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A New Subspecies of the Amur Grayling *Thymallus grubii flavomaculatus* ssp. nova (Thymallidae)

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Abstract—A new subspecies of the Amur grayling is described, the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n. populating the upper reaches of large tributaries of the Lower Amur basin and some rivers flowing to the Tatar Strait, the Sea of Okhotsk, and the Sea of Japan. From the nominative subspecies *T. g. grubii* populating the basin in the upper reaches of the Amur and from other representatives of the genus *Thymallus*, this subspecies differs in the dorsal fin pattern whose principal trait is a yellow spot on the last two–five interray membranes, in the body coloration, and in some morphological characters. The yellow-spotted grayling in the upper reaches of tributaries sympatrically coexists with the Lower Amur grayling *Thymallus* sp. No specimens with intermediate characters are found. The sympatric forms spawn at different times, thus being isolated reproductively. Isolation of the yellow-spotted grayling as a subspecies of the Amur grayling *T. grubii* is confirmed by the results of molecular–genetic investigations.

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A representative of the genus *Thymallus* with a special coloration of the dorsal fin, with an yellow or orange–yellow spot situated between the last two–five interray membranes, was found for the first time by Antonov (Antonov et al., 1997) in June 1996 in the upper reaches of the Anyui River (the Lower Amur basin). Later, "a yellow-spotted grayling" was mentioned in some papers on the diversity of fish in the Amur basin and Primor'e rivers (Antonov, 1999, 2001a, 2001b; Shed'ko, 2001; Froufe et al., 2003, 2005; Bogutskaya and Naseka, 2004; Knizhin et al., 2004). More detailed data on the morphological and genetic traits, body coloration, the dorsal fin pattern, and on distribution of the yellow-spotted form are available in the articles by Froufe and Knizhin et al. (Froufe et al., 2003; Knizhin et al., 2004). They consider this grayling to be a representative of one of two forms of the Amur grayling *T. grubii*. The latter was initially described by Dybowski (1869) from the Onon and Ingoda rivers (the basin of the Amur upper reaches).

There is a different viewpoint on the taxonomic state of the yellow-spotted grayling. Shed'ko (2001) and Bogutskaya and Naseka (2002, 2004) believe that its rank is a species one "*Thymallus* sp. 2." However, these studies report some data on values of morphometric characters, meristic characters, and a fragmentary description of coloration but no information on morphology and biology.

Comparative morphological and molecular–genetic investigations (Froufe et al., 2003, 2005; Knizhin et al., 2004) demonstrated that the yellow-spotted grayling and the nominative subspecies of the Amur grayling *T. g. grubii* are closely related in spite of some differences, while the Lower Amur grayling (supposed by Knizhin et al. (2004) to have a species rank) and the Bureya grayling *T. burejensis* (Antonov, 2004) significantly diverged from them. In many rivers, the yellow-spotted grayling exists sympatrically with the Lower Amur grayling. However, their spawning time is different and no specimens with intermediate coloration were reported.

The aforementioned data testify that the yellow-spotted form is characterized by a complex of characters indicating that it belongs to the species Amur grayling *T. grubii* and thus may be considered as its subspecies. The description of the latter is the subject of the present study.

MATERIAL AND METHODS

The material was collected in the years 1996–2004 in tributaries of the Amur lower reaches: Anyui, Gur, Khor, Bikin, Merek, and Kerbi (the Amgun basin) rivers, and in the Buta, Ashmar (the Tumnin basin), and Botchi rivers flowing to the Tatar Strait (Fig. 1). In addition, dried dorsal fins of graylings from the Kiran and Nemui rivers (the basin of the Sea of Okhotsk), and color photographs of graylings from the Tugur and Dzhana rivers (the Uda basin).

