct because they were kept for a very long time in a preserving solution.

Many investigators noted the differences between the graylings inhabiting the Lena River. Borisov (1928) noted a difference in the linear size of the fish of the upper and lower reaches. Karantonis et al. (1928), according to the results of morphological comparison, proposed to distinguished the grayling from the middle current of the Lena River into a specific tribe "natio *juchtae*." Kirillov (1972) and Tyaptirgyanov (1980) discovered morphological differences in grayling of the Aldan River from populations of the East Siberian subspecies and other water bodies of Yakutia. The hypothesis that there exist two spatially distinct morphologically different groups of East Arctic grayling in the Lena River has been proposed by Tugarina and Knizhin (1986). They also concluded that the graylings from the lower reaches of the Lena River are close to the fish inhabiting the rivers Kolyma and Khroma. Makoedov (1999) noted that graylings from the upper and lower current of the Lena River are not identical with respect

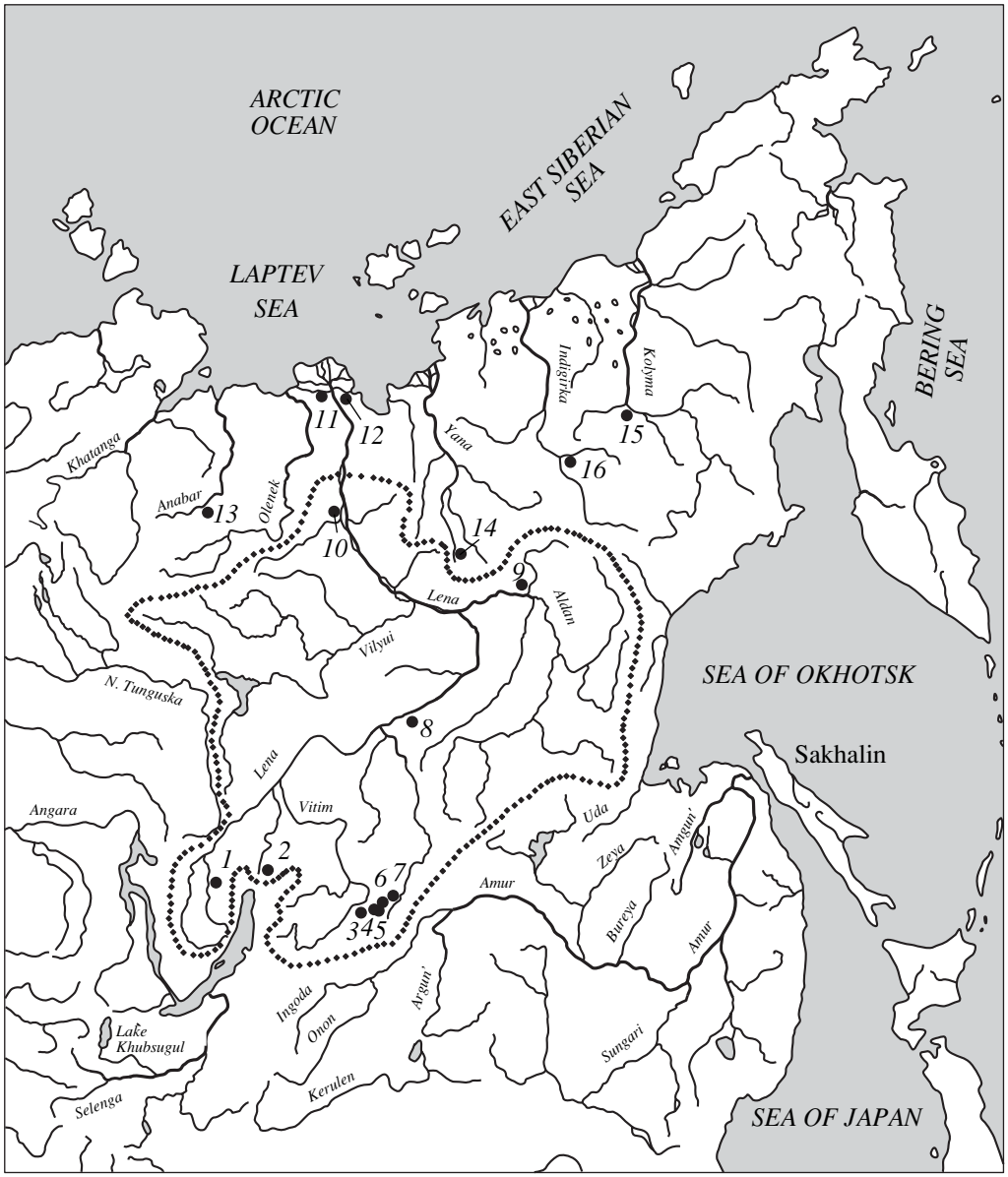

Fig. 1. Map of material collection: (*1*) Kutima River, (*2*) Lake Ogiendo, (*3*) Lake Leprindokan, (*4*) Lake Amudisa, (*5*) Kalar River, (*6*) Lake Chitkanda, (*7*) Lake Olongdo, (*8*) Pilka River, (*9*) Aldan River, (*10*) Sakhandzha River, (*11, 12*) Lena River delta, (*13*) Anabar River, (*14*) Yana River, (*15*) Kolyma River, (*16*) Indigirka River. The dashed line depicts the range of the upper Lena form.

to the pattern on the dorsal fin. Also, in his opinion, Lena River graylings differ in this trait from the Kolyma fish.

In this work we analyzed the diversity of the grayling forms in the Lena River basin to ascertain their taxonomic status.

MATERIALS AND METHODS

For this study, we used samples of graylings caught in different areas of the Lena River, from upper courses to the lower reaches, from 1998 to 2003; upper courses: the Kutima River (Kirenga River basin); middle current: Ogiendo Lake (Chaya River basin), Lake Leprindokan, Lake Davatchan, Lake Amudisa, Kalar River (Vitim River basin), Olongdo River, Lake Chitkanda (Olekma river basin), Pilka River, Aldan River; lower reaches: Sakhandzha River, Kengdei River, Tyusser River and the delta (Fig. 1). On the whole, 280 individual adult fish were used in the study. The length and body weight of some samples are given in Table 1. For comparison, we have also presented unpublished data on the morphology of grayling from other water bodies: the Khatyryn'ya River and Lake Inderkei (Yana River basin), the Khonu River and the Sygannakh River (Indigirka River basin), the Anabar River, and other water

Table 1. Linear and weight growth of graylings *Thymallus* in the basin of the Lena River (based on the observed data)

Water body (form)	Age, years							Number of fish, specimens
	2+	3+	4+	5+	6+	7+	8+	
Kutima River (UL)		194.9 / 89.5	216.4 / 125.4	234.8 / 173.6				28
Lake Leprindokan (UL)		216.1 / 111.4	236.6 / 146.2	280.0 / 223.0	292.0 / 245.0			16
Olongdo River (UL)	127.0 / 21.0	149.9 / 34.9	193.3 / 69.0	198.8 / 78.8	201.2 / 81.3			63
Pilka River (UL)		213.1 / 114.0	230.8 / 152.1	247.0 / 185.2				20
Aldan River (UL)		193.7 / 75.3	215.9 / 121.3	245.6 / 176.5				11
Sakhandzha River (UL)		204.5 / 95.0	226.5 / 133.8				317.8 / 425.0	10
Lena River (LL)		250.1 / 175.0	288.5 / 286.8	327.5 / 415.5	359.6 / 534.0	367.2 / 615.0		23

Note: the fork length is above the line, body weight, below the line.

bodies of Siberia. To determine the geographical ranges of the forms, we used dried dorsal fins of graylings from the Lena River and basins of other northern rivers of Siberia. To describe the body coloration, the pattern of the dorsal fin, and determination of the ranges in water bodies of northeastern Russia, we also used photographs of different subspecies of grayling kindly provided by M.B. Skopets. The figures were drawn on the basis of dried fins and photos of the fish.

