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Morphological Characteristics and Ecological Peculiarities of Nonparasitic Lampreys of the Genus *Lethenteron* (Petromyzontidae) from the Angara River Basin

Yu. V. Loshakova and I. B. Knizhin

Irkutsk State University, bul. Gagarina 20, Irkutsk, 664003 Russia
e-mail: Loshakova_Julia@mail.ru

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Abstract—Evidence on morphology, biological characteristics, and ecological peculiarities of monocyclic, nonparasitic resident form of lamprey of the genus *Lethenteron* inhabiting the Amur River basin is presented for the first time. The studied sample includes mature individuals and three size groups of larvae. Maximum length and weight of larvae comprise 191 mm and 9.5 g, respectively; that of adult individuals is 182 mm and 8.2 g. Sex dimorphism was determined according to several characters, of them the most significant are anteanal and antedorsal distances, as well as the distance from the anus to the end of the body. Reproduction takes place at the end of May—beginning of June at the water temperature 13–15°C. At different spawning grounds, density of individuals averages 96–133 ind/m^2; males are greater than of females by a factor of 1.5. The individual absolute fecundity is 1683 (1042–3166) eggs with a diameter of 0.83 (0.79–0.87) mm. The lamprey inhabits both the main channel of Angara (up to the inflow into it of the Kitoi River) and its tributaries.

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Keywords: amprey *Lethenteron*, morphology, ecology, Amur River basin

INTRODUCTION

Biology and distribution of the lamprey of the genus *Lethenteron* in water bodies of Eastern Siberia have been studied insufficiently. The issue of the taxonomic status of forms inhabiting Siberian rivers is debated. This is mainly related to the absence of data on their phenetic and genetic diversity. The causes of it are specific features of ontogenesis and ecology of these organisms that lead a secretive mode of life most of the time. Their migration is mainly associated with spawning taking place in a brief period of time, and individuals perish after its termination. Therefore, observations of lampreys and collection of material necessary for studies involve great difficulties, and episodic findings are usually explained by their small numbers. Evidence on the biology and ecology of lampreys for several water bodies is most frequently a compilation of published data having no direct relation to the characterized habitats. This leads to the unjustified inclusion of lampreys into lists of animals requiring special measures of protection, which hinders their study (Knizhin et al., 2012).

Lamprey from Siberian rivers Tom and Kirgizka (basin of the Ob River) was first described by Anikin (1905) in the rank of species *Petromyzon kessleri*. Berg (1911, 1948) considered this form as a subspecies of Pacific lamprey *Lampetra japonica kessleri* Anikin, 1905. Subsequently studies of morphometric characters and ecology of individuals from the Ob River allowed Poltorykhina (1971, 1979) to conclude its species rank—*Lethenteron kessleri* (Anikin, 1905). Evidence on lampreys of the Angara basin is limited to only mentioning their habitation in different locations (Mamontov, 1977; Egorov, 1985; Pankratov and Panasenkov, 2008). In this connection, the study of ecological-biological characteristics, taxonomic status, and phylogenetic relations of Angara populations with other forms and species of the genus are urgent.

For the taxonomy of lampreys, besides traditional phenotypic characters, specific features of their life strategy were taken into account. On this basis, the so-called groups of satellite species were distinguished, in which larvae are phenetically identical, while adult individuals have several differences (Hardisty, 2006). Recently, data were obtained that made it possible to conclude that small nonparasitic forms inhabiting Siberian rivers should be regarded in the composition of the species *Lenthenteron camtschaticum* (Tilesius, 1811) (Artamonova and Kucheryavyi, 2010; Artamonova et al., 2011).

In the paper, morphological characteristic, biological indices, evidence on specific features of distribution, migrations, and reproduction of lamprey inhabiting rivers of the Amur basin are presented for the first time.

MATERIALS AND METHODS

Material on the biology and ecology of lamprey was collected in the Chuksha River and other rivers of the