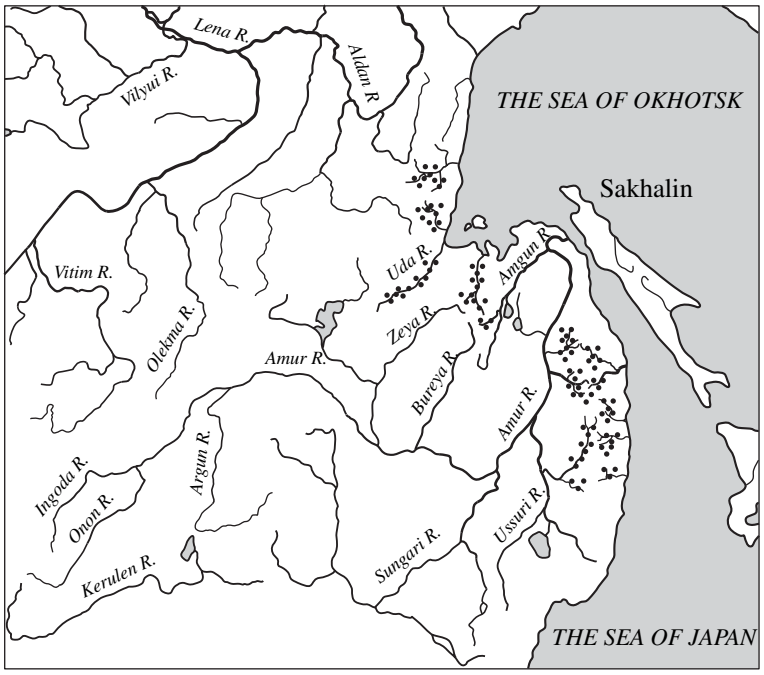

Fig. 1. The area of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n.

The fish were caught with a fishing rod. Altogether, 48 specimens of the yellow-spotted grayling were investigated (17 from the Anyui River, 8 from the Merek River, 8 from the Buta River, and 15 from the Botchi River) at ages from 2+ to 6+. All specimens were subjected to complete morphological analysis according to Pravdin (1966) and Svetovidov (1936). All estimations of the characters were obtained by one operator. Additional information on techniques of investigation of morphological characters are reported by Knizhin et al. (2004).

The food composition was studied according to recommendations of *Methodical Handbook…* (1974). The age was determined according to Chugunova (1959).

Statistical treatment and comparison with graylings from other water bodies as made according to standard methods (Plokhinskii,1970; Rokitskii, 1973) using software Statistica 5.5A (Borovikov and Borovikov, 1998) and SPSS 8.0. Analysis of morphological characters was made using principal components analysis (PCA) using a variance–covariance matrix. Significance of differences and their value were determined by the *t*-test assuming $p \le 0.001$ and by the *CD* coefficient (Mayr et al., 1956).

For elucidation of the area of the yellow-spotted grayling, the collections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) and of the Zoological Museum of Moscow State University (Moscow) were examined.

Thymallus grubii flavomaculatus Knizhin, Antonov et Weiss spp. nova—the yellow-spotted grayling

(Figs. 2, 3)

"A grayling morphologically different from the Amur one"—Antonov et al., 1997: 15 (Anui); Antonov, 1999: 98 (Anyui).

"A yellow-spotted form"—Antonov, 2001a: 267; Froufe et al., 2003: 2348 (the Lower Amur, the Anyui, Buta, Merek); Knizhin et al., 2004: Figs. 3c, 4d, 4e, 4f (Anyui, Merek, Buta).

"*Thymallus* sp. 2"—Shed'ko, 2001: 238 (Maksimovka, probably the Ussuri basin, Edinka, and probably Samarga, Primor'e).

"*Thymallus* sp. 2" the yellow-spotted grayling—Bogutskaya and Naseka, 2004, 149 (Maksimovka, Edinka, probably Ussuri and Samarga, the basin of the Sea of Japan).

Holotype. Zoological Museum ISU no. R-3. Male AC 274 mm, Anyui, coll. A.L. Antonov.

Paratype. Zoological Museum ISU no. R-4. Female AC 240 mm, Anyui, coll. A.L. Antonov.

Diagnosis. There is a yellow–orange spot with vague outlines in the upper posterior part of the dorsal fin on the last two–five interray membranes. A narrow red-vinous fringe 1–2 mm wide along the upper edge of the fin. From the fin base upwards there are four–five rows of small round spots with dull fringing. The upper row of spots begins from the base of the first unbranched rays and continues upwards to the middle of the fin, then it continues almost in parallel to the lower rows. Posterior edge of dorsal fin wide, often