The fish were caught with rods and gill nets. The fish were either measured fresh (the rivers Tyusser, Aldan, Indigirka, Anabar, and Yana) or preserved in 4% formaldehyde solution (all other samples). According to external morphology, shape and pattern of the dorsal fin and body coloration, all graylings were identified as upper Lena (UL) and lower Lena (LL) forms.

Details of the study of the plastic and meristic characters and statistical analyses have been published by Knizhin et al. (2004). Nonbranched (D_1) and branched (D_2) rays of the dorsal fin are not included in the cluster analysis or the principal components analysis.

RESULTS

Description of the Forms

The morphometric and meristic characters of the two forms of graylings from different areas of the Lena River are presented in Tables 2 and 3.

Lower Lena form (Fig. 2a). ll 84–98; D VIII–XII 11–15, total 22–26; P I 13–17; VII 9–11; A III–V 8–11; sp. br. 17–22; r. br. 8–10; vert. 52–58; pc 13–22.

Length of adult fish more than 300 mm. Body relatively deep 19.0–23.1% of fork length (L_{Sm}), massive. Head length from 16.9 to 18.6% L_{Sm}. Snout slightly sharpened, 4.9–6.2% of the body length. Small teeth are easily discernible on jaws. Upper jaw bone does not overlap with the vertical of the middle of eye; its length is 4.4–5.4%, lower jaw, 7.7–9.3% of body length. Antedorsal distance from 29.0 to 32.8% L_{Sm}. Length of dorsal fin base ranges from 22.9 to 27.8% L_{Sm}; its depth in the anterior part 8.2–12.7%; in posterior part, 12.9–25.0%. First 8–9 nonbranched rays of dorsal fin shortened. Its anterior margin overlaps with fatty fin and in some individuals may even protrude farther, reaching the base of dorsal fin rays. Length of pectoral fins 14.5–18.3%, abdominal, 14.2–19.2% L_{Sm}; they often reach vent. Caudal peduncle deep, 7.1–8.8% L_{Sm}.

Body coloration silverish with slight turquoise or olive shimmer. Small roundish black spots on scales noted mostly in the anterior part, at the head, more rarely overlapping the middle of the body. Gill covers, like scales above the lateral line, with dark turquoise shine. There is a black oval spot on the lower jaw. Large dark maroon spot of irregular shape is located above the abdominal fins. Caudal peduncle, anal and caudal fins dark maroon. Abdominal fins with oblique cherry-colored stripes. Pectoral fins gray-yellow. There are 6–9, sometimes more, parallel rows of maroon spots of different size going along the dorsal fin: in the anterior part, the spots are small, rounded, with not wide dim edging; closer to the last rays, the size of the spots increases and they become somewhat elongated. The upper fin fold narrow, maroon. It becomes discernible

Table 2. Morphometric traits of the popULations of grayling *Thymallus* from the Lena River basin

Character	Water body (form)						
	Kutima River (UL) (n = 28)	Vitim River (UL) (n = 74)	Olongdo River (UL) (n = 61)	Pilka River (UL) (n = 20)	Aldan River (UL) (n = 11)	Sakhandzha River (UL) (n = 10)	Lena River (LL) (n = 14)
L_{Sm}, mm	211.1 184.5–244.0	214.4 156.1–292.0	193.8 136.6–373.0	232.2 199.8–257.4	215.2 191.8–245.9	229.0 200.5–317.8	300.2 245.5–371.5
	In % L_{Sm}						
l	95.1 ± 0.09 0.46, 93.9–95.9	95.3 ± 0.08 0.64, 94.2–97.5	95.3 ± 0.08 0.61, 93.8–96.8	94.8 ± 0.11 0.48, 93.5–95.8	95.2 ± 0.16 0.55, 94.5–96.6	93.9 ± 0.19 0.61, 93.1–95.2	93.9 ± 0.18 0.88, 92.8–96.6
l_2	79.2 ± 0.15 0.77, 77.2–80.6	78.9 ± 0.13 1.08, 76.7–81.2	77.9 ± 0.2 1.49, 75.5–82.1	78.9 ± 0.26 1.17, 77.3–81.6	78.2 ± 0.4 1.33, 76.5–81.2	78.1 ± 0.29 0.93, 76.6–79.6	78.4 ± 0.28 1.33, 76.5–81.4
ao	5.8 ± 0.05 0.25, 5.3–6.3	5.4 ± 0.06 0.48, 4.2–6.3	5.6 ± 0.04 0.31, 4.8–6.0	5.4 ± 0.08 0.37, 4.8–6.1	5.9 ± 0.06 0.18, 5.6–6.4	5.8 ± 0.15 0.47, 5.0–6.6	5.5 ± 0.07 0.32, 4.9–6.1
o	4.4 ± 0.04 0.22, 3.9–4.7	4.5 ± 0.03 0.25, 3.9–5.1	4.8 ± 0.06 0.47, 3.2–5.8	4.2 ± 0.04 0.19, 3.8–4.6	4.8 ± 0.1 0.34, 4.1–5.3	4.2 ± 0.08 0.26, 3.6–4.6	3.8 ± 0.04 0.21, 3.4–4.2
f	9.0 ± 0.06 0.3, 8.6–9.7	9.3 ± 0.06 0.49, 7.9–10.2	9.6 ± 0.06 0.47, 8.5–10.9	9.2 ± 0.05 0.23, 8.7–9.6	9.7 ± 0.09 0.3, 9.2–10.4	9.7 ± 0.1 0.31, 9.2–10.1	9.4 ± 0.09 0.42, 8.6–10.0
c	18.6 ± 0.08 0.42, 17.8–19.8	18.5 ± 0.07 0.56, 17.0–19.8	19.3 ± 0.09 0.71, 17.6–20.9	18.1 ± 0.09 0.42, 17.2–18.9	19.5 ± 0.18 0.6, 18.7–20.8	18.8 ± 0.15 0.47, 17.9–19.5	17.7 ± 0.10 0.49, 16.9–18.6
ch_2	13.8 ± 0.11 0.56, 12.8–15.1	13.2 ± 0.07 0.53, 12.0–14.9	13.4 ± 0.08 0.57, 12.1–14.7	14.4 ± 0.15 0.65, 12.5–15.4	14.6 ± 0.17 0.56, 13.5–15.7	14.1 ± 0.27 0.84, 12.8–15.2	13.4 ± 0.14 0.65, 12.1–14.8
ch	9.9 ± 0.11 0.57, 8.9–11.2	9.3 ± 0.06 0.52, 8.4–11.3	9.8 ± 0.07 0.5, 8.8–10.9	10.1 ± 0.11 0.48, 9.0–10.7	10.2 ± 0.17 0.56, 8.8–10.7	9.7 ± 0.15 0.47, 9.0–10.7	8.9 ± 0.11 0.52, 8.1–10.0
k	6.0 ± 0.05 0.27, 5.5–6.5	5.7 ± 0.06 0.48, 4.4–6.3	5.6 ± 0.05 0.35, 4.4–6.2	5.9 ± 0.09 0.41, 5.0–6.8	5.5 ± 0.14 0.46, 5.0–6.7	5.5 ± 0.1 0.31, 5.0–5.9	5.4 ± 0.05 0.25, 4.8–5.8
lmx	5.0 ± 0.04 0.2, 4.6–5.4	5.1 ± 0.05 0.39, 4.0–5.8	5.3 ± 0.04 0.29, 4.6–5.8	4.9 ± 0.05 0.23, 4.6–5.3	5.2 ± 0.06 0.2, 4.8–5.6	5.0 ± 0.08 0.25, 4.6–5.4	4.9 ± 0.05 0.24, 4.4–5.4
i/lmx	1.9 ± 0.02 0.12, 1.6–2.1	1.7 ± 0.02 0.17, 1.3–2.0	1.9 ± 0.02 0.17, 1.5–2.4	1.9 ± 0.04 0.17, 1.5–2.4	1.9 ± 0.03 0.11, 1.7–2.0	1.9 ± 0.05 0.16, 1.7–2.2	1.7 ± 0.03 0.15, 1.4–2.0
lmd	8.9 ± 0.04 0.23, 8.5–9.5	9.1 ± 0.06 0.48, 8.0–10.2	9.4 ± 0.07 0.55, 8.1–10.5	8.6 ± 0.09 0.4, 7.9–9.4	9.4 ± 0.12 0.38, 8.8–10.0	9.0 ± 0.16 0.51, 8.0–9.9	8.3 ± 0.08 0.36, 7.7–9.2
H	19.4 ± 0.17 0.9, 17.7–21.3	19.2 ± 0.13 1.03, 16.1–21.6	19.2 ± 0.15 1.12, 17.0–22.2	20.3 ± 0.22 1.01, 18.9–22.4	20.0 ± 0.29 0.96, 18.5–21.4	19.4 ± 0.5 1.57, 16.9–21.4	21.1 ± 0.21 0.99, 19.0–23.1
h	6.6 ± 0.04 0.24, 6.0–7.1	6.6 ± 0.04 0.29, 5.7–7.2	6.8 ± 0.03 0.23, 6.3–7.4	6.5 ± 0.06 0.25, 6.0–6.9	6.8 ± 0.07 0.22, 6.4–7.3	6.8 ± 0.12 0.38, 6.3–7.6	7.8 ± 0.07 0.35, 7.1–8.7
w	13.7 ± 0.11 0.57, 12.5–14.7	11.6 ± 0.11 0.87, 9.9–14.5	11.5 ± 0.15 1.14, 9.7–14.3	12.7 ± 0.18 0.82, 11.5–14.8	11.9 ± 0.36 1.19, 10.9–14.0	12.9 ± 0.32 1.01, 11.5–14.6	12.1 ± 0.17 0.80, 10.7–13.6