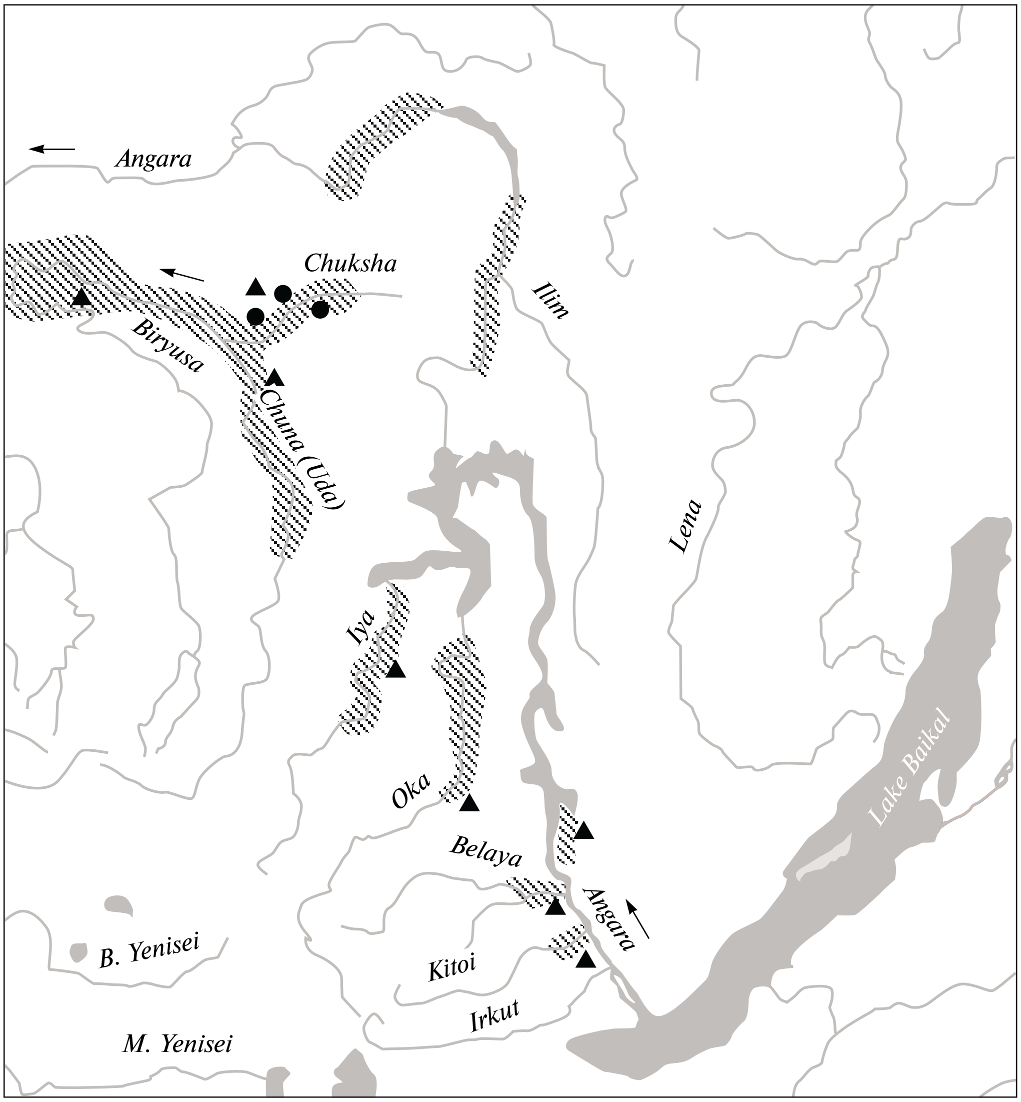

Fig. 1. Map scheme of the study area: (●) sites of material collection, (▲) sites of observation, (▧) sites where, according to observations of the authors and survey data, lampreys occur, (→) current direction.

Angara River basin in the spring and summer periods from 2008 to 2012 (Fig. 1). The Chuksha River is the right tributary of the Chuna River into which it inflows 540 km away from the site of its fusion with the Biryusa River. Its extent is approximately 190 km. Its bottom is rocky-sandy with small silting. Rapids are alternated by stretches with a depth to 2 m. In habitats of lamprey, current speed averages 0.5 (0.2–1.2) m/s, pH 7.4–7.5. In May, increase in water level to 1.5 m, on average, is observed. In this period, it assumes a dark brown color, while it remains slightly turbid in summer (transparency 0.2–0.3 m).

Lampreys were fished in the light time of the day using a small fry drag seine and landing net. Absolute length (*TL*) and body weight, as a rule, were determined directly after catch. For the subsequent processing under laboratory conditions, individuals were fixed in a 4% solution of formaldehyde. Count of individuals at spawning grounds was performed on August 15–19, 2012, in the Chuksha River using a metallic frame (25 × 25 cm) that was placed on the bottom in ten replications.

For analysis of morphometric characters, a sample (120 individuals) collected in the Chuksha River (56°03′; N 99°38′ E) in 2008–2010 was used: 49 larvae[1], 44 mature males, and 27 females. Measurements were performed by one operator with an accuracy to 0.1 mm. The scheme presented in the paper of Kuch-

[1] We also had at our disposal two larvae at the stage of completion of metamorphosis that were not included into the analysis of morphometric characters.

