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Biological and Morphological Characteristic of the Arctic Grayling *Thymallus arcticus* (Thymallidae) from Alpine Lakes of the Basin of the Upper Reaches of the Angara River

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Abstract—Specific morphological and biological features of the populations of the Arctic grayling *Thymallus arcticus* from lakes Urunge Nur, Mongosha, Sadaiskoe, and Gusinoe situated in the Upper Sayan Mountains in the sources of the Oka and Kitoi rivers (the basin of the upper reaches of Angara) that have been not studied previously are considered. The results of the multivariate analysis indicated the uniformity of all samples by 12 meristic characters. Graylings of the studied lakes are similar to graylings from the Angara and Nizhnyaya Tunguska rivers and the Irkutsk Reservoir, as well as to the Baikal grayling *T. a. baicalensis* in body coloration and pattern of the dorsal fin. The samples studied and *T. a. baicalensis* considerably differ in the above characters from populations inhabiting the basin of the upper reaches of the Ob that belong to the nominative subspecies *T. a. arcticus*. The differences established between the Angara-Yenisei and the Upper Ob graylings give grounds to doubt the justification of including them into one taxon, *T. a. arcticus*. The same is evidenced by the results of molecular-genetic studies of graylings from the Palearctic (Froufe et al., 2005). The data obtained indicate the necessity of ascertaining the boundaries of the ranges of different forms of graylings in the Angara-Yenisei and Ob basins and of the revision of their taxonomic status. Populations inhabiting the Angara and Yenisei rivers, except their sources and the section of the lower reaches, should be assigned to the Baikal subspecies, *T. a. baicalensis*. Graylings from different lakes in the upper reaches of Oka and Kitoi differ in their linear-weight indices. The indices of growth are highest where they occupy a dominant position. Their food in the summer consists mainly of the larval and imaginal stages of amphibiotic and aerial-terrestrial insects. Only in Lake Urunge Nur do graylings of elder age groups use fish of other species for food. The extreme conditions of habitation of the grayling in Lake Gol'tsovoe are the cause of food deficiency, which determines its dwarfism.

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According to modern concepts, the basins of the Ob, Yenisei, Angara, as well as Kobdo rivers in western Mongolia are inhabited by a nominative subspecies of the Arctic grayling *Thymallus arcticus arcticus* (Svetovidov, 1931, 1936; Ioganzen, 1945; Berg, 1948; Kafanova, 1970; Shatunovskii, 1983; Egorov, 1985; Popov, 1997; Dorofeeva, 1998, 2002; Romanov, 2001, 2002, 2004). In the Baikal basin, its range is limited by the Irkutsk Reservoir (Svetovidov, 1936; Egorov, 1985) and the Selenga River basin in Mongolia (Shatunovskii, 1983). The sympatry of the nominative subspecies with the East Siberian grayling *T. a. pallasii* in the lower reaches of Yenisei (Khantai Lake) (Romanov, 1990, 2000, 2002, 2004; Romanov and Brus'yanina, 1996) and with Mongolian grayling *T brevirostris* in the Kobdo River is noted; Svetovidov (1936) suggests their possible hybridization there. In the basin of the upper reaches of the Yenisei (the Shishkhid Gol River, Mongolia), Koskinen et al. (2002) found a form of the grayling[1] that, based on results of molecular-genetic analysis, cannot yet be assigned with assuredness either to an Arctic or to a Mongolian species (Froufe et. al., 2005).

The populations of graylings inhabiting the upper reaches of the Ob, as well as the middle and lower reaches of the Yenisei have been studied most comprehensively (Ioganzen, 1945; Gundrizer, 1967, 1979; Kafanova, 1970; Gundrizer et al., 1981; Mitrofanov et al., 1986; Popov, 1997; Zadelenov and Gulimov, 2000; Romanov, 2001, 2002, 2004). The study of morphological characters and biological indices of graylings from these rivers led to the description of several forms and subspecies (Dorogostaiskii, 1923; Ioganzen, 1945; Gundrizer, 1967, 1979; Kafanova, 1970; Egorov, 1985) that are not mentioned in the last taxonomic reviews of freshwater fish in Russia (Dorofeeva, 1998, 2002;

[1] Morphological characters and biological indices of this form were not studied.

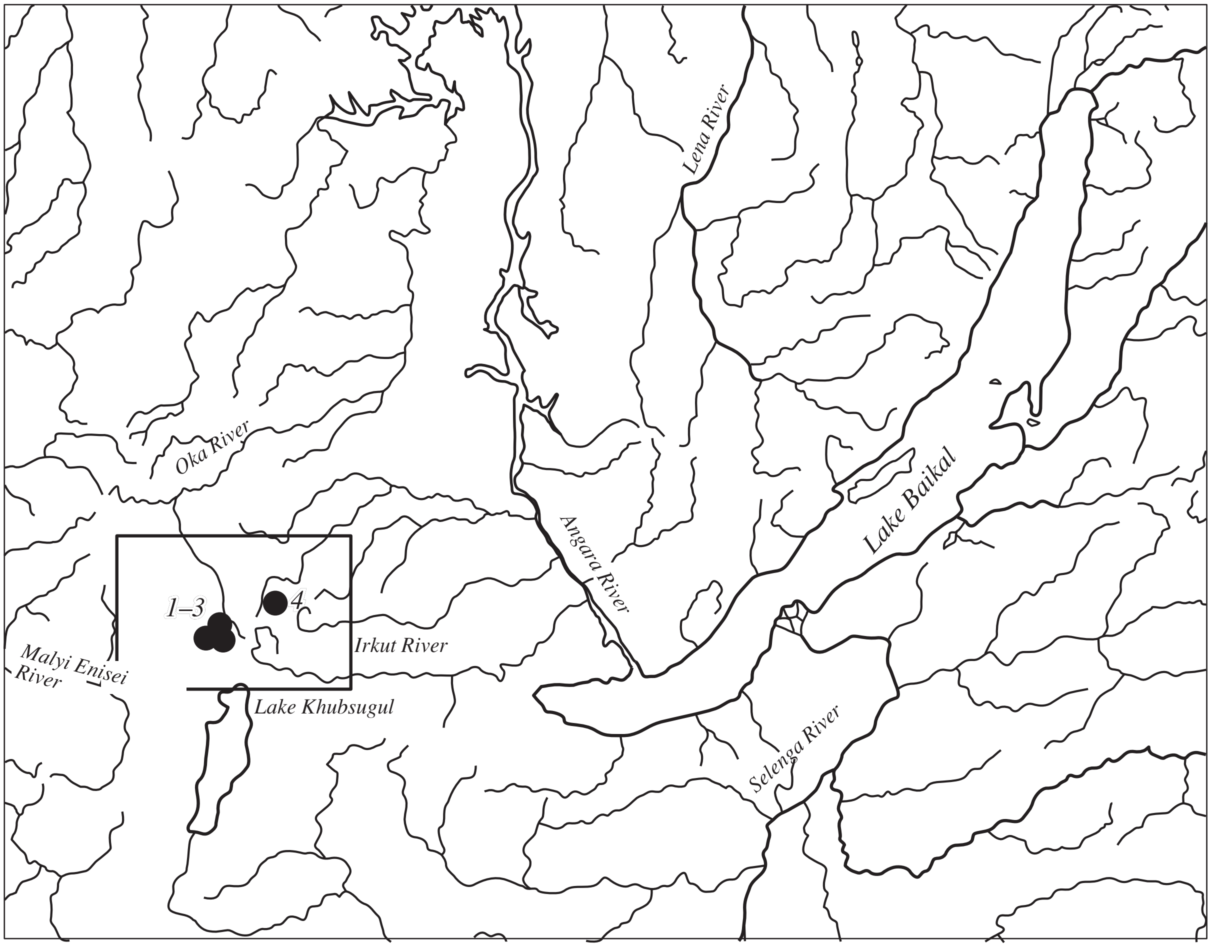

Fig. 1. The map–scheme of the study area: (*1–3*) Lake Mongosha, Lake Urunge Nur, Lake Sadaiskoe; (4) Lake Gusinoe.

