

# JAWLESS FISHES OF THE WORLD

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EDITED BY  
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# Jawless Fishes of the World:

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## CHAPTER SEVEN

### REVIEW OF WESTERN TRANSCAUCASIAN BROOK LAMPREY, *LETHENTERON NINAE* NASEKA, TUNIYEV & RENAUD, 2009 (PETROMYZONTIDAE)

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#### Introduction

Lampreys constitute a small group of about 40–45 species depending, in part, on the methodological approach used (Docker et al. 2015) and the availability of reliable data to infer the boundaries between species. For example, Renaud (2011) recognized 40 species, Potter et al. (2015) recognized 41 species, and Maitland et al. (2015) list 44 species recognizing three recently-described brook lamprey species from Portugal (Mateus et al. 2013) as distinct from *Lampetra planeri* (Bloch 1784). All three publications treated *Eudontomyzon vladykovi* Oliva & Zanandrea, 1959, considered a distinct species by some authors (e.g., Kottelat & Freyhof 2007), as a synonym of *Eudontomyzon mariae* (Berg 1931). Also, a number of putative lamprey species, either extant (e.g., Yamazaki et al. 2003, 2006; Boguski et al. 2012) or extinct (e.g., Kottelat et al. 2005), have not yet been formally described. If one accepts the more liberal taxonomy of Kottelat and Freyhof (2007) and Maitland et al. (2015), 21 of the 45 species, belonging to six genera, are distributed in Eurasia. Interestingly, only seven species are parasitic while the majority, 14, are nonparasitic. In the Black Sea-Sea of Azov basin, the following nonparasitic species occur: Danubian brook lamprey *E. vladykovi* (Danube), Ukrainian brook lamprey *E. mariae* (Dniester, Dnieper in the Black Sea basin to Don and Kuban' in the Sea of Azov basin), Western Transcaucasian brook lamprey *Lethenteron ninae* Naseka, Tuniyev &

Renaud, 2009 (Psezuapse, Shakhe, Mzymta, Psou, Bzipi (Bzyb'), and Mokvi (Mokva) rivers in Russia and Georgia), and Turkish brook lamprey *Lampetra lanceolata* Kux & Steiner, 1972 (İyidere and İkizdere streams west of Rize, north-eastern Turkey, and a stream in Lake Sapanca basin in north-western Turkey) (e.g., Lang et al. 2009; Naseka et al. 2009; Renaud 2011; Freyhof 2014b).

Morphological and evolutionary affinities between several parasitic and nonparasitic species have been suggested for a long time (e.g., Hubbs 1925); these species were termed “paired species” (Zanandrea 1959). Vladykov & Kott (1979) introduced the more general term “stem-satellite species” because they identified, based on morphological criteria, several cases in which more than one brook lamprey (satellite) species had apparently been derived from a single parasitic (stem) species; several so-called relict species (nonparasitic lampreys that occur at the southern limits of distribution of the Northern Hemisphere lampreys) could not be unambiguously paired with extant parasitic species (e.g., Docker 2009; Potter et al. 2015). Based on morphological criteria, among the four nonparasitic lampreys distributed in the Black Sea basin, *E. mariae* (including *E. vladykovi* when synonymized with the latter species) is paired with the Carpathian lamprey *Eudontomyzon danfordi* Regan, 1911, *L. lanceolata* is, probably, a derivative of the European river lamprey *Lampetra fluviatilis* (Linnaeus, 1758) though the two species do not occur sympatrically, while the affinity of *L. ninae* is unclear (e.g., Potter et al. 2015).

The Black Sea nonparasitic species were traditionally assigned to three genera (or subgenera of *Lampetra* according to some authors, such as Bailey (1980)) representing distinct morphological clades (Gill et al. 2003; Monette & Renaud 2005; Renaud 2011). Diagnostic morphological characters in adults are limited to few character sets among which the pattern and morphology of teeth in the oral disc is the most informative. *Eudontomyzon* Regan, 1911 is characterised by numerous labial teeth commonly present on all fields of the oral disc; in *Lampetra* Bonnaterra, 1788, the labial teeth are present only in the anterior field while exolaterals and posterials are absent; and in *Lethenteron* Creaser & Hubbs, 1922, anterials are present, exolaterals are usually absent but if present, only one or two occur per lateral field, exceptionally a complete row, and a single row of posterials is present, either complete or incomplete (Gill et al. 2003; Renaud 2011). Additionally, European species of *Eudontomyzon* typically have unicuspid upper endolateral teeth and bicuspid middle endolateral teeth, European species of *Lampetra* (including the Po brook lamprey *L. zanandreae* Vladykov, 1955) typically possess bicuspid upper

endolateral teeth and tricuspid middle endolateral teeth, while Eurasian *Lethenteron* commonly have both the upper and middle endolaterals bicuspid.

Molecular methods have been used to help resolve the phylogeny and taxonomy of lampreys of the genera *Eudontomyzon*, *Lethenteron*, and *Lampetra* at different taxonomic levels (e.g., Docker et al. 1999; Yamazaki et al. 2006; Lang et al. 2009; Li 2014; White 2014). For the Black Sea brook lampreys, especially important were data from the mitochondrial cytochrome *b* gene by Lang et al. (2009), who showed that some nonparasitic species formed clades with parasitic species which, from their morphology, had been allocated by taxonomists to different genera. Thus, *L. zanandreai* placed in the genus *Lethenteron* because its endolaterals are usually bicuspid and because posteriors are commonly present (e.g., Bianco 1986; Renaud 2011), was returned to *Lampetra* and Asian Pacific *E. morii* was shown to have no affinity with true European *Eudontomyzon*. Additionally, based on unpublished results deposited in GenBank (GQ206176 from the Chakhtsutsyr Stream, misidentified as *L. lanceolata*), *L. ninae* was transferred to *Lampetra* (Freyhof 2014a). These data (Lang et al. 2009) suggested that some morphological characters may be homoplasious within lampreys contrary to what had been previously hypothesised. Recently, Li (2014), based on phylogenetic trees using the cytochrome *b* gene, supported the hypothesis that *L. zanandreai* and *L. ninae* had derived from a *Lampetra fluviatilis*-type ancestor. Her cytochrome *b* gene analyses did not include any *L. lanceolata* specimen, but using the nuclear TAP2 gene intron *L. ninae* and *L. lanceolata* were not reciprocally monophyletic. However, the resolution of the TAP2 trees was not high enough to resolve the species-level relationships since *L. fluviatilis* and *L. zanandreai* were not retrieved as monophyletic either.

In summary, the molecular data (Lang et al. 2009; Li 2014) have considerably changed traditional taxonomic concepts in three major aspects as far as *Eudontomyzon*, *Lampetra*, and *Lethenteron* are concerned, namely: 1. *Lampetra* from the Pacific drainage of North America and *Lampetra aepyptera* (Abbott, 1860) should each be separated from *Lampetra* from the Atlantic drainage of Eurasia as distinct genera; 2. *Lampetra* from the Atlantic drainage of Eurasia includes *Lampetra zanandreai*; 3. *Lethenteron* includes *Eudontomyzon morii*. With regard to morphology, it supports the hypothesis (Kottelat & Freyhof 2009) that those types of dentition, which were traditionally accepted for distinguishing genera, might have evolved convergently in different clades and may be useful in diagnosing species rather than in defining lineages.

As shown above, although both *L. ninae* and *L. lanceolata* have close molecular phylogenetic affinities with *L. fluviatilis* (Lang et al. 2009; Li 2014), it is still unclear if the latter species represents their immediate "stem-species". Sequences of the mitochondrial COI gene (1,072 bp) in two larvae of *L. ninae* from the Mzymta River showed that these shared some haplotypes with Arctic lamprey *Lethenteron camtschaticum* (Tilesius, 1811) (Artamonova et al. 2011). The authors proposed three hypotheses to explain their observation and synonymisation of *L. ninae* with *L. camtschaticum*. The first hypothesis, which they called the least probable, was that *L. camtschaticum* in the rivers of the Caucasian Black Sea coast is a relict of the ancient Tethys Sea; the second was that the Arctic lamprey dispersed into the Black Sea basin during a glacial period; and the third suggested a human-mediated introduction of *L. camtschaticum* into the Black Sea basin. Synonymization of *L. ninae* and *L. camtschaticum* has already been accepted in subsequent publications by Makhrov et al. (2013) and Parin et al. (2014). However, Li (2014) showed that the mean genetic (Kimura 2-parameter) distance (cytochrome *b* gene) between *L. ninae* and Asian *Lethenteron* species was at least 7.79%, while between *L. ninae* and *L. fluviatilis* it was much less, 3.91%, and between *L. ninae* and *L. zanandrei* only 1.63%. Also, with regards to their third hypothesis, Artamonova et al. (2011) provided no explanation for the presence of the nonparasitic species among geographically isolated river drainages across a wide area during a short period of time since the supposed lamprey introduction(s) in the last century. It is known that nonparasitic lampreys possess very low dispersal ability within and between river basins (Schreiber & Engelhorn 1998; Mateus et al. 2011). Artamonova et al. (2011) also ignored the fact that a resident brook lamprey has been reported in the eastern Black Sea area long before any fish introductions started (De Filippi 1865, p. 360, under the name *Petromyzon* sp.; Barach 1939, p. 60, and Barach 1941, p. 71, under the name *Lampetra mariae*).

