A New Nonparasitic Species of the Holarctic Lamprey Genus LETHENTERON Creaser and Hubbs, 1922, (Petromyzonidae) from Northwestern North America with Notes on Other Species of the Same Genus

VADIM D. VLADYKOV AND EDWARD KOTT

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by

Vadim D. Valdykov
Department of Biology
University of Ottawa

and

Museum of Natural Sciences
National Museums of Canada
Ottawa, Ontario,
Canada

and

Edward Kott
Department of Biology
Wilfrid Laurier University
Waterloo, Ontario,
Canada

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**ABSTRACT**

A new nonparasitic lamprey, *Lethenteron alaskense* from Alaska and Northwest Territories is described and illustrated. The holotype (No. NMC 76-614) is deposited in the National Museum of Natural Sciences, Ottawa, Canada. The study was based on 67 metamorphosed specimens. The species, by its permanently non-functional intestinal tract and weak dentition, smaller disc and much smaller size (maximum 188 mm), is easily separable from the parasitic *Lethenteron japonicum* (maximum length 625 mm) found in the same areas. It is distinguishable from nonparasitic *L. lamottenii*, found in eastern and southern North America, by 1) a generally weaker dentition but possessing more anterials and supplementary marginals; 2) typically with five velar tentacles as opposed to seven in *L. lamottenii*; 3) differences in pigmentation pattern of the second dorsal fin and a lack of dark pigmentation on the gular region; 4) smaller size in comparison to 299 mm maximum length in *L. lamottenii*; and 5) distinct areas of geographical distribution separated from each other by 2400 km. All three, *L. alaskense*, *L. lamottenii*, and *L. japonicum* have usually 66 to 72 trunk myomeres. *L. alaskense*, by its higher number of myomeres is separable from two other nonparasitic species: *L. reissneri* from Asia with less than 64 myomeres and *L. meridionale* from eastern tributaries of the Gulf of Mexico with 50 to 58 myomeres.
Introduction

The occurrence and distribution of the Arctic lamprey *Lethenteron japonicum* (Martens), a parasitic species, in Alaska and northwestern Canada is well documented (Walters, 1953, 1955; Wilimovsky, 1954; Heard, 1966; Buchwald, 1968; McPhail and Lindsey, 1970; Nursall and Buchwald, 1972; Quast and Hall, 1972; Scott and Crossman, 1973; Morrow, 1974). Several authors have also noted a second form of the genus *Lethenteron* from these regions. Some have concluded that this second form is indistinguishable from *L. lamottenii* (Le Sueur), a nonparasitic species of eastern and southern North America (Wilimovsky, 1954; Hubbs and Lagler, 1964; Quast and Hall, 1972).

McPhail and Lindsey (1970), compared *L. japonicum* and *L. lamottenii* and were unable to find significant differences between the two species. They suggested also that further studies may show that the two forms are not specifically distinct.

Heard (1966) on the basis of extensive material from the Alaska Peninsula found that *L. japonicum* located in the Naknek River system, is represented by both anadromous and dwarfed land-locked forms. The latter is the more common of the two. In abstract he states that “Mature, spawning, and spent lampreys of this form (land-locked) are morphologically almost identical with nonparasitic *L. lamottenii*”. Further on (page 332) he concludes that “available evidence suggests, however, that all lampreys in the Naknek system are parasitic *L. japonica*”.

With Heard's kind cooperation we reexamined his material as well as specimens obtained from several other areas. We disagree with Heard's final conclusion and have recognized the existence of a new, nonparasitic species of the genus *Lethenteron* in North America.

Although this new species is closer to *L. lamottenii* than to any other species of the genus, it is clearly distinct at the species level.
Materials and Methods

The material of the new species consists of 67 transformed (i.e. metamorphosed) lampreys of which 36 are from the Naknek River system, Alaska Peninsula, 9 transformed lampreys from Chatanika River near Fairbanks, Alaska, and 22 transformed individuals and 4 ammocoetes from Martin River of the Mackenzie River basin, Northwest Territories. Collection details are discussed in the section dealing with the description of the holotype and paratypes.

For comparison only transformed individuals of all known species of Lethenteron were examined as follows:

(a) *L. lamotteni* (Le Sueur) — 185 specimens from Quebec and New Hampshire to Alabama (Tables 15, 16, 23).
(b) *L. japonicum* (Martens) — 107 specimens from Beaufort Sea of the Mackenzie River system, Alaska, Japan (Hokkaido), Amur River (U.S.S.R.) and Kara Sea (Tables 9, 10, 22).
(c) *L. reissneri* (Dybowski) — 23 specimens from Japan (Hokkaido) and Sakhalin Island (Tables 17, 18, 24).
(d) *L. meridionale* Vladykov, Kott and Coad-Pharand — 81 specimens, for details see Vladykov, et al. (1975)

Measurements

Measurements and meristic counts were made typically on the left side of the specimen and follow the procedures outlined by Vladykov and Follett (1965). Measurements are expressed as percentages of the total length of the specimen: the disc length (d) is also expressed as a percentage of the branchial length (B1-B7). The following abbreviations are used, as in Vladykov and Follett (1965).

a-C *Tail length*, the distance from the posterior edge of the cloacal slit to the end of the caudal fin.

B7-a *Trunk length*, the distance from the posterior edge of the last (seventh) branchial opening to the anterior edge of the cloacal slit.

B1-B7 *Branchial length*, the distance from the anterior edge of the first branchial opening to the posterior edge of the last (seventh) branchial opening.

d *Disc length*, longitudinal diameter, with the oral fimbriae included, measured with the disc closed.

d-B1 *Prebranchial length*, the distance from the anterior edge of the disc (in transformed individuals) or of the upper lip (in ammocoetes) to the anterior edge of the first branchial opening.
NEW SPECIES OF LAMPREY

O  *Eye length*, the horizontal diameter of the eye.

TL  *Total length*, the distance from the anteriormost oral fimbria to the end of the caudal fin.

The terminology of lamprey teeth is that of Vladykov and Follett (1967). All cusps of different disc laminae were counted, if they were sufficiently developed or not damaged. In the case of a pair of longitudinal lingual laminae, the number of cusps on the left and right sides was not always identical. Therefore, cusps on a single lamina (irrespective of its position) were counted and results are presented in Table 26. In the description of the holotype, the number of cusps on both laminae is given.

For the study of the velar tentacles the following two cuts on the ventral surface of the head of transformed lampreys were made: a) a transverse cut to the first pair of branchial openings; then b) a horizontal cut forward to the level of the eye. The flap thus obtained can be flipped forward to expose the velar apparatus. This method does very little damage to a specimen and does not affect the observation of the teeth on the sucking disc. The number and shape of the velar tentacles are not affected by sex, size, and locality.

All specimens studied were marked with our plastic tags, having different colors and bearing letters and numbers.
**Taxonomy Of The Genus Lethenteron**  
Creaser And Hubbs, 1922

Creaser and Hubbs (1922) proposed a new subgeneric name *Lethenteron* based on the orthotype *Lampetra wilderi* Gage (= *Petromyzon appendix* DeKay). This orthotype is commonly accepted today under the specific designation *lamottenii* (Le Sueur) (Hubbs and Trautman, 1937).

Jordan, *et al.*, (1930) elevated the subgenus *Lethenteron* to generic status. *Lethenteron*, with three pairs of inner laterals and with a greatly enlarged median cusp on the transverse lingual lamina looks rather similar to the genus *Lampetra* Gray (1851) but differs in having a row of unicuspid posterial teeth, which are completely absent in *Lampetra* (Vladykov and Follett, 1967). In spite of this and a difference in geographical distribution several authors (Berg, 1931, 1948; Hubbs and Potter, 1971), to mention the most important, considered *Lethenteron* as a subgenus within the genus *Lampetra*.

Regan (1911) considered *Lampetra* Gray (1851) and *Entosphenus* Gill (1861) as two distinct genera. In the latter genus, in addition to *Entosphenus tridentatus*, several other species including the Arctic lamprey known then as *Lampetra japonica* were combined. As explained above we consider the Arctic lamprey to be *Lethenteron japonicum*. It must be stated that the genus *Entosphenus* as originally established by Gill (1862) has four pairs of enlarged laterals while *Lethenteron* has only three. Hence we cannot agree with Regan’s treatment. Moreover in *Entosphenus* the transverse lingual lamina has no greatly enlarged median cusp and some teeth of the posterial row are bicuspid. The supraoral lamina, at least in parasitic species, has typically three cusps instead of two as in *Lethenteron* and there are typically five cusps on the infraoral lamina instead of seven-eight in *Lethenteron*.