Bogutskaya and Naseka, 2004). The morphological similarity and the genetic closeness of the Yenisei and Angara graylings with Baikal grayling *T. a. baicalensis* were reported by several researchers (Dorogostaiskii, 1923; Svetovidov, 1936; Skurikhina, 1984; Romanov, 2000, 2004; Koskinen et al., 2002; Froufe et al., 2005; Knizhin et al., 2006). Bogutskaya and Naseka (2004) assign graylings inhabiting the Angara and the black Baikal grayling to the species *T. baicalensis*, but do not determine the taxonomic status of the populations inhabiting the Yenisei Proper.

A site of interest in the zoogeographical aspect are the Eastern Sayan Mountains where watersheds of the largest basins of Asia: Central-Asiatic, Baikal, and Angara-Yenisei pass. Svetovidov (1936), based on the main theses of Vavilov's learning (1987) on the "centers of origin", considered this region a place wherefrom graylings dispersed over the continent. In this region, namely during multiple glaciations, main routes passed via which they could penetrate in the basins of most Siberian rivers.

The main task of our work was to study specific morphological and biological features of graylings inhabiting mountain water bodies of the basin of the upper reaches of the Angara and to determine their taxonomic status.

MATERIAL AND METHODS

Material was collected in the summer period from 2000 to 2003 in water bodies belonging to the basin of the upper reaches of the Angara River: lakes Urunge Nur, Mongosha, Sadaiskoe (the basin of the upper reaches of the Oka River), as well as Lake Gusinoe (the basin of the Kitoi River) situated in the mountains of the Eastern Sayany Ridge (Fig. 1).

Fish were seined with gill nets with a mesh of 18 to 40 mm. The collected material was preliminarily preserved in 4% formaldehyde. For the morphological analysis, we used 145 mature individuals of the grayling; for the biological and trophological analyses, 184 individuals. For comparison, we used the materials of authors on the morphology of grayling populations from rivers: the Angara (20 km downstream Irkutsk), the Taltsinka (Irkutsk Reservoir), the Tompuda (northern Baikal), Lake Soblinoe (southern Baikal), Lower

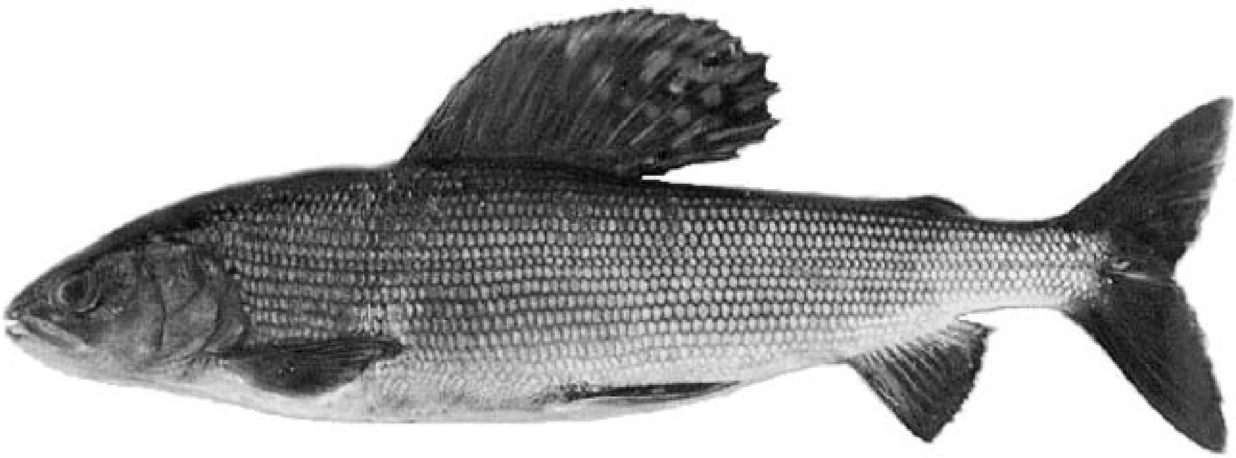

Fig. 2. Arctic grayling *Thymallus arcticus* from Lake Urunge Nur (male, AC 292 mm, weight 300 g, age 5+).

Tunguska (the basin of the Yenisei River), Biya, Bashkhaus (the basin of the upper reaches of the Ob River), Lake Khubsugul (the basin of the Selenga River, Mongolia), and Lake Khokh Nur (the Central-Asiatic basin, Mongolia); and the data of other researchers (Kafanova, 1970; Romanov, 2002) were used.

External features were assessed in the field conditions of freshly caught individuals. Special attention was paid to the pattern and form of the dorsal fin, since it was shown that taxa of a species group can be differentiated according to these features (Makoedov, 1983, 1999; Antonov, 2004; Knizhin et al., 2004; Romanov, 2004). We had at our disposal dried dorsal fins and photographs of graylings from other bodies of water belonging to the basin of the upper reaches of the Angara. A more detailed description of the methods of morphological analysis and statistical processing of the materials is given in the papers of Froufe and Knizhin et al. (Froufe et al., 2003; Knizhin et al., 2004).

Characteristics of lakes. Lake Urunge Nur has an area of about 7.5 km^2. The altitude above sea level is 1992 m, maximal depth, 16 m. It is connected with the Oka River by an underground channel, which determines its isolation. The western coast of the lake is a steep mountain slope with thickets of spruce and cedar and with thickets of Japanese stone pine, shrubs, and sedges in relief depressions. The eastern, southern, and northern coasts are flat, without arboreal vegetation, with a wide sandy coastal belt, which apparently indicates the existence at this site of a deeper water body in the past. Higher aquatic vegetation occurs only in a shallow zone. The lake, besides *T. arcticus* (Fig. 2), is inhabited by the common minnow *Phoxinus phoxinus* and the Arctic char *Barbatula toni*.

Lake Mongosha is 3 km to the northwest from Lake Urunge Nur in a swampy floodplain of a small stream having the same name that flows in the Oka River downstream. The altitude above sea level is 1756 m. The area of the lake is about 0.4 km^2, depth up to 3 m. The bottom is silty, sandy, oozy, and covered with sunk remnants of aquatic vegetation (horsetails, pondweeds, awlwort, and sedges). Around the lake on hilly elevations, alder, spruce, cedar, fir, and birch grow. In the source of the stream flowing out from the lake and downstream, stone sculpin *Paracottus knerii* seldom occurs, in addition to *P. phoxinus*.