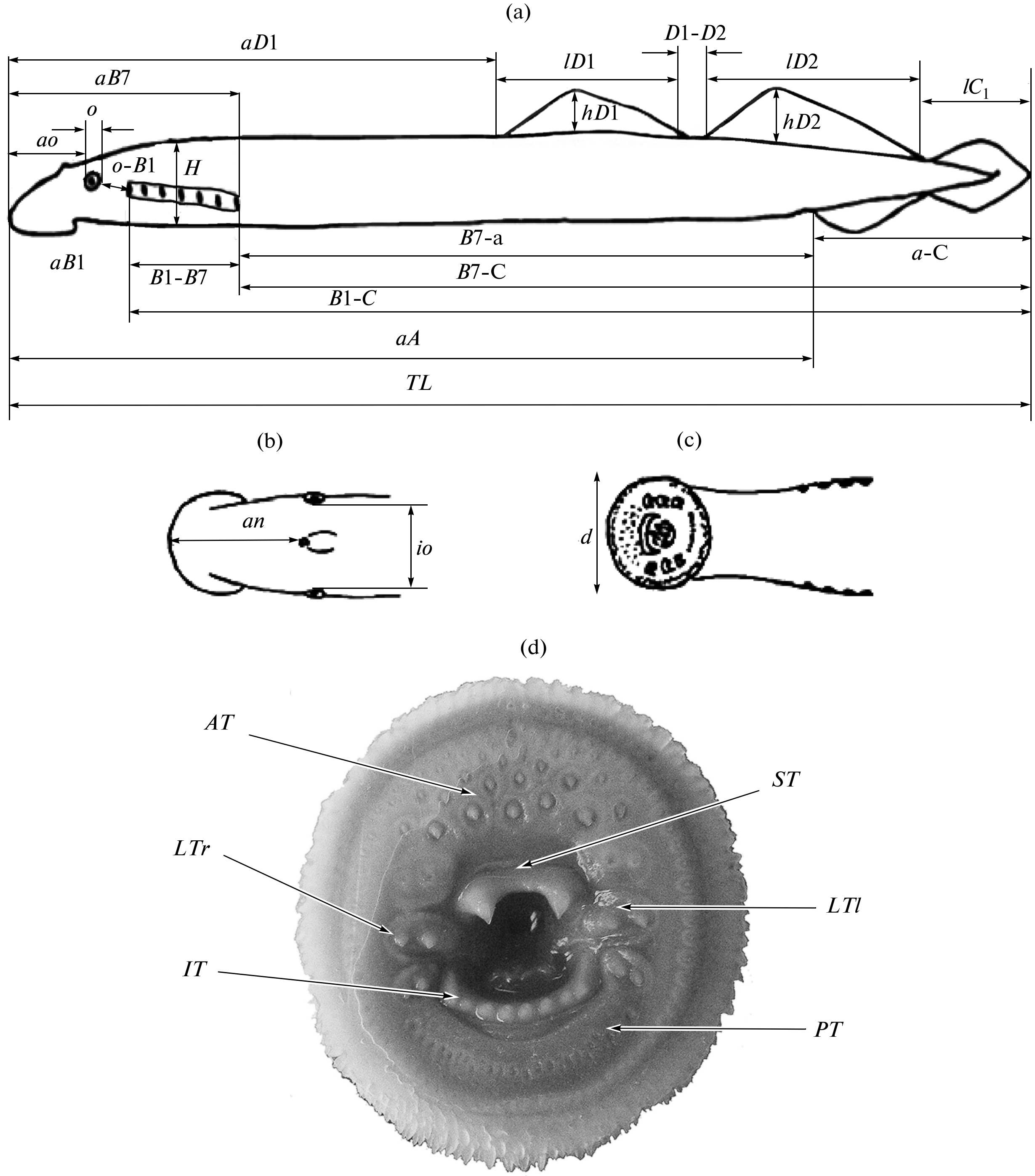

Fig. 2. Scheme of morphometric measurements of lamprey of the genus *Lethenteron*: (a) lateral general view; (b) head, top view; (c) head, bottom view; (d) oral infundibulum. Designations: *TL*—absolute body length, *H*—body height between the 3rd and 4th gill openings, *aB*l—distance from the snout end to the 1st gill opening, *ao*—snout length, *B*l–*B*7—length of gill apparatus, *o*—horizontal eye diameter, *a*–*B*l—distance from the posterior eye margin to the 1st gill opening, *d*—oral disc diameter, *aB*7—length of head with gill apparatus, *B*l–*C*—distance from the 1st gill opening to the body end, *B*7–*C*—distance from the 1st gill opening to the body end, *io*—forehead width, *an*—distance from the snout end to nasal opening, *aD*—antedorsal distance, *aA*—anteanal distance, *D*1–*D*2—space between the 1st and 2nd dorsal fins; *l lD*1, *lD*2—length of insertions of the 1st and 2nd dorsal fins, *hD*1 and *hD*2—their maximum height, lC_1—length of dorsal part of caudal fin, *a*–*C*—distance from anus to the body end, *B*7–*a*—distance from the last gill opening to anus. *o*–*B*1—space between eye and the 1st gill opening; teeth: *AT*—anteoral, *PT*—posterioral, *LTr, LT*l—lateral right and left, *ST*—supraoral (maxillary), *IT*—infraoral (mandibular).