In the present article we consider *Lethenteron* as a distinct genus as it was defined by Vladykov and Follett (1967) and Vladykov and Kott (1976). We recognize the following species in the genus *Lethenteron*.

(a) *L. japonicum* (Martens, 1868) a parasitic species found in North America (Buchwald, 1968; McPhail and Lindsey, 1970; Nursall and Buchwald, 1972; Morrow, 1974) and Eurasia. Berg (1931: 98-103) recognized three forms of *L. japonicum*, which differ, in addition to their distribution, by their sizes. The largest form (*L. japonicum japonicum*) is found along the western Pacific coasts. *L. japonicum septentrionale* (Berg, 1931) distributed along the Arctic Ocean from the White Sea to the Ob basin, is intermediate in size, and *L. japonicum kessleri* (Anikin, 1905) found in the rivers of Siberia from the Ob to the Kolyma and Anadyr and also on Sakhalin Island, is the smallest. No doubt, there are distinct local populations of *L.*
*NEW SPECIES OF LAMPREY*

_**japonicum**_ in Eurasia and North America some of which are anadromous in habit, while others are non-migratory and possibly land-locked (Johansen, 1935a; b; c; Morozova, 1956; Nickolsky, 1956; Poltorykhina, 1971, 1974).

However, further more critical studies are required to elucidate these important points. Lacking sufficient material for comparison, we do not differentiate subspecies in the present study as recognized by Berg (1931).

(b) _L. lamottenii_ (Le Sueur, 1827) a nonparasitic species found in eastern and southern North America. Formerly this species was referred to as _wilderi_ Gage (in Jordan and Everman, 1896).

(c) _L. reissneri_ (Dybowski, 1869) a nonparasitic species found in Japan, Sakhalin Island, and Amur River basin (Jordan and Hubbs, 1925*; Berg, 1931; Sato, 1951; Morozova, 1956; Nickolsky, 1956; Abakumov, 1960; Okada, 1960; Hensel, 1963).

(d) _L. meridionale_ Vladykov, Kott and Coad-Pharand, 1975, a nonparasitic species from eastern tributaries of the Gulf of Mexico (Vladykov, et al., 1975).

(e) A new nonparasitic species the description of which follows.

*These authors called this species _mitsukurii_ (Hatta) instead of the specific name _reissneri_ (Dybowski). However the description given by the authors, and particularly the low number of myomeres (56-59) unquestionably refers to the true _reissneri_.*
Description of
Lethenteron alaskense sp. nov.

This new nonparasitic species is named alaskense since the holotype and topotypic paratypes were collected in Alaska (Figs. 1 - 3).

Holotype
A male, 164 mm long with tag VDV4620 from West Creek, a tributary of Brooks Lake, Alaska; June 11, 1964; collected by W. Heard. Its present catalogue number is NMC76-614 and the specimen is deposited in the National Museum of Natural Sciences, Ottawa, Canada.

Diagnosis
This new nonparasitic species belongs to the genus Lethenteron Creaser and Hubbs, 1922. Transformed specimens are distinguishable from the parasitic species of the same genus, L. japonicum (Martens), by a permanently non-functional intestinal tract, weak dentition, smaller disc, and much smaller size.

It is separable from two other nonparasitic species by a higher number of trunk myomeres (66-72): L. reissneri has less than 64 myomeres, and L. meridionale has 50 to 58 myomeres.

The new species has about the same number of trunk myomeres as L. lamottenii, a third nonparasitic species, limited in distribution to eastern and southern North America. Our new species differs from L. lamottenii by: (1) smaller size; (2) a generally weaker dentition (infraoral and lingual laminae, and posteriors) but possessing more anteriors and supplementary marginals; (3) different number of velar tentacles: typically 5 in the new species and 7 in L. lamottenii; (4) differences in pigmentation pattern of the second dorsal fin and gular region (posterior ventral portion of disc), and (5) a different geographical distribution.

Description of Holotype

The holotype (Tag VDV4620), a male 164 mm in total length, is in spawning condition. Its nonfunctional intestine is reduced to an outside diameter of less than 1 mm. Measurements (in percentage of total length) are: disc length 6.1, prebranchial length 11.0, eye length 2.1, branchial length 10.4, trunk length, 46.3, and tail length 32.3. Disc length as a percentage of branchial length is 58.1. It has 69 trunk myomeres.

Since the holotype is in spawning stage, the two dorsal fins are touching one another and the genital papilla and disc are well developed. The anteriors field has about 31 anteriors, three of which nearest the supraoral lamina are larger than the rest. The supraoral lamina has a cusp at each end. There are three enlarged inner laterals on each side of the disc, all of which are bicuspid and
blunt. A few supplementary marginals are present along the right and left lateral sides of the disc. The infraoral lamina has seven small rounded cusps. On the posterior field there is a single row, somewhat irregular, of 22 unicuspid teeth which are blunt and weakly cornified. The transverse lingual lamina carries 13 weakly cornified cusps and those on the longitudinal lingual laminae were not equally developed: on the left were present six blunt cusps, while on the right there were nine.

Colour of the specimen preserved in 4-5% formalin is grey brown on the back and flanks with a whitish colored ventral surface.

Fig. 1 Lateral view of the holotype of *Lethenteron alaskense*, Tag VDV 4620, a male in spawning condition, TL (Total Length) 164 mm., West Creek, a tributary of Brooks Lake, Alaska.

Fig. 2 Enlargements of the head (a) and tail (b) regions of the holotype of *Lethenteron alaskense*, TL 164 mm.
NEW SPECIES OF LAMPIREY

There are 18 oral papillae dispersed around the disc, among the fimbriae. The buccal cavity and tongue are not pigmented and the gular region also lacks dark pigmentation. The first dorsal fin is without a distinct anterior dark blotch, while the second dorsal fin has a distinct dark blotch only in the upper anterior region. About one-half of the caudal fin, closest to the notochord, is darkly pigmented, and the fin itself is sharply triangular in shape.

Paratypes

The first 24 paratypes are toptotypic and the remaining are general paratypes, some of which were obtained close to the type locality while the others are from more distant places. Tags VDV4616-4619, 4621-4640 (16♂, 137-185 mm; 8♀, 122-172 mm): collected with holotype, same data and collector. Tags VDV4612-4614 (10♂, 143 mm; 2♀, 137-155 mm): Brooks River below outlet of Brooks Lake, Alaska; June 15, 1964; W. R. Heard. Tags B1891-1900 (4♂, 125-147 mm; 6♀, 128-168 mm): Brooks River, Alaska; August 22-September 25, 1962; W. R. Heard and Gissberg. Tags W1467-1475 (6♂, 155-179 mm; 3♀, 154-175 mm): Chatanika River, 1.5 km below Elliot Highway Bridge, Fairbanks area, Alaska; June 12, 1976; K. T. Alt and E. A. Roguski. Tags W851-865, 867, 869-873 (11♂, 140-188 mm; 10♀, 140-174 mm): Martin River, Mackenzie River system; Northwest Territories; November-December 1972 and January 1973; T. Rex Porter.

Transformed (Metamorphosed) Specimens

Total length – A sample composed of 38 males collected from both Alaska and the Mackenzie River ranged in total length from 125 to 188 mm (average 158.7 mm), while 30 females from the same area ranged from 122 to 175 mm (average 153.0 mm).

Body proportions (Tables 1-8) – For mean measurements in percentages of total lengths the first number refers to 38 males and the second to 30 females: disc length 5.7, 5.1; prebranchial length 11.4, 10.7; eye length 2.3, 2.3; branchial length 9.9, 10.1; trunk length 48.1, 50.9; tail length 30.8, 28.6; disc length in percentage of branchial length is 56.7 and 50.5.

The disc lengths of 11 males and 10 females from Martin River of Mackenzie River system, expressed in percentage of total lengths, were considerably shorter than disc lengths of specimens from other areas. The Martin River lampreys had recently undergone transformation and their discs did not reach full development. This has also affected the disc length/branchial ratio of the Martin River specimens.