Table 2. (Contd.)

Character	Water body (form)						
	Kutima River (UL) (n = 28)	Vitim River (UL) (n = 74)	Olongdo River (UL) (n = 61)	Pilka River (UL) (n = 20)	Aldan River (UL) (n = 11)	Sakhandzha River (UL) (n = 10)	Lena River (LL) (n = 14)
aD	33.2 ± 0.14 0.75, 31.7–34.7	32.7 ± 0.15 1.2, 29.2–35.8	34.5 ± 0.17 1.25, 31.8–36.8	31.8 ± 0.28 1.25, 29.5–34.0	32.6 ± 0.16 0.54, 31.8–33.3	31.6 ± 0.32 1.01, 29.2–32.7	30.6 ± 0.16 0.79, 29.0–32.8
pD	42.2 ± 0.27 1.41, 39.1–44.9	43.4 ± 0.19 1.66, 39.3–46.9	41.8 ± 0.2 1.49, 38.4–46.3	42.0 ± 0.27 1.19, 39.0–44.4	40.2 ± 0.3 0.98, 39.1–42.6	39.8 ± 0.49 1.56, 37.1–42.5	40.6 ± 0.32 1.55, 38.2–43.8
aA	70.2 ± 0.21 1.13, 67.9–73.0	70.7 ± 0.13 1.04, 68.6–72.9	71.5 ± 0.18 1.36, 67.9–75.6	70.7 ± 0.26 1.14, 68.4–73.7	70.8 ± 0.29 0.95, 69.1–72.0	70.4 ± 0.33 1.05, 68.5–71.7	70.4 ± 0.34 1.61, 68.2–75.5
aV	45.1 ± 0.24 1.29, 42.4–47.7	45.1 ± 0.12 0.98, 43.4–47.5	46.2 ± 0.2 1.48, 43.3–51.6	45.5 ± 0.4 1.77, 42.9–50.4	45.5 ± 0.34 1.12, 43.7–47.5	44.8 ± 0.38 1.2, 41.9–46.1	45.6 ± 0.33 1.57, 42.9–48.8
lp	16.8 ± 0.14 0.72, 15.2–18.0	16.9 ± 0.13 1.05, 14.3–18.7	16.5 ± 0.14 1.08, 14.7–18.5	16.7 ± 0.17 0.76, 14.3–17.8	15.7 ± 0.24 0.79, 14.4–17.3	15.6 ± 0.16 0.5, 14.4–16.3	15.9 ± 0.14 0.67, 14.7–17.6
PV	27.9 ± 0.23 1.23, 25.3–30.0	27.9 ± 0.17 1.33, 22.4–31.1	28.5 ± 0.15 1.1, 26.2–31.2	29.2 ± 0.23 1.04, 27.4–31.5	27.9 ± 0.42 1.38, 26.4–30.4	28.4 ± 0.4 1.28, 25.9–30.7	30.2 ± 0.28 1.34, 26.9–33.3
VA	26.8 ± 0.16 0.83, 25.3–28.9	26.2 ± 0.13 1.06, 23.3–29.0	26.2 ± 0.18 1.33, 22.8–28.8	26.6 ± 0.42 1.86, 24.5–34.0	25.5 ± 0.33 1.09, 23.2–27.3	26.0 ± 0.21 0.68, 24.8–26.9	26.3 ± 0.36 1.72, 23.3–29.0
lD	21.9 ± 0.23 1.22, 19.3–24.8	20.3 ± 0.18 1.44, 17.5–24.0	20.6 ± 0.19 1.44, 18.3–25.2	23.3 ± 0.38 1.69, 20.3–27.2	23.7 ± 0.46 1.52, 21.4–27.6	24.9 ± 0.63 2.0, 22.8–29.5	24.8 ± 0.28 1.34, 22.9–27.8
hD_1	10.0 ± 0.12 0.65, 8.5–11.5	10.5 ± 0.14 1.09, 8.6–13.9	10.5 ± 0.15 1.12, 8.5–13.4	10.9 ± 0.21 0.92, 9.4–12.2	11.4 ± 0.28 0.93, 9.0–12.5	11.2 ± 0.39 0.95, 9.5–12.7	10.1 ± 0.24 1.17, 8.2–12.7
hD_2	12.4 ± 0.45 2.39, 8.6–17.7	10.8 ± 0.38 3.06, 7.2–21.6	9.7 ± 0.34 2.53, 6.3–18.2	12.8 ± 0.77 3.36, 7.4–18.3	16.4 ± 1.18 3.9, 8.4–21.4	16.3 ± 1.59 3.55, 11.9–22.8	17.8 ± 0.77 3.69, 12.1–25.0
lA	9.6 ± 0.09 0.49, 8.7–10.7	8.9 ± 0.08 0.62, 7.6–10.7	8.9 ± 0.1 0.73, 7.5–10.9	9.8 ± 0.12 0.56, 8.5–10.9	9.9 ± 0.19 0.64, 8.8–10.7	9.8 ± 0.2 0.64, 8.8–11.4	8.9 ± 0.16 0.78, 7.3–11.3
hA	11.9 ± 0.2 1.08, 9.6–14.6	11.4 ± 0.11 0.88, 9.8–13.8	12.0 ± 0.14 1.02, 10.1–14.1	11.9 ± 0.19 0.87, 10.2–13.4	12.4 ± 0.16 0.54, 11.5–13.3	12.2 ± 0.36 0.63, 11.3–12.7	12.3 ± 0.15 0.73, 11.0–13.7
lP	14.6 ± 0.13 0.7, 12.9–15.5	15.1 ± 0.1 0.78, 11.4–17.0	15.1 ± 0.07 0.55, 13.9–16.6	14.7 ± 0.15 0.68, 12.3–15.6	15.7 ± 0.25 0.84, 14.1–16.9	15.7 ± 0.24 0.64, 14.8–16.5	15.8 ± 0.21 1.02, 14.5–18.3
lV	14.6 ± 0.13 0.67, 13.5–15.9	14.8 ± 0.14 1.14, 12.5–17.5	14.9 ± 0.18 1.37, 12.7–20.7	14.9 ± 0.26 1.17, 12.5–17.0	16.6 ± 0.48 1.59, 14.1–19.6	15.2 ± 0.39 1.17, 13.9–17.3	16.2 ± 0.29 1.39, 14.2–19.2