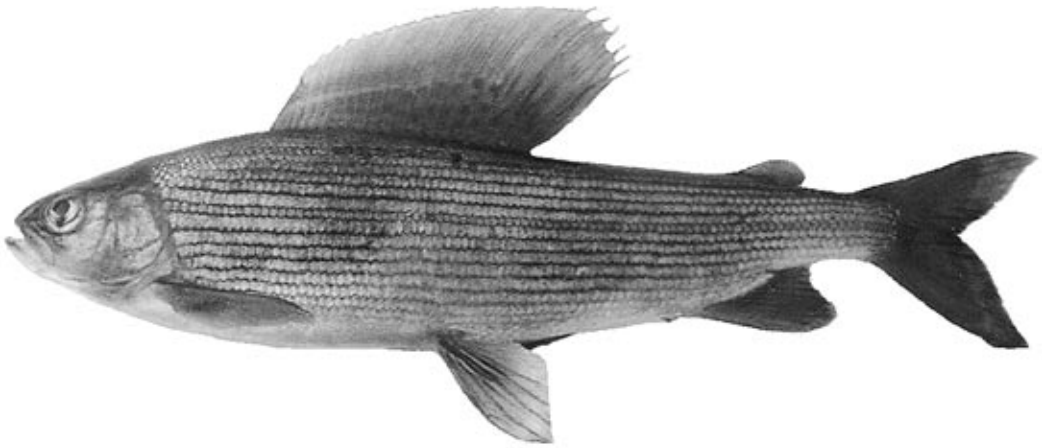

Fig. 2. The yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n. AC 305 mm, Gobili River, October 2002 (photograph by A. L. Antonov).

with deep emarginations or rounded notches (Fig. 3). Clear bright orange sinuous bands among rows of scales. Scales average-sized. Upper jaw reaches beyond anterior eye edge and attains the pupil. Dorsal fin base large. Body relatively deep, slightly cylindrical, on an average 21.0% AC. No teeth on vomer and tongue.

Etymology. The subspecies is named by its diagnostic character—the orange–yellow spot on the dorsal fin.

Description of the holotype. There are small black spots on the body situated mainly in anterior part below lateral line. Above ventral fins there is a large red-vinous spot of 14–15 scales in width, extending along ventral part onto caudal peduncle. Folded dorsal fin almost attains adipose fin.

Meristic characters: ll 94, sb 18, rb 9, D_1 10, D_2 13, P_2 14, V_2 9, A_1 4, A_2 9.

Morphometric characters, in % AC: trunk length (l) 95.3, length up to end of scale cover (l_2) 79.2, anteanal distance (aA) 67.5, antedorsal distance (aD) 27.8, anteventral distance (aV) 43.2, postdorsal distance (pD) 44.5, pectovental distance (PV) 26.1, ventroanal distance (VA) 25.3, pectoral fin length (lP) 16.8, ventral fin length (lV) 19.8, dorsal fin base length (lD) 27.3, its depth in anterior part (hD_1) 13.6, its depth in posterior part (hD_2) 24.2, anal fin base length (lA) 10.1, its depth (hA), 13.3, caudal peduncle length (lp) 16.5, greatest body length (H), 24.3, least body length (h) 7.5, and head length (c) 16.8.

In % c: snout length (ao) 31.9, postorbital region (f) 51.7, eye diameter (o) 22.5, upper jaw length (lmx) 29.8, its width (i/lmx) 10.7, lower jaw length (lmd) 49.8, forehead width (k) 28.8, head width at occiput (cH) 81.3, and head width at eye (ch) 53.6.

Description of the paratype. Small black spots on the body are situated closer to the head below lateral line. Above ventral fins there is a vague reddish–crimson spot, 14–16 scales in width, passing over along ventral part into caudal peduncle. Folded dorsal fin does not attain adipose fin.

Meristic characters: ll 93, sb 17, rb 8, D_1 9, D_2 13, P_2 14, V_2 9, A_1 4, A_2 8.