Trunk myomeres (Table 21) – The number of trunk myomeres in 67 transformed specimens varies from 66 to 72 (average 69.4).

Dentition (Table 26) – Since this species is nonparasitic, its teeth are typically weakly cornified and blunt.
Fig. 3  Enlarged photograph of the disc of the holotype of *Lethenteron alaskense*, TL 164 mm. Note weakly developed and blunt cusps on the infraoral and transversal lingual laminae. Compare this figure with Fig. 4, the disc of *Lethenteron lamottenii*. 
Fig. 4  Enlarged photograph of the disc of *Lethenteron lamottenii*, a male, Tag W 681, TL 162 mm, Gatineau River, Quebec. Note strongly developed cusps on the infraoral and transversal lingual laminae.
The teeth on the anterior field are small, blunt and poorly cornified and only in a few specimens they may be better developed. They are in two series with larger teeth near the supraoral lamina and smaller ones towards the marginals. In three specimens only, the larger teeth are barely distinguishable in size from the smaller ones (VDV4612, VDV4617, VDV4625).

The average number of teeth on the anteriors field was 30.4 (range 23-38). A single row of posteriors teeth, 17-24 (average 20.2), small, rounded, weakly developed and often difficult to count, is present.

Among different types of teeth, the supraoral cusps are the best developed in our new species: among 34 specimens, 21 had rather sharp cusps, one at each end. An exception was one specimen, tag B1892, which had a pointed cusp at each end of the supraoral lamina and two small supplementary cusps in the middle.

Cusps on the infraoral lamina were blunt and poorly developed, averaging 8.6 (range 6-11).

All specimens have six enlarged inner laterals, three on each side of the disc, as is characteristic of the genus *Lethenteron*. The cusp formula was invariably 2-2-2.

The median cusp of the transverse lingual lamina is enlarged, whereas its lateral cusps are low, rounded and often obsolete, and in many specimens uncountable. The height of the transverse lingual lamina is relatively low compared to the width. The average number of cusps on this lamina in the 18 specimens was 12.0 (range 9-15).

The cusps of the longitudinal lingual laminae were low, rounded and often obsolete. Their average number per lamina was 8.5 (range 6-13).

Supplementary marginals are present on the lateral fields of the disc. In one specimen VDV4636, the marginals form a double row about the whole disc, approaching the condition seen by us in *L. meridionale* (Fig. 7).

**Velar tentacles** (Table 27) — Five velar tentacles were found most often, and the next frequent number was seven; the average being 5.8 (range 5-7). The tentacles were relatively short and slender with a median tentacle not very different from the lateral ones.

**Coloration** — The sides and backs of specimens fixed in 4-5% formalin are greyish brown and the lower surface is whitish. In most specimens the first dorsal fin is nonpigmented but an anterior dark blotch is present on the second dorsal fin. Specimens from Chatanika River differed from other areas in that on the rest of the second dorsal fin were some additional chromatophores. The caudal fin is heavily pigmented, usually covering the whole fin. In all specimens no dark pigmentation was present in the buccal cavity or on the tongue. In *L. alaskense* dark pigmentation is typically absent from the gular region of the disc, (Fig. 6) while in *L. lamotteni* it is always present, as noted by Kott (1974).
Sexual dimorphism (Tables 1-6) – The external appearances of males and females are similar to those described for *L. lamottenii* (Vladykov, 1949; Kott, 1974).

As Figs. 5 (a, b) clearly show, spawning males of *L. alaskense*, in addition to a well-developed genital papilla, have rather high second dorsal fin with an arch-like outline. In contrast, spawning females have a triangular shaped second dorsal fin and a well-developed anal fin-like fold.

There are also secondary sexual differences in body proportions. Disc length, prebranchial length, and tail length are greater in males; females have a relatively longer trunk.

**Fecundity** – Two females (Tags B1900 and B1897) from Brooks River, Alaska, maturity stage 5, 150 and 168 mm in length, collected during August 22 to September 25, 1962, had 2188 and 3477 eggs respectively, averaging 0.9 mm in diameter in both cases. Two females (Tags W865 and W867) from Martin River, Northwest Territories, maturity stage 3, 175 mm and 164 mm length, collected between November 1972 and January 1973 had 2700 (0.65 mm in diameter) and 3017 (0.55 mm in diameter) eggs respectively. The average for the four specimens is 2846 eggs.

**Ammocoetes** – Since our material of the larval stage of different species of *Lethenteron* is inadequate to make a comprehensive study, we shall omit in the present publication, any treatment of the ammocoetes.

**Comparison between Lethenteron alaskense and other species of the genus**

**Feeding habits** – *L. alaskense*, like *L. lamottenii*, *L. reissneri*, and *L. meridionale* is a nonparasitic species. *L. japonicum* is the only parasitic species in the genus. According to several authors (Richardson, 1836; Birman, 1950; Heard, 1966; McPhail and Lindsey, 1970; Nursall and Buchwald, 1972), it parasitizes different types of fishes in fresh and salt water.

**Number of myomeres** (Tables 21-25) – The number of myomeres in *L. alaskense* ranges from 66 to 72 (average 69.4). This is similar to that of *L. lamottenii* (range 66 to 74, average 68.9) and *L. japonicum* (range 65 to 73, average 69.5) but significantly higher than that found in *L. reissneri* (range 57 to 63, average 60.4) and *L. meridionale* (range 50 to 58, average 54.0; Vladykov, et al., 1975).

Since *L. lamottenii* is closest to *L. alaskense*, more details on its number of myomeres would be desirable. For different populations of *L. lamottenii* the number of trunk myomeres were given by the following authors: Vladykov, 1949 (range 64-70), McPhail and Lindsey, 1970* (range 64-76)*, Manion and Purvis, 1971 (range 70-73), Kott, 1974 (range 65-74), Rohde, *et al.*, 1975 (range 66-72), and Rohde, *et al.*, 1976 (range 64-72).

* These authors give data not for myomeres proper but for “muscle grooves”, the counts for which are somewhat higher than for myomeres.
For *L. japonicum* from Hokkaido, Japan, Sato (1951) found 68 to 77 myomeres; Heard (1966) reported 68 to 72 myomeres in anadromous *L. japonicum* from Alaska; McPhail and Lindsey counting muscle grooves, instead of myomeres give the following numbers: 68-74 grooves for Mackenzie River specimens and 65-80 for Alaskan specimens. *L. japonicum kessleri*, a land-locked form, has been reported to have 64 to 74 myomeres by Sato (1951) and 67 to 72 by Poltorykhina (1971, 1974).

*L. reissneri* definitely has a smaller number of trunk myomeres than *L. alaskense*. Jordan and Hubbs (1925) give 56 to 59 myomeres for *L. reissneri* from Japan. Okada (1960) reports 56 to 60 myomeres. In our material of 18 specimens the myomere range is 57 to 63 (average 60.3). The following three authors considerably extend the upper limit of trunk myomeres for *reissneri*: Berg (1931) mentions 56 to 67; Sato (1951) reported 57 to 66 and Poltorykhina (1974) 66 to 72. In our opinion the first two authors had mixed material of *L. reissneri* and perhaps *L. japonicum*. Data of Poltorykhina is not applicable for *L. reissneri*.

On the basis of trunk myomere number, the species of *Lethentron* can be divided into three groups: a) *L. meridionale* with an average of 54; b) *L. reissneri* with an average near 60; and c) the remaining three species with an average near 70.

**Total length** (Tables 1-20) — Specimens of *L. alaskense* range in total length from 122 to 188 mm. The size of *L. lamottenii* available for the present study (Tables 15-16), varies from 102 to 192 mm. There is considerable geographical variation in the lengths of specimens. A population from New Hampshire consists of the shortest individuals — 102 to 125 mm (Tables 15-16); from Lake Michigan tributaries, Manion and Purvis (1971) reported “giant” specimens 260-299 mm; the medium sized populations, 140-170 mm, are found in several states from New York to Tennessee.

*L. reissneri*, principally from Japan ranged from 116 to 172 mm (Tables 17-18). The largest specimen of 200 mm was reported by Okada (1960).