Note: L_{Sm}—fork length; l—trunk length; l_2—the length to the termination of the scale cover; ao—snout length; o—orbit diameter, horizontal; f—postorbital head area; c—head length; ch_2—head depth at the occiput; ch—head depth at the eye; k—forehead width; lmx—upper jaw length; i/lmx—lower jaw width; lmd—lower jaw length; H—the maximum body depth; h—minimum body depth; w—body width; 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 depth of the anterior part of the dorsal fin; hD_2—the depth 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 abdominal fin. The mean value with the standard error is above the line, standard deviation and the range, below the line; n the number of individuals.

Table 3. Meristic traits in populations of the graylings *Thymallus* from the basin of the Lena River

Character	Water body (form)							
	Kutima River (UL) (n = 28)	Lake Ogiendo (UL) (n = 32)	Vitim River (UL) (n = 74)	Olongdo River (UL) (n = 61)	Pilka River (UL) (n = 20)	Aldan River (UL) (n = 11)	Sakhandzha River (UL) (n = 10)	Lena River (LL) (n = 44)
ll	91.8 ± 0.73 3.88, 86–103	91.4 ± 0.7 3.95, 84–99	95.8 ± 0.53 4.37, 87–104	91.1 ± 0.53 3.99, 82–102	93.2 ± 0.93 4.17, 82–104	92.8 ± 1.54 5.1, 88–104	94.4 ± 0.79 2.5, 89–98	90.5 ± 0.51 3.41, 84–98
D_1	7.8 ± 0.1 0.54, 7–9	8.2 ± 0.13 0.75, 7–10	7.9 ± 0.09 0.77, 7–10	7.8 ± 0.1 0.72, 7–9	9.2 ± 0.18 0.77, 8–11	8.5 ± 0.2 0.66, 8–10	8.2 ± 0.24 0.75, 7–10	9.7 ± 0.18 1.16, 8–12
D_2	12.5 ± 0.19 0.98, 11–14	13.1 ± 0.17 0.97, 12–16	12.5 ± 0.08 0.67, 11–14	12.9 ± 0.11 0.84, 12–15	12.6 ± 0.25 1.09, 10–14	13.2 ± 0.13 0.45, 13–14	13.7 ± 0.38 1.19, 11–15	13.8 ± 0.15 1.00, 11–15
D	20.4 ± 0.17 0.9, 19–22	21.4 ± 0.16 0.93, 19–23	20.4 ± 0.1 0.81, 19–22	20.8 ± 0.13 1.0, 19–23	21.8 ± 0.24 1.06, 20–24	21.8 ± 0.17 0.57, 21–23	21.9 ± 0.48 1.51, 19–24	23.5 ± 0.13 0.87, 22–26
P	14.1 ± 0.13 0.69, 13–15	14.4 ± 0.11 0.61, 13–15	14.3 ± 0.08 0.7, 13–16	14.2 ± 0.1 0.73, 12–16	14.2 ± 0.14 0.62, 13–15	14.7 ± 0.23 0.75, 14–16	14.6 ± 0.15 0.49, 14–15	15.2 ± 0.11 0.72, 13–17
V	8.9 ± 0.04 0.19, 8–9	8.9 ± 0.05 0.3, 8–10	9.0 ± 0.04 0.34, 8–10	9.1 ± 0.04 0.29, 9–10	9.0 ± 0.07 0.32, 8–10	9.1 ± 0.09 0.29, 9–10	9.1 ± 0.09 0.3, 9–10	9.5 ± 0.08 0.54, 9–11
A_1	3.8 ± 0.07 0.38, 3–4	4.4 ± 0.1 0.54, 3–5	4.1 ± 0.07 0.55, 3–5	4.1 ± 0.06 0.48, 3–5	4.1 ± 0.11 0.48, 3–5	4.1 ± 0.09 0.29, 4–5	4.1 ± 0.17 0.54, 3–5	4.1 ± 0.07 0.49, 3–5
A_2	9.3 ± 0.09 0.48, 9–10	9.2 ± 0.1 0.58, 8–10	9.2 ± 0.08 0.63, 8–11	8.8 ± 0.09 0.67, 7–10	9.4 ± 0.11 0.49, 9–10	9.4 ± 0.2 0.66, 8–10	9.4 ± 0.15 0.49, 9–10	9.1 ± 0.11 0.70, 8–11
sp. br.*	18.6 ± 0.17 0.9, 17–20	19.0 ± 0.19 1.06, 17–21	19.1 ± 0.14 1.13, 17–22	18.7 ± 0.14 1.08, 16–22	19.3 ± 0.28 1.27, 17–22	18.5 ± 0.35 1.16, 17–20	19.4 ± 0.43 1.36, 18–23	18.8 ± 0.32 1.53, 17–22
r. br.	9.1 ± 0.14 0.74, 8–11	9.1 ± 0.08 0.44, 8–10	9.1 ± 0.08 0.65, 8–11	9.1 ± 0.09 0.64, 8–10	8.9 ± 0.12 0.54, 8–10	9.4 ± 0.2 0.66, 8–10	8.7 ± 0.2 0.64, 8–10	8.9 ± 0.10 0.65, 8–10
vert*	55.3 ± 0.13 0.71, 54–57	55.6 ± 0.15 0.85, 54–57	55.4 ± 0.11 0.85, 54–57	55.7 ± 0.11 0.86, 54–57	55.6 ± 0.23 1.02, 54–57	51.2 ± 0.13 0.45, 51–52	54.5 ± 0.32 1.02, 53–56	55.1 ± 0.25 1.68, 52–58
pc*	15.9 ± 0.37 1.96, 12–19	16.4 ± 0.36 2.02, 13–23	16.4 ± 0.24 1.86, 13–24	14.7 ± 0.24 1.73, 12–19	16.3 ± 0.52 2.31, 12–20	13.6 ± 0.59 1.97, 12–19	15.3 ± 0.57 1.79, 13–19	16.9 ± 0.48 2.30, 13–22