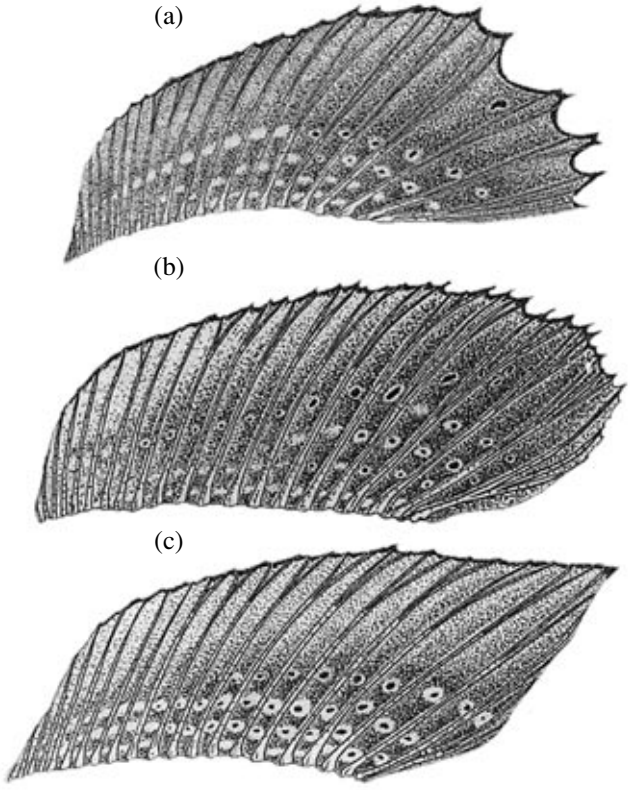

Fig. 3. Variants of the dorsal fin pattern of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n.: (a) the Chuken River (the basins of the Khor and Amur rivers), (b) the Gobili River (the basins of the Anyui and Amur rivers), (c) the Nemui River (the basin of the Sea of Okhotsk).

Table 1. Morphometric and meristic characters of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. nova ($n = 48$)

Characters	$M \pm m$	σ	*min–max*	Characters	$M \pm m$	σ	*min–max*
AC	221.8	36.5	159.9–321.3	lA	9.3 ± 0.13	0.9	7.6–12.2
In % AC				hA	11.9 ± 0.12	0.9	9.6–13.9
l	94.9 ± 0.11	0.8	91.5–95.9	lP	15.6 ± 0.11	0.8	13.6–17.5
l_2	78.1 ± 0.14	1.0	75.6–80.0	lV	15.8 ± 0.25	1.8	12.4–19.4
ao	5.8 ± 0.05	0.3	5.3–6.5	In % c			
o	4.8 ± 0.05	0.3	4.3–5.7	ao	30.7 ± 0.17	1.2	27.9–32.4
f	9.5 ± 0.06	0.4	8.9–10.7	o	25.3 ± 0.19	1.3	22.8–28.0
c	19.0 ± 0.09	0.6	17.8–20.6	f	50.2 ± 0.23	1.6	46.9–52.9
cH	14.8 ± 0.11	0.8	13.2–16.5	cH	77.9 ± 0.55	3.8	69.6–84.4
ch	10.5 ± 0.08	0.6	9.2–11.8	ch	55.3 ± 0.44	3.0	49.1–60.1
k	5.7 ± 0.05	0.3	4.9–6.2	k	29.8 ± 0.21	1.4	25.9–32.9
lmx	5.7 ± 0.05	0.3	5.0–6.5	lmx	30.2 ± 0.19	1.3	26.4–32.4
i/lmx	1.9 ± 0.02	0.1	1.6–2.2	i/lmx	10.0 ± 0.10	0.7	8.6–12.3
lmd	9.7 ± 0.06	0.4	8.8–10.6	lmd	51.0 ± 0.21	1.5	48.4–54.2
H	20.9 ± 0.22	1.5	18.3–25.5	Meristic characters			
h	7.0 ± 0.05	0.3	6.2–7.6	ll	90.5 ± 0.59	4.1	82–101
w	12.1 ± 0.12	0.8	10.2–14.9	D_1	10.4 ± 0.16	1.1	9–15
aD	29.3 ± 0.12	0.8	27.6–30.8	D_2	13.3 ± 0.14	1.0	10–15
pD	43.4 ± 0.22	1.5	39.4–48.2	D	23.7 ± 0.15	1.1	21–25
aA	69.3 ± 0.18	1.3	66.5–72.4	P_2	14.4 ± 0.10	0.7	13–16
aV	44.6 ± 0.16	1.1	41.7–47.2	V_2	9.3 ± 0.08	0.6	8–11
lp	18.1 ± 0.14	1.0	15.6–19.7	A_1	4.4 ± 0.08	0.5	4–6
PV	27.6 ± 0.20	1.4	25.4–30.9	A_2	9.3 ± 0.09	0.6	8–10
VA	25.3 ± 0.15	1.0	22.7–27.3	sb	18.3 ± 0.19	1.3	16–22
lD	24.6 ± 0.21	1.5	21.2–28.2	rb	9.5 ± 0.08	0.6	9–11
hD_1	10.4 ± 0.17	1.1	7.8–12.0	vert.	55.0 ± 0.13	0.9	53–57
hD_2	13.0 ± 0.47	3.1	8.3–20.1	pc	17.3 ± 0.33	2.3	14–24