The size of *L. japonicum* available for our study (Tables 9-10), varies from 130 to 460 mm. The largest specimen on record was reported by Berg (1948) as 625 mm. The smallest recorded species in the genus is *L. meridionale*, ranging in size from 96 to 141 mm (Vladykov, *et al.*, 1975).

In conclusion it could be stated that *L. japonicum* could be easily separated from other species of the genus by its large size. Any specimen longer than 350 mm belongs to this parasitic species.

**Body proportions** — a) General considerations: Many authors have considered the problem of variations in body proportions of different holarctic lampreys. Some of these authors include: Cotronei, 1926, 1927; Vladykov, 1927, 1949, 1955, 1973; Berg, 1931; Ivanova-Berg, 1933; Hubbs and Trautman, 1937; Leach, 1940; Vladykov and Roy, 1948; Dendy and Scott, 1953; Hall and
NEW SPECIES OF LAMPREY

Moore, 1954; Morozova, 1956; Vladikov and Follett, 1958, 1965; Pletcher, 1963; Wigley, 1959; Abakumov, 1960; McPhail and Lindsey, 1970; Hardisty and Potter, 1971; Bond and Kan, 1973; Kott, 1974; Beamish and Potter, 1975; Kan, 1975; Vladikov, et al., 1975; Rohde, et al., 1976. A useful index to separate the nonparasitic and the parasitic species is the change in body proportions (total length, disc length, etc.) after metamorphosis has occurred. Nonparasitic species of Lethenteron include meridionale, alaskense, lamottrenii, and reissneri. In all of these species, the maximum size of individuals is found at the time of metamorphosis from larva (amnocoetes) to adult. The length gradually diminishes to the time of spawning when a sexually mature individual of either sex is the shortest (Tables 19-20; Fig. 12).

In the case of all adult parasitic species, for instance L. japonicum, the length of newly transformed individuals is the shortest. By regular feeding, the lengths of individuals increases considerably, at least three or four times for L. japonicum (Tables 9 and 10; Fig. 12) and even six times for Petromyzon marinus until the prespawning time. However during the spawning period, a shrinkage of the body occurs, particularly in the posterior section from the end of the first dorsal fin to the end of the caudal fin. This shrinkage which is observed in all species of lampreys during the reproductive period is particularly pronounced in parasitic species — up to 22% in Ichthyomyzon unicuspis (Vladikov and Roy, 1948) and 23.4% for male and and 21.3% for female Petromyzon marinus (Parker and Lennon, 1956).

Among the body proportions the length of the disc is particularly variable, depending first on the sex (males have a larger disc than females) and second, in the case of parasitic species, on their feeding activity. Since disc length varies with feeding activity, young individuals of L. japonicum have a relatively larger disc than old individuals at prespawning time (Table 9 and 10). During the spawning period in all lampreys, both parasitic and nonparasitic, the disc becomes relatively larger. This is especially true of male lampreys. To ascertain differences in body proportions and especially discs between parasitic and nonparasitic lampreys, only individuals of similar size and the same sex should be compared (Tables 13 and 14).

Body proportions — b) Comparisons between species: The information on body proportions of L. alaskanse are given in Tables 1 to 8. Males and females are considered separately. In this species the ratio is less than 1:2 between the minimum and maximum lengths of metamorphosed specimens. For this reason it appears that differences in body proportions, especially disc length, depend more on sex of the individual and stage of maturity, rather than lengths of individuals.

Due to the fact that in the type locality for L. alaskanse, namely the Naknek River system, L. japonicum is frequently present, it is important to make a comparison between these two species. It is especially important since
Heard (1966) considered both species to belong to *L. japonicum*. Our data on *L. japonicum* are summarized in Tables 9-12. As previously mentioned, the body proportions and especially disc length, depend on the sex and feeding (smaller specimens) as well as spawning (larger specimens) activities (Tables 11 and 12).

Differences in body proportions between *L. alaskense* and *L. japonicum* are particularly noticeable in eye and disc lengths of individuals of corresponding size (Tables 13 and 14). Therefore, body proportions alone can confirm the specific identity of *L. alaskense* and *L. japonicum*.

The body proportions of *L. alaskense* are not strikingly different from other nonparasitic species of the genus (Tables 19-20). Detailed information on body proportions of individual species can be found in Tables 15 and 16 for *L. lamottenii*, and 17 and 18 for *L. reissneri*.

In general, for nonparasitic species, body proportions are less important in separating species than are dentition, myomeres and number of velar tentacles.

**Dentition** (Table 26) — *L. alaskense* has a weak dentition with most of the cusps being rounded rather than pointed and in some specimens the teeth approach the condition found in *L. meridionale*, the species of *Lethenteron* with the most degenerate dentition.

In *L. alaskense*, cusps on the infraoral and transverse lingual laminae are typically blunt and poorly developed. This condition contrasts greatly with *L. lamottenii* where teeth are well cornified and sharp. This strong dentition in certain specimens of the latter species has led some authors (Manion and Purvis, 1971) to believe that these lampreys may be partially parasitic (Figures 4 and 10).

The number of anterials is very characteristic of different nonparasitic species (Table 26), and the species may be ranked in order of increasing number of anterials: *L. meridionale*, 5-34 (average 16.1); *L. lamottenii*, 19-33 (average 25.7); *L. alaskense*, 23-38 (average 30.4); and *L. reissneri*, 38-44 (average 41.7).

Among other sets of teeth the number of supplementary marginals along lateral sides of the disc is equally important in separating nonparasitic species. Supplementary marginals are lacking completely in *L. lamottenii* while they are present in the three other species. Their number is especially high in *L. meridionale* (Vladykov, et al., 1975), while in *L. alaskense* and *L. reissneri* the number is approximately similar but somewhat lower than in *L. meridionale*.

In contrast with nonparasitic species, *L. japonicum* has the strongest dentition with cusps sharp, well developed, heavily cornified and of an orange-brown color. The principal teeth — inner laterals, supraoral and infraoral laminae, and transverse lingual lamina — are very well developed with sharp cusps. The number of cusps on lingual laminae are more numerous than in other species of the genus numbering 13-18 (average 14.9) on transverse and 10-14 (average 12.1) on each lingual lamina respectively. Thus it should be stressed that in dentition, *L. japonicum* is entirely different from *L. alaskense* and the other nonparasitic species.
In general, dentition of parasitic species of lampreys is particularly well developed and sharp during the period of active feeding and growth.

**Velar tentacles** (Table 27) — Five velar tentacles was the number most frequently counted in *L. alaskense* (Fig. 11). The average for 11 specimens was 5.8, ranging from five to seven. They are relatively short and slender, with the median of the same length as the lateral ones. In *L. reissneri* and *L. lamottenii* the number of tentacles most often observed was seven. The shape of the tentacles are similar to those of *L. alaskense*. The range in *L. lamottenii* was five to nine and averaging 7.3. This is the highest average for any species of *Lethenteron*. *L. japonicum* has an average of 6.6 tentacles, range of five to seven, with seven being the most frequent count. *L. japonicum* has tentacles which are relatively longer and more slender than in other species of the genus. Only three short, slender tentacles are found in *L. meridionale* (Vladykov, et al., 1975).

**Coloration** (Table 28) — All species of *Lethenteron* have dark pigmentation on the caudal fin. On the other hand, pigmentation on the second dorsal fin in the form of a dark blotch varies with the species. It is most strongly developed in *L. japonicum* and *L. alaskense*. This dark blotch may be absent or only weakly developed in *L. lamottenii*. It is completely lacking in *L. reissneri*. In *L. meridionale*, dark pigmentation rather than being a blotch of small dark chromatophores, consists of a series of vertically elongated narrow dark spots (Vladykov, et al., 1975).

The gular region (ventral surface of the posterior portion of the disc) is always darkly pigmented in *L. lamottenii* (Kott, 1974). It is absent in all other species. Only rarely in *L. alaskense* (in two specimens of 64), can a weak pigmentation be noted (Fig. 6).
Geographical Distribution

*Lethenteron japonicum* is properly named the “Arctic lamprey”. It is well adapted to Arctic conditions, being found as far north as 70° latitude North. The anadromous and land-locked populations of this most broadly distributed lamprey species in the Holarctic region are found in salt and fresh waters of northern sections of three continents: Europe, Asia and North America. In Europe, it is present in Pasvik River, East Finmark (Tambs-Lyche, 1963) and White Sea Basins. According to Berg (1948) in the Barents Sea Basin, its range is from Varanger Fjord to the Pechora River; in Asia, it is found in the Arctic Ocean and its rivers from the Ob to the Kolyma; it is abundant on Anadyr territory, Kamchatka, in Okhotsk Sea Basin, Sakhalin, in the basin of the Sea of Japan on Hokkaido and Honda; in the Amur (including Sungary River, China, according to Hensel, 1963) and to the southern extremity of Korea (Fusan).