Sadaiskoe Lake is situated on a tundra plateau, 5 km to the south of Lake Urunge Nur. The altitude of the lake above sea level is 2030 m. The area is about 0.12 km^2, depth 16 m. It is a component of the chain of numerous small lakes interconnected by narrow channels no more than 1.0–1.5 m wide and with a depth of up to 1 m. The Sade River, rising in the lake system, inflows the Khore River in its lower reaches, and the latter inflows the Oka River. The vegetation setting off the coasts of the lake consists mainly of dwarfish herbaceous communities typical of the tundra zone; low spruces and dwarf birches seldom occur. The lake, besides grayling, is inhabited by the lenok *Brachymystax lenok*, common minnow *P. phoxinus*, and *B. toni*.

Lake Gusinoe is one of the sources of the Kitoi River inflowing the Angara. It is situated in the zone of bald mountains, at an altitude of about 2000 m above sea level, and has a shape of a short arc enclosed between the mountain slopes. The area is 0.3 km^2, with a depth of about 20 m. Vegetation in the lake and along the coasts is not developed.

RESULTS

Morphology. The estimates of meristic and morphometric characters of the lake populations of graylings from the basins of the Oka and Kitoi rivers are cited in Table 1.

The pattern and form of the dorsal fin. The location of spots on the dorsal fin and its coloration and form in graylings inhabiting the studied lakes have the following specific features (Fig. 3). In most individuals,

Table 1. Morphometric and meristic characters of populations of the Arctic grayling *Thymallus arcticus* from the Alpine lakes of the basin of the upper reaches of the Angara

Characters	Lake (sample size, individuals)			
	Urunge-Nur (n = 44)	Mongosha (n = 12*)	Sadaiskoe (n = 27)	Gusinoe (n = 62)
AC, mm	270 / 207–370	253 / 207–303	198 / 149–266	163 / 143–218
Morphometric characters, in % AC				
l	95.2 ± 0.09 / 0.5, 93.5–96.5	95.3 ± 0.16 / 0.5, 94.3–96.2	95.2 ± 0.15 / 0.8, 93.3–96.8	95.0 ± 0.10 / 0.8, 92.6–97.6
l_2	76.4 ± 0.19 / 1.2, 73.3–78.7	77.5 ± 0.45 / 1.4, 74.4–79.4	77.3 ± 0.22 / 1.1, 74.7–79.2	75.9 ± 0.21 / 1.6, 71.3–80.6
ao	6.6 ± 0.05 / 0.3, 5.9–7.3	6.2 ± 0.08 / 0.3, 5.7–6.6	6.1 ± 0.06 / 0.3, 5.5–6.6	6.7 ± 0.03 / 0.2, 6.25–7.2
o	4.5 ± 0.05 / 0.33, 3.6–5.3	4.4 ± 0.07 / 0.2, 3.9–4.7	5.3 ± 0.05 / 0.3, 4.7–5.8	5.7 ± 0.06 / 0.5, 4.2–6.8
f	10.4 ± 0.05 / 0.3, 9.5–11.1	9.9 ± 0.10 / 0.3, 9.3–10.5	9.9 ± 0.08 / 0.4, 9.4–11.6	10.6 ± 0.06 / 0.48, 9.3–11.7
c	20.6 ± 0.08 / 0.5, 18.7–21.4	19.5 ± 0.16 / 0.5, 18.4–20.4	20.2 ± 0.11 / 0.6, 18.9–22.3	22.0 ± 0.10 / 0.7, 20.3–23.7
ch_2	15.3 ± 0.10 / 0.7, 14.1–16.6	14.6 ± 0.16 / 0.5, 13.7–15.2	14.5 ± 0.16 / 0.8, 12.8–15.8	15.1 ± 0.08 / 0.6, 12.5–16.5
ch_1	11.0 ± 0.11 / 0.7, 9.9–14.0	10.2 ± 0.08 / 0.3, 9.8–10.5	10.0 ± 0.09 / 0.5, 9.3–11.0	11.3 ± 0.08 / 0.6, 9.9–12.7
k	6.5 ± 0.04 / 0.3, 5.8–7.2	6.2 ± 0.08 / 0.3, 5.8–6.6	6.1 ± 0.07 / 0.4, 5.2–6.8	6.5 ± 0.04 / 0.3, 5.5–7.2
lmx	6.3 ± 0.04 / 0.2, 5.7–7.0	5.4 ± 0.07 / 0.2, 4.9–5.7	5.8 ± 0.07 / 0.4, 5.4–7.3	6.5 ± 0.06 / 0.4, 5.4–7.4
i/lmx	2.2 ± 0.02 / 0.1, 1.9–2.6	2.0 ± 0.04 / 0.1, 1.8–2.2	2.0 ± 0.03 / 0.1, 1.8–2.3	2.2 ± 0.03 / 0.2, 1.7–2.8
lmd	10.51 ± 0.06 / 0.4, 9.5–11.3	9.6 ± 0.06 / 0.2, 9.2–9.9	10.4 ± 0.06 / 0.3, 9.8–11.1	11.1 ± 0.06 / 0.5, 10.08–12.2
H	20.8 ± 0.21 / 1.3, 17.4–25.0	22.4 ± 0.28 / 0.9, 20.2–23.6	20.8 ± 0.30 / 1.5, 18.1–25.0	19.0 ± 0.13 / 1.0, 16.5–21.5
h	6.7 ± 0.05 / 0.3, 5.9–7.4	7.3 ± 0.06 / 0.2, 7.0–7.6	6.8 ± 0.09 / 0.5, 6.0–8.0	6.5 ± 0.04 / 0.3, 6.0–7.3
w	12.5 ± 0.13 / 0.9, 10.9–14.09	11.5 ± 0.17 / 0.5, 10.8–12.4	12.1 ± 0.17 / 0.9, 10.4–14.3	11.7 ± 0.10 / 0.8, 8.05–13.4
aD	35.9 ± 0.14 / 0.9, 33.7–38.1	35.2 ± 0.23 / 0.7, 34.3–36.8	35.1 ± 0.17 / 0.9, 33.1–36.6	35.9 ± 0.18 / 1.4, 32.66–38.4
pD	42.1 ± 0.22 / 1.4, 38.9–45.4	42.2 ± 0.54 / 1.7, 38.4–44.7	42.0 ± 0.33 / 1.7, 38.0–46.2	38.8 ± 0.21 / 1.6, 33.6–42.9
aA	71.6 ± 0.15 / 0.9, 69.4–73.5	70.6 ± 0.42 / 1.3, 68.6–72.0	71.1 ± 0.16 / 0.8, 69.1–72.7	72.1 ± 0.16 / 1.3, 69.1–76.2
aV	48.0 ± 0.16 / 1.0, 45.6–50.8	45.7 ± 0.23 / 0.7, 44.5–47.0	45.8 ± 0.16 / 0.9, 44.2–47.8	48.1 ± 0.17 / 1.3, 45.8–51.4
lp	17.0 ± 0.14 / 0.9, 14.3–19.2	17.5 ± 0.32 / 1.0, 16.1–18.8	17.6 ± 0.27 / 1.4, 15.8–23.3	16.4 ± 0.11 / 0.8, 14.2–18.5
PV	28.2 ± 0.21 / 1.3, 25.1–30.7	27.7 ± 0.39 / 1.2, 25.4–30.4	26.9 ± 0.26 / 1.3, 21.8–28.6	27.8 ± 0.18 / 1.4, 24.4–32.2
VA	24.9 ± 0.17 / 1.1, 21.4–27.4	25.4 ± 0.55 / 1.7, 22.7–28.4	25.6 ± 0.23 / 1.2, 22.3–27.6	25.0 ± 0.17 / 1.3, 21.9–28.06

Table 1. (Contd.)