Note: AC—fork length, l—trunk length, L_2—length up to the end of scale cover, ao—snout length, o—horizontal eye diameter, f—postorbital region of head, c—head length, cH—head depth at occiput, ch—head depth at eye, k—forehead width, lmx—upper jaw length, i/lmx—upper jaw width, lmd—upper jaw length, H—greatest body depth, h—minimum body depth,w—body thickness, aD—antedorsal distance, pD—postdorsal distance, aA—anteanal dostance, aV—anteventral distance, lp—caudal opeduncle length, PV—pectoventral distance, VA—ventroanal distance, lD—dorsal fin base length, hD_1—depth of anterior part of dorsal fin, hD_2—depth of posterior part of dorsal fin, lA—anal fin base length, hA—anal fin depth, lP—pectoral fin length, lV—ventral fin length, ll—number of perforated scales in lateral line, D_1—number of unbranched rays in dorsal fin, D_2—number of branched rays in dorsal fin, D—total number of rays in dorsal fin, P_2—number of branched ray in pectoral fin, V_2—number of branched rays in ventral fin, A_1—number of unbranched rays in anal fin, A_2—number of branched rays in anal fin, sb—number of gill rakers, rb—number of branchiostegal rays, vert.—number of vertebrae, pc—number of pyloric caecae. $M \pm m$—mean value and its error, σ—standard deviation, *min–max*—limits of variation of a character.

Morphometric characters, in % AC: l 94.5, l_2 79.5, aA 69.5, aD 30.9, aV 43.5, pD 44.4, PV 28.7, VA 26.8, lP 14.1, lV 16.9, lD 24.3, hD_1 9.3, hD_2 15.3, lA 8.1, hA 14.5, lp 17.7, H 23.0, h 6.6, c 17.6.

In % c: ao 30.8, f 50.4, o 24.7, lmx 28.4, i/lmx 10.9, lmd 47/5, k 30.2, cH 82.3, ch 51.8.

Description of the subspecies (composed from all captured specimens).

Body relatively deep, slightly rounded. Scales average-sized. Head at occiput deep, snout short. Mouth terminal. Upper jaw reaches beyond anterior eye edge. Teeth on jaws small, absent on tongue and vomer.

Dorsal fin comparatively deep and long, its posterior edge wide, often with deep notches, in mature fish usually reaching adipose fin. In mature males in its posterior part, it is considerably deeper than that in its anterior part. Dorsal fin base shorter in females than in males. Pectoral fins shorter than ventral fins. Caudal peduncle long. Morphometric and meristic characters are shown in Table 1.

Upper side of head dark gray. Operculum steel colored, with a slight green–violet shade. Lower jaw light gray, black in anterior part. Tongue light. A very narrow red-vinous fringe along an upper edge of dorsal fin. In its posterior part, closer to upper edge there is a large yellow–orange spot with blurred outline. Dorsal side with greenish shade. Sides light gray or dark gray, in large fish (over 300 mm) dark steel with turquoise shade. In anterior body part below lateral line, there are small (smaller than pupil) black spots, absent in especially large specimens. Interrupted bright orange bands between rows of scales along the body. Above ventral fin base there is a large red-vinous spot with irregular outline, 12–16 scales in width continuing upwards to three–four rows above lateral line. Caudal peduncle and anal fin of the same color. In mature specimens the bottom of body from ventral fins to anal fin red-vinous too. Belly light, with two parallel yellow–brown bands extending from head to ventral fins. In mature fish, lower part of branchiostegal rays and head yellow–brown. Pectoral fins gray–yellow, ventral fins—dark, with light vinous shade. Four–five violet–red bands along rays of ventral fins.