On the North American continent, *L. japonicum* is found in southern Alaska; Kenai Peninsula (Morrow, 1974) and Alaska Peninsula, especially in the Naknek River system (Heard, 1966) and along Bering Sea (St. Lawrence Island) and Bering Strait. According to McPhail and Lindsey (1970) it is present along the Bering Sea drainages and east along the Arctic Ocean drainage as far as Anderson River, Northwest Territories. It extends up the Yukon River into Yukon Territory and up the Mackenzie River to Great Slave and Artillery Lakes and to Fort Smith on Slave River. Formerly (around 1879) it was economically very important for native peoples along the Yukon River at Mission and Anvik (Turner, 1886; Nelson, 1887).

It should be mentioned also that populations of *L. japonicum* are frequently found in the same water systems as other, but nonparasitic lampreys of the same genus: *L. reissneri* in Asia and *L. alaskense* in North America.

*L. reissneri*, living exclusively in freshwater, is found in Asia along the Pacific Ocean. In comparison with *L. japonicum*, it has a restricted distribution. According to Berg (1948) and Okada (1960) it occurs in rivers of the Amur Basin, on Sakhalin, and on the islands of Japan in rivers and lakes (Biwa and others), within both the Pacific Ocean and the Sea of Japan drainages, but absent from Ryukyu Islands.

The characteristic habitats of *L. alaskense* are poorly known at present, but it appears to have a distribution largely coincident with that of *L. japonicum* in North America. We have specimens from the Alaska Peninsula (mainly from the Brook River basin), from the Chatanika River of the Yukon River drainage near Fairbanks, and from Martin River, Mackenzie River system in the Northwest Territories. On the whole our material clearly shows that the distribution of *L. alaskense* is limited to northwestern North America.

The known distribution of *L. lamottenii* is as follows: on the Atlantic slope from New Hampshire (Sawyer, 1960; Scarola, 1973) to Roanoke River in
Virginia (Jenkins et al., 1972; Rohde et al., 1975); in the St. Lawrence drainage it is found in several Quebec rivers (Vladykov, 1952, 1972), in Lake Champlain and in New York State (Greeley, 1930); it is present in tributaries of all of the Great Lakes* (Dymond et al., 1929; Radforth, 1944; Thomas, 1961, 1966; Applegate et al., 1961; Hubbs and Lagler, 1964; Manion and Purvis, 1971; and Kott, 1971), with the exception of the eastern portion of Lake Ontario (Greeley, 1940; Scott and Crossman, 1973) and the states of Wisconsin (Johnson and Becker, 1970) and Minnesota (Eddy and Underhill, 1974).

In the Mississippi drainage it is found in southern and eastern Minnesota (Eddy and Underhill, 1974); in Wisconsin it occurs as far north as the centre of the state (Greene, 1935; Johnson and Becker, 1970); it is present also in Iowa (Harlan and Speaker, 1951); in Illinois (Smith, 1965); in Indiana (Nelson and Gerking, 1968); in Ohio (Trautman, 1957); in Pennsylvania (Eddy and Underhill, 1974); in Missouri (Pflieger, 1971); in Kentucky (Clay, 1975); in Arkansas (Buchanan, 1973; Harp, 1975); in the Tennessee River system of Tennessee (Vladykov et al., 1975) and Alabama (Smith-Vaniz, 1968).

In contrast to L. alaskense, L. lamottienii is found only in eastern and southern sections of North America, hence their areas of respective distribution are separated by a distance of about 2400 km (1500 miles) (Fig. 13).

L. meridionale has a southern and a very restricted distribution, partially overlapping the southern range of L. lamottienii. It has been found in tributaries of the Tennessee River of the Mississippi system in the state of Tennessee, and the Tombigbee and Alabama Rivers in Alabama and Georgia (Vladykov et al., 1975).

* On the Canadian side of Lake Superior the most northerly and westerly distribution of L. lamottienii is reported by J. J. Tibbles (personal communication) to be Westman's creek, a small tributary of Batchawana Bay, about 80 km. north of Sault Ste. Marie, Ontario.
Conclusions

Since *L. alaskense* is often found in the same streams as *L. japonicum*, and there are some authors (Heard, 1966) who consider that both belong to the same species, it would be advisable to make a brief comparison between these two species.

*L. japonicum* is a parasitic species with a functional digestive tract after metamorphosis. It has pointed, very sharp and well cornified teeth on the disc, however it lacks supplementary marginals. The transverse lingual lamina has 13-18 (14.9) cusps and there are 10-14 (12.1) cusps on the longitudinal lingual laminae. It has 65-73 (69.5) trunk myomeres. The maximum recorded length is 625 mm. In specimens less than 180 mm the disc is rather large, being at least 72% of the branchial length in males and 64% of the branchial length in females. There are typically seven rather long velar tentacles.

*L. alaskense*, on the other hand, is a nonparasitic species reaching its maximum length at metamorphosis of 188 mm and decreasing gradually in size throughout post-metamorphosis. The teeth are blunt and weakly cornified with supplementary marginals present. Cusps on the lingual laminae are often obsolete but in some specimens were countable. The transverse lamina has 9-15 (12.0) cusps and there are 6-13 (8.5) cusps on each longitudinal lamina. There are 66 to 72 (69.4) trunk myomeres, about the same number as in *L. japonicum*. In specimens shorter than 180 mm in length the disc is rather small, being less than 67% of branchial length in males and less than 63% in females. There are typically five rather short velar tentacles. (Fig. 11).

Among the nonparasitic species of *Lethenteron*, *L. alaskense* is nearest to *L. lamottenii*. Moreover several authors (Wilimovsky, 1954; Hubbs and Lagler, 1964; Quast and Hall, 1972) incorrectly identified *L. alaskense* as *L. lamottenii*. For these reasons we are making a brief comparison between these two species. Both are nonparasitic with a similar myomere count.

The teeth of *L. alaskense* are blunt while in *L. lamottenii* they are sharp and well cornified but supplementary marginals are lacking. The cusps on the lingual laminae in *L. lamottenii* are pointed and there are 9-14 (11.8) on the transverse lamina and 5-9 (7.2) on each longitudinal lamina. Being the largest nonparasitic species, the maximum recorded length for *L. lamottenii* is 299 mm (Manion and Purvis, 1971). There are typically seven velar tentacles. Another distinctive character between *L. lamottenii* and *L. alaskense* is pigmentation. In the former, dark pigmentation on the second dorsal fin is typically lacking but on the gular region dark chromatophores are always present (Fig. 6). The opposite is true for *L. alaskense*.

The area of distribution of the above two nonparasitic species is broadly separated. *L. alaskense* has a known distribution limited to northwestern North America, and is separated by about 2400 km from the area of distribution of *L. lamottenii* which is limited to eastern and southern areas of North America. (Fig. 13).
Acknowledgments

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Members of Wilfrid Laurier University, Department of Geography, helped in preparing the distribution map and Mrs. N. Spoltore, Department of Biology, had the arduous task of typing the manuscript.

