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FAO FISH FINDER

LAMPREYS OF THE WORLD

AN ANNOTATED AND ILLUSTRATED CATALOGUE OF LAMPREY SPECIES KNOWN TO DATE

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AN ANNOTATED AND ILLUSTRATED CATALOGUE OF LAMPREY SPECIES KNOWN TO DATE

by

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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PREPARATION OF THIS DOCUMENT

This catalogue was prepared under the FAO Fisheries Department Regular Programme by the FishFinder Programme in the Marine Resources Service of the Fishery Resources Division. Financial support came from the Canadian Museum of Nature.

It represents the first comprehensive and updated publication concerning the Lampreys (order Petromyzontiformes), providing an identification key for the adults, a partial key for the larvae as well as an account for all species.

Lampreys are an evolutionary ancient group of jawless vertebrates displaying a temperate distribution. A number of lamprey species are of significant interest to fisheries and most of them play an important ecological role in their habitats. They are a food source for numerous species and the parasitic species can affect the distribution and abundance of some commercially important fishes. In the last decades, the populations of lampreys have dramatically declined due to human disturbances to the extent that, to date, many of them are threatened or endangered. In this context, management and conservation plans are being carried out for several species all over the world. Given that correct identification is of primary importance in resource management, the purpose of this catalogue is to help fishery workers and conservation biologists to identify the 39 species belonging to this order.

The author, Dr. Claude B. Renaud, is a research scientist at the Canadian Museum of Nature. He is an internationally recognized expert on lamprey taxonomy, systematics and morphology as confirmed by the large number of scientific articles published in the last 30 years.

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ABSTRACT

Lampreys are aquatic, jawless vertebrates belonging to the Order Petromyzontiformes. The order comprises 39 species widely distributed in the Northern and Southern hemispheres, but virtually absent in the intervening tropical zone. There is one family in the Northern Hemisphere (Petromyzontidae) comprising 35 species and two families in the Southern Hemisphere (Geotriidae and Mordaciidae) comprising, respectively, one and three species. Lampreys undergo a radical metamorphosis from the larval to the adult form. While lamprey larvae (ammocoetes) of all species are very similar in their habits (filter–feeding on microorganisms in a freshwater habitat), the adults vary considerably in their mode of life. Some are parasitic and anadromous, others parasitic but restricted to fresh water, while still others are nonparasitic (non–feeding) and restricted to fresh water. The taxonomic characters used to describe ammocoetes and adults are fully explained and illustrated. A key to adults and a partial key to larvae are presented. This catalogue provides an account for each of the 39 species. Each species account gives information on the taxonomy including synonyms, common names, diagnostic features of ammocoetes and adults (with drawings of the adult body and oral disc), habitat and biology, geographic distribution (with map), interest to fisheries and references.

Distribution

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[1] The information on this new species became available too late in the publishing process to make any changes to the species accounts or keys. Reference: Renaud, C.B. and P.S. Economidis. 2010. *Eudontomyzon graecus*, a new nonparasitic lamprey from Greece (Petromyzontiformes: Petromyzontidae). Zootaxa 2477: 37–48.

FAO Species Catalogue of Lampreys of the World

Claude B. Renaud

1. INTRODUCTION

The only two extant jawless (agnathan) orders, the hagfishes and the lampreys, belong to the phylum Chordata and subphylum Craniata. The relationship between the two clades, however, has not been resolved. There are two competing views: the cyclostome (circular mouth) hypothesis (Fig. 1) and the vertebrate hypothesis (Fig. 2). In the first, hagfishes and lampreys form a monophyletic group, the Cyclostomata (see Yalden, 1985; Stock and Whitt, 1992; Mallatt *et al.*, 2001; Hedges, 2001; Delarbre *et al.*, 2002; Takezaki *et al.*, 2003). In the second, lampreys are sister to jawed fishes and all other jawed animals (Gnathostomata) and together form the clade Vertebrata; the hagfishes, which lack vertebrae, are the sister–group to the Vertebrata (see Janvier, 1981, 1999; Maisey, 1986; Jamieson, 1991; Forey, 1995; Donoghue *et al.*, 2000). The data in support of the cyclostome hypothesis are mostly molecular, whereas those in support of the vertebrate hypothesis are mostly morphological. The issue will persist and is not likely to be settled until a phylogeny is constructed that is based on total evidence. The problem of establishing homologies within and among the ingroups and outgroups remains a challenge. It is of interest to note that Linnaeus (1758) classified hagfishes in the class Vermes and the order Intestina (intestinal worms) and lampreys in the class Amphibia and the order Nantes (swimming amphibians), erroneous placements that nevertheless reflect on their great divergence.