The allocation by Naseka et al. (2009) of *L. ninae* to the genus *Lethenteron* and of *L. lanceolata* to the genus *Lampetra* was based principally on the usual presence of a row of posterials, albeit incomplete, in the former and its absence in the latter; the same reasoning that had caused the transfer of *Lampetra zanandrei* to the genus *Lethenteron* mentioned above. While the parasitic stem species of *L. ninae* has not been identified, that of *L. lanceolata* is inferred to be *L. fluviatilis* (Potter et al. 2015). This contrasts with the treatment by some authors (e.g., Artamonova et al. 2011; Makhrov et al. 2013) of *L. camtschaticum*, widely distributed across Eurasia, comprising both an anadromous parasitic form

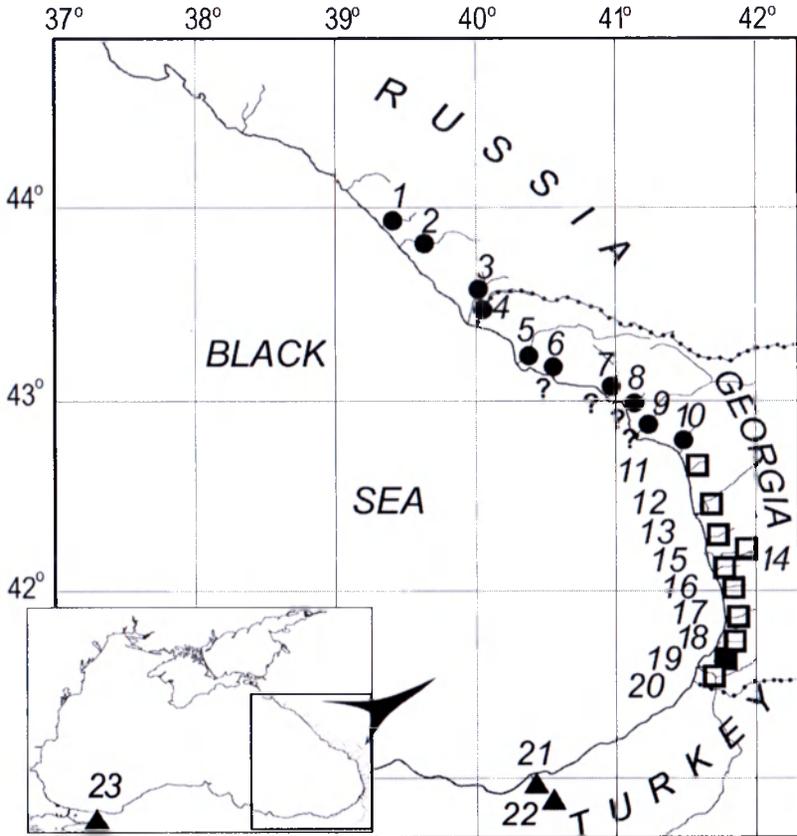
and two allopatric nonparasitic resident forms; the latter (*L. reissneri* (Dybowski, 1869) and *L. kessleri* (Anikin, 1905)) having been described as distinct species. Molecular data (Li 2014) also revealed that *L. camtschaticum camtschaticum*, *L. camtschaticum septentrionalis* (Berg, 1931), *L. reissneri*, and *L. kessleri* were not reciprocally monophyletic because their relationships had not been resolved in the cytochrome *b* tree. In contrast, although two putative species from Japan, *Lethenteron* sp. S and *Lethenteron* sp. N are morphologically indistinguishable from each other, they were shown to be genetically distinct using both allozyme and mitochondrial sequence data (Yamazaki & Goto 1998; Yamazaki et al. 2006; Li 2014). Apparently, more genes, and in particular nuclear genes, should be used to help resolve the basis for these differences between morphological and molecular phylogenies, and taxonomic changes need not be made hastily (Potter et al. 2015).

## Historical data on the distribution of the eastern Black Sea lampreys

Geographic localities mentioned below can be found in Fig. 7-1.

A lamprey was first recorded in Western Transcaucasia (an area south of the Greater Caucasus Range from Novorossiysk to the Çoruh River (Chorokh, Chorokhi), which includes river drainages of the Black Sea in Russia, Georgia, and the Abkhazia region) under the name *Petromyzon* sp. by De Filippi (1865) who collected "many individuals at the larval stage in a stream near Batumi. Overall, they resemble the common small lamprey of Europe (*Lampetra planeri* (Bloch, 1784)) but differ only by their larger size" (p. 360, translated from Italian). Berg (1911) referred to De Filippi (1865) and Yashchenko (1895); the latter author, in a catalogue of the St. Petersburg University zoological collection, listed (p. 99) a lamprey larva identified as "*Petromyzon ponticus* ?" from "Novorossiysk". Since that time, the locality of Novorossiysk (a town on the north-eastern or Caucasian coast of the Black Sea in Russia) had been commonly given whenever distribution of the Transcaucasian lamprey was discussed (e.g. Berg 1931, 1948). However, Yashchenko's specimen is absent from the collection in St Petersburg University at present (our data), and we know of no extant lamprey specimens collected near Novorossiysk. Most probably, the label "Novorossiysk" refers not to the locality where the specimen was sampled but to the collection from which this specimen was obtained – i.e., Novorossiyskiy University located in the city of Odessa, north-western Black Sea coast, where the donator of the specimen, Ernst von Ballion (1816–1901), an entomologist, worked at the time (Kottelat et

al. 2005). The former Novorossiia Province (with Odessa as its capital; now in Ukraine) is an area of distribution of *E. mariae*. Berg (1931), when he described the species *E. mariae*, did not have any specimens of lamprey from Western Transcaucasia but extended its range to include this area.



**Figure 7-1.** Geographic distribution of brook lampreys in eastern and south Black Sea basin. *Lethenteron ninae* (solid circles): Psezuapse (1), Shakhe (2), Mzynta (3), Psou (4), Bzipi (5), Mchishta (6), Gumista (7), Kelasuri (8), Kodori (9), Mokvi (10); unidentified (no diagnostic characters known) species (square): Lake Bebesiri (11), Inguri (12), Khobi (13), Tsivi (Rioni tributary, 14), Lake Paliastomi (15), Supsa (16), Kintrishi (17), Chakvis-tskali with Chelta tributary (18), Chorokhi (20); *Eudontomyzon* species as described by Kokotshashwili (1942) (solid square): Makhindzhauris-tskali (19); *Lampetra lanceolata* (solid triangle): İyidere (21), İkizdere (22), stream running to Lake Sapanca (23). Question marks indicate unverified taxonomic identification.

Barach (1939, 1941) reported a lamprey under the name *E. mariae* from Lake Bebesyr (Bebesiri) in the Abkhazia region and Lake Paliastomi in Georgia based on information from local people only and gave no description of any original material. Later, Barach (1960) mentioned a lamprey from Mchishta River and Sharashidze (1960) recorded one individual 160 mm long under the name *Lampetra planeri* from a tributary of the Kodori (both localities are in the Abkhazia region) but, again, the authors provided no information on whether adults or larvae were found. Sharashidze (1960) also provided a list of other rivers from where this brook lamprey was known (Khobi, Inguri, Kelasuri, Gumista).

The first description of a lamprey specimen (a spent adult female) was made by Kokotshashwili (1942) who collected, on the 4th of March 1935, two specimens (male and female) in the Makhindzhauris-tskali (Makhindzhauri) River north of the town of Batumi in Georgia. He provided a drawing of the oral disc of the lamprey, which clearly shows the diagnostic characters of *Eudontomyzon* (a broad supraoral lamina and the presence of exolaterals and posterials), as was already mentioned by Naseka et al. (2009). It is important to note that his drawing does not seem to be either a reproduction or a modified re-drawing of Berg's specimen of *E. mariae* from the Don River drainage (e.g., Berg 1931, 1932) although Kokotshashwili (1942) identified his specimen as *E. mariae*.

Elanidze & Demetrashvili (1973) and Shervashidze (1980) briefly listed rivers in Georgia (including the Abkhazia region) where a lamprey identified as *Lampetra mariae* is distributed, namely, Chorokhi, Chakvis-tskali (Chakvi) with a tributary at the village of Chaisubani, Khobi, Inguri, Kodori, Makhindzhauri, Bzipi, Gumista, and Kelasuri; neither examined material nor developmental stage was mentioned. Elanidze (1983) reported the finding of two larvae and one adult specimen identified as *L. mariae* from the middle reaches of the Inguri River in Georgia – this was the second known report of an adult lamprey from Western Transcaucasia. However, the description provided does not allow determination of the specimen even to genus. Elanidze (1983) also reported three larvae from the middle Kodori River (the Abkhazia region) identified as *L. mariae* but "different in external appearance and some characters from the specimens from the Inguri River" (p. 19, translated from Russian) and numerous larvae in the Chelta River at Chaisubani, one adult (no description was given) in the mouth of the Chorokhi River and two specimens (no indication as to larvae or adults) in the Chakvis-tskali River, as well as the probable occurrence of a lamprey in the Supsa River, Georgia. *Lampetra lanceolata* Kux & Steiner, 1972 was described from the İyidere stream in the Black Sea basin near Rize, Turkey, and Bogutskaya & Naseka (2004)

concluded that this species rather than *E. mariae* is the one distributed in Russian Western Transcaucasia.