Comparative remarks. The results of comparison of morphological characters of different forms of Amur graylings and investigation of mitochondrial and nuclear DNA suggest that the yellow-spotted form from tributaries of the Lower Amur reaches and the Upper Amur grayling from the Ingoda and the Onon belong to one species—the Amur grayling *T. grubii* (Froufe et al., 2003; Knizhin et al., 2004). These forms differ in absolute size of the body and in coloration. The yellow-spotted grayling is significantly larger than the Upper Amur grayling. On its body, there are longitudinal bright orange bands along the rows of scales. In contrast, the Upper Amur grayling is silvery, with black spots grouped into rows. These spots are diagnostic characters of the nominative subspecies *T. g. grubii*, in yellow-spotted specimens a few of them are present only on the anterior body part, below the lateral line. Detailed examination of coloration of the Upper Amur grayling revealed that its posterior part, similarly to the yellow-spotted one, is slightly yellow, which is not so in the Lower Amur and Bureya graylings. In some specimens of the yellow-spotted grayling and the Lower Amur grayling, this character may be expressed less or more, frequently in immature specimens. There is a certain similarity in the arrangement of spots on the fin. Both the yellow-spotted grayling and the Lower Amur grayling are characterized by the ascending direction of the upper row. The difference is in the size of spots and of the fin (Knizhin et al., 2004).

In speaking of the presence of numerous spots on the body sides of the Upper Amur form, it should be noted that this character may manifest itself in specimens from small rivers and streams with rapid currents, such as the mountain tributaries of the Onon, Ingoda, Bureya, and Zeya rivers. A similar spot pattern is recorded in the Lower Amur grayling *Thymallus* sp.: in the fish of this species from large tributaries of the Lower Amur, there are no spots on the body sides, while they are present, though in a small number, in some specimens from small streams. It may be supposed that the difference in this character is a consequence of biotopic localization of these forms and of specific living conditions.

Table 2. Loads of eigenvectors on two principal components for 12 meristic characters of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n.

Characters	Principal components	
	1	2
ll	–0.994	0.060
D_1	0.280	0.579
D_2	0.557	0.231
D	0.588	0.536
P	0.093	0.268
V	0.516	0.122
A_1	0.063	0.174
A_2	–0.065	0.194
sb	0.069	0.262
rb	0.208	–0.129
vert.	–0.582	–0.203
pc	–0.078	0.845

In comparison with the Upper Amur graying, the yellow-spotted grayling possesses on average more numerous unbranched rays and their total number in the dorsal fin is more numerous. In comparison of these forms by the aforementioned characters, the value of the CD coefficient is close to 1.28 or surpasses it. By the morphometric characters, differences exceeding the conventional subspecies level of 1.28 were also noted (Knizhin et al., 2004). In contrast to the Upper Amur grayling, the yellow-spotted grayling possesses greater antedorsal distance and dorsal fin base, and a minimum body depth. Still, no hiatus in any of the analyzed characters is determined and the results of multivariate analysis indicate the undisputable closeness of these forms (Knizhin et al., 2004).

For determination of the level of morphological similarity with previously studied samples of the yellow-spotted grayling, the specimens from the Botchi River flowing to the Tatar Strait were included in the principal component analysis (PCA) by 12 meristic characters. The two first components explain 79.6% of total variance. The highest loads of eigenvectors are indicated in Table 2. The scatter diagram demonstrates that the graylings from this river make a common group with the yellow-spotted grayling from the Anyui, Merek, and Buta rivers and with the specimens from the Ingoda and Onon rivers representing the Upper Amur