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Sexual dimorphism of *Lethenteron alaskense* taken during the spawning period, Chatanika River, Alaska.

a) spawning male, Tag W 1471, TL 164 mm, has a well-developed genital papilla and high second dorsal fin with arch-like free edge;

b) spawning female, Tag W 1469, TL 175 mm, has anal fin-like fold and a triangular-shaped second dorsal fin.
Fig. 6 Dark pigmentation of the gular region in two metamorphosed nonparasitic species of *Lethenteron*: a) *L. alaskense*, Tag VDV 4612, lacks pigmentation, while b) *L. lamottenii*, Tag W 1532, has strong pigmentation.
Enlarged discs of four species of *Lethenteron*:

a) *L. japonicum*, Tag VDV 6544, female, in feeding stage, TL 173 mm, Brooks River, Alaska.

b) *L. alaskense*, Tag VDV 4623, spawning male, TL 185 mm, West Creek, a tributary of Brooks Lake, Alaska.

c) *L. reissneri*, Tag W1547, spawning male, TL 147 mm, Chitose River, Hokkaido.

d) *L. meridionale*, Tag W667, male, TL 104 mm, Blue Springs Creek, a tributary of the Tennessee River, Tennessee.
Enlargements of the head region of males of four species of *Lethenteron*:

a) *L. japonicum*, Tag J 734, recently metamorphosed male, TL 190 mm., Hokkaido.

b) *L. lamottaei*, Tag W 681, male, TL 162 mm., Gatineau River, Quebec.

c) *L. reissneri*, Tag W 1547, spawning male, TL 147 mm., Chitose River, Hokkaido.

d) *L. meridionale*, Tag W 667, male, TL 104 mm., Blue Springs Creek, a tributary of the Tennessee River, Tennessee.
Fig. 9  Enlargements of the tail region of males of four species of *Lethenteron* (the same specimens as in Fig. 8):

a) *L. japonicum*; b) *L. lamottenii*; c) *L. reissneri*, and d) *L. meridionale*.
Fig. 10 Comparison between the cusps on the lingual and infraoral laminae of four species of *Lethenteron*:
*L. japonicum*: a and c, Tag VDV 6544, female, in feeding stage, TL 173 mm., Brooks River, Alaska; b, Tag W 696, spawning female, TL 422 mm., Amur River, USSR.
*L. alaskense*: d, Tag W 1475, spawning male, TL 179 mm., Chatanika River, Alaska.
*L. lamuttenii*: e, without tag, male, TL 189 mm., Big Creek, Lake Erie, Ontario; f, Tag W 999, male, TL 162 mm., Gatineau River, Quebec.
*L. reissneri*: g, Tag W 684, spawning male, TL 143 mm., Tym River, Sakhalin, USSR.

Remarks: i – infraoral lingual lamina
l – longitudinal lingual laminae
t – transverse lingual lamina
Fig. 11  Comparison between velar tentacles of four species of *Lethenteron*:

*L. japonicum*: a — ventral view of tentacles (only 5 tentacles visible) and

b — dorsal view of tentacles (all 7 tentacles visible), Tag W 693, female, TL 437 mm., Amur River, USSR.

*L. alaskense*: c — ventral view (all 5 tentacles visible, Tag W 1467, spawning female, TL 154 mm., Chatanika River, Alaska.

*L. lamottenii*: d — dorsal view (all 7 tentacles visible), Tag W 995, spawning male, TL 154 mm., Sturgeon Bay, Wisconsin.

*L. reissneri*: e — ventral view (only 5 tentacles visible), Tag W 682, male, TL 154 mm., Tym River, Sakhalin, USSR.
Fig. 12 Different trends in changes of total length during the life cycle of two hypothetical species of lampreys (Petromyzonidae), one of which is a nonparasitic species (A) and the other a parasitic species (B).

*The dashed lines:* O - a represents the progressive increase in length of ammocoetes from hatching to the onset of metamorphosis.

*The solid lines:* a - m represents the duration of metamorphosis from ammocoete to adult stage (decrease in length of an ammocoete);

m - P: in parasitic species, represents the increase in length of adults during the feeding period and in nonparasitic species, the decrease in length of adults which never feed after completing metamorphosis;

P - S: represents the decrease in length of adult lampreys of both types during prespawning period to time of spawning, which is followed by death.

**Note:** The duration of the ammocoete stage — differs between parasitic and nonparasitic species, the metamorphosis period is generally the same for both types, and the adult stage (post-metamorphosis) is less than one year for nonparasitic, and one to two years for parasitic species.
Fig. 13  Areas of distribution of *L. lamottenii* (B) and *L. alaskense* (A). Black triangles indicate exact localities where specimens of *L. alaskense* were collected.
TABLE 1. Body proportions (in percentage of total length) of 21 spawning males of *Lethenteron alaskense* from Naknek River drainage system, Alaska.

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*For definition of measurements, see Materials and Methods

** holotype
### Table 2

Body proportions (in percentage of total length) of 17 spawning females of *Lethenteron alaskense* from Naknek River drainage system, Alaska.

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**Mean**

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TABLE 3.  Body proportions (in percentage of total length) of 6 spawning males and 3 spawning females of *Lethenteron alaskense* from Chatanika River (Yukon drainage system), Alaska.

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TABLE 5. Body proportions (in percentage of total length) of 10 recently transformed females of *Lethenteron alaskense* from Martin River of Mackenzie River System, Northwest Territories.

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### TABLE 6
Summary of body proportions (in percentage of total length) of males and females of *Lethenteron alakense*
from three different localities, based on Tables 1-5.

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<th>(\frac{a-C}{TL})</th>
<th>(\frac{O}{TL})</th>
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TABLE 7. Variation in body proportions (in percentage of total length) according to size in 21 spawning males of *Lethenteron alaskense* from Naknek River drainage system. Data based on Table 1.

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<th>( \frac{B_7-a}{TL} )</th>
<th>( \frac{a-C}{TL} )</th>
<th>( \frac{O}{TL} )</th>
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TABLE 8. Variation in body proportions (in percentage of total length) according to size in 17 spawning females of *Lethenteron alaskense* from Naknek River drainage system. Data based on Table 2.

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<th>O TL</th>
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Feeding Stage

Alaska – Naknek River System

Beaufort Sea

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1) V3444 is from Aklavik, Northwest Territories.

Japan (Hokkaido)

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| U.S.S.R. – Amur River

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TABLE 11. Variations in body proportions (in percentage of total length) according to size in 11 feeding males of *Lethenteron japonicum* from North America. Data based on Table 9.

<table>
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<tr>
<th>Stage</th>
<th>No. of Specimens</th>
<th>Total length in mm (TL)</th>
<th>d-B/ TL</th>
<th>B1-B/ TL</th>
<th>B7-a/ TL</th>
<th>a-C/ TL</th>
<th>0/ TL</th>
<th>d/ TL</th>
<th>d/ B1-B/</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding 1</td>
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<td>130</td>
<td>14.8</td>
<td>10.0</td>
<td>46.5</td>
<td>28.8</td>
<td>3.5</td>
<td>7.3</td>
<td>73.1</td>
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<tr>
<td>Feeding 3</td>
<td>3</td>
<td>169.0</td>
<td>13.2</td>
<td>9.7</td>
<td>48.0</td>
<td>29.0</td>
<td>2.9</td>
<td>7.0</td>
<td>72.2</td>
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<tr>
<td>Feeding 4</td>
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<td>28.7-29.2</td>
<td>2.7-3.0</td>
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<td>71.9-72.3</td>
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<td>27.5</td>
<td>2.8</td>
<td>6.6</td>
<td>72.4</td>
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<td>26.8-28.6</td>
<td>2.5-3.0</td>
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<tr>
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TABLE 12. Variations in body proportions (in percentage of total length) according to size in 24 females of *Lethenteron japonicum* from North America. Some are feeding while others are in spawning condition. Data based on Table 10.

Note: Among specimens of corresponding sizes, spawning individuals have smaller discs than feeding ones.

<table>
<thead>
<tr>
<th>Stage</th>
<th>No. of Specimens</th>
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<th>B7-a TL</th>
<th>a-C TL</th>
<th>0 TL</th>
<th>d TL</th>
<th>d B1-B7</th>
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<td>10.0</td>
<td>48.5</td>
<td>28.1</td>
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<td>27.9-28.7</td>
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<td>71.9-73.3</td>
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### TABLE 13. Comparison between males of *L. alaskense* and *L. japonicum* of corresponding sizes, based on Tables 7 and 11.