Note: ll the number of perforated rays in the lateral line; D_1 the number of non-branched rays in the dorsal fin; D_2 the number of branched rays in the dorsal fin; D total number of rays in the dorsal fin; P the number of branched rays in the pectoral fin; V the number of branched rays in the abdominal fin; A_1 the number of nonbranched rays in the anal fin; A_2 the number of branched rays in the anal fin; sp. br. the number of gill rakers; r. br. the number of gill rays; vert. vertebral number; pc the number of pyloric ceca; * in the sample from the basin of the Vitim River, we counted vert in 60 specimens, pv, in 55 specimens; in the united sample of the lower Lena form from the delta pf the Lena River and Tyusser River, we counted sp. br. and pc in 23 specimens. Mean value and its standard error is above the line, standard deviation and range, below the line; n. the number of individuals.

only from the 6th–8th ray and, slightly widening, continues up to the end of the fin (Fig. 3a). On the belly, two parallel wide brown stripes go from pectoral to abdominal fins. The grayling of this form inhabit the delta part of the Lena River and the adjacent tributaries.

Upper Lena form (Fig. 2b). ll 82–104; D VII–XI 10–16, total 19–24; P I 12–16; V II 8–10; A III–V 7–11; sp. br. 16–23; r. br. 8–11; vert. 51–57; pc. 12–24.

Fish usually not longer than 350 mm. Body not deep, from 16.1 to 22.4% L_{Sm}, oblong. Head length from 17.0 to 20.9% L_{Sm}. Snout rounded, 4.2–6.6% of body length. Teeth on jaws small, poorly discernible. Upper jaw bone does not overlap the vertical of the middle of eye, its length 4.1–5.8%, and lower jaw, 7.9–10.5% of body length. Antedorsal distance from 29.2 to 36.8% L_{Sm}. Length of dorsal fin base ranges from 17.5 to 29.5% L_{Sm}, its posterior tip is usually pointed and in the lowered state does not overlap with fatty fin. Anterior part of dorsal fin relatively deep, 8.5–13.9% L_{Sm}, posterior part 6.3–22.8 L_{Sm} in depth. The length of pectoral fins from 11.4 to 17.0%, abdominal, from 12.5 to 20.7% L_{Sm}. Pectoral fins never attain vent. Caudal peduncle not deep, from 5.7 to 7.7% of body length.

Body coloration silverish with dominance of dark colors with violet shine. Slightly dashed, black, and

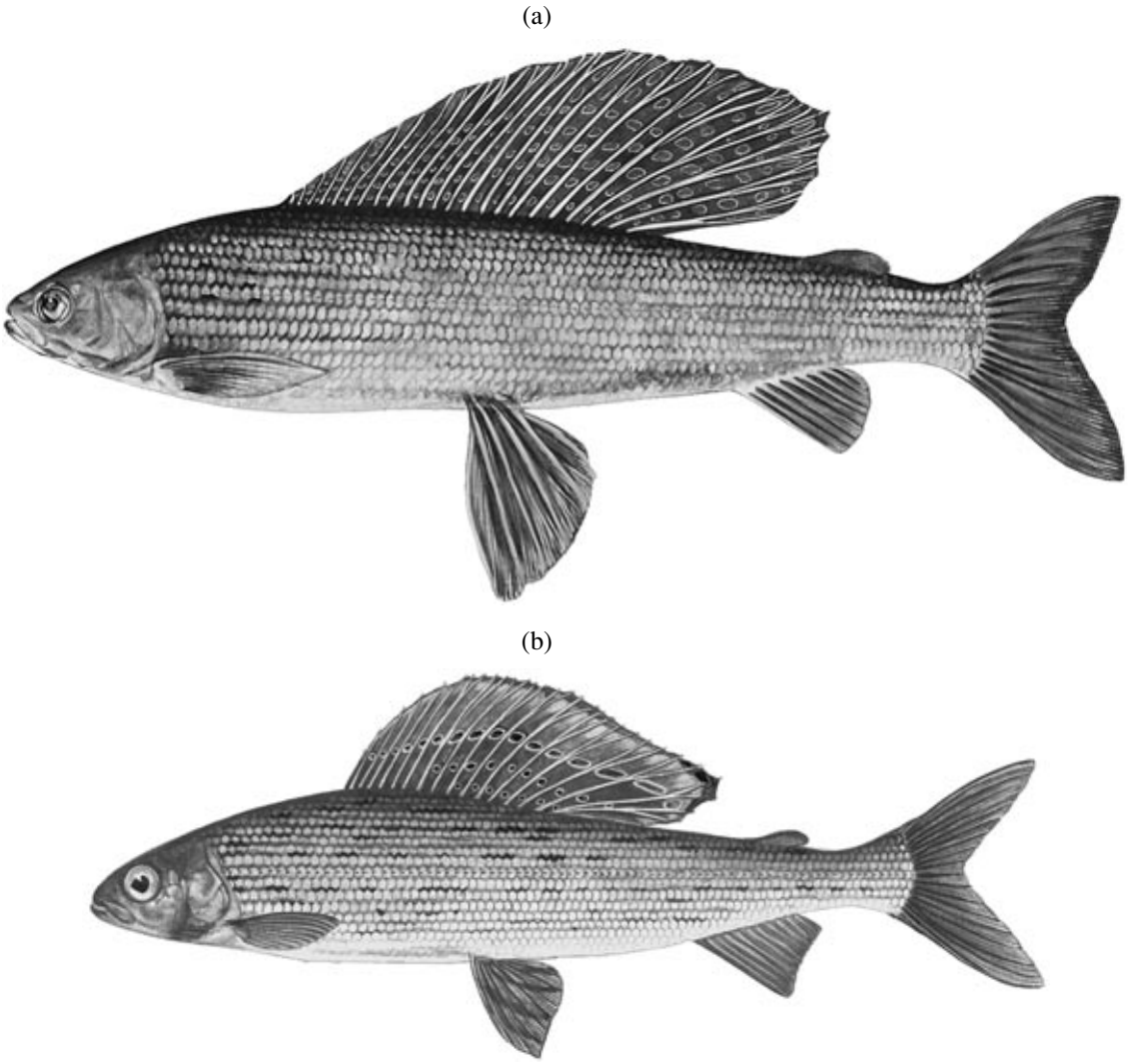

Fig. 2. Graylings *Thymallus* from the Lena River: (a) lower Lena form, (b) upper Lena form.

slightly meandering stripes made of small spots run along the scale rows from head to the tail. Gill covers with vivid violet steel shine. Black oval spot on the lower jaw. Several rows of scales from abdominal fins to the end of the caudal peduncle have copper maroon shine. Oblique reddish-violet bands on abdominal fins. Pectoral fins grayish-yellow in color. From three to five (usually 3–4) parallel stripes consisting of elongated oval spots of different size run along the dorsal fin base. Small spots constitute the third row, creating a "sling." In most individuals, the spots of this row do not fuse with the relatively wide maroon border at the edge of the fin (Figs. 3b, 3c, 3d). Two wide grayish-yellow stripes run along the belly from the pectoral to abdominal fins. Graylings of this form inhabit water bodies of the upper, middle, and lower reaches of the Lena, and the upper courses of certain northeastern tributaries of Lake Baikal.