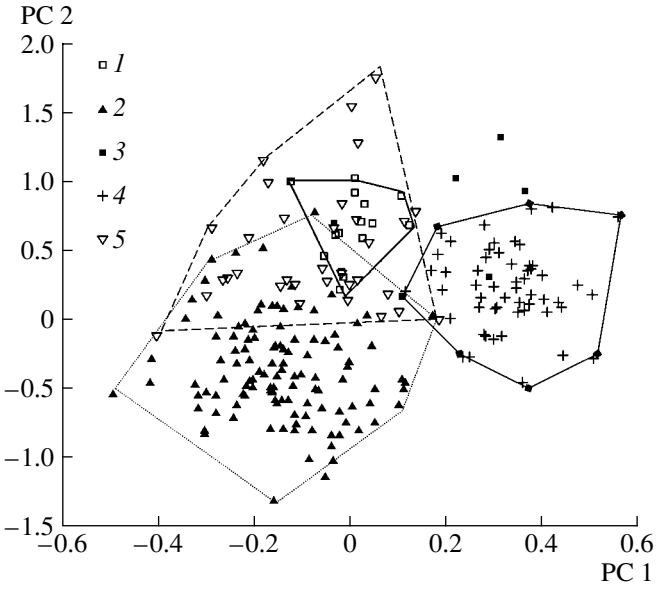

Fig. 4. The scatter diagram of different forms of the Amur grayling of the genus *Thymallus* in the space of two first principal components (PC) by 12 meristic characters: (*1*) the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n., the Buta River; (*2*) the Amur grayling *Thymallus grubii grubii*, the Onon and Ingoda rivers; (*3*) the Bureya grayling *T. burejensis*, the Bureya River; (*4*) the Lower Amur graling *Thymallus* sp., the Anyui River; (*5*) *T. grubii flavomaculatus* ssp. n., the Anyui, Buta, and Merek rivers.

form (Fig. 4). The body coloration of the dorsal fin pattern of the grayling from the Botchi River is close to that of the yellow-spotted grayling from the Lower Amur basin. This indicates their similarity in these characters too. The same conclusion on the grayling from the Botchi River follows from the results of molecular–genetic investigation made by Froufe et al. (2005).

The results of cluster analysis (UPGMA) of all samples of the yellow-spotted grayling in comparison with those of graylings of different species from the basin of the Amur and of other Siberian rivers by 11 meristic characters are shown in Fig. 5[1].

The dendrogram shows that clusterization of graylings of the yellow-spotted form and of the Upper Amur form of *T. grubii* occurs at a lower value of Euclidean distance than their combination with other species.

Considering the problem of phylogenetic relationships of the yellow-spotted grayling with the Upper Amur and Lower Amur graylings, it is possible to make some suggestions about reasons for their divergence. The Upper Amur and the yellow-spotted form of the Amur grayling *T. grubii* are known to be closer to each other than to the Lower Amur grayling (Froufe et al., 2003, 2005; Knizhin et al., 2004). However, all of them represent one phyletic line. Their similarity is also confirmed by some characters in the body coloration: orange–yellow bands along scales all over the body in the yellow-spotted and the Lower Amur grayling, the presence in them of red-vinous spots over ventral fins, black spots in stream populations. Still, in these form they are present in different combinations, characteristic of each of them. The morphological and genetic divergence of the Lower Amur grayling in relation to the yellow-spotted and the Upper Amur graylings has advanced much further than the divergence of the two latter forms in relation to each other (Froufe et al., 2003; Knizhin et al., 2004). The remoteness of the areas of the yellow-spotted form and of the Upper Amur forms and the specificity of their biotopes should also be taken into consideration, leading to formation of the aforementioned differences.

On the basis of the above data it may be concluded that the subspecies of the Amur grayling *T. grubii flavomaculatus* ssp. n. is characterized both by the characters indicating that it belongs to the species *T. grubii* and by characters differing it from the Upper Amur form populating the upper and middle reaches of the Amur. The former are the number of scales in the lateral line and the number of branched rays in the dorsal fin, the coloration of this fin, and the distribution of spots on it. The second groups of characters comprises the total number of rays and the number of unbranched rays in the dorsal fin, the dorsal fin base length, a narrower dark red fringe on its upper edge, fewer black spots on the body sides (in larger specimens their absence), and the linear size.

The diagnostic characters of the subspecies are the presence of a yellow spot on the last membranes between rays of the dorsal fin and deep notches of its posterior margin (Fig. 3) in combination with a narrow dark red fringe and bright orange bands along the body sides.

Molecular–genetic investigation of the Amur graylings indicates the reproductive isolation of the yellow-spotted and the Lower Amur graylings. However, the probability of its hybridization with the Upper Amur form in the contact zone is not excluded (Froufe et al., 2003). No such zone is known in the Amur basin yet.

Distribution. The yellow-spotted grayling populates some tributaries of the Lower Amur basin, upstream to the Ussuri basin (the upper reaches of the Khor and Bikin rivers). In addition, it lives in some large rivers flowing into the southwestern part of the Sea of Okhotsk—the Tugur River (M.B. Skopets, E. Machino, personal communications), the Kiran and Nemui rivers (V.M. Sapaev, personal communication), the Uda River (V.V. Boiko, personal communication), and in large rivers of the basin of the Sea of Japan—the Koppi River (V.I. Kim, personal communication), the Botchi River (E.V. Adnagulov, personal communication; our data), the Samarga River (A.Yu. Semenchenko, personal communication), and the Edinka and Maksimo-

[1] Due to different methods of counting, the number of vertebrae was not considered (vert.).