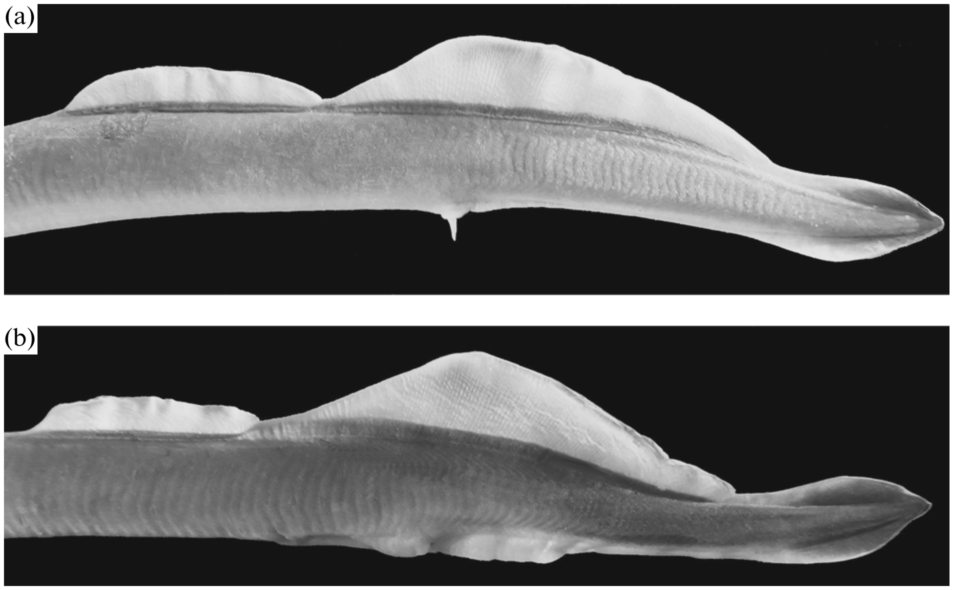

Fig. 3. External genital organs of males (a) and females (b) of lamprey *Lethenteron* from the Angara River basin.

eryavyi et al. (2007) with some changes was taken as the basis (Fig. 2). The number of trunk myomeres was calculated, preliminarily removing skin. Description of teeth was made according to the scheme of Vladykov and Follet (1967).

In adult individuals (71 individuals), sex was determined from external characters: presence of urogenital papilla in males, anal fin (keel) in females (Fig. 3), and after dissection in larvae (25 individuals). Individual absolute fecundity (27 females) was determined by the meristic-gravimetric method: number of oocytes in the sample (0.2–0.3 g) was recalculated per weight of gonads. The intestine contents were analyzed in 32 larvae, 13 males and 24 females.

Statistical processing was performed by standard methods using Excel v. 6.0, Statistica v. 6.0, and SPSS v. 8.0 software. Significance of differences was estimated according to *t*-test at $p \leq 0.001$ (Rokitskii, 1967), and their magnitude was estimated according to *CD* coefficient (Mayr, 1969).

RESULTS AND DISCUSSION

D e s c r i p t i o n. Coloration of larvae olive-brown. Mouth shaped as triangular slit, without horny teeth, first dorsal fin not pronounced, eyes poorly pronounced, covered with skinny membrane, gill openings located in groove (Fig. 4a). Among larvae collected in June, two individuals that had not completed metamorphosis were found. They had open eyes and round gill openings (Fig. 4b). Nevertheless, their mouth was horseshoe-shaped, typical of larvae. Silvery body coloration, as in smolts of Pacific lamprey (Kucheryavyi et al., 2007), well distinguished these individuals among other amoecete larvae. Apparently, some larvae terminate metamorphosis later than a majority of individuals that either mature completely towards the beginning of summer or pass to this stage of development in early spring.

In mature lampreys, dorsal fins light with yellowish tint, they come in contact by their insertions. Coloration along body sides from light brown to olive. Basic tint of caudal fin dark (Figs. 4c and 4d).

Length of larvae in our catches within 35–191 (on average, 139.4) mm (Fig. 5), weight within 0.1–9.5 (3.8) g. Analyzed sample with three size groups representing II, III, and IV generations. Average values of length and weight of larvae of II generation comprise 57.1 mm and 0.44 g; of III—132.7 mm and 3.31 g; and of IV—173.2 mm and 7.57 g; sizes of two larvae at stage of metamorphosis 170.6 and 171.2 mm and 6.6 and 7.9 g. Mature individuals with *TL* 135–182 mm and weight 6.0–8.2 g. Average sizes of females (153.4 mm, 6.5 g) and males (161.5 mm, 7.5 g) smaller than in larvae directly before metamorphosis (IV).

In adult individuals, teeth blunt. On labial plate, 18–26 teeth; on maxillary plate, 2 teeth (1 + 1). Dental formula on mandibular plate: 2 + (4–5) + 2 (median teeth 4, less frequently 5), labial—18–26. Lateral left and right have three bimodal teeth on each side. Trunk myomeres 66–77. The values of meristic characters obtained by us enter into the limits of variation determined for the Siberian lamprey *L. kessleri* from the Ob basin (Poltorykhina, 1979) and resident form of Pacific lamprey *L. camtschaticum* (Kucheryavyi et al., 2007). Egorov (1985), in Siberian lamprey from the Selyakh River (Syalakh, Yakutia), recorded the presence of median tooth at the maxillary

Fig. 4. Lamprey of the genus *Lethenteron* from the Angara River basin: (a) ammocoete larva, *TL* 126 mm; (b) ammocoete larva at the stage of metamorphosis, *TL* 171 mm; (c) mature male, *TL* 169 mm; (d) mature female, *TL* 152 mm.