The first vouchered records of a lamprey from the Black Sea coast in the Russian Federation were those of B. Tuniyev (1999)—he collected lamprey larvae in four rivers near the towns of Sochi and Adler: Psezuapse, Shakhe, Mzymta, and Psou. Drogan (2002) collected larvae from the same rivers but no adults were found. The first adult specimen of a lamprey from Russian Western Transcaucasia (and only the third report of an adult in 150 years of ichthyological investigation from the entire Western Transcaucasia) was collected by S. Tuniyev on the 20 September 2006 in the Mzymta River near the village of Kazachiy Brod. Since then, 1 adult and 12 larvae reared in aquaria to the postmetamorphic stage have been collected and were the basis for the original description of *L. ninae* together with larvae collected in the Shakhe, Mzymta, Psou (Chakhtsutsyr Stream), Bzyb', and Mokva rivers (Naseka et al. 2009). To summarise, a lamprey originally described as *L. ninae* is known from rivers of the Black Sea coast in Russia and north-western Georgia (Abkhazia region), from west to east: Psezuapse, Shakhe, Mzymta, Psou (Chakhtsutsyr Stream), Bzyb', and Mokva rivers (Tuniyev 1999; Drogan 2002; Bogutskaya & Naseka 2004; Tuniyev 2005, 2006, 2008; Naseka et al. 2009). Within this range, a lamprey identified as *L. mariae* is also known from the Mchishta River, which is located east of the Bzyb' (Barach 1960), and, south-eastwards, in Gumista, Kelasuri, and Kodori rivers (Elanidze & Demetrashvili 1973; Elanidze 1983) (Fig. 7-1).

Further southwards, a lamprey is known (De Filippi 1865; Kokotshashvili 1942; Barach 1960; Elanidze 1983; Ninua & Japoshvili 2008) from Lake Bebesyr, the Inguri (Enguri) River, a tributary of the Rioni River (the Tsivi River), Lake Paliastomi (south of the Rioni River delta), the Supsa River (probably), the Kintrishi River (our data, only larvae), the Chakvis-tskali River, the Makhindzhauri River, the Chelta River and rivulets near Batumi, the Khobi River, and in the Chorokh River at the border between Georgia and Turkey. However, identification of this lamprey still needs to be established because only four adults have been recorded from the entire area and only one (the Makhindzhauri female specimen) of these was described and it refers to a *Eudontomyzon* species. Further along the Black Sea coast, the species *L. lanceolata* is distributed in the İyidere and İkizdere, streams flowing into the Black Sea west of Rize, north-eastern Turkey, and ~800 km westwards from these localities—in a stream running to Lake Sapanca in north-western Turkey (Kux & Steiner 1972; Lang et al. 2009; Freyhof 2014b; Li 2014).

Thus, our knowledge of the brook lamprey(s) along the Black Sea coast from Psezuapse River (Russia) to the İyidere River and Lake

Sapanca (Turkey) (Fig. 7-1) is rather fragmentary. Two morphologically distinct "relict" nonparasitic species (*Lethenteron*-like and *Lampetra*-like) are respectively distributed in the north and in the south of the area and separated from each other by a poorly known form morphologically close to *Eudontomyzon*. Therefore, we believe that an increase in our knowledge of morphological variability within the known range of the species formally described as *L. ninae* will help to clarify the taxonomy of the Eastern Black Sea lampreys, the limits of their ranges, and their phylogenetic relationships.

## Material and Methods

All measurements on specimens were taken within a short period of time to avoid problems due to differential shrinkage of body sections, which occur during initial fixation in 4–5% formalin followed by preservation in 70% ethanol. For methods for description of body measurements and counting of the teeth, trunk myomeres, and oral fimbriae and evaluation of the extent of pigmentation coverage and the defined areas for those various characters in ammocoetes see Naseka et al. (2009). Note, however, that we refer here to the bulb of the tongue precursor as the middle prong. Also, the following characters not recorded by Naseka et al. (2009) were added here: urogenital papilla length, cloacal slit length, myomeres to origin of first dorsal fin and to insertion of first dorsal fin, oral papillae, and pigmentation in the area between upper lip and cheek, the predorsal and the lower lip. Velar wings are defined as one or more tentacles that are folded onto the dorsal surface of the velar apparatus and should not be confused with the tentacles that lie on the ventral surface of the velar apparatus (see Renaud 2011, fig. 5). For discussion on terms used to describe the stages of a lamprey life cycle – ammocoetes (=larvae), metamorphosing individuals (=transformers), and adults (=metamorphosed individuals) – see Docker et al. (2015). Statistic calculations were done using the Excel application for Microsoft Office 2003. Correlation coefficient (Pearson's  $r$ ) values from 0.50 to 0.75 and from -0.50 to -0.75 indicate moderate to good correlation, and  $r$  values from 0.75 to 1 and from -0.75 to -1 indicate very good to excellent correlation between variables (Dawson & Trapp 2004).

Abbreviations: CMNFI, Canadian Museum of Nature Fish Collection, Ottawa; NMW, Naturhistorisches Museum Wien, Vienna; SNP, Sochi National Park; TGU, Tomsk State University; ZIN [formerly, abbreviation ZISP was used as in Naseka et al. (2009)], Zoological Institute of Russian

Academy of Sciences, St Petersburg; and ZMB, Museum für Naturkunde, Berlin. TL, total length; b, bicuspid tooth; u, unicuspid tooth.

For intraspecific comparisons, specimens described by Naseka et al. (2009) are used (holotype ZIN 54431, paratypes ZIN 54432, 54433, 54434, 54435, 54436; CMNFI 2008-0059, non types SNP 23, 65) supplemented by the following newly collected specimens (99 ammocoetes, 1 recently metamorphosed individual, and 14 adults):

SNP 253 (15 ammocoetes TL 95.3–144.3 mm, 3 adult males TL 115–153 mm; Mzymta River near Galitsino, Sochi District, Russia, 17 Oct. 2009, coll. A.N. Pen'kovskiy).

SNP 258a (27 ammocoetes TL 55.3–135.5 mm; Mzymta River near Galitsino, Sochi District, Russia, 17 Oct. 2009, coll. A.N. Pen'kovskiy).

SNP 258b (20 ammocoetes TL 95.4–160.1 mm, 2 adult males and 1 adult female, TL 139.0–155 mm; same data as 258a, coll. S.B. Tuniyev).

SNP 286 (8 ammocoetes TL 81–122 mm; Shakhe River, Sochi District, Russia, 2009, coll. S.B. Tuniyev).

SNP 377 (1 recently metamorphosed individual TL 172.5 mm, 4 adult males and 1 adult female, TL 116–140 mm; Mokva River, Abkhazia region, Georgia, Oct. 2014, coll. S.B. Tuniyev).

SNP 378 (1 adult male and 2 adult females, TL 134.8–139.1 mm; Psiya River near Khartsyz, tributary of Shakhe River, Sochi District, Russia, 23 Sept. 2014, coll. S.B. Tuniyev).

SNP 379 (3 ammocoetes TL 139.3–162.2 mm; Shakhe River at Malaya Kienka, Sochi District, Russia, Oct. 2014, coll. S.B. Tuniyev).

SNP 380 (9 ammocoetes TL 115.6–162.0 mm; Shakhe River at Kirov, Sochi District, Russia, 17 Feb. 2014, coll. S.B. Tuniyev).

SNP uncat. (8 ammocoetes TL 90.5–126.6 mm; Shakhe River at Kirov, Sochi District, Russia, 17 Feb. 2014, coll. S.B. Tuniyev).

NMW 98630 (9 ammocoetes TL 129.4–157.8 mm; Mzymta River, Sochi District, Russia, 09 Nov. 2009, coll. S.B. Tuniyev).

These specimens (except for the Mokva sample) were collected in large oxbow lakes formed in the Shakhe and Mzymta river systems due to recent constructions that changed the direction of watercourses.

The comparative material only included the genus *Lethenteron*, mostly types of nominal taxa to avoid any misidentification; other data are principally taken from Renaud (2011) and Renaud & Naseka (2015).

***Comparative description of the 2009–2014 samples versus the holotype and paratypes***

*Ammocoetes*. Morphometric and meristic characters are given in Tables 7-1 and 7-2. The maximum size of ammocoetes was 162.2 mm TL; this means that ammocoetes can reach at least the latter size. Trunk myomeres 57–61 with a modal range of 58–60, similar to the counts found in the type series; myomeres to origin of first dorsal fin (32)33–35 and myomeres to insertion of first dorsal fin 45–49 with a modal range 46–48 (Table 7-2).

The middle prong of the tongue precursor is clearly triangular, with a wide base and a pointed apex bearing few cirrhi (examined in 45 specimens) (Fig. 7-2, centerfold, page xiv). The pigmentation coverage is absent on the tongue precursor middle prong in all examined specimens (Fig. 7-2, centerfold, page xiv, Table 7-2). Pigmentation of the areas lateral to the elastic ridge is rarely slight (2) and sometimes moderate (10, Fig. 7-2, centerfold, page xiv), but usually strong (19, 61% of specimens) (Table 7-2). The character, thus, is variable but with a clear mode of strong pigmentation coverage. Although Naseka et al. (2009) reported only slight coverage in the areas lateral to elastic ridge, re-examination of the type series revealed that these areas had the following condition: + (1), ++ (3), +++ (5), in line with the present observations.

**Table 7-1.** Measurements in ammocoetes of *Lethenteron ninae*. Numbers in parentheses following the catalogue numbers represent the sample size.