Comparative notes. The two forms of the Lena River grayling differ in the following traits.

The upper Lena graylings usually have the following characteristics: a roundish snout; the upper part of the body and the gill covers are violet steelish; short black meandering stripes run along the scale rows from head to the caudal fin; the anterior part of the dorsal fin is relatively deep; the number of spot rows does not exceed five and their upper row forms a "sling"; spots from adjacent rows never join; posterior margin of the dorsal fin pointed and in the folded state does not reach the fatty fin; there is no dark maroon spot above the pectoral fins.

The lower Lena graylings have the following characteristics: sharpened snout; the upper part of the body and gill covers are olive turquoise; there are several black spots in the anterior part of the body between the scale rows; the anterior part of the dorsal fin is gently sloping; the number of spot rows on the dorsal fin is

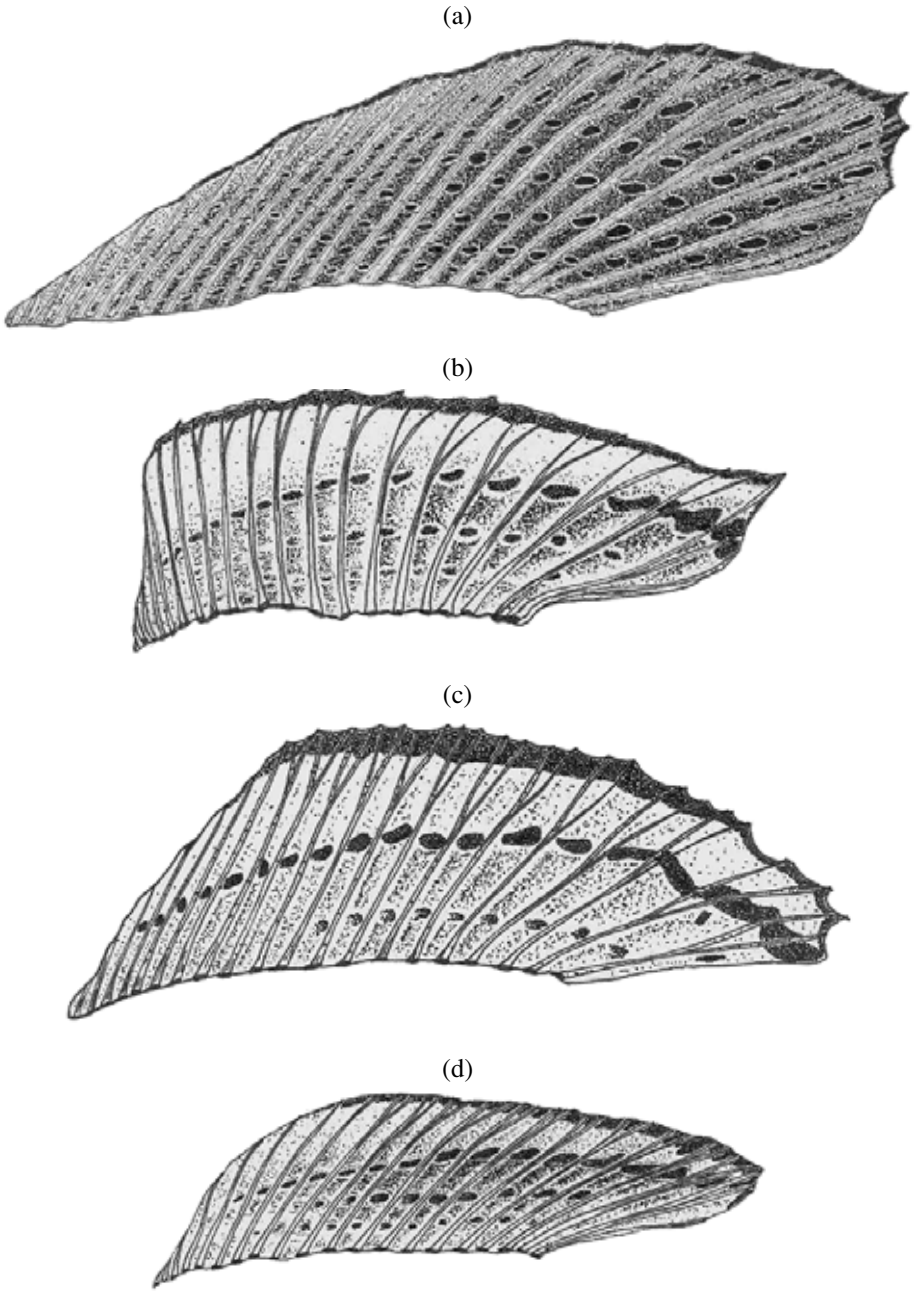

Fig. 3. Variants of the dorsal fin pattern in graylings *Thymallus* of the Lena River basin. Lower Lena form: a. Lena delta, Tyusser River; upper Lena form: b. Kutima River (basin of the Kirenga River, upper courses), c. Olongdo River (basin of the Olekma River, middle courses), d. Pilka River (Lena River tributary, middle course).

more than five and the "sling" is absent; spots from neighboring rows in the posterior part sometimes merge in the form of short elongated lines; the posterior margin of the dorsal fin is sharpened and in the folded state overlaps with the fatty fin; there is a dark maroon spot above the abdominal fins.

Significant ($p \leq 0.001$) differences between the lower and upper Lena forms were found in the number of branching and non-branching rays in the dorsal fin and their overall number. The comparison of the lower Lena form with the upper Lena form from the basins of the rivers Kirenga, Chaya, Vitim, and Olekma in the latter trait revealed a difference coefficient CD of more than 1.28. The lower Lena form also has more pyloric ceca and fewer scales in the lateral line.

With respect to the number of scales, the upper Lena form from the Aldan is distinct (Table 3). Its difference formally exceeds the subspecies level (CD ≥ 1.28).

The principal components analysis of the meristic traits of the Lena River populations revealed that three

Table 4. Loadings of the first three principal components for 10 meristic traits in graylings *Thymallus* from the basin of the Lena River

Trait	Principal component		
	1	2	3
ll	0.999	−0.051	−0.004
D	0.005	0.169	0.625
P	0.118	0.109	0.364
V	−0.092	0.159	0.319
A_1	−0.053	0.003	0.023
A_2	0.186	0.104	0.101
sp. br.	0.148	0.187	−0.043
r. br.	−0.027	0.044	0.089
vert	−0.095	−0.135	−0.897
pc	0.238	0.964	−0.099

first components accounting for 84.3% of the variance in the data. The factor loadings are presented in Table 4. The maximum loadings on the first principal component were found for the number of scales in the lateral line, for the second, for pyloric ceca, and for the third, for the number of rays in the dorsal fin. The scatterplot of the first three principal components indicates that the grayling of the Lower Lena form somewhat deviate from the main data cloud, represented by the upper Lena form. This is true for the fish from the Aldan River, which also occupy a somewhat distinct position (Fig. 4).