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<th>No. of Specimens</th>
<th>Total length (mm)</th>
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<th>B&lt;sub&gt;1&lt;/sub&gt;-B&lt;sub&gt;7&lt;/sub&gt;</th>
<th>B&lt;sub&gt;7&lt;/sub&gt;-a</th>
<th>a-C</th>
<th>0</th>
<th>d</th>
<th>d-B&lt;sub&gt;1&lt;/sub&gt;-B&lt;sub&gt;7&lt;/sub&gt;</th>
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<tbody>
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<td>11.0</td>
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<td>30.3</td>
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<td>5.8</td>
<td>52.6</td>
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<td>130</td>
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<td>10.0</td>
<td>46.5</td>
<td>28.8</td>
<td>3.5</td>
<td>7.3</td>
<td>73.1</td>
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<tr>
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<td>9.7</td>
<td>47.4</td>
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<td>5.8</td>
<td>58.8</td>
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<td>27.9-32.7</td>
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<td>51.6-63.6</td>
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<td>9.7</td>
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<td>2.9</td>
<td>7.0</td>
<td>72.2</td>
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<td>12.8-13.7</td>
<td>9.6-9.8</td>
<td>47.4-48.5</td>
<td>28.7-29.2</td>
<td>2.7-3.0</td>
<td>6.9-7.1</td>
<td>71.9-72.3</td>
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### TABLE 14. Comparison between females of *L. alaskense* and *L. japonicum* of corresponding size based on Tables 8 and 12.

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<th>No. of Specimens</th>
<th>Total length (mm)</th>
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<th>B&lt;sub&gt;1&lt;/sub&gt;-B&lt;sub&gt;7&lt;/sub&gt;</th>
<th>B&lt;sub&gt;7&lt;/sub&gt;-a</th>
<th>a-C</th>
<th>0</th>
<th>d</th>
<th>d-B&lt;sub&gt;1&lt;/sub&gt;-B&lt;sub&gt;7&lt;/sub&gt;</th>
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</thead>
<tbody>
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<td>4</td>
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<td>11.0</td>
<td>9.9</td>
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<td>27.9</td>
<td>2.4</td>
<td>5.6</td>
<td>56.1</td>
</tr>
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<td>9.2-10.6</td>
<td>48.5-52.4</td>
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<td>1.9-2.9</td>
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<td>135</td>
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<td>10.0</td>
<td>48.5</td>
<td>28.1</td>
<td>3.7</td>
<td>7.4</td>
<td>74.1</td>
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<td>10.1</td>
<td>50.1</td>
<td>29.4</td>
<td>2.2</td>
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<td>9.3-11.1</td>
<td>9.5-11.3</td>
<td>47.6-52.0</td>
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<td>13.3</td>
<td>9.9</td>
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<td>27.9</td>
<td>2.8</td>
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<td>26.3-29.6</td>
<td>2.6-2.9</td>
<td>6.2-7.5</td>
<td>63.9-76.5</td>
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TABLE 15. Body proportions (in percentage of total length) of 15 prespawning and 14 spawning males of *Lethenteron lamottenii* from Quebec, Ontario and some States.

<table>
<thead>
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<th>Tag No.</th>
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<th>Total length (mm) (TL)</th>
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<th>B1-B7 TL</th>
<th>B7-a TL</th>
<th>a-C TL</th>
<th>O TL</th>
<th>d TL</th>
<th>d B1-B7</th>
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Prespawning

Quebec – “Petites Chutes” – Gatineau River

NEW SPECIES OF LAMPREY
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Spawning

New Hampshire - Wednesday Brook

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|                | W414    | 108    | 11.6 | 10.2 | 47.7 | 30.6 | 2.3 | 6.9 | 68.2 |
|                | W412    | 111    | 12.0 | 10.8 | 45.9 | 30.6 | 2.3 | 7.2 | 66.7 |
|                | W416    | 112    | 12.9 | 10.3 | 45.5 | 31.3 | 2.2 | 7.1 | 69.6 |
|                | S421    | 113    | 11.9 | 10.8 | 50.4 | 27.4 | 2.2 | 7.1 | 69.6 |
|                | W420    | 125    | 12.4 | 10.4 | 48.4 | 28.8 | 2.0 | 7.2 | 69.2 |
| MEAN           | 112.2   | 12.1   | 10.4 | 47.8 | 29.8 | 2.2 | 7.0 | 68.9 |
| RANGE          | 104-125 | 11.5-12.9| 9.6-10.8| 45.5-50.4| 27.4-31.3| 2.0-2.4| 6.7-7.2| 66.7-70.0|</p>
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COMBINED

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**Spawning**

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## New Hampshire – Wednesday Brook

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## New York – Casadoga Creek

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## Ontario – Furnace Creek – Lake Superior

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TABLE 17. Body proportions (in percentage of total length) of 10 spawning males of *Lethenteron reissneri* of Japan (Hokkaido) and Sakhalin.

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TABLE 18. Body proportions (in percentage of total length) of 9 spawning females of *Lethenteron reissneri* of Japan (Hokkaido) and Sakhalin.

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<th>a-C/TL</th>
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<th>d/TL</th>
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TABLE 19. Comparison of body proportions (as percentages of total length) of metamorphosed males of five species of *Lethenteron*. Data refer to means and ranges (in parentheses) for each character, and are based on our present study, except for *L. meridionale*, which were taken from Vladykov et al (1975).

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<td>28.2 (24.6-30.8) 27.7 (25.3-30.2) 31.3 (27.9-33.5) 30.1 (28.0-31.4) 29.8 (27.4-32.1) 29.8 (28.1-31.4) 30.6 (29.5-31.6) 28.9 (27.6-30.1) 30.2 (27.3-33.9)</td>
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<tr>
<td>Eye length</td>
<td>1.7 (1.4-2.1) 2.7 (2.1-3.5) 2.3 (1.8-2.8) 2.4 (2.1-2.9) 2.3 (2.0-2.5) 2.1 (1.7-2.3) 1.8 (1.2-2.4) 2.2 (1.9-2.4) 1.8 (1.5-2.1)</td>
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<tr>
<td>Disc length</td>
<td>6.0 (5.1-7.7) 6.6 (5.4-7.3) 5.8 (5.0-6.3) 4.9 (4.4-5.7) 6.0 (5.3-7.2) 5.3 (4.8-6.0) 5.7 (5.1-6.4) 5.9 (5.4-6.4) 5.2 (4.2-6.5)</td>
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<tr>
<td>Disc length/branchial length</td>
<td>57.8 (48.8-70.7) 67.2 (56.7-73.1) 59.0 (50.6-65.7) 48.4 (44.4-62.0) 57.7 (51.4-70.0) 54.0 (50.0-58.8) 57.0 (50.0-65.0) 59.4 (53.3-65.4) 51.5 (41.2-66.7)</td>
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TABLE 20. Comparison of body proportions (as percentages of total length) of metamorphosed females of five species of *Lethenteron*. Data refer to means and ranges (in parentheses) for each character, and are based on our present study, except for *L. meridionale* which were taken from Vladykov *et al* (1975).

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<tr>
<th>Number of specimens</th>
<th><em>L. japonicum</em></th>
<th><em>L. alaskense</em></th>
<th><em>L. lamottenii</em></th>
<th><em>L. reissleri</em></th>
<th><em>L. meridionale</em></th>
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<td>Nonspawning</td>
<td>Spawning</td>
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<td>18</td>
<td>17</td>
<td>10</td>
<td>37</td>
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<tr>
<td>Total length (mm)</td>
<td>344.5 (256-460)</td>
<td>205.6 (135-295)</td>
<td>148.7 (122-172)</td>
<td>156.1 (140-174)</td>
<td>140.9 (102-173)</td>
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<td>Prebranchial length</td>
<td>11.0 (9.4-12.4)</td>
<td>12.5 (11.6-14.2)</td>
<td>10.5 (9.3-11.6)</td>
<td>10.9 (10.1-12.1)</td>
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<td>Branchial length</td>
<td>9.7 (8.4-10.7)</td>
<td>9.2 (7.8-10.1)</td>
<td>10.1 (9.2-11.3)</td>
<td>9.9 (9.1-11.2)</td>
<td>10.1 (9.2-11.2)</td>
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<td>Trunk length</td>
<td>52.2 (49.5-55.7)</td>
<td>49.9 (46.8-52.9)</td>
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<td>51.0 (47.3-53.8)</td>
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<td>Tail length</td>
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<td>28.4 (26.3-29.8)</td>
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<td>Disc length/branchial length</td>
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<td>67.5 (59.4-76.5)</td>
<td>51.7 (36.0-62.5)</td>
<td>47.5 (40.5-53.3)</td>
<td>51.7 (40.0-65.0)</td>
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TABLE 21. Number of trunk myomeres of transformed *Lethenteron alaskense* of Alaska and N.W.T., sexes combined.