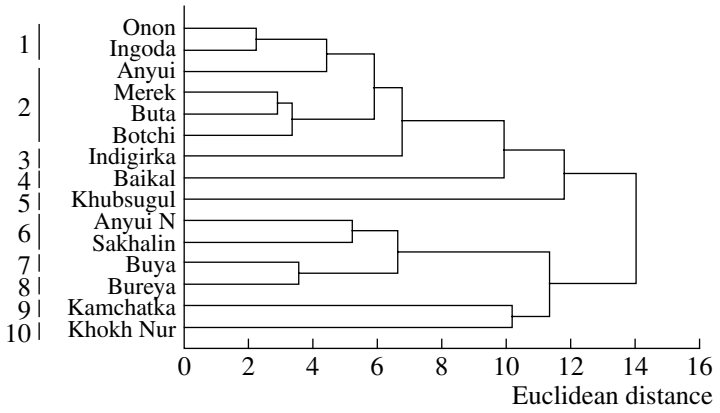

Fig. 5. Dendrogram of similarity of populations of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n. and of other taxa of the family Thymallidae by 11 meristic characters constructed by UPGMA method (the number of vertebrae is not considered): (1) *T. g. grubii*, (2) *Thymallus grubii flavomaculatus* ssp. n., (3) *T. a. pallasii*, (4) *T. a. baicalensis*, (5) *T. a. nigrescens*, (6) *Thymallus* sp. the Lower Amur grayling, (7) *T. a. arcticus*, (8) *T. burejensis,* (9) *T. a. mertensii*, and (10) *T. brevirostris.*

vka rivers (Shed'ko, 2001). The southern boundary of its distribution in the Amur basin is the tributaries of the Ussuri River, and in the north, the boundary is the upper tributaries of the Amgun River (Fig. 1). The northernmost river along the coast of the Sea of Okhotsk populated by this subspecies is the Mute River (our unpublished data). The yellow-spotted grayling is not found in mountain lakes. In the Lower Amur basin, in the upper reaches of all its large tributaries, it is sympatric with the Lower Amur grayling (Antonov, 2001a; Shed'ko, 2001; Froufe et al., 2003, 2005; Knizhin et al., 2004). It is absent in their lower reaches. Upstream, it penetrates to an absolute altitude of about 800–850 m.

Some traits of biology and ecology. Spawning in the rivers of the Lower Amur basin takes place from the middle of May till late May, seven–ten days later than that in the Lower Amur grayling. The autumn downstream migration in tributaries of the Lower Amur occurs in October–November.

The food spectrum of the yellow-spotted grayling is rather diverse. The basis of its diet consists of representatives of zoobenthos, predominantly larvae and subimagoes of amphiobitic insects. In addition, a large part

Table 3. Composition of the diet of the yellow-spotted grayling *Thymallus grubii flavomaculatus* ssp. n. in July

Food item	Rivers					
	Gobili		Merek		Buta	
	1	2	1	2	1	2
Trichoptera	9.5	93.3	3.79	100	13.1	87.5
Ephemeroptera	9.9	93.3	0.55	87.5	10.0	100
Plecoptera	34.0	73.3	0.89	62.5	3.1	87.5
Diptera	7.5	46.7	0.6	62.5	2.7	87.5
Chironomidae	10.5	46.7	0.02	12.5	0.1	62.5
Simulidae	3.4	80.0	0.03	25.0	1.2	75.0
Blepharoceridae	1.5	73.3	0.02	12.5	0.3	75.0
Tipulidae	9.7	33.3	–	–	0.3	12.5
Coleoptera	6.5	80.0	4.5	100	2.6	87.5
Formicidae	1.9	53.3	84.3	100	55.5	100
Fragments of vegetation	0.2	13.3	0.39	12.5	1.3	25.0
Fish eggs	–	–	0.07	25	0.3	37.5
Other organisms	4.4	86.6	3.84		8.5	100
Number of fish	15		8		8	

Note: (1) weight of food items, %; (2) frequency of occurrence, %.

is played by aerial insects, namely hymenopterans, coleopterans, and dipterans. In different tributaries in the diet of the yellow-spotted grayling, larvae and imagoes of caddisflies, stoneflies, mayflies, and ants were recorded. Sometimes, remains of fish and their eggs were present in the stomachs (Table 3).

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