Character	SNP 379 (3), SNP 380 (3), SNP 253 (8), SNP 258 (10), NMW 98630 (9), n=33		
	range	mean	SD
Total length, mm	97.1–162.2	132.3	18.98
% TL			
Prebranchial length	6.2–7.8	6.9	0.47
Prenostril length	2.0–2.9	2.4	0.21
Branchial length	10.8–12.6	11.8	0.45
Interbranchial opening length	1.1–1.8	1.4	0.15
Trunk length	49.0–54.3	51.9	1.33
Tail length	26.0–30.5	27.8	1.07
Cloacal slit length	0.9–1.6	1.3	0.19

**Table 7-2.** Pigmentation coverage and myomeres in ammocoetes of *Lethenteron ninae*. Degree of pigmentation coverage is absent (-), slight (+), moderate (++), and strong (+++).

Character	SNP 379 (3), SNP 380 (3), SNP 253 (8), SNP 258 (10), NMW 98630 (9), n=33
Middle prong of tongue precursor pigmentation	- (33)
Pigmentation of areas lateral to elastic ridge	+ (2), ++ (10), +++ (19), undetermined (2)
Upper lip pigmentation	+ (1), ++ (31), +++ (1)
Lower lip pigmentation	- (2), + (30), ++ (1)
Area between upper lip and cheek pigmentation	++ (1), +++ (32)
Cheek pigmentation	+++ (33)
Subocular pigmentation	+ (3), ++ (5), +++ (25)
Upper prebranchial pigmentation	++ (4), +++ (29)
Lower prebranchial pigmentation	+ (7), ++ (12), +++ (14)
Upper branchial pigmentation	++ (3), +++ (30)
Lower branchial pigmentation	- (17), + (16)
Ventral branchial pigmentation	- (9), + (22), ++ (2)
Predorsal pigmentation	+++ (33)
Caudal fin pigmentation	+ (12), ++ (20), +++ (1)
Lateral line neuromasts	unpigmented (33)
Trunk myomeres	57 (2), 58 (15), 59 (4), 60 (9), 61 (3)
Myomeres to origin of first dorsal fin	32 (1), 33 (9), 34 (15), 35 (8)
Myomeres to insertion of first dorsal fin	45 (4), 46 (14), 47 (7), 48 (6), 49 (2)

Body colouration (in live and freshly preserved specimens) is without mottling. External pigmentation is generally well developed (Fig. 7-3A, B, centerfold, page xv). In most specimens the pigmentation coverage of the area between the upper lip and cheek, cheek, subocular, upper prebranchial, upper branchial, and predorsal (anterior to first dorsal fin) areas is 75% or more (Table 7-2). Naseka et al. (2009) did not record the

pigmentation between the upper lip and cheek or the predorsal, but their evaluation of the cheek, upper prebranchial and upper branchial pigmentations agree with the present observations, while for the subocular, pigmentation coverage was equally moderate or strong. Pigmentation coverage of other areas is usually either slight (1% to <25%) (lower lip, ventral branchial) or moderate (25% to <75%) (upper lip, caudal fin); both moderate and strong states are equally present in the lower prebranchial area and equally present states of absent to trace (< 1%) and slight in the lower branchial area. Naseka et al. (2009) did not record the pigmentation of the lower lip, but, in contrast to the present observations, the pigmentation of the ventral branchial area showed a strong mode of absent to trace and the caudal fin was invariably slightly pigmented. Both the recent samples and the type series showed moderate pigmentation in the lower prebranchial and absent to trace pigmentation in the lower branchial areas, but the recent samples also showed strong modes of higher states of pigmentation coverage while the type series did not. We believe that the generally higher pigmentation coverage observed in the recent samples is at least in part the result of the larger sample size. However, in the case of the upper lip pigmentation, re-examination of the type series revealed that the original evaluation of the pigmentation coverage had been overestimated because the free margin of the upper lip was often curled and prevented a proper evaluation of the entire area. The re-evaluation of this character in the type series [i.e., + (1), ++(7), +++(1)] is in agreement with the present observations.

Lateral line neuromasts are unpigmented as was also reported in Naseka et al. (2009). The caudal fin shape is spade-like, while Naseka et al. (2009) found it to be either spade-like or rounded.

*Adults.* See Fig. 7-4, centerfold, page xv, for general appearance, Table 7-3 for morphometric data and Table 7-4 for meristic data.

One recently metamorphosed individual is 172.5 mm TL; it belongs to stage 6 according to Bird & Potter (1979) and is characterised by high dorsal fins, a colouration similar to that in adults, an enlarged oral disc with fully developed supraoral lamina but slightly differentiated labial teeth, and clearly defined but small fimbriae around the disc perimeter.

Lamprey individuals described herein were collected at the end of September and in October and kept in aquaria until they became fully metamorphosed; this was attained in December of the same year. When preserved and examined, they had TL of 115–155 mm (see Table 7-3) with a mean of 132.6 mm (excluding the recently metamorphosed individual above), which is considerably less than the mean of 151.3 mm for the type series specimens, which comprised only very recently metamorphosed individuals. As

is well known, natural shrinkage occurs in lampreys not only when they go through metamorphosis, but also when adults become sexually mature. In the sample of adults described herein (excluding the recently metamorphosed individual), smaller individuals (the smallest one is a male 115 mm TL in SNP 253) had their gonads at stage of development IV (prespawning condition with fully developed vitellogenous oocytes in females), a conspicuous urogenital papilla and a downturned tail in males, a distended trunk and an upturned tail in females.

It can be seen in Table 7-3 that, with the reduction in size from the end of metamorphosis, during the process of maturation and the approach of spawning, 10 measurements display a clear ( $r > 0.50$  and  $< -0.50$ ) correlation with total length (negative in nine characters and positive in one). In the sample examined, very good negative correlation was found in snout (preorbital) length, prebranchial length, prenostril length; good negative correlation was found with oral disc length, eye length, maximum depth of caudal fin, interorbital width, postocular length and urogenital papilla length; and good positive correlation was revealed only with tail length.

The oral disc is shown in Fig. 7-5, A–D, centerfold, page xvi.

Transverse lingual lamina u-shaped with 5–16 (commonly 9–12) unicuspid teeth, the median one markedly enlarged (Table 7-4), while in Naseka et al. (2009) the overall range was smaller 9–15. The cusps are commonly well developed and prominent; in the cases the cusps were poorly developed, the tooth formulae were 2u-I-2u or 3u-I-2u. Longitudinal lingual laminae straight, each with 5–9 unicuspid teeth, as also reported in Naseka et al. (2009).

**Table 7-3.** Measurements in recently metamorphosed individual and mature adults of *Lethenteron ninae* (specimens arranged in decreasing order according to their total length). Pearson's  $r$  refers to correlation with total length.

Character	SNP 377*	Mature adults: SNP 253 (3 males), SNP 258b (2 males and 1 female), SNP 377 (4 males and 1 female), SNP 378 (1 male and 2 females)															Range	M	SD	$r^{**}$
Total length, mm	172.5	155	153	146	140	139.1	139	137.6	136	134.8	122	119	118	116	115	115–155	132.6	15.17		
% TL																				
Prebranchial length	7.8	9.4	9.7	9.7	11.6	10.4	9.9	10.4	10.6	9.7	10.6	11.1	10.9	10.0	11.3	9.4–11.6	10.4	0.68	-0.77	
Branchial length	10.6	9.6	11.4	10.3	11.3	9.5	10.6	10.1	11.1	10.2	11.0	11.1	11.4	9.7	11.4	9.5–11.4	10.6	0.71	-0.23	
Interbranchial opening length	1.4	1.3	1.6	1.5	1.4	1.2	1.4	1.1	1.6	1.2	1.4	1.3	1.7	1.5	1.5	1.1–1.7	1.4	0.16	-0.16	
Branchial depth	6.5	5.5	5.2	6.2	6.8	6.1	5.1	6.4	6.5	5.8	6.6	7.2	5.4	5.4	6.2	5.1–7.2	6.0	0.63	-0.09	
Disc length	2.6	3.9	4.1	4.3	4.9	3.8	4.2	4.3	5.2	3.8	4.2	5.1	5.7	4.2	5.7	3.8–5.7	4.5	0.65	-0.73	
Eye length	1.2	1.6	1.8	1.7	2.0	1.4	2.1	2.0	2.0	1.6	2.0	2.1	1.9	1.8	2.2	1.4–2.2	1.9	0.22	-0.69	
Interocular width	3.2	3.7	3.4	3.4	4.0	4.0	3.7	4.1	4.2	3.9	3.5	4.7	4.0	3.9	4.2	3.4–4.7	3.9	0.35	-0.64	
Snout length	3.9	5.0	5.7	5.4	6.6	5.6	6.0	5.8	6.2	5.4	6.0	6.8	7.3	5.5	7.0	5.0–7.3	6.0	0.68	-0.78	
Postocular length	2.9	2.6	3.1	3.1	3.4	3.1	2.7	2.9	3.2	3.0	3.1	3.8	3.3	2.9	3.7	2.6–3.8	3.1	0.34	-0.56	
Prenostril length	3.1	4.0	4.5	4.7	5.3	4.7	4.7	4.7	4.2	4.4	4.6	5.4	5.6	4.6	5.5	4.0–5.6	4.8	0.49	-0.76	
Trunk length	51.0	52.3	49.5	50.5	48.0	50.7	50.4	48.5	49.4	50.4	49.1	50.8	52.0	49.7	52.6	48.0–52.6	50.3	1.37	-0.06	