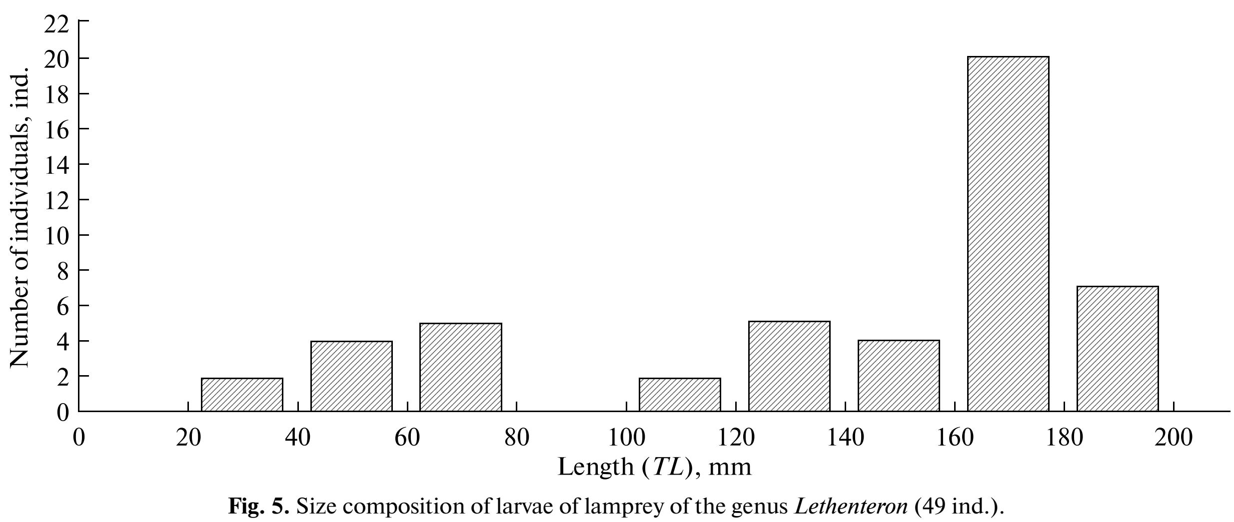

Fig. 5. Size composition of larvae of lamprey of the genus *Lethenteron* (49 ind.).

plate (character typical of representatives of the genus *Entosphenus*) that was absent in individuals of our sample (Fig. 6).

Differences between mature males and females were revealed according to 11 plastic characters from 20 studied (Table 1). In males, compared to females, the relative values (in % *TL*) of body height (*H*), snout length (*ao*), oral disc diameter (*d*), length of insertion of the first dorsal fin (*lD*1) and its height (*hD*1), length of second dorsal fin (*lD*2), length of dorsal part of cau-

Table 1. Plastic characters of lamprey *Lethenteron* from the Angara River basin

Character	Ammocoete larvae ($n = 49$)	Males ($n = 44$)	Females ($n = 27$)	Comparison of males and females	
				t_{st}	*CD*
TL, mm	35–191 / 139.4 ± 6.9	141–182 / 161.5 ± 1.4	135–177 / 153.4 ± 1.7		
Weight, g	0.1–9.5 / 3.8 ± 0.6	6.3–8.2 / 7.5 ± 0.2	6.0–7.7 / 6.5 ± 0.2		
		In % *TL*			
H	4.5–9.8 / 5.87 ± 0.16(1.1)	5.1–6.4 / 5.8 ± 0.04(0.3)	4.5–6.9 / 5.3 ± 0.09(0.5)	4.8*	0.64
*aB*1	5.3–10.1 / 6.96 ± 0.17(1.2)	1.1–13.9 / 12.0 ± 0.28(1.9)	10.6–12.4 / 11.8 ± 0.08(0.4)	0.7	0.08
ao	–	6.9–9.3 / 7.7 ± 0.07(0.4)	6.5–8.1 / 7.3 ± 0.08(0.4)	4.3*	0.52
*B*1–*B*7	9.6–21.8 / 12.6 ± 0.35(2.4)	7.3–10.7 / 9.9 ± 0.008(0.5)	9.5–10.7 / 10.1 ± 0.06(0.3)	1.9	0.23
o	–	1.7–2.8 / 2.5 ± 0.03(0.2)	2.0–2.8 / 2.4 ± 0.04(0.2)	2.2	0.27
o–*B*1	–	2.0–2.9 / 2.4 ± 0.03(0.2)	2.1–3.0 / 2.5 ± 0.04(0.2)	1.6	0.19
d	–	4.3–6.2 / 5.0 ± 0.06(0.4)	4.1–6.1 / 4.6 ± 0.07(0.4)	3.9*	0.47
*aB*7	15.9–29.3 / 19.21 ± 0.45(3.1)	20.9–23.4 / 21.9 ± 0.10(0.6)	20.3–22.7 / 21.7 ± 0.10(0.5)	1.5	0.18
*B*1–*C*	–	86.9–91.5 / 88.3 ± 0.13(0.9)	86.5–91.5 / 88.6 ± 0.17(0.9)	1.5	0.18
*B*7–*C*	–	76.5–81.4 / 78.2 ± 0.14(1.0)	73.5–80.2 / 78.1 ± 0.29(1.0)	0.3	0.04
io	–	3.3–4.5 / 4.06 ± 0.04(0.3)	3.5–4.5 / 3.9 ± 0.05(0.3)	2.1	0.25
an	1.5–5.0 / 2.43 ± 0.1(0.7)	5.9–7.8 / 6.9 ± 0.06(0.4)	5.6–7.0 / 6.3 ± 0.07(0.4)	6.6*	0.80
*aD*1	–	46.8–51.2 / 48.4 ± 0.15(1.0)	47.6–53.3 / 50.9 ± 0.22(1.1)	9.5*	1.18
aA	69.5–79.4 / 72.83 ± 0.37(2.6)	68.4–72.1 / 70.0 ± 0.14(1.0)	69.9–75.9 / 73.2 ± 0.26(1.3)	10.8*	1.40
*D*1–*D*2	1.5–5.3 / 3.07 ± 0.2(0.8)	–	–	–	
*lD*1	0–15.0 / 11.14 ± 1.19(5.5)	12.2–16.8 / 15.2 ± 0.12(0.8)	12.8–15.7 / 14.5 ± 0.14(0.7)	3.8*	0.47
*hD*1	0.–1.2 / 0.49 ± 0.08(0.3)	1.8–2.8 / 2.3 ± 0.03(0.2)	1.7–2.4 / 2.0 ± 0.04(0.2)	6.0*	0.72
*lD*2	16.2–24.7 / 21.15 ± 0.35(1.9)	22.3–25.9 / 24.6 ± 0.11(0.7)	21.4–25.7 / 23.6 ± 0.19(1.0)	4.6*	0.59