Characters	Lake (sample size, individuals)			
	Urunge-Nur (*n* = 44)	Mongosha (*n* = 12*)	Sadaiskoe (*n* = 27)	Gusinoe (*n* = 62)
lD	18.6 ± 0.19 / 1.2, 15.7–20.9	21.4 ± 0.63 / 2.0, 17.7–25.5	20.7 ± 0.24 / 1.3, 18.9–24.2	21.3 ± 0.18 / 1.4, 18.2–25.7
hD_1	10.6 ± 0.11 / 0.7, 8.9–12.8	11.4 ± 0.23 / 0.7, 10.2–12.5	11.6 ± 0.22 / 1.1, 8.7–15.0	13.5 ± 0.17 / 1.3, 10.8–16.6
hD_2	13.5 ± 0.38 / 2.5, 8.7–18.03	14.7 ± 1.28 / 4.1, 10.2–20.8	10.8 ± 0.79 / 4.1, 6.6–21.0	12.3 ± 0.46 / 3.6, 7.30–20.0
lA	8.8 ± 0.09 / 0.6, 7.5–9.88	9.2 ± 0.20 / 0.6, 8.4–10.7	9.0 ± 0.17 / 0.9, 7.8–11.1	9.3 ± 0.10 / 0.7, 7.5–10.89
hA	11.2 ± 0.15 / 1.0, 9.26–13.1	12.5 ± 0.39 / 1.2, 10.9–14.8	11.7 ± 0.16 / 0.8, 10.5–14.4	12.0 ± 0.14 / 1.1, 10.2–15.97
lP	16.5 ± 0.09 / 0.6, 15.1–17.7	16.6 ± 0.23 / 0.7, 15.1–17.4	15.8 ± 0.22 / 1.2, 12.7–18.5	16.9 ± 0.14 / 1.1, 14.3–19.9
lV	15.0 ± 0.11 / 0.7, 13.6–16.7	16.3 ± 0.46 / 1.4, 13.6–18.2	14.8 ± 0.28 / 1.5, 12.4–18.8	15.9 ± 0.17 / 1.3, 13.0–19.09
	Meristic characters			
ll	91.8 ± 0.50 / 3.3, 84–98	90.8 ± 1.50 / 5.2, 80–97	96.0 ± 0.55 / 2.8, 91–102	89.7 ± 0.42 / 3.3, 80–98
D_1	7.4 ± 0.14 / 0.9, 6–9	7.8 ± 0.20 / 0.7, 7–9	7.5 ± 0.13 / 0.7, 6–9	7.9 ± 0.09 / 0.7, 7–10
D_2	12.2 ± 0.13 / 0.8, 10–14	13.0 ± 0.26 / 0.9, 12–15	13.5 ± 0.13 / 0.7, 1–15	13.6 ± 0.09 / 0.7, 12–15
D	19.6 ± 0.15 / 0.9, 17–21	20.8 ± 0.31 / 1.1, 19–23	21.0 ± 0.13 / 0.7, 19–22	21.5 ± 0.09 / 0.7, 20–23
P	15.1 ± 0.10 / 0.6, 14–17	14.3 ± 0.17 / 0.6, 13–15	15.2 ± 0.12 / 0.6, 14–17	14.4 ± 0.09 / 0.7, 13–16
V	9.2 ± 0.07 / 0.4, 9–10	9.8 ± 0.16 / 0.6, 9–11	9.4 ± 0.09 / 0.5, 9–10	8.9 ± 0.03 / 0.2, 8–9
A_1	4.7 ± 0.10 / 0.6, 3–6	4.8 ± 0.17 / 0.6, 4–6	4.5 ± 0.10 / 0.5, 4–5	4.2 ± 0.06 / 0.4, 3–5
A_2	9.1 ± 0.08 / 0.5, 8–10	9.3 ± 0.13 / 0.4, 9–10	9.7 ± 0.09 / 0.5, 9–10	9.1 ± 0.07 / 0.5, 8–10
sb	19.5 ± 0.16 / 1.0, 17–22	18.8 ± 0.29 / 1.0, 17–21	18.2 ± 0.17 / 0.9, 16–20	18.0 ± 0.14 / 1.0, 16–20
rb	9.6 ± 0.10 / 0.6, 8–11	8.6 ± 0.25 / 0.9, 7–10	9.8 ± 0.14 / 0.7, 9–12	9.0 ± 0.07 / 0.5, 8–10
vert.	55.1 ± 0.13 / 0.9, 54–57	56.1 ± 0.25 / 0.9, 55–58	56.3 ± 0.15 / 0.8, 55–58	55.1 ± 0.11 / 0.8, 54–57
pc	18.6 ± 0.30 / 1.9, 15–25	17.3 ± 0.46 / 1.6, 14–19	17.5 ± 0.31 / 1.6, 14–20	15.6 ± 0.17 / 1.3, 12–19

Note: *, Morphometric characters were measured in ten individuals. AC, fork length; l, trunk length; l_2, length to the end of scale cover; ao, snout length; o, horizontal eye diameter; f, length of the postorbital region of the head; c, head length; ch_2, ch_1, head depth near occiput and the eye; k, forehead width; lmx, i/lmx, length and width of upper jaw; lmd, length of lower jaw; H, h, maximum and minimal body depth; w, body thickness; distances: aD, antedorsal; pD, postdorsal; aA, anteanal; aV, anteventral; PV, pectoventral; VA, ventroanal; lp, length of caudal peduncle; lD, length of insertion of dorsal fin; hD1, hD2, depth of the anterior and posterior parts of dorsal fin; lA, length of insertion of the anal fin; hA, depth of the anal fin; lP, length of the pectoral fin; lV, length of the ventral fin; ll, number of perforated scales in the lateral line; D_1, number of unbranched rays in the dorsal fin; D_2, number of branched rays in the ventral fin; P, number of branched rays in pectoral fin; V, number of branched rays in ventral fin; A_1, number of unbranched rays in the anal fin; A_2, number of branched rays in the anal fin; sb, number of gill rakers; rb, number of branchiostegal rays; vert., number of vertebrae; pc, number of pyloric caeca. Above the line is the mean value and error of the mean; below the line, standard deviation and limits of variation.