The results of the cluster analysis of meristic traits using the unweighted pair-group average method (UPGMA) revealed the division of the studied samples into two branches, one of which is formed by graylings from the delta areas of the Lena River (lower Lena form), and the rivers Yana, Anabar, Indigirka, and Aldan, and the second, by other populations of the upper Lena form (Fig. 5).

DISCUSSION

Comparative analysis of the two forms of graylings from the Lena River, differentiated by coloration and certain morphological characteristics revealed significant overlap in ranges of meristic traits with some differences in the mean values. A similar situation with the absence of a clear hiatus in the basic diagnostic traits is observed in subspecies of the Arctic grayling *T. arcticus* inhabiting the water bodies of northeastern Russia (Kirillov, 1972; Tyaptirgyanov, 1980; Chereshnev et al., 2001, 2002); these include the East Arctic grayling *T. a. pallasii*, the Alaskan grayling *T. a. signifer*, and the Kamchatka grayling *T. a. mertensii* (Table 5). This is probably the reason some researchers (Walters, 1955; Barsukov, 1958) combined all these subspecies into one taxon *T. a. pallasii.*

Along with clear division by several biological and morphological characters, Chereshnev et al. (2002) noted certain similarity between all northeastern subspecies of graylings. Furthermore, biochemical genetics methods provided evidence of the divergence of the Kamchatka and Eastern Arctic graylings (Makoedov, 1999; Makoedov and Korotaeva, 1999).

The results of phenetic studies of graylings (Makoedov, 1985, 1999; Makoedov and Korotaeva, 1999) and our data on the analysis of Amur populations

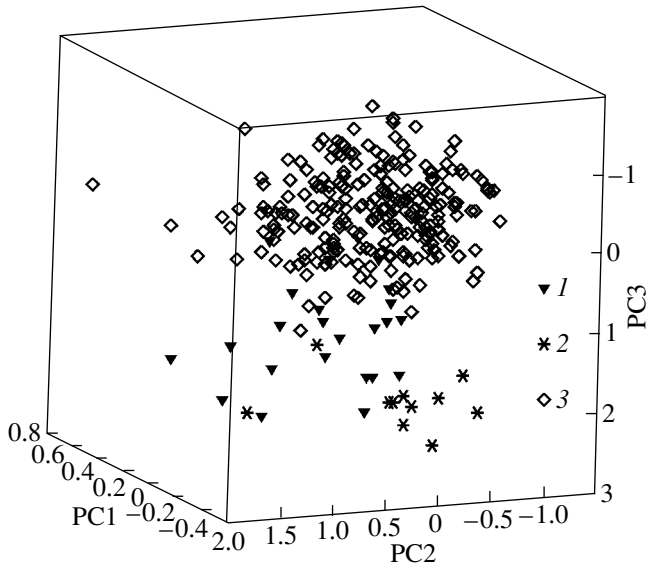

Fig. 4. Distribution of the grayling forms *Thymallus* in the three principal components (PC) in 11 meristic traits: (1) Lower Lena form (delta of the Lena River, Tyusser River), (2) Upper Lena form (Aldan River), (3) Upper Lena form (all other samples). Only the overall number of rays D was not included into the analysis.

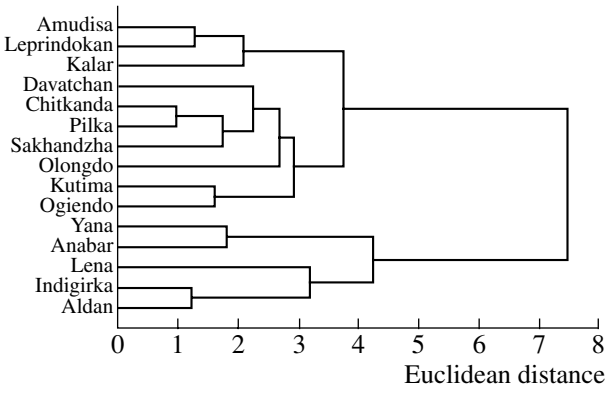

Fig. 5. Dendrogram of the Lena River grayling's *Thymallus* similarity with cartain populations of the eastern Arctic grayling *T. arcticus pallasii* from adjacent basins by 10 meristic traits, cluster analysis using the UPGMA method. Only the overall number of rays D is included into the analysis.

Table 5. Variability of certain meristic traits in subspecies and forms of the Arctic grayling *Thymallus arcticus* in rivers of Eastern Siberia and Northeastern Russia

Trait	Subspecies and forms											
	Upper Lena Form			Lower Lena Form	*T. a. pallasii*						*T. a. mertensii*	*T. a. signifer*
	Lena River				Anabar River	Indigirka River	Yana River	Yakutia	Kolyma River	Northeast of Russia	Northeast of Russia	
	references											
	our data	Kalashnikov, 1978	Karantonis et al., 1956	our data				Kirillov, 1972	Novikov, 1966	Chereshnev et al., 2002		
ll	82–104	89–105	83–101	84–98	79–91	87–110	79–97	80–102	80–102	76–103	69–94	77–98
D_1	7–11	7–11	7–11	8–12	8–12	9–11	8–10	8–15	8–15	9–16	7–14	8–13
D_2	10–16	11–16	11–14	11–15	12–16	12–15	12–15	8–17	10–16	10–17	10–16	10–15
D	19–24	–	–	22–26	22–25	22–25	21–25	18–28	–	21–28	19–27	20–28
P	12–16	12–16	–	13–17	14–16	14–15	14–17	–	–	13–17	13–17	12–15
V	8–10	8–10	–	9–11	8–10	9–10	8–10	–	–	8–10	8–10	8–10
A_1	3–5	3–5	3–4	3–5	4–5	3–4	3–5	2–5	2–5	3–6	3–5	3–5
A_2	7–11	8–11	8–12	8–11	8–10	8–10	8–10	8–12	8–12	7–11	8–11	8–11
sp. br.	16–23	15–21	15–18	17–22	17–22	16–20	18–22	17–24	17–24	16–23	14–23	17–24
pc	12–24	–	–	13–22	14–25	17–25	17–27	–	–	13–26	14–33	14–21

(Knizhin et al., 2004) indicated that the color pattern on the dorsal fin can be used for diagnosis. Having analyzed the dorsal fins of several species and forms of grayling, one can note that the stripes on the last interray membranes in the east Arctic grayling (noted in several descriptions, see Borisov, 1928; Svetovidov, 1936; Kirillov, 1972; Tyaptirgyanov, 1980; Chereshnev et al., 2001, 2002) are noted in the Kolyma River graylings, in graylings from the Indigirka River (Figs. 6b, 6c), and in the Kamchatka grayling. However, the Lena River forms and the fish from the rivers Yana (Fig. 6a) and Anabar do not have such stripes, which has been noted by Makoedov (1999). Also, only the pattern on the fin in the lower Lena form is comparable with that in graylings from the rivers Yana (Fig. 6a) and Anabar.

The pattern of spots in the anterior part of the dorsal fin is similar in all analyzed forms except that of the upper Lena. A similar situation is noted in body coloration. The lower Lena form and graylings from the rivers Yana and Anabar have much in common with the Alaska and Kamchatka graylings, the depictions of which are presented in works by Chereshnev et al. (2001, 2002), as well as with the fish from the Koolen' River, Chukot Peninsula (Fig. 6d).