Table 1. (Contd.)

Character	Ammocoete larvae ($n = 49$)	Males ($n = 44$)	Females ($n = 27$)	Comparison of males and females	
				t_{st}	*CD*
*hD*2	0.5–2.5 / 1.29 ± 0.1(0.4)	3.3–4.9 / 4.1 ± 0.05(0.3)	3.4–4.9 / 4.0 ± 0.07(0.4)	1.1	0.14
*lC*1	8–13.7 / 11.46 ± 0.24(1.3)	10.6–14.5 / 12.4 ± 0.12(0.8)	7.0–12.4 / 10.8 ± 0.23(1.2)	6.4*	0.83
a–C	20.1–30.0 / 26.23 ± 0.34(2.4)	26.0–31.4 / 28.8 ± 0.13(0.9)	23.9–28.8 / 26.4 ± 0.26(1.3)	8.5*	1.11

Designations of characters here and in Table 2: *TL*—total length, *H*—body height between the 3rd and 4th gill openings, *aB*1—distance from the snout end to the 1st gill opening, *ao*—snout length, *B*1–*B*7—length of gill apparatus, *o*—horizontal eye diameter, *o–B*1—distance from the posterior eye margin to the 1st gill opening, *d*—oral disc diameter, *aB*7—length of head with gill apparatus, *B*1–*C*—distance from the 1st gill opening to the body end, *B*7–*C*—distance from the last gill opening to the body end, *io*—forehead width, *an*—distance from the snout tip to nasal opening, *aD*2—antedorsal distance, *aA*—anteanal distance, *D*1–*D*2—space between the 1st and 2nd dorsal fins, *lD*1 and *lD*2—length of insertions of the 1st and 2nd dorsal fins, *hD*1 and *hD*2—their maximum height, lC_1—length of dorsal part of caudal fin, *a–C*—distance from anus to the body end, *—differences are significant at $p \leq 0.001$. Above the line—limits of character variation, below the line beyond parentheses–mean value and its error, in parentheses–standard deviation.

dal fin (lC_1), distance from anus to the end of dorsal fin (*a–C*) are greater, but antedorsal (*aD*1) and anteanal (*aA*) distances are smaller. According to *CD* coefficient, the magnitude of value exceeded 1.28 only for one character—*aA*. Rather high values of this index were also found for *aD*1 and *a-C*.

For visualization of differences of phenotypes of males and females according to a complex of 20 plastic characters, similar comparison using the method of principal components (PC) was performed. The first and second PC explain 69.5% of the total dispersion of characters. Loads their vectors are presented in Table 2. At PC1, *TL* and *lC*1 gave maximum positive loads; *aA* and *aD*1 gave negative; at PC2, *aD*1 and *aB*7 gave maximum positive loads; *B*7–*C* and *aA* gave negative. On the dissemination diagram (Fig. 7), division of individuals into two discrete generalities representing males and females is seen.

Preliminary results of molecular-genetic studies on the gene *COI* mtDNA of the lamprey from the Angara basin and other water bodies of the Palearctic indicate the absence of significant differences from *L. reissneri, L. kessleri,* and *L. camtschaticum* (Loshakova and Pudovkina, 2012), which does not contradict the opinion of assigning resident nonparasitic forms inhabiting Siberian rivers to *L. camtschaticum* (Artamonova and Kucheryavyi, 2010).