Trunk depth	6.0	5.9	5.6	5.2	7.2	6.8	5.2	7.8	6.5	6.3	6.3	8.7	5.8	6.4	5.6	5.2-8.7	6.4	1.00	-0.26
Tail length	28.1	27.5	28.7	26.8	27.5	27.0	28.0	27.4	28.4	27.4	26.2	26.1	26.9	26.9	26.9	26.1-28.7	27.3	0.74	0.66
First dorsal fin length	10.8	12.1	13.7	12.0	13.0	12.3	13.3	15.9	10.9	11.2	12.0	14.2	10.2	12.5	14.3	10.2-15.9	12.7	1.51	-0.17
First dorsal fin depth	1.2	2.1	2.0	1.7	1.6	1.6	1.4	1.8	2.0	1.6	1.8	1.6	1.7	1.4	2.2	1.4-2.2	1.7	0.25	-0.15
Second dorsal fin length	23.2	21.6	25.6	25.8	26.6	23.7	22.9	25.7	23.3	21.4	24.2	22.6	27.0	24.4	26.3	21.4-27.0	24.4	1.84	-0.26
Second dorsal fin depth	2.6	3.6	3.9	3.3	3.2	3.0	3.2	3.6	3.3	2.5	2.7	3.4	4.1	2.6	4.1	2.5-4.1	3.3	0.52	-0.16
Caudal fin length	9.1	10.3	9.1	9.2	11.6	10.3	9.2	9.4	10.2	10.0	9.5	9.7	10.1	9.6	10.7	9.1-11.6	9.9	0.69	-0.25
Tail depth at junction of second dorsal and caudal fins	3.2	2.6	2.4	2.5	3.4	2.7	2.4	2.3	2.6	2.8	3.3	3.7	3.1	2.6	3.1	2.3-3.7	2.8	0.43	-0.28
Maximum depth of caudal fin	4.5	4.7	4.2	4.8	5.3	5.1	5.0	5.7	5.0	5.1	5.0	6.1	5.4	4.7	6.5	4.2-6.5	5.2	0.59	-0.66
Tail depth at maximum depth of caudal fin	1.4	1.4	2.0	1.4	1.4	1.5	1.5	1.5	1.5	1.6	1.6	1.8	2.0	1.3	1.8	1.3-2.0	1.6	0.24	-0.33
Urogenital papilla length	0.2	0.2	0.3	0.4	0.7	0.4	0.3	0.4	0.6	0.5	0.4	0.8	0.7	0.2	1.0	0.2-1.0	0.5	0.24	-0.55
Cloacal slit length	1.1	1.8	1.6	1.3	1.1	1.0	1.1	0.9	1.1	1.0	1.5	1.2	1.6	1.0	1.5	1.1-2.8	1.7	0.46	0.04

**Table 7-4.** Dentitional characters, myomere counts, oral fimbriae and papillae, and caudal fin pigmentation in recently metamorphosed individual and adults of *Lethenteron ninae*; u = unicuspid, b = bicuspid.

Character	Recently metamorphosed individual, SNP 377	Mature adults, SNP 253, SNP 258b, SNP 377, SNP 378, n=14
Transverse lingual lamina	undetermined	5u-I-6u (2), 4u-I-5u (2), 4u-I-4u (2), 6u-I-5u, 7u-I-5u, 4u-I-3u, 8u-I-7u, 2u-I-2u, 3u-I-2u, undetermined (2)
Longitudinal lingual laminae	undetermined (2)	5 (3), 6 (2), 7 (1), 8 (2), 9 (1), undetermined (19)
Supraoral lamina	I-I	I-I (14)
Infraoral lamina	undetermined	1b3u1b (4), 7u (3), 1b5u, 5u1b, 1b1u1b1u1b, 6u1b, 1b4u1b, undetermined (2)
Endolaterals	undetermined (2)	2-2-2 (10), 2-3-2 (14), undetermined (4)
Rows of anterials	undetermined	1 (7), 2 (5), undetermined (2)
First arterial row	undetermined	4 (4), 5 (6), 6 (2) undetermined (2)
Rows of posterials	0	0 (1), 1 (13)
First posterial row	absent	absent (1); incomplete (9): 1u-gap, 1u-gap-1u, 2u-gap-2u, 3u-gap-3u, 1b-gap-3u, 1b4u-gap-3u1b, 6u-gap-9u, 6u-gap-2u-gap-8u, 1b-gap-1u-gap-3u-gap-5u; complete (2): 3b15u1b, 1b18u1b; undetermined (2).
Trunk myomeres	58	58 (3), 59 (8), 60 (2), 61 (1)

Myomeres to origin of first dorsal fin	35	32(3), 33(8), 34 (1), 35(2)
Myomeres to insertion of first dorsal fin	46	46(3), 47(7), 48(3), 49(1)
Oral fimbriae	90	70, 79, 81, 85, 88, 90 (2), 91 (2), 94 (2), 95, undetermined (2)
Oral papillae (n=8)	18	16, 19, 23, 24(2), 25, 26
Caudal fin pigmentation	+	+ (8), ++ (5), +++ (1)

Supraoral lamina with two unicuspid teeth, which can be either blunt (Fig. 7-5A, B, centerfold, page xvi) or sharp (Fig. 7-5C, D, centerfold, page xvi), separated by a toothless bridge, as was reported in Naseka et al. (2009), which is relatively short being less than (Fig. 7-5 A, B, centerfold, page xvi) or about equal to the length of the tooth base (Fig. 7-5 C, D, centerfold, page xvi).

Infraoral lamina comprises 5–7 teeth, usually arranged in a variable order of unicuspid and bicuspid teeth (75% of specimens), but also may occur as unicuspid teeth only (25%). The same range was found in Naseka et al. (2009) and the percentage of specimens with unicuspid-bicuspid versus only unicuspid teeth was very similar (i.e., 69% : 31%).

Three endolaterals on both sides of the oral disc either all bicuspid (in 4 specimens) or middle endolateral tricuspid (in 6 specimens); in 2 specimens, the middle endolaterals are asymmetrically developed—bicuspid on one side and tricuspid on the other side. Naseka et al. (2009) also reported the endolateral tooth formulae 2–2–2 and 2–3–2, but in contrast to the present study, the former formula was the modal condition instead of the latter formula. Additionally, Naseka et al. (2009) found a less frequent formula (i.e., 2–2–3) not found in the present study. Size and shape of the middle tricuspid endolateral vary: in some specimens (as in Fig. 7-5C, D, centerfold, page xvi) the three cusps are sharp and prominent, while sometimes one of the three cusps can be very small and poorly developed.

Rows of anterials 1–2, as was also reported by Naseka et al. (2009), but in contrast to the present study, the latter was the mode. First row of anterials with 4–6 unicuspid teeth, while Naseka et al. (2009) reported 5–7 unicuspid teeth; however, the mode of 5 is identical in both studies.

Exolaterals absent in all specimens, as was also reported in Naseka et al. (2009).

Posterials absent (in one specimen) or in a single row, either incomplete (9) or complete (2) (Table 7-4). Another specimen, still in an aquarium, from the Psiya River also possessing a complete row of posterials, as ascertained when attached by its oral disc to the glass of the aquarium. The number and pattern of posterials vary considerably – from a single cusp at one end of the row (1u-gap) to almost complete (e.g. 6u-gap-2u-gap-8u) and complete (3b15u1b or 1b18u1b). There are 19–20 teeth in the two preserved specimens with a complete posterial row and 23 in the aquarium specimen (Fig. 7-5D, centerfold, page xvi). Therefore, the number of posterials in a complete row in *L. ninae* is 19–23. While Naseka et al. (2009) also reported wide variability in the number and pattern of teeth in the first posterial row, from absent to incomplete, the

latter either comprising only unicuspid teeth or a mixture of unicuspid and bicuspid teeth, they did not report any cases of a complete row, in contrast to the present study.

In two specimens, there is an additional cusp next to the single posterior row (Fig. 7-5D, centerfold, page xvi).

Velar tentacles (in four specimens dissected) 5–7: 2-1-2 (2), 2-1-3 or 2-1-4 (3-1-3 was reported in two paratypes by Naseka et al. (2009)). The median tentacle shorter than adjacent lateral ones; tentacles with tubercles on the dorsal aspect; no wings as reported in Naseka et al. (2009).

Number of trunk myomeres 58–61 with a mode of 59 (Table 7-4), similarly to those reported by Naseka et al. (2009), except that in the latter the range was 58–62. Number of myomeres to origin of first dorsal fin 32–35 with a mode of 33 and number of myomeres to end of first dorsal fin 46–48 with a mode of 47. Neither of these characters were assessed in Naseka et al. (2009).

Oral fimbriae 70–95 (90–94 in 54% of specimens) (Table 7-4), while Naseka et al. (2009) reported a wider range of 69–99 (89–94 in 46% of specimens). Oral papillae 16–26 (Table 7-4). Oral papillae were not assessed by Naseka et al. (2009).

Caudal fin shape spade-like (Figs. 7-4, 7-6A), while Naseka et al. (2009) also reported rounded.

Colouration of live and freshly preserved adults not mottled, greyish, back darker than belly; caudal fin pigmentation varies from slight (1% to < 25% coverage, in 9 specimens) to moderate (25% to < 75%, in 5) to strong ( $\geq 75\%$ , in 1) (Figs. 7-4, 7-6A). Some caudal fins though pigmented at the base look almost hyaline (Fig. 7-6A, centerfold, page xvii) compared to the condition in *E. mariae* (Fig. 7-6B, centerfold, page xvii) in which the pigmentation often covers the entire fin.