The results of mitochondrial DNA analysis in the upper Lena (basin of the Olekma River) and lower Lena (delta of the Lena River) forms, conducted by Froufe et al. (2005) as a part of a wider study of phylogenetic relationships between graylings of the Palaearctic, clearly indicate that they are genetically different. Additionally, this work provides evidence that the lower Lena graylings are similar to graylings from the rivers of Canada and Alaska. This supports our hypothesis that the lower Lena form is related to the Alaska grayling, with which it shares the same pattern on the dorsal fin.

Further studies of the diversity of forms and phylogenetic relations are necessary to obtain a clearer picture of the species structure in the Arctic grayling *T. arcticus* in water bodies of Palaearctic. Such studies will make it possible to reveal the origin and the paths of dispersal of graylings. An interesting problem is the mosaic distribution of graylings in northern rivers of Siberia. Probably, this is a consequence of the history of their distribution during the Pleistocene glaciations; glaciers covered the central part of Eastern Siberia from the Yenisei to the ridges, separating the Lena River from the rivers of the Sea of Okhotsk and Chukot basins.

The differences of the grayling population living in the Aldan River from the Lena river populations in the number of vertebrae points to a certain uniqueness of this population. The data on Aldan graylings are based on a small number of individuals (11 specimens). However, it seems obvious that they represent the upper Lena form because they are characterized by identical

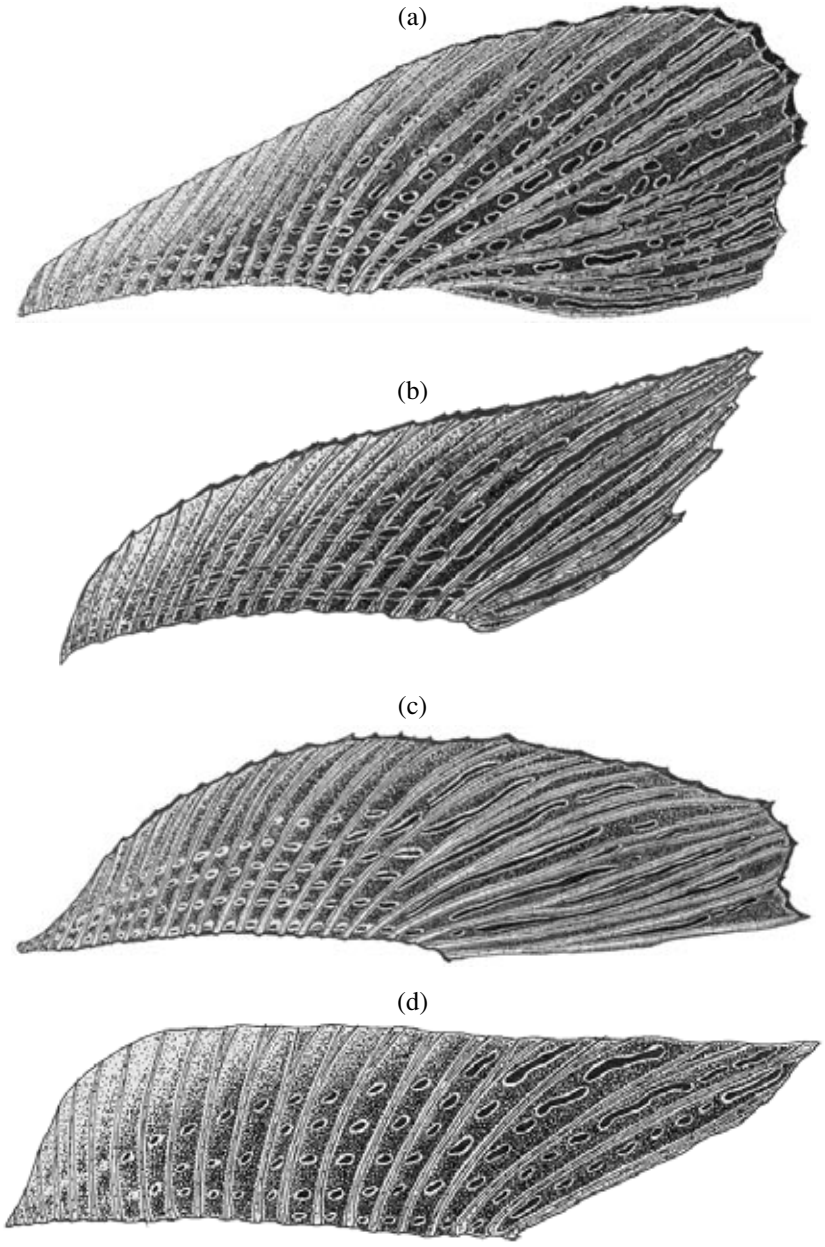

Fig. 6. Variations of the dorsal fin pattern in the Eastern Arctic grayling *Thymallus arcticus pallasii* in certain water bodies of Northeastern Russia: (a) Yana River, (b) Indigirka River, (c) Kolyma River, (d) Koolen' River (Chukot Peninsula).

body coloration and the pattern on the dorsal fin as well as by similar biological characteristics.

In conclusion, we may posit that two spatially and genetically distinct lineages inhabit the Lena River. The Upper Lena form lives in most of the basin from the upper courses almost to the delta, and the Lower Lena form is noted only in the delta and by the complex of traits representing the Eastern Arctic grayling *T. a. pallasii.* The Lower Lena form is similar to the populations of grayling inhabiting the rivers Anabar and Yana, as well as to the Alaskan grayling from rivers of the Chukot Peninsula, Alaska, and the Missouri. The Upper Lena form is characterized by a pattern on the dorsal fin different from that of graylings of all other populations, which suggests that it may represent an individual subspecies. However, the taxonomic status of the upper Lena form may be determined only after detailed study of the diversity and phylogenetic relations of the graylings of Palaearctic.

ACKNOWLEDGMENTS

We are grateful to S.S. Alekseev, V. P. Samusenok, A. L. Yur'ev for materials from Lake Ogiendo, Amudisa, Kalar, Davatchan, and Chitkanda (collected with

support from the Russian Foundation for Basic Research, grant 01-04-49376) provided for morphological analysis; M.B. Skopets for the photos of graylings from waters of northeastern Russia; S.D. Bezdubnyi, B.E. Bogdanov, V.V. Vanin, V.I. Grishchenko, A.Yu. Gukov, D.N. Gubanov, G.M. Markov, A.N. Matveev, A.I. Savvinov, B.N. Sleptsov, N.M. Solomonov, and V.V. Khodulov for invaluable help in collection of the materials; D.V. Kuznetsova for help in the preparation of the figures of the fish, S.S. Alekseev and P.Ya. Tugarina† for helful advice during the work on the manuscript; N.G. Bogutskaya and A.V. Balushkin for making available the collection of graylings in the museum of the Zoological Institute of the Russian Academy of Sciences. We are especially indebted to W.P. Dwyer (USFWS, Bozeman, Montata) for providing the materials on the Arctic grayling from the Big Hole River (Montana, USA), and D. DeHart and K. Kostow (Oregon department of Fish and Wildlife, USA) for assistance during the research; the comments and criticism of E. D. Vasil'eva significantly improved the manuscript.

This study was supported by the Federal Program Integratsiya, grant no. K0 788, the Ministry of Education of the Russian Federation, grant A03-2.12-265, the program "Universities of Russia," grant UR.07.01.009 and the Ministry of Sciences of Portugal, grant FCT POCT 1/33364/BSE/2000.

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Translated by S. V. Budaev