Ecology. Larvae of lampreys inhabit silted river sites with a weak current and small bays, and they are frequently found near washed out coasts. Most of the time, they are in the silt that they seldom leave in the light time. According to our observations of the distribution of lampreys in different biotopes, amocete larvae of junior generations prefer sites where the bottom is covered by fine-dispersed sludge and there is outflow of spring waters. Larvae of elder generations occurred

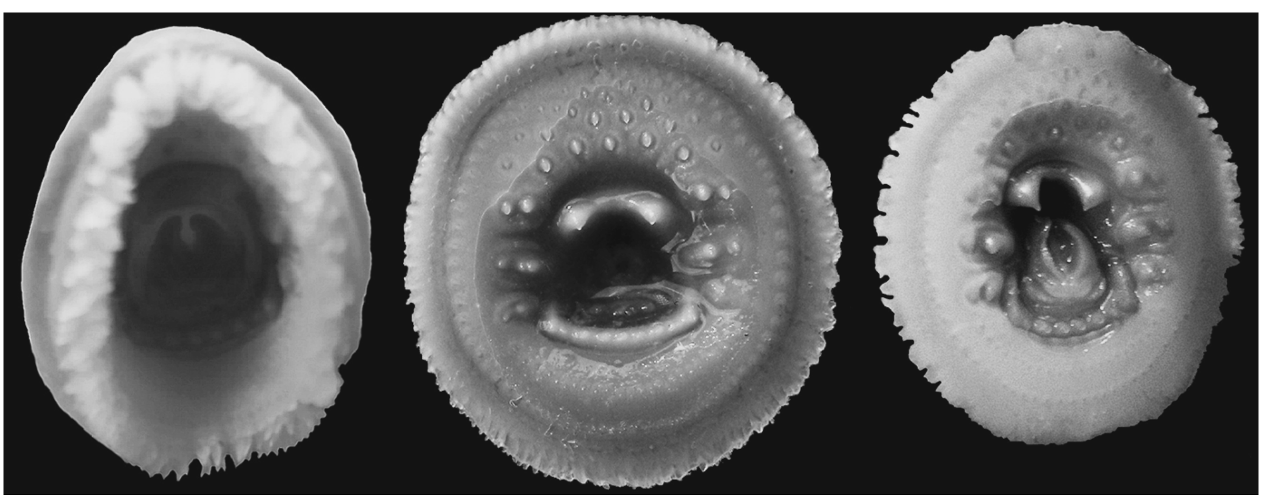

Fig. 6. Oral infundibulums of mature individuals of lamprey of the genus *Lethenteron* from the Angara River basin.

more frequently at sites where there was sludge with large fragments of organics (fallen off leaves, small branches) and specific saprogenic smell. Adult individuals usually were found at sites with rapid current and rocky or sandy-pebble bottom shaded by coastal vegetation. The pronounced migration of lampreys was associated only with spawning; at another time, no noticeable migrations of adult individuals were recorded.

At spawning grounds, mature lampreys appeared at the end of May—the first days of June after fall of abundant precipitation, increase in water level, and onset of clear weather. Water temperature in the river in this period was 13–15°C, which was also previously recorded for the lamprey from the Ob basin (Poltorykhina, 1971, 1979). Spawning took place at sites with relatively rapid current and sandy-pebble bottom at a depth of 0.2–0.5 m: in 2010—from May 28 to June 4; in 2011—from June 3 to June 8; and in 2012—from June 15 to June 20. Spawning behavior of lampreys from the Chuksha River is in many respects similar to that described for the resident form *L. camtschaticum* (Kucheryavyi et al., 2010). Directly before spawning, caudal fin of females ascended and descended in males, which was also noted by Morozova (1956) in Pacific lamprey. Sex ratio at the spawning grounds is 1 : 1.5 with domination of males.

In 2012, 60 km away from the estuary of the Chuksha River at a site with an extent of approximately 1 km, five spawning grounds with an area of 12 to 116 m^2 were found. At two spawning grounds with an area of 116 and 12 m^2 located at a distance of approximately 200 m from each other, the density of lampreys varied within 80–160 (133) and 64–128 (96) ind./m^2.

Among 27 examined females, seven individuals had not yet proceeded to spawn, while 20 had already spent some amount of eggs. Individual absolute fecundity of the former varied within 1042–3166 (on average, 1683) eggs. Gonads of the latter contained 770 to 2028 (958) eggs. The diameter of mature oocytes was 0.79–0.87 (0.83) mm.

Intestines of mature lampreys at the spawning grounds were empty. In larvae, it was filled with fine-dispersed fraction of detritus and larger inclusions of undecomposed plant remains. The spectrum of consumed components in all individuals had a similar pattern. Organic detritus was formed mainly by bacteria, while the proportion of diatom and green algae was insignificant; mineral particles were also present. Among benthic diatoms, species of the genera *Navicula*, *Nitzschia*, *Cymbella* occurred most frequently; green algae were recorded singly.