Dark blotch near the apex of the second dorsal fin (Figs. 7-4, centerfold, page xv and 7-6A, centerfold, page xvii) in all specimens, as was also reported in Naseka et al. (2009). Lateral line neuromasts darkly pigmented on the ventral surface and in the prebranchial region (Fig. 7-5, centerfold, page xvii) in some individuals and unpigmented in others, as was also reported in Naseka et al. (2009).

Based on data from both the type series and the additional material described above, a revised diagnosis of *L. ninae* is as follows:

*Lethenteron ninae* possesses in adults an oral disc 3.8–5.7% of TL; a transverse lingual lamina with an enlarged median cusp and two to eight cusps on either side; a broad supraoral lamina with two marginal cusps separated by a toothless bridge; an infraoral lamina with 5–7 teeth usually arranged in a variable order of unicuspid and bicuspid teeth; an endolateral

tooth formula 2–2–2 (52% of specimens) or 2–3–2 (41%); 1 or 2 rows of anterials with 4–7 unicuspid teeth in the first row (mode of 5); no exolateral rows; usually a single row of posterials (absent in 22% of specimens), either incomplete (65%) with 1–16 teeth or complete (13%) with 19–23 teeth; an additional cusp next to the posterial row may be present (9%); a typically spade-like and slightly to moderately pigmented caudal fin; 58–62, with a mode of 59, trunk myomeres; and reaches total lengths of 115–172.5 mm. The ammocoetes have a body colouration without mottling; the area between the upper lip and cheek, cheek, subocular, upper prebranchial, upper branchial, and predorsal areas strongly pigmented; the lower prebranchial area moderately or strongly pigmented; the lower branchial area unpigmented or slightly pigmented; the lower lip area slightly pigmented; the ventral branchial area pigmentation absent to trace or slight; a usually spade-like caudal fin; an unpigmented triangular middle prong of the tongue precursor and usually strongly pigmented areas lateral to the elastic ridge; 56–61 trunk myomeres, with a mode of 58; and reach at least 172.5 mm TL based on a recently metamorphosed individual, although our longest ammocoete was 162.2 mm TL.

It undergoes metamorphosis in September–December at 166–173 mm TL; mature adults are 115–155 mm TL.

### **Diagnostic characters of *Eudontomyzon*, *Lampetra*, and *Lethenteron* and generic assignment of *L. ninae***

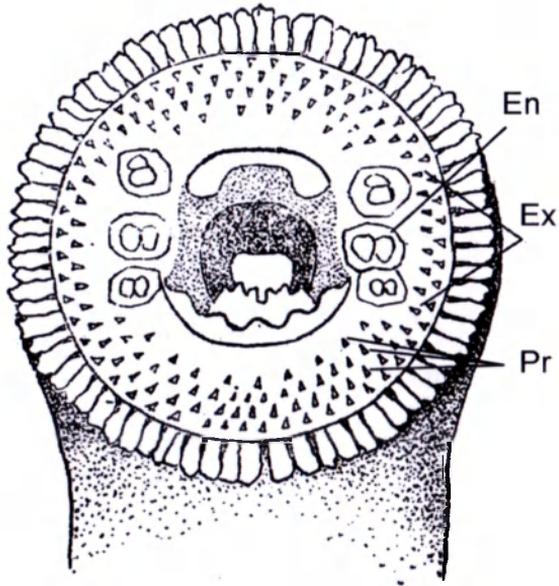
Though the pattern and morphology of teeth in the oral disc are the most informative morphological characters in adults of lamprey of the family Petromyzontidae, there are no character states that delimit species commonly assigned to *Eudontomyzon*, *Lampetra*, and *Lethenteron* with a complete gap between the genera.

*Exolaterals* (Table 7-5). The genus *Eudontomyzon* is usually diagnosed by the presence of numerous exolateral teeth arranged in 1–6 rows on either side of the oral disc, although a few cases in which exolaterals were absent have been reported in *E. stankokaramani* by Holčík & Šorić (2004). The presence of exolateral rows (also known as alate rows in the lateral fields) was the only derived character defining the monophyly of parasitic species of *Eudontomyzon* (Gill et al. 2003). However, in both *Lampetra* and *Lethenteron*, there are also species possessing exolaterals – *Lampetra aepyptera* with 1–2 rows and *L. zanandreae* sometimes with 1 row and *Lethenteron alaskense* Vladykov & Kott, 1978 occasionally with 1–2 teeth or rarely 1 row, and *L. appendix* (DeKay, 1842), *L. reissneri*, *L. mitsukurii*

(Hatta, 1901) (traditionally synonymized with *L. reissneri*), and *Lethenteron* sp. from Sakhalin (ZIN 25204), often with one or two teeth. Exolaterals have not been found in *L. ninae* thereby excluding it from *Eudontomyzon*. A geographically close lamprey described by Kokotshashwili (1942, fig. 1) from the Makhindzhauris-tskali River (Fig. 7-1, locality 19), representing a *Eudontomyzon* lamprey, possesses a single row of 8 exolaterals on both sides of the oral disc (Fig. 7-7).

*Posterials* (Table 7-5). Besides the absence of exolaterals, the genus *Lampetra* is usually diagnosed by the absence of posterials which are commonly present in *Lethenteron* (typically a single row) and *Eudontomyzon* (1–4 rows, but in 10% of *E. mariae* and in most *E. stankokaramani* they are absent). The drawing of the *Eudontomyzon* lamprey described by Kokotshashwili (1942, fig. 1) (Fig. 7-7) from the Makhindzhauris-tskali River shows three complete rows of posterials. In a number of *Lampetra* species, both parasitic and nonparasitic – *L. ayresii* (Günther, 1870), *L. fluviatilis*, *L. pacifica* Vladykov, 1973, *L. planeri* – posterials are invariably absent. However, in *L. aepyptera* one row of posterials is sometimes present being either complete, but usually incomplete, with 1–22 teeth. In *L. richardsoni* Vladykov & Follett, 1965 the usual condition is for posterials to be absent, but a single case was reported where two posterial teeth were found in an incomplete row and in *L. zanandreae* (recently returned to *Lampetra* from *Lethenteron*) the row of posterials is incomplete, with 2–5 teeth. In *L. hubbsi* (originally described in *Entosphenus*) the row of posterials is usually complete, with 8–12 teeth, but can also be incomplete with 6 teeth. The character state in *L. lanceolata* is known only from one specimen in which a single very small posterial tooth was found.

Typically, *Lethenteron* species (*L. camtschaticum* and its satellite species *L. alaskense*, *L. kessleri*, *L. reissneri*, and *L. appendix*) possess a single and complete first row of posterials with 16–29 teeth. Furthermore, a second row of posterials may also be present in *L. reissneri* (Renaud & Naseka 2015, fig. 4) and in *L. mitsukurii*, and *Lethenteron* sp. from Sakhalin (ZIN 25204). As described above, *L. ninae* usually has one row of posterials, incomplete (with 1–16 teeth) or complete (with 19–23), and, in two cases, next to this posterial row an additional tooth was present (such a condition may be classified as a single tooth in the second posterial row). The presence of a row of posterials was the main argument for assigning this species to *Lethenteron*.



**Figure 7-7.** From Kokotshashwili (1942, fig. 1): oral disc of lamprey identified as *Eudontomyzon mariae* from Makhindzhauris-tskali River characterized by a complete row of exolaterals (Ex), bicuspid middle endolateral (En), and three rows of posterials (Pr).

**Table 7-5.** Diagnostic characters of oral disc dentition and trunk myomeres in *Eudontomyzon*, *Lampetra*, and *Lethenteron* species (summarized original data and from literature sources). The cusp formula for each endolateral is given (1 = unicuspid, 2 = bicuspid, 3 = tricuspid).

Species	Endolaterals	Exolaterals	First posterial row	Trunk myomeres	Longitudinal lingual laminae	Velar wings	Source
<i>Eudontomyzon danfordi</i>	1-2-2, 2-2-2, 1-2-1, rarely 1-1-2, 2-2-1, 2-3-2, 1-2-2-1, 2-2-2-1, 1-2, 1-3-2, 1-3-1	2-5 rows	Complete (15-28 teeth)	59-68	Straight	Present	Gill et al. (2003), Renaud (2011)
<i>Eudontomyzon graecus</i>	2-2-2, 2-2-2-2, rarely 2-2-2-1, 1-2-2, 3-2-2, 2-2-2-3	3-4 rows	Complete (10-15 teeth)	53-61	Undetermined	Absent	Renaud & Economidis (2010)
<i>Eudontomyzon hellenicus</i>	2-2-2, 1-2-2, rarely 2-2-3, 1-2-1, 1-1-1, 2-3-2	2-6 rows	Complete (10-15 teeth)	54-62	Undetermined	Absent	Renaud & Economidis (2010)
<i>Eudontomyzon mariae</i>	highly variable, most commonly 1-2-2, 1-2-1, 2-2-1, 2-2-2	1-4 rows	Absent (rarely), complete (11-20 teeth) or incomplete (1-17)	60-73	Undetermined	Present or absent	Salewski et al. (1995), Renaud (2011)