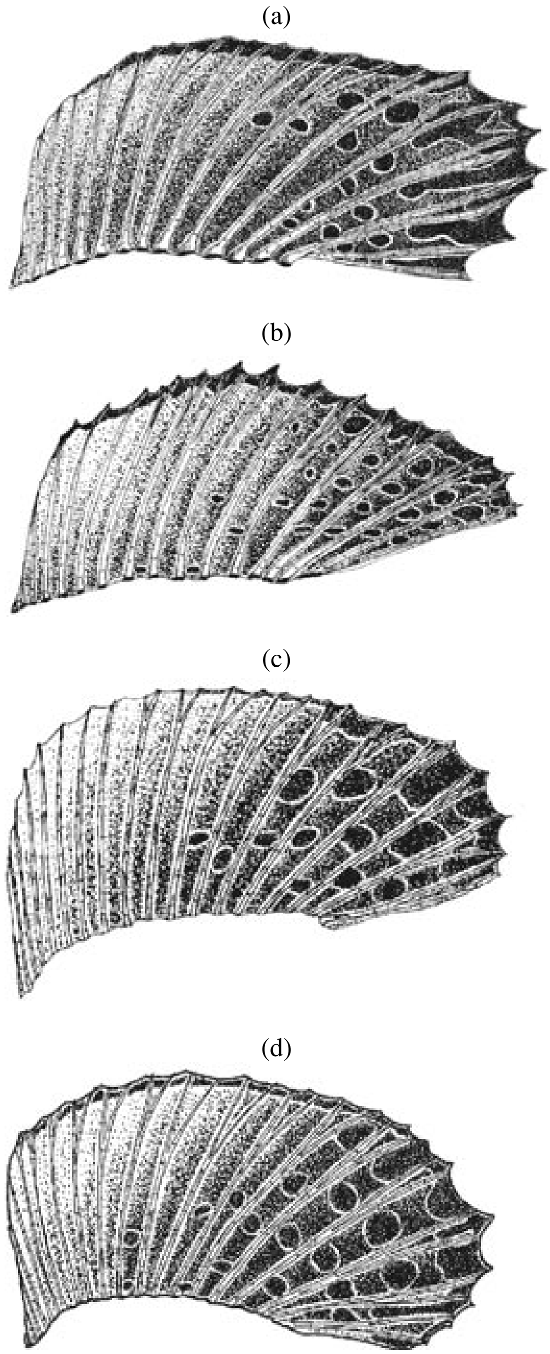

Fig. 3. Patterns of the dorsal fin in the Arctic grayling *Thymallus arcticus* from Alpine lakes of the basin of the upper reaches of the Angara: (a, b) Lake Urunge Nur; (c) Lake Gusinoe; (d) Lake Il'chir (the source of the Irkut River, the tributary of the Angara River).

the anterior part of the fin is almost free of spots; in some fish that have spots, the latter are located as a slightly ascending row. In the posterior part of the fin, spots are rounded and claret red; their size gradually increases towards the last rays. Most spots are grouped into 2–5 incomplete rows. A narrow scarlet margin passing along the upper edge of the fin, on fusing with adjacent spots, forms short and wide, sometimes meandering stripes, extending inward up to the middle of the rays. In the light, spots have a bright turquoise-dull shade. The general background of interradial membranes is dark or almost black. The posterior edge of the fin in mature males is deep and relatively wide; in the folded form, it does not extend to the adipose fin.

Comparative remarks. The comparison of the studied samples by the *t*-criterion ($p \leq 0.005$) indicated in them the presence of significant differences in a great number of morphometric and meristic characters.

Comparison of samples from lakes Urunge Nur, Mongosha, and Sadaiskoe between themselves, as well as with graylings from the Angara, Nizhnyaya Tunguska, and Taltsinka rivers, and Lake Baikal by the *CD* coefficient (Mayr et al., 1956) indicated the absence of noticeable differences. The exception is the sample from Lake Gusinoe, the comparison of which with graylings from all the abovementioned water bodies by different characters shows an excess of the formal subspecies level. Samples from the populations of the Angara-Yenisei Basin and of the black Baikal grayling differ from the samples of graylings of the upper reaches of the Ob in many meristic characters (Table 2).

The multivariate analysis of 12 meristic characters performed by the method of principal components (PCA) revealed no noticeable differences between graylings from the basins of the Oka and Kitoi rivers, on the one hand, and from Lake Baikal, Irkutsk Reservoir (the Taltsinka River) and the Nizhnyaya Tunguska rivers, on the other hand (Fig. 4). The first two principal components accounted for 79.2% of the total dispersion of characters. The greatest load on the first principal component is made by the number of scales in the lateral line; on the second, by the number of pyloric caeca (Table 3).

On the dendrogram constructed by the UPGMA method, several clusters can be discerned. One is formed by samples from the populations from lakes Mongosha, Urunge Nur, Gusinoe, Sadaiskoe, and Baikal (the Tompuda River, Lake Sobolinoe) and the Angara, Nizhnyaya Tunguska, and Taltsinka rivers (Irkutsk Reservoir). Individual clusters are formed by the Kosogol grayling *T. a. nigrescens* (Lake Khubsugul), the Mongolian grayling *T brevirostris* (Lake Kokh Nur, Mongolia), and the "Upper Ob" grayling (the Biya River, the Bashkaus River, the basin of the upper reaches of the Ob River) (Fig. 5).

The estimates of meristic characters in the samples of Alpine lakes of the basin of the upper reaches of the Angara River vary in the same limits as in graylings from Lake Baikal and the Angara and the Nizhnyaya Tunguska rivers. The limits of variation in individuals from the abovementioned water bodies differ considerably in the number of scales in the lateral line from graylings in Lake Dod Tsagan Nur (the upper reaches of the Yenisei River, Mongolia), Lake Kulagash-Bazhi, as well as the Biya and Bashkaus rivers (the basin of the

Table 2. Meristic characters of graylings *Thymallus* according to which the value of the *CD* coefficient exceeded 1.28

Populations	Populations									
	Lake Urunge Nur	Lake Mongosha	Lake Sadaiskoe	Lake Gusinoe	Angara River	Taltsinka River	Nizhnyaya Tunguska River	Lake Baikal	Biya River, Bashkaus River	Lake Kulagash-Bazhi
Lake Urunge Nur										
Lake Mongosha	–									
Lake Sadaiskoe	–	–								
Lake Gusinoe	D_2, D	V	ll							
Angara River	vert.	–	–	V						
Taltsinka River	–	–	–	ll, vert.	–					
Nizhnyaya Tunguska River	–	rb	P	ll, V	–	–				
Lake Baikal	–	–	sb	ll, V, sb	–	–	sb			
Biya River, Bashkaus River	ll, D_2, D, V, vert.	ll, D_2, D, vert.	ll, D_2, D, vert.	ll, D_2, D, V, vert., pc	ll, D_2, D, vert.	ll, D_2, D, vert.	ll, D_2, D, vert., pc	ll, D_2, D, vert., pc		
Lake Kulagash-Bazhi	ll	ll, P	ll	ll, P	ll	ll	ll, P	ll, sb	–	
Basin of Khantaika River	ll, D, V	ll	–	ll, V	–	–	–	sb	ll, D_2, D	ll, P

Note: Character designations are the same as in Table 1.

upper reaches of the Ob River); in the number of branched rays and the total number of rays in the dorsal fin from graylings in the Biya and Bashkaus rivers; and in the number of gill rakers from the Kosogol grayling