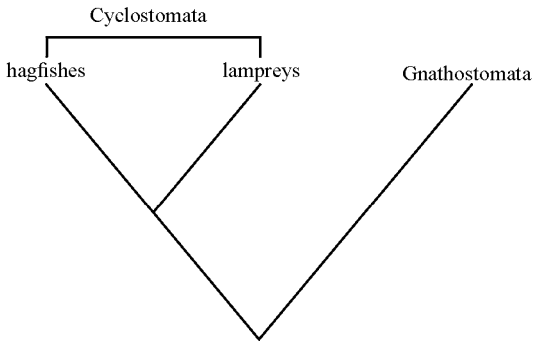

Fig. 1. Relationships among living agnathans and gnathostomes according to the cyclostome hypothesis.

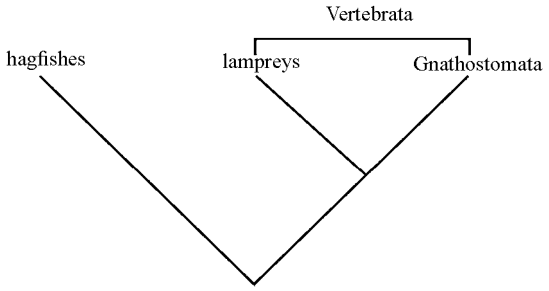

Fig. 2. Relationships among living agnathans and gnathostomes according to the vertebrate hypothesis.

1.1 General remarks on the order Petromyzontiformes

Lampreys belong to the order Petromyzontiformes (or Hyperoartia, from the Greek meaning palate complete or entire, in that the single median nostril ends blindly without perforating the palate). Petromyzont is derived from the Greek meaning stone sucker in reference to the behaviour of adults that attach to stones using their oral disc. Lampreys have no jaws but possess an annular cartilage that supports the supraoral and infraoral laminae. Their body is naked and elongate. They possess seven branchial openings (or pores) on either side of the body. The seven pairs of gill pouches (basis for the old order Marsipobranchii from the Greek meaning pouched gills) are supported by a surrounding branchial basket consisting of an elaborate network of fused cartilaginous elements. Lamprey cartilage is unique to the group and is termed lamprin. The skeleton contains no bone, only cartilage, although this cartilage may be calcified. The main axial support for the body is the notochord, which is persistent throughout the life of the animal. Rudimentary vertebral elements termed arcualia are arranged two per myomere on either side along the dorsal nerve cord. The myomeres are w-shaped, with the median apex pointing anteriorly, and entire (i.e. not subdivided by a horizontal septum). The lateral line system consists of individual neuromasts. The internal ears have two semicircular canals. The teeth on the oral disc and tongue-like piston of the adult lamprey are made of keratin. They possess a hollow core allowing for a number of replacement teeth to occur one on top of the other. It has been estimated that over the course of two years, an adult Sea Lamprey, *Petromyzon marinus*, may replace its teeth about 30 times. The darker color of the teeth, orangish or brownish, indicates an increased hardness relative to the lighter colors, whitish and yellowish. There are two (Geotriidae and Petromyzontidae) or three (Mordaciidae) buccal glands. The two buccal glands in the former are bean-shaped, hollow sacs embedded within the basilaris muscles and each possesses a duct that empties into the oral cavity behind the infraoral lamina. The three buccal glands in the latter are solid, of two different shapes (a small central gland and two club-shaped lateral glands), all three lying just behind the infraoral lamina and outside of the basilaris muscles. The intestine is straight and its interior possesses a typhlosole arranged in a spiraling fashion, thereby greatly increasing the absorptive surface. One dorsal fin (genus *Ichthyomyzon*) or two (all others) and one caudal fin. In the former, the posterior lobe is higher than the anterior lobe and in the latter, the second dorsal fin is higher than the first. There are no paired fins. Lampreys have a generally antitropical distribution related to the fact that their larvae have relatively low thermal