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<th>No. of Specimens</th>
<th>Number of myomeres</th>
<th>Mean</th>
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<td>Brooks River</td>
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<td>125-168</td>
<td>9</td>
<td>- - 1 2 4 2 -</td>
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<td>Brooks River (near outlet of Brooks Lake)</td>
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<td>137-155</td>
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<td>- - 1 1 - 1 -</td>
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<td>West Creek (Trib. of Brooks Lake)</td>
<td>June 11, 1964</td>
<td>122-185</td>
<td>25</td>
<td>- 2 7 6 6 3 1</td>
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<td>122-185</td>
<td>37</td>
<td>- 2 9 9 10 6 1</td>
<td>69.4</td>
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<td>Alaska (Fairbanks area)</td>
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<td>June 12, 1976</td>
<td>154-179</td>
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<td>- - - 3 3 2 1</td>
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<tr>
<td>Martin River</td>
<td>Nov. 1972-Jan. 1973</td>
<td>148-188</td>
<td>21</td>
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<td>67</td>
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**Japan (Hokkaido)**

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TABLE 23. Number of trunk myomeres of transformed *Lethenteron lamottenii* from Quebec, Ontario and some States, sexes combined.

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<th>Mean</th>
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**TABLE 24. Number of trunk myomeres of transformed *Lethenteron reissneri* from Japan, sexes combined.**

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<th>61</th>
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<td>2</td>
<td>3</td>
<td>2</td>
<td>6</td>
<td>4</td>
<td>1</td>
<td>-</td>
<td>60.4</td>
</tr>
</tbody>
</table>

1) A misplaced specimen from this river apparently had 66 myomeres. This count has been excluded from this table.
TABLE 25. Comparison of number of trunk myomeres of transformed specimens of five species of *Lethenteron*, sexes combined. Data are based on our present study, except for *L. meridionale* which were taken from Vladykov *et al.* (1975).

<table>
<thead>
<tr>
<th>Species</th>
<th>TL mm</th>
<th>Number of specimens</th>
<th>Number of myomeres</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. meridionale</em></td>
<td>96-142</td>
<td>77</td>
<td>1 7 6 16 18 11 16 1 1</td>
<td>54.0</td>
</tr>
<tr>
<td><em>L. reissneri</em></td>
<td>116-172</td>
<td>18</td>
<td>- - - - - - 2 - 3 2 6 4 1</td>
<td>60.4</td>
</tr>
<tr>
<td><em>L. lamottenii</em></td>
<td>102-192</td>
<td>89</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>68.9</td>
</tr>
<tr>
<td><em>L. alaskense</em></td>
<td>122-188</td>
<td>67</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>69.4</td>
</tr>
<tr>
<td><em>L. japonicum</em></td>
<td>110-498</td>
<td>67</td>
<td>- - - - - - - - - - - - - - - -</td>
<td>69.5</td>
</tr>
</tbody>
</table>
TABLE 26. Comparison between number of cusps on the various types of teeth in a parasitic species, *Lethenteron japonicum* and four nonparasitic species of the same genus. Data refer to means and ranges for each character. Numbers in parentheses are numbers of specimens.

<table>
<thead>
<tr>
<th>Species</th>
<th><em>L. meridionale</em></th>
<th><em>L. reissneri</em></th>
<th><em>L. lamottenii</em></th>
<th><em>L. alaskense</em></th>
<th><em>L. japonicum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Authority</td>
<td>Vladykov, et al (1975)</td>
<td>present study</td>
<td>present study</td>
<td>present study</td>
<td>present study</td>
</tr>
<tr>
<td>Antericals</td>
<td>16.1 (70)</td>
<td>41.7 (4)</td>
<td>25.7 (18)</td>
<td>30.4 (40)</td>
<td>25.2 (34)</td>
</tr>
<tr>
<td></td>
<td>5-34</td>
<td>38-44</td>
<td>19-33</td>
<td>23-38</td>
<td>20-33</td>
</tr>
<tr>
<td>Infraoral</td>
<td>9.9 (67)</td>
<td>7.7 (11)</td>
<td>8.5 (33)</td>
<td>8.6 (42)</td>
<td>8.4 (41)</td>
</tr>
<tr>
<td></td>
<td>6-13</td>
<td>6-11</td>
<td>8-10</td>
<td>6-11</td>
<td>8-10</td>
</tr>
<tr>
<td>Posterials</td>
<td>15.4 (36)</td>
<td>23.5 (4)</td>
<td>21.4 (80)</td>
<td>20.2 (47)</td>
<td>19.4 (41)</td>
</tr>
<tr>
<td>Transverse</td>
<td>poorly developed</td>
<td>13 (1)</td>
<td>11.8 (30)</td>
<td>12.0 (18)</td>
<td>14.9 (24)</td>
</tr>
<tr>
<td>lingual lamina</td>
<td>and not countable</td>
<td>13</td>
<td>9-14</td>
<td>9-15</td>
<td>13-18</td>
</tr>
<tr>
<td></td>
<td>7-8</td>
<td>5-9</td>
<td>6-13</td>
<td>6-13</td>
<td>10-14</td>
</tr>
<tr>
<td>Supplementary marginals on lateral fields</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Infraoral and transverse lingual lamina cusps</td>
<td>blunt, poorly developed</td>
<td>blunt, poorly developed</td>
<td>pointed, well developed</td>
<td>blunt, poorly developed</td>
<td>pointed, very sharp, and well developed</td>
</tr>
</tbody>
</table>

1) Total number of laminae (not specimens) counted are indicated in brackets.
<table>
<thead>
<tr>
<th>Species</th>
<th>No. of specimens</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. meridionale</td>
<td>2</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3.0</td>
</tr>
<tr>
<td>L. reissneri</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>7.0</td>
</tr>
<tr>
<td>L. lamottenii</td>
<td>102</td>
<td>-</td>
<td>1</td>
<td>2</td>
<td>77</td>
<td>14</td>
<td>8</td>
<td>-</td>
<td>7.3</td>
</tr>
<tr>
<td>L. alaskense</td>
<td>11</td>
<td>-</td>
<td>6</td>
<td>1</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>5.8</td>
</tr>
<tr>
<td>L. japonicum</td>
<td>13</td>
<td>-</td>
<td>1</td>
<td>3</td>
<td>9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>6.6</td>
</tr>
</tbody>
</table>
TABLE 28. Variation in dark pigmentation of second dorsal and caudal fins, and gular region in four species of *Lethenteron* (−, no pigmentation; +, weak pigmentation; ++, moderate pigmentation; +++; strong pigmentation).

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of specimens studied</th>
<th>Second dorsal fin</th>
<th>Caudal fin</th>
<th>Gular region</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>−</td>
<td>+</td>
<td>++</td>
</tr>
<tr>
<td><em>L. alaskense</em></td>
<td>64</td>
<td>4</td>
<td>22</td>
<td>38</td>
</tr>
<tr>
<td>Number</td>
<td></td>
<td>6.3</td>
<td>34.2</td>
<td>59.4</td>
</tr>
<tr>
<td>%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. lamottenii</em></td>
<td>40</td>
<td>25</td>
<td>14</td>
<td>1</td>
</tr>
<tr>
<td>Number</td>
<td></td>
<td>62.5</td>
<td>35.0</td>
<td>2.5</td>
</tr>
<tr>
<td>%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. reissneri</em></td>
<td>10</td>
<td>10</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Number</td>
<td></td>
<td>100.0</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>L. japonicum</em></td>
<td>28</td>
<td>−</td>
<td>1</td>
<td>18</td>
</tr>
<tr>
<td>Number</td>
<td></td>
<td>−</td>
<td>3.6</td>
<td>64.3</td>
</tr>
<tr>
<td>%</td>
<td></td>
<td>−</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Abakumov, V.A. 1960. On the systematics and ecology of the far-eastern brook lamprey from the Amur basin. Vop. Ikhtiol. 15:43-54. [In Russian]


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<th>Price</th>
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<td>1973</td>
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<td></td>
<td>1973 Out of Print</td>
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<tr>
<td>15</td>
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<td>$2.25</td>
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<tr>
<td>18</td>
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<td>Henning Thing</td>
<td>1977</td>
<td>$3.75</td>
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