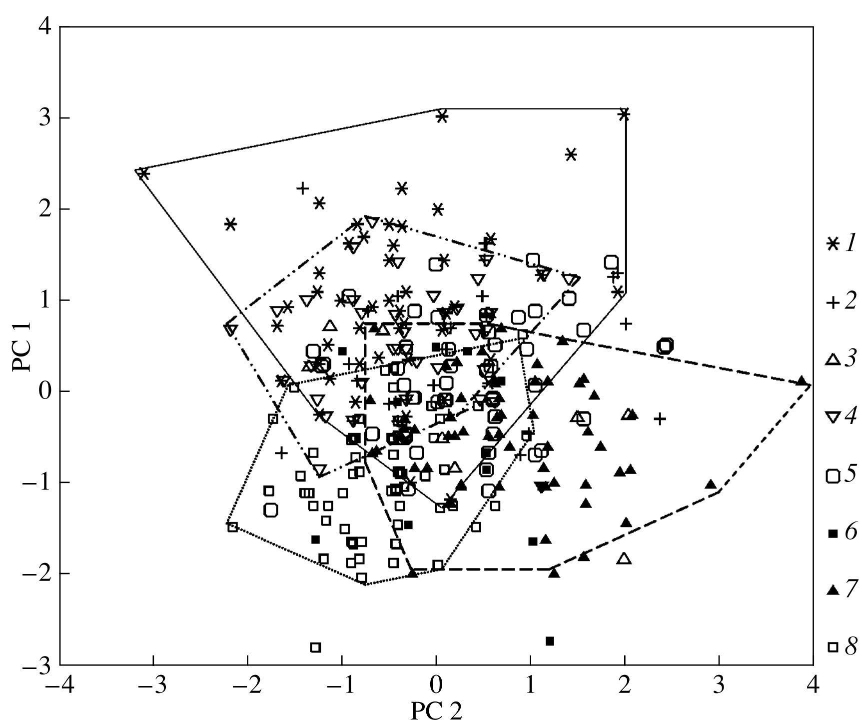

Fig. 4. Diagram of dispersal of the Arctic grayling *Thymallus arcticus* from populations of the basin of the Angara and Baikal in the space of two first principal components (PC) by 12 meristic characters: (*1*) Tompuda River (northern Baikal); (*2*) Taltsinka River (Irkutsk Reservoir); (*3*) the Angara River; (*4*) the Nizhnyaya Tunguska River; (*5*) Lake Sadaiskoe; (*6*) Lake Mongosha; (*7*) Lake Urunge Nur; (*8*) Lake Gusinoe.

Table 3. Loads of eigenvectors on the first two principal components for 12 meristic characters

Characters	Principal components	
	1	2
ll	0.986	–0.048
D_1	0.000	–0.011
D_2	–0.005	–0.022
D	–0.005	–0.040
P	0.004	0.037
V	0.005	–0.001
A_1	0.001	0.012
A_2	–0.001	0.016
sb	0.023	0.028
rb	0.006	0.025
vert.	0.011	0.023
pc	0.003	0.971

(Lake Khubsugul, Mongolia) (Table 4).

The coloration and pattern of the dorsal fin in graylings from the basins of the Oka and Kitoi rivers are almost identical (Fig. 3). Note a great similarity of these populations in the abovementioned characters with the black Baikal grayling *T. a. baicalensis*, as well as with populations from the Taltsinka River (Irkutsk Reservoir), the Nizhnyaya Tunguska River (Knizhin et al., 2006), and the Khantaika River (Romanov, 2004). Conversely, graylings of the upper reaches of the Ob noticeably differ from the Angara-Yenisei and Baikal forms in this character. In contrast to the graylings studied from the basin of the upper reaches of the Angara and Nizhnyaya Tunguska rivers, as well as from Lake Baikal, in individuals of the Upper-Ob populations, three to four even rows of oval red-scarlet spots delimited from the upper fringe pass along the dorsal fin insertion (Fig. 6).

Body coloration of individuals from the studied Alpine lakes differs insignificantly from that of *T. a. baicalensis* and graylings of the Angara-Yenisei Basin. They are characterized by the presence of a claret red large spot above the ventral fins and an adequate coloration of the caudal peduncle, a light turquoise-dull shade of the dorsal part of the body and gill covers, as well as the presence on scales of small dark spots that are more numerous on the head than on the trunk. In graylings of the Upper Ob populations, in contrast to the Angara-Yenisei and Baikal populations, claret red spots above the ventral fins and the same coloration of the caudal peduncle are lacking. In individuals from the basin of the upper reaches of the Ob, there are several small black spots only near the head. The posterior edge of the dorsal fin, in comparison with that in the Angara-Yenisei graylings, is not deep, round, and does not extend far to the adipose fin.

Specific biological features. Among the studied graylings, graylings from Lake Gusinoe are the most slow-growing. Their length at the age of six years does not exceed 182 mm and the weight, 76 g. Maximum values of these parameters are recorded in fish from Lake Urunge Nur in which eight-year individuals have a length of about 370 mm and a weight of 686 g. Graylings from Lake Mongosha are close by the growth

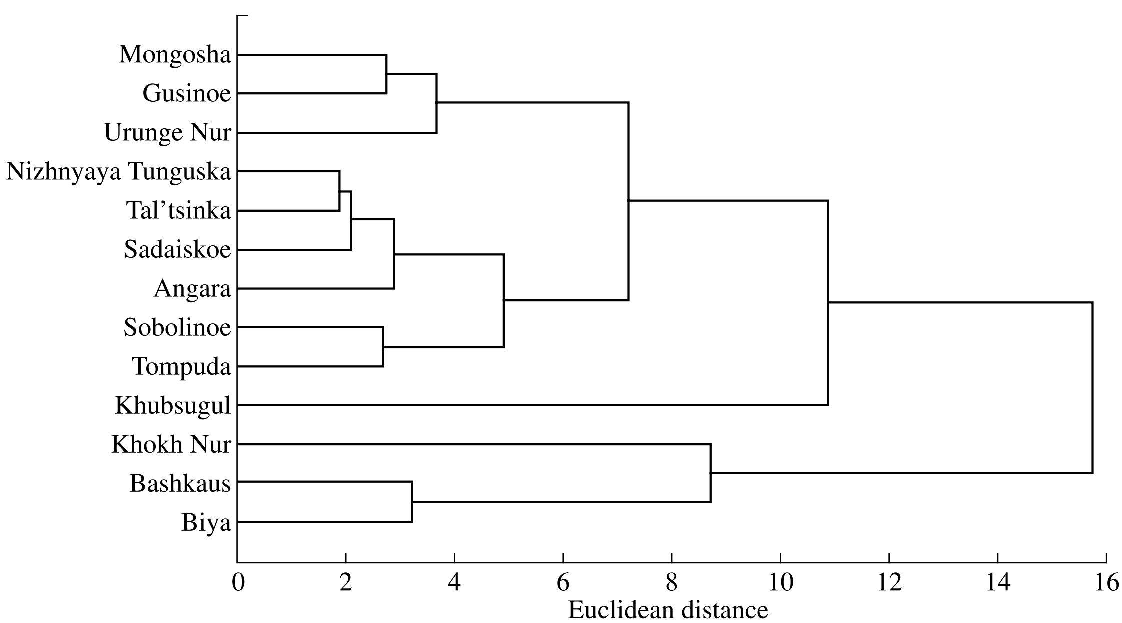

Fig. 5. Dendrogram of the distinctions of populations of graylings *Thymalus* from several water bodies of Siberia by 12 meristic characters.