Lampreys are objects of feeding of fish and birds. According to our observations, at river shoals, they are hunted by magpies and crows that collect larvae that turned to be at coastal sites in the periods of decrease in the water level. Ammocoete larvae were also found in stomachs of burbot *Lota lota*, perch *Perca fluviatilis*, and pike *Esox lucius* caught by fishermen in the tributaries of the Chuna River. In the Angara basin, they are a feeding component of taimen *Hucho taimen*, sharp-snout lenok *Brachymystax lenok*, and whitefish *Coregonus pidshian* (Mamontov, 1977; Egorov, 1985). Mitrofanov et al. (1986) indicate that the importance

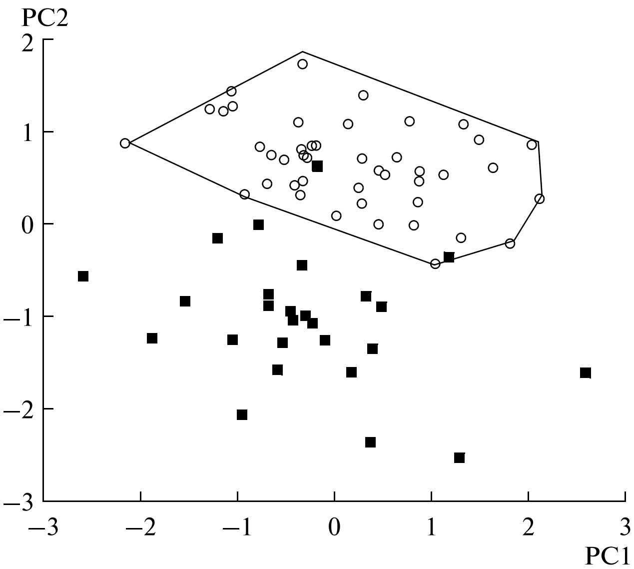

Fig. 7. Diagram of scattering reflecting differences between males (■) and females (○) of the genus *Lethenteron* according to a complex of 20 plastic characters in the area of the first two principal components (PC)>

Table 2. Loads of own vectors on the first main components for 20 plastic characters of lamprey *Lethenteron* from the Angara River basin

Character	Principal component	
	1	2
H	0.010	0.024
*aB*1	0.009	0.130
ao	0.007	0.076
*B*1–*B*7	–0.006	0.045
o	0.001	0.008
o–*B*1	–0.001	0.007
d	0.004	0.042
*aB*7	–0.004	0.177
*B*1–*C*	–0.009	–0.151
*B*7–*C*	0.014	–0.569
io	0.001	0.011
an	0.012	0.084
*aD*1	–0.243	0.218
aA	–0.371	–0.270
*lD*1	0.019	0.075
*hD*1	0.003	0.016
*lD*2	0.053	–0.058
*hD*2	0.001	0.027
*lC*1	0.143	–0.011
a–*C*	0.256	–0.105

Table 3. Recordings of catches of lamprey *Lethenteron* in the rivers of the Angara basin

River	Coordinates		Information source
	N	E	
Irkut	52°17′54	104°16′23	Egorov, 1985; interrogatory data
Kitoi	52°28′33	103°46′25	Our data
Angara (near Buret settlement)	52°58′57	103°31′19	Egorov, 1985
Belaya	52°54′34	103°39′53	Egorov, 1985; our data
Oka	52°22′55	102°16′22	Egorov, 1985
Zima	53°41′50	101°20′50	Interrogatory data
Angara, Shaman rapid*	57°08′36	102°20′12	Egorov, 1985
Kimeltei	54°08′49	102°00′47	Our data
Khokta	53°28′28	103°59′16	The same
Iya	54°36′01	100°44′31	Interrogatory data
Chuna	57°43′35	95°25′46	The same
Chuksha	56°10′28	99°56′19	Our data

* At the present time it is a zone of flooding of Ust-Ilim reservoir.

of lampreys in the food of fish can be underestimated, since it is difficult to identify them in the contents of stomachs.

Distribution. On the basis of our own, published, and interrogatory data, we can gain an idea of the occurrence of lamprey in the rivers of the Angara basin (Table 3). It is a common, widespread species inhabiting both the main channel of the Angara and many of its tributaries. In the upper reaches of the river, upstream the estuary of the Kitoi River, lamprey was not discovered.

Thus, morphometric characters of monocyclic nonparasitic form of lamprey inhabiting water bodies of the Angara basin are within limits established for Siberian lamprey from the Ob basin *L. kessleri*, Asiatic lamprey *L. reissneri*, and Pacific lamprey *L. camtschaticum*. The biological indices of the studied form and some features of its ecology in many respects correspond to data cited for lampreys of the Ob basin, as well as in part to ecological features indicated for the resident form of lamprey from the rivers of Kamchatka. Preliminary results of molecular-genetic studies of individuals from the Angara River testify in favor of the opinion of reducing of the aforementioned taxa into synonymy. It is expedient to derive final conclusions of the taxonomic rank of the lamprey from the Angara basin after completion of comparative and molecular-genetic studies.

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