<i>Eudontomyzon morii</i>	2-2-2, 1-1-1	1-2 rows	Complete (19-24 teeth)	68-74	Straight	Present	Gill et al. (2003), Renaud (2011)
<i>Eudontomyzon stankokaramani</i>	1-2-1, rarely 1-1, 1-2, 1-1-1	Absent or 1-3 rows	Absent or complete (15 teeth)	58-65	Undetermined	Present	Renaud & Economidis (2010)
<i>Lampetra aepyptera</i>	2-1-2, 1-1-1, 2-3-2, 2-3-3	1-2 rows	Absent or 1 row, incomplete or, less often, complete (1-22 teeth)	53-62	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)
<i>Lampetra ayresii</i>	2-3-2, very rarely 2-2-2	Absent	Absent	60-71	Straight	Absent	Vladykov & Kott (1976), Gill et al. (2003), Renaud (2011)
<i>Lampetra fluviatilis</i>	2-3-2, very rarely 1-3-2, 2-3-1	Absent	Absent	58-66	Straight or parentheses shaped	Absent	Renaud (2011)
<i>Lampetra hubbsi</i>	1-1-1-1, occasionally middle endolateral tricuspid	Absent	Complete (8-12 teeth) or incomplete (6)	50-57	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)
<i>Lampetra lanceolata</i>	2-2-2	Absent	Incomplete (1 tooth)	58-64	Undetermined	Absent	Naseka et al. (2009), Renaud (2011)

<i>Lampetra pacifica</i>	highly variable, upper and middle teeth 1-3, lower tooth 1-2	Absent	Absent	53-58	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)
<i>Lampetra planeri</i>	2-3-2	Absent	Absent	60-65	Undetermined	Absent or present	Vladykov & Kott (1976), Kappus et al. (1995), Renaud (2011)
<i>Lampetra richardsoni</i>	1-2-1, 2-2-1, 2-2-2, 2-3-2, rarely 2-3-1	Absent	Absent, rarely incomplete (2 teeth)	60-67	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)
<i>Lampetra zanandreaei</i>	2-3-2 or 2-2-2	Absent or 1 row	Incomplete (2-5 teeth)	54-60	Undetermined	Absent	Renaud (2011)
<i>Lethenteron (?) ninae</i>	2-2-2 or 2-3-2, rarely 2-2-3	Absent	Commonly incomplete (1-16 teeth); also complete (19-23) or absent	58-62	Straight	Absent	Naseka et al. (2009), this study
<i>Lethenteron alaskense</i>	2-2-2	Absent or 1-2 teeth or rarely 1 row	Complete (17-24 teeth)	66-72	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)
<i>Lethenteron appendix</i>	2-2-2	Absent, more rarely 1 or 2 teeth	Complete (20 teeth)	64-74	Undetermined	Absent	Vladykov & Kott (1976), Renaud (2011)

<b><i>Lethenteron camtschaticum</i></b>	2-2-2, rarely 2-2-1, 2-2-2-2, 2-2-2-1	Absent	Complete (12-22 teeth)	65-77	Parentheses shaped	Present	Gill et al. (2003), Renaud (2011)
<b><i>Lethenteron camtschaticum septentrionalis</i></b>	2-2-2, rarely 2-2-1	Absent	Complete (18-22 teeth)	75	Undetermined	Undetermined	This study
<b><i>Lethenteron kessleri</i></b>	2-2-2, rarely 2-2-3	Absent	Complete (24-29 teeth)	70-74	Undetermined	Undetermined	This study
<b><i>Lethenteron mitsukurii</i></b>	2-2-2	Absent or 1-2 teeth	Complete (20-21 teeth)	66-67	Undetermined	Undetermined	This study
<b><i>Lethenteron reissneri</i></b>	2-2-2	Absent, rarely 1 or 2 teeth	Complete (24 teeth)	70-72	Undetermined	Undetermined	Renaud & Naseka (2015)
<b><i>Lethenteron</i> sp. (brook lamprey, Sakhalin)</b>	2-2-2	Absent or 1 tooth	Complete (20 teeth)	68	Undetermined	Present	Vladykov & Kott (1978), this study

*Endolaterals* (Table 7-5). The presence of tricuspid middle endolaterals (also known as second lateral circumorals) was one of two synapomorphic characters defining the parasitic species of the genus *Lampetra* (Gill et al. 2003). The nonparasitic *Lampetra* species, *L. aepyptera*, *L. pacifica*, *L. planeri*, *L. richardsoni*, *L. zanandreae*, exhibit some variability in this character, but commonly possess tricuspid middle endolaterals, while *L. hubbsi* only occasionally does. However, *L. lanceolata* only exhibits the bicuspid condition. This is perhaps not surprising given the inherent variability of the character and the low number of specimens of this species studied. In species of *Eudontomyzon* the character states for the middle endolateral are either bicuspid or unicuspid (*E. graecus*, *E. morii* and *E. stankokaramani*) or in those species for which a tricuspid state for the middle endolateral is known (*E. danfordi*, *E. hellenicus*, *E. mariae*), it occurs in less than 5% of the cases. For example, Naseka et al. (2009) studied 31 syntypes of *E. mariae* and found only two cases out of a total of 62 middle endolaterals (3%) with a tricuspid condition. In *Lethenteron* the middle endolateral is invariably bicuspid. While the original description of *L. ninae* reported tricuspid endolaterals in 4 cases out of 20 (20%), this study found even more cases (14 of 24 or 58%) for a combined occurrence of 41%. The high value of tricuspid middle endolateral presence in *L. ninae* versus invariable bicuspid occurrence in *Lethenteron* species indicates that *L. ninae* should be aligned with *Lampetra* rather than *Lethenteron*.

*Trunk myomeres* (Table 7-5). *Eudontomyzon* species have 53–74 trunk myomeres, while *Lampetra* species have 50–71, and *Lethenteron* species (excluding *L. ninae*) have 64–77. *Lethenteron ninae* has 58–62 trunk myomeres and this character aligns the species with *Lampetra* rather than *Lethenteron* since *Eudontomyzon* had previously been excluded on the basis of the absence of exolaterals in *L. ninae*.

*Longitudinal lingual lamina* (Table 7-5). A straight longitudinal lingual lamina was the single synapomorphy defining parasitic species of *Lampetra* + *Eudontomyzon* (Gill et al. 2003), and this is the character state also found in *L. ninae*, while the plesiomorphic state (i.e., parenthesis-shaped lamina) occurred in parasitic *Lethenteron*. Unfortunately, the character state in other nonparasitic species of *Eudontomyzon*, *Lampetra*, and *Lethenteron* is undetermined, in part because of the poor development of this structure in these species. Additionally, parentheses-shaped laminae, the plesiomorphic state, have also been reported in *L. fluviatilis*. These two points notwithstanding, the presence of straight longitudinal lingual laminae in *L. ninae* is evidence for its alignment with *Lampetra* + *Eudontomyzon* rather than *Lethenteron*.

*Velar wings* (Table 7-5). The absence of velar wings was the other character, besides the tricuspid middle endolateral tooth (see above), defining the monophyly of the parasitic species of the genus *Lampetra* (Gill et al. 2003), and this is also the character state found in *L. ninae*. Velar wings are also absent in the nonparasitic *Lampetra aepyptera*, *L. hubbsi*, *L. lanceolata*, *L. pacifica*, *L. richardsoni*, and *L. zanandreae*, and may either be absent or present in *L. planeri*. The plesiomorphic condition of possessing velar wings occurs in *Eudontomyzon* and *Lethenteron*. However, the absence of velar wings has also been reported in nonparasitic *E. graecus*, *E. hellenicus*, *E. mariae* (although they may also be present in this species), *L. alaskense*, and *L. appendix*. Notwithstanding the possible independent losses of velar wings in the aforementioned species, absence of wings in *L. ninae* aligns it with *Lampetra* rather than *Lethenteron*.

This study establishes in *L. ninae* the usual presence of a row of posterial teeth (either complete, but more often incomplete), which is typical for the genus *Lethenteron*. However, it cannot be excluded that this characteristic is a homoplastic character independently evolved in *Lethenteron* and *Lampetra*. Similar to *Lampetra*, but in a contrast to *Lethenteron*, *L. ninae* often has a tricuspid middle endolateral, a low number of trunk myomeres, straight longitudinal laminae, and no velar wings. This morphological evidence suggests that *L. ninae* should be assigned to *Lampetra* rather than *Lethenteron*. We delay doing so until a total evidence cladistic analysis that includes both parasitic and nonparasitic species and integrates both morphological and molecular characters has been completed. This will ensure that species are not continuously being re-allocated to various genera on the basis of incomplete information.

## Comparative Material

*Lethenteron camtschaticum septentrionalis* (Arctic Ocean basin, Europe): ZIN 12159, **syntypes**, 8 adults, TL 281–374 mm; Onega River at Podporozhye, White Sea basin, Russia, Dec. 1901, N.A. Varpakhovskiy.

*Lethenteron kessleri* (Arctic Ocean basin, Asia): TGU 3 [No 3699 in Ioganzen (1935, tabl. 3)], **syntype**, adult female, TL 182 mm; Kirgizka River at Tomsk, Tom' River system, Ob' River drainage, Russia, 24 Dec. 1899, A. Neiland; TGU 9 [No 3696 in Ioganzen (1935, tabl. 3)], **syntypes**, 6 adults (from 10), TL 128.0–165.0 mm; River Tom' mouth at Kozyulino (from gull's crop?), Ob' River drainage, 28 June 1903, G. Ioganzen.

*Lethenteron mitsukurii* (Pacific Ocean basin): ZMB 20638, **syntypes**, 2 adults, TL 138.3–140.1 mm; Hondo (=Honshu) and Hokkaido, Japan.