Table 4. Limits of variation of meristic characters of graylings *Thymallus* from some water bodies of Siberia

Character	Water body (sample size, individuals)										
	Oka and Kitoi rivers (*n* = 143)	Angara River (*n* = 21)	Taltsinka River (*n* = 38)	Nizhnyaya Tunguska River (*n* = 30)	Lake Baikal black grayling (*n* = 265)	Khantaika River[1] (*n* > 500)	Lake Dod-Tsagan-Nur, Mongolian People's Republic[2] (*n* = 100)	Lake Kulagash-Bazhi[3] (*n* = 70)	Biya River (*n* = 27)	Bashkaus River (*n* = 12)	Lake Khubsugul (*n* = 35)
ll	80–102	85–101	89–104	89–104	88–110	89–120	70–89	68–89	76–91	80–87	87–100
D_1	6–10	7–9	6–8	6–8	6–10	6–10	4–8	6–10	7–10	6–9	7–9
D_2	10–15	11–14	11–15	11–15	10–15	11–17	12–14	11–17	14–16	14–17	10–13
D	17–23	20–23	19–23	21–23	18–23	19–24	–	–	22–25	21–25	18–22
P	13–17	13–16	14–15	13–16	13–17	13–16	13–15	11–16	14–17	14–16	13–16
V	8–11	9–10	9–11	9–11	8–11	9–11	8–9	7–11	9–11	10–11	9–11
A_1	3–6	3–5	4–5	4–5	3–6	3–5	2–4	3–4	4–5	4–5	4–5
A_2	8–10	8–10	8–10	8–10	7–11	8–11	8–10	8–11	8–10	9–10	8–11
sb	16–22	17–22	16–21	16–20	16–23	15–21	16–21	13–20	17–21	18–21	21–30
rb	7–12	8–11	9–12	9–12	8–11	–	8–10	–	9–10	9–10	8–10
vert.	54–58	55–58	55–58	55–58	52–60	–	–	–	52–55	51–52	54–57
pc	14–25	14–21	12–20	12–20	10–21	–	17–26	–	17–25	18–27	16–29

Note: The source of information: (1) Romanov, 2002; (2) Shatunovskii, 1983; (3) Kafanova, 1970.

indices to individuals from Lake Urunge Nur, and the population from Sadaiskoe Lake is slightly inferior to fish from Mongosha and Urunge Nur lakes. This lagging behind becomes noticeable only after the onset of sexual maturity (Table 5). No considerable differences were found between females and males in the growth rate.

The feeding of graylings in all lakes takes place mainly in the shallow coastal part, at depths up to 3–5 m. A comparatively narrow range of food organisms was established in fish from Lake Mongosha. It reflects the specifics of the water body that is distinguished by a developed aquatic vegetation and the abundance of larval amphibiotic insects. In graylings from this water body, of all organisms comprising its food, larval dragonflies had the largest proportion by weight (33.2%). In food boluses, hymenopterans and bugs were also recorded (29.2 and 26.6% by weight, respectively). The food of graylings from Sadaiskoe Lake, besides the abovementioned organisms, consisted of caddis larvae and chironomids (17.2 and 7.5% by weight). The most diverse food components were found in fish from Lake Urunge Nur. In stomachs of graylings from this lake, bugs (27.8%) and different species of Hymenoptera (13.1%) were dominant; beetles and other insects, mollusks, and zooplankton were of secondary importance. Only here the individuals of elder age groups used fish as food, namely *B. toni* and *P. phoxinus*, whose total portion accounted for 29.3% of the weight of the stomach content. In the food of graylings from Lake Gusinoe, representatives of zoobenthos dominated, of which larval stone flies (31.7%)

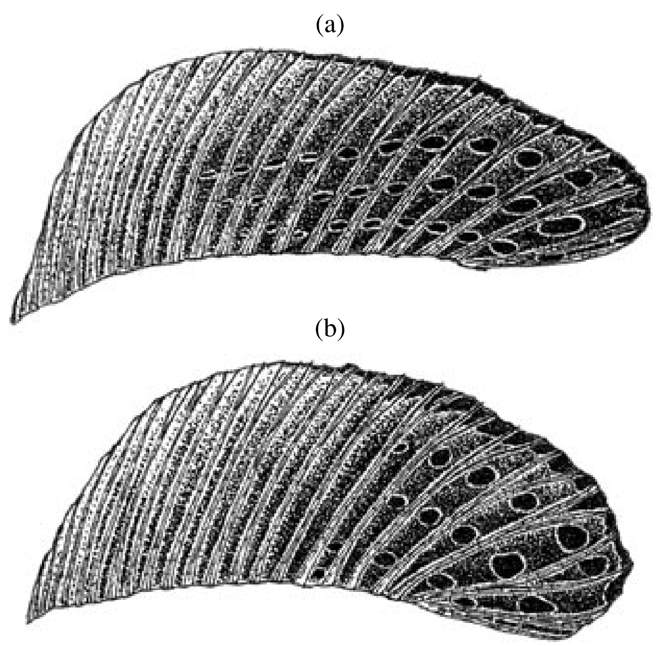

Fig. 6. Variants of pattern of dorsal fin in the grayling *Thymallus* sp. from the Biya River (the basin of the upper reaches of the Ob River).

Table 5. Length (AC, mm) and weight (*W*, g) of the Arctic grayling *Thymallus arcticus* from Alpine lakes of the basin of the upper reaches of the Angara (based on observed data)

Lake	Parameter	Age, years							Number of fish
		1+	2+	3+	4+	5+	6+	7+	
Urunge Nur	AC	136.9 / 115.0–155.0	169.2 / 160.1–176.4	225.9 / 207.3–240.5	242.1 / 220.2–270.8	271.1 / 235.0–304.5	312.8 / 265.5–339.4	368.2 / 365.9–370.5	65
	W	26.7 / 14.3–38.0	48.1 / 43.0–59.0	134.7 / 94.0–158.0	158.4 / 120.0–234.0	236.7 / 158.0–354.0	401.8 / 227.0–617.0	686.0 / –	
Mongosha	AC	–	189.7 / 179.0–200.5	207.7 / –	248.7 / 218.0–290.4	250.0 / –	293.6 / 283.4–303.9	–	12
	W	–	74.5 / 58.0–91.0	100.0 / –	200.0 / 124.0–324.0	180.0 / –	331.0 / 310.0–352.0	–	
Sadaiskoe	AC	122.6 / 96.5–148.0	162.2 / 149.0–183.3	187.4 / 180.5–193.3	214.3 / 196.4–237.0	239.1 / 216.9–266.5	–	–	56
	W	20.7 / 8.8–33.0	48.4 / 33.0–68.0	73.0 / 66.0–84.0	128.0 / 94.0–170.0	173.2 / 110.0–264.0	–	–	
Gusinoe	AC	–	150.2 / 149.3–151.2	154.2 / 142.8–170.5	168.3 / 149.5–218.2	181.8 / 170.8–186.8	–	–	62
	W	–	37.9 / 37.8–38.0	42.3 / 31.5–56.5	57.3 / 39.2–117.0	69.1 / 54.5–75.9	–	–	

Note: Above the line is the mean value; below the line, limits of variation.

and chironomids (24.0%) had the most importance by weight. Graylings consumed, in smaller amounts, other insects—bugs, dipterans, and hymonopterans. In the spawning period, the eating by fish of their own eggs was recorded (5.1% by weight).

In all individuals of the studied populations, stomachs contained sand that got there apparently while collecting organisms from the bottom; in lakes Urunge Nur and Mongosha, fragments of higher aquatic vegetation were frequently found.

DISCUSSION

The biological indices of graylings inhabiting lakes of the upper reaches of the Oka and Kitoi reflect specific features of their habitation. The factor determining the differences between the studied populations is the absolute height at which water bodies are situated. Mostly differences in the growth of graylings, the time of their spawning, and the intensity of feeding depend on the duration of the period of open water, the area of the littoral zone, and the abundance of vegetation near the water body.

Graylings from Lake Mongosha and Urunge Nur are under relatively favorable conditions since the lakes have a rather wide littoral, and diverse taiga vegetation is present along their coasts. Complete breakup in these water bodies terminates in the first days of July and the period of open water continues up to mid-September. All this promotes a better food availability for graylings in the summer period due to insects blown off by the wind to the water surface. Throughout their life, the graylings from the abovementioned lakes almost do not experience an impact on the part of predators, except for fish-eating birds. The populations from the Sadaiskoe and Gusinoe lakes exist in more rigid conditions. If in food availability of graylings from Sadaiskoe Lake, entomofauna of the tundra zone plays a great role in the summer, for the individuals of Lake Gol'tsovoe, this resource is actually inaccessible because of its almost complete absence. In both lakes, the littoral is very narrow, and the deep-water part occupies 95% of the bottom area. The breakup in them terminates by mid-July, and the period of open water continues for about two months, sometimes less. The population of *B. lenok* that actively uses all fish species as food is undoubtedly a factor limiting the increase in the population of Sadaiskoe Lake.

The highest indices of growth are typical of populations from lakes where graylings eat other fish and are a dominant species by numbers and the occupied area, for instance, as in Lake Urunge Nur.

The spectra of food organisms of graylings from the lakes studied differ insignificantly. In individuals of all populations, food is mainly composed of larvae and imago of amphibiotic and aerial-ground insects. Differences between fish from different lakes are observed only in proportions of the food components.

Despite the recorded ecological differences of the populations studied, the results of the study of their morphology, as well as of the body coloration and the pattern of the dorsal fin testify to their phenetic and possibly genetically close relationship. The same conclusion also follows from their comparison with *T. a. baicalensis*, as well as with populations of the nominative subspecies *T. a. arcticus* from the Irkutsk Reservoir, and the Angara and Nizhnyaya Tunguska rivers. The absence between the abovementioned subspecies of a reproductive isolation and the presence of gene exchange are supported by results of molecular-genetic studies (Skurikhina, 1984; Koskinen et al., 2002; Froufe et al., 2005). It may be asserted that all of them are a unique group morphologically and genetically. However, the issue of reducing them to one taxon, despite the fact that there were objective grounds for this, has not been seriously discussed until recently. The established differences in some characters between the population from Lake Gusinoe and graylings from other water bodies of the basin are possibly the result of their isolation and habitation under extreme conditions that have determined their dwarfism.

As was mentioned above, the morphological closeness of the West Siberian and Baikal graylings was noted by Romanov (2004). In his paper, he cites arguments evidencing that in the upper and lower reaches of the Yenisei there are graylings that do not belong to the West Siberian subspecies; and that the middle reaches, and in part, the lower reaches are inhabited by populations similar to the two forms of the Baikal grayling. Our data mostly support this suggestion.

It is expedient to touch on causes responsible for assigning graylings inhabiting a vast Angara-Yenisei basin to a nominative subspecies. In the course of revision of the European-Asiatic taxa, Svetovidov (1936), based on the analysis of 23 individuals from collections of the Zoological Institute, Russian Academy of Sciences and the Ichthyology Room of the Moscow Technical Institute of Fishing Industry, described morphological characters of the West Siberian grayling. The diagnosis of the nominative subspecies cited by him in this paper resulted from a generalized consideration of morphological characters of different forms of graylings and, thereby, reflected their variation in the basins of the Ob, Yenisei, Angara, and Kobdo rivers (the Central-Asiatic basin). A small size of the analyzed samples and the absence at the same time of distinct ideas of the phenetic diversity of graylings inhabiting the abovementioned rivers led to erroneous conclusions on the range of the nominative subspecies and its morphological characteristics.

In our opinion, the attempts to describe new subspecies in the Yenisei basin have not been supported and given due attention because the diagnosis suggested by Svetovidov (1936) determined a very broad range of variation of characters of graylings inhabiting basins of rivers from the Ob to Baikal. It follows that distinguishing new taxa could not have been performed without a detailed revision of the views of Svetovidov (1936) on the intraspecific structure of *T. arcticus*.

The results of our comparison of graylings from Alpine lakes of the basin of the upper reaches of the Angara, the Irkutsk Reservoir, and the Nizhnyaya Tunguska with the grayling from the Biya River are one more argument against uniting them within a nominative subspecies. The data obtained demonstrated an excess of the formal value of the subspecies level ($CD \geq 1.28$) in the Angara-Yenisei and Upper-Ob populations in 5 of 12 meristic characters (Table 2). In the body coloration and pattern of the dorsal fin, individuals from these basins differ without overlapping. The fact that graylings from the Yenisei and Angara, similar to the Baikal grayling, considerably differ from the Upper-Ob populations is supported by results of the molecular-genetic analysis performed by Froufe et al. (2005). The position of the grayling from the Biya River on the phylogenetic tree presented in the aforementioned paper testifies to its considerable divergence from the individuals of the Baikal and Angara-Yenisei basins. It is more closely related to the Mongolian species *T. brevistrotis* and grayling from the Shishkhid Gol River (the upper reaches of the Yenisei in Mongolia). The description of the dorsal fin of the Mongolian grayling from the Bogdoin-Gol River (Tugarina and Dashidordzhi, 1972), Lake Khar-Nur (Shatunovskii, 1983), and the pattern of the individual from the Kobdo River (Svetovidov, 1936) testify to their closeness to graylings of the upper reaches of the Ob (Fig. 6).

It follows that the greater part of the Yenisei basin, except the sources of the river and the lower reaches proper[2], as well as the Angara, are inhabited by populations that should be assigned to the Baikal subspecies of the Arctic grayling—*T. a. baicalensis*. It is urgent to elucidate to what extent the Upper-Ob populations are phenetically and genetically close to graylings of the middle and lower reaches of the Ob and whether they are actually a nominative subspecies of the Arctic grayling. The solution of these issues will permit clarifying the ranges of the subspecies of the Arctic grayling, which will possibly lead to the revision of the taxonomic status of several forms, reducing them to the synonymy or distinguishing new species.

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[2] The habitation of either *T. a. pallasi* or *T. a. mertensii* is suggested in the lower reaches of the Yenisei (Romanov, 2004).

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