*Lethenteron* sp. (Pacific Ocean basin): ZIN 25204, adult female, TL 146.0 mm; Tym' River, Sakhalin Island, Russia, A.Ya. Taranets [possibly a new species according to Berg (1948, p. 43, fig. 30)].

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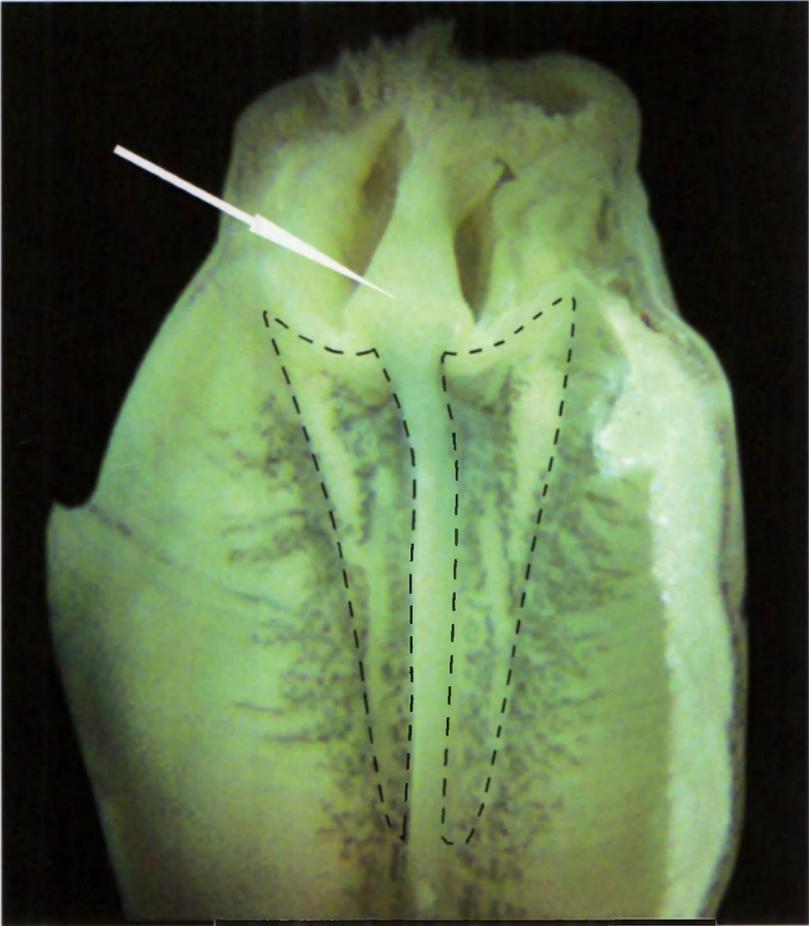
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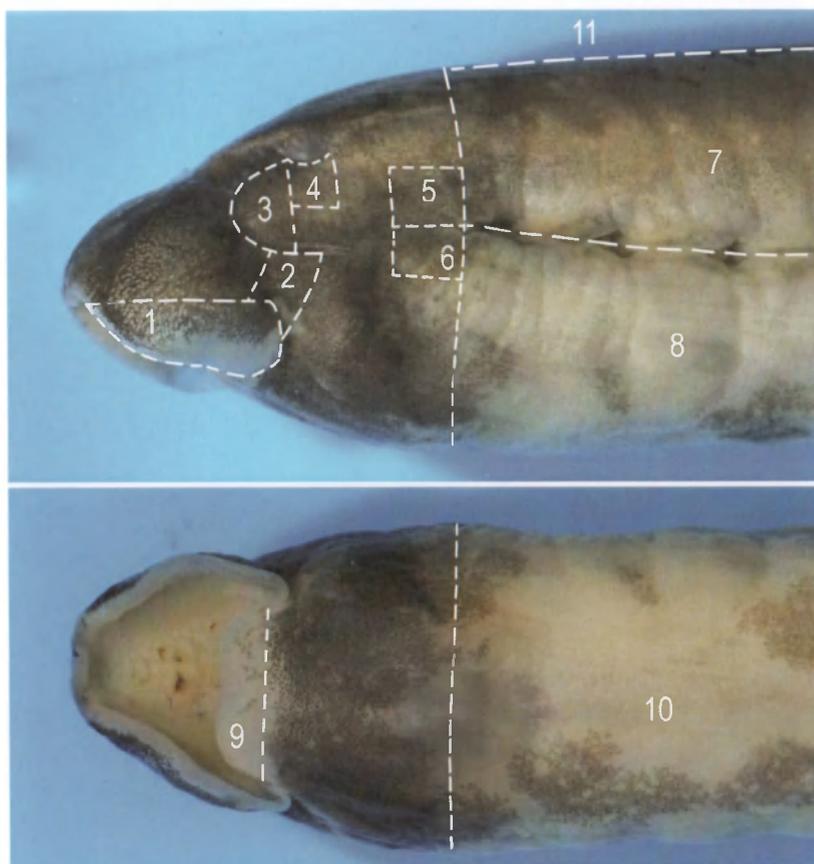
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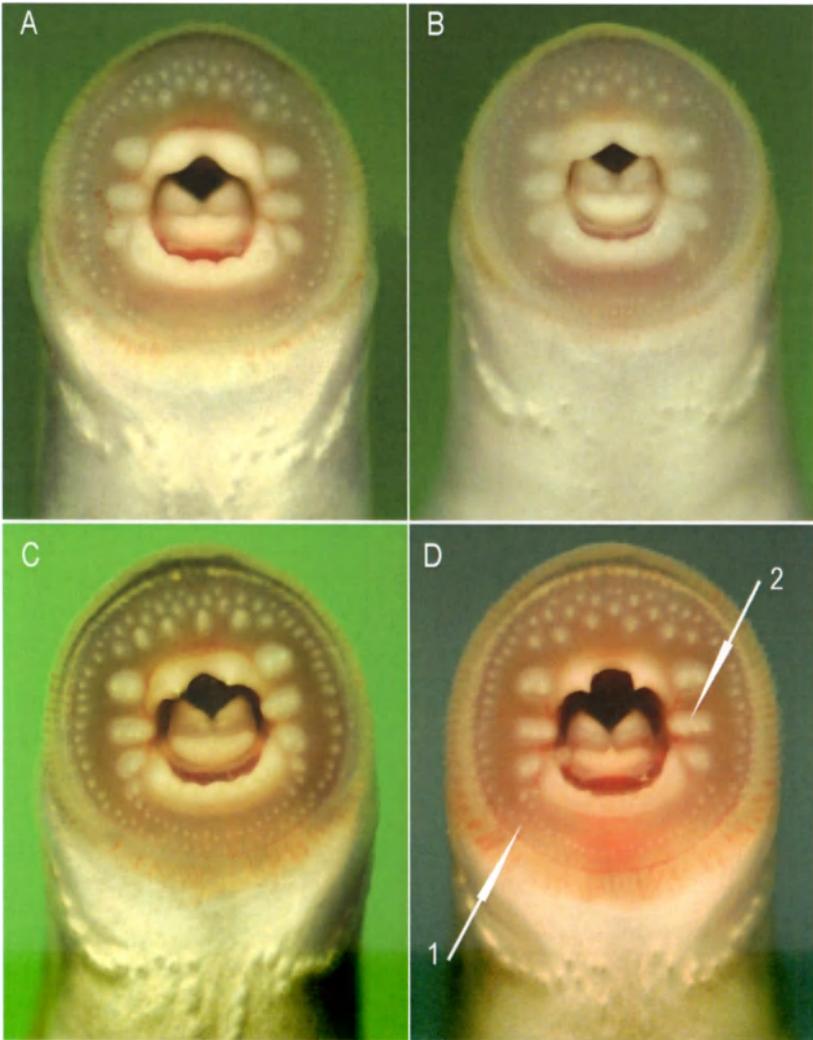
**Figure 7-2.** Tongue precursor in ammocoete of *Lethenteron ninae*. Arrow indicates middle prong of the tongue precursor, dashed line indicate areas lateral to elastic ridge.



**Figure 7-3.** Pigmentation areas in ammocoetes of *Lethenteron ninae*: 1, upper lip; 2, between upper lip and cheek; 3, cheek; 4, subocular; 5, upper prebranchial; 6, lower prebranchial; 7, upper branchial; 8, lower branchial; 9, lower lip; 10, ventral branchial; 11, predorsal.



**Figure 7-4.** *Lethenteron ninae* adult, TL ca. 140 mm (aquarium specimen), Psiya River near Khartsyz, tributary of Shakhe River, Sochi District, Russia.



**Figure 7-5.** Oral disc in adult *Lethenteron ninae*: (A) incomplete first posterial row 2u-gap-2u, Mokvi River; (B) incomplete first posterial row 1b-gap-1u-gap-3u-gap-5u, Psiya River; (C) complete first posterial row 1b-18u-1b, Mzymta River; (D) complete first posterial row 1b-22u, Psiya River (aquarium specimen). Arrows indicate an additional cusp next to the single posterial row (1) and tricuspid middle endolateral tooth (2).



**Figure 7-6.** Posterior section of body in live adults of (A) *Lethenteron ninae* (TL ca. 140 mm, Psiya River near Khartsyz, tributary of Shakhe) and (B) *Eudontomyzon mariae* (TL ca. 190 mm, Ubinka River, tributary of Kuban).