tolerance (max. 31.4 °C), and hence, they are compelled to spawn in cool or cool temperate river systems. The only exceptions to this rule are in the Northern Hemisphere; the genus *Tetrapleurodon* that occurs in the tropical zone at 20º lat. N, but is restricted to high altitude cool watersheds and one record of *Entosphenus tridentatus*, at about 18° lat. N, in marine waters off the west coast of Mexico. There are 40 species of extant lampreys in the world.

Fossil Record. Unambiguous lampreys are known from the Carboniferous of North America (280-310 MYA) by two species, *Mayomyzon pieckoensis* Bardack and Zangerl, 1968 and *Hardistiella montanensis* Janvier and Lund, 1983, from the Cretaceous of China (125 MYA), by one species, *Mesomyzon mengae* Chang *et al.*, 2006, and from the Devonian of South Africa (360 MYA), also by one species, *Priscomyzon riniensis* Gess *et al.*, 2006.

Life History. Lampreys undergo a radical metamorphosis from a larva, called ammocoete (derived from the Greek meaning sleeping in sand), to an adult. A fully metamorphosed individual is here termed an adult whether or not it has achieved sexual maturity. Some authors are more restrictive and use the term adult to mean only sexually mature individuals. In the literature, adults are often refered to as transformed or metamorphosed individuals. So radical is this metamorphosis that 19th century ichthyologists believed that the larva and the adult belonged to different genera of lampreys. For example, Kirtland (1840), DeKay (1842), and Agassiz (1850), respectively described *Ammocoetes concolor*, *A. unicolor*, and *A. borealis* on the basis of the ammocoete of unidentifiable species of *Ichthyomyzon*. Müller (1856) is credited as the first to recognize that the ammocoete was the larval stage of the adult lamprey. The habit of describing species on the basis of the ammocoete stage, or using *Ammocoetes* as a genus name, persisted for some time after that however, as demonstrated by the descriptions of *Ammocoetes caeruleus* Philippi 1858 (= *Geotria australis*), *A. cibarius* Girard 1858 (= *Entosphenus tridentatus* or *Lampetra ayresii*), *A. aepyptera* Abbott 1860 (= *Lampetra aepyptera*), and *A. aureus* Bean 1881 (= *Lethenteron camtschaticum*).

There are three main stages of development, regardless of mode of life, in the life cycle of lampreys: larval or ammocoete stage, metamorphosing ammocoete or juvenile stage, and metamorphosed individual or adult stage. Ammocoetes possess a horseshoe-shaped mouth (the upper lip is termed an oral hood), a triangular median nostril, have either one or two low dorsal fin(s) and the second dorsal or posterior lobe of the single dorsal fin, as appropriate, is continuous with the caudal fin, their branchial openings are triangular with the apex oriented anteriorly and lie connected in a groove, a gall bladder, and possess eyes that are covered by a layer of skin rendering them blind. Ammocoetes are filter-feeding microphagous detritivores, the entrance to their mouth consisting of a network of cirrhi. The ammocoete stage lasts a number of years. Once the ammocoete reaches a certain length, certain individuals go through a period of arrested growth, called by some a resting phase, lasting at least one year, during which time the ammocoete no longer grows but accumulates lipids in preparation for metamorphosis. The age at which a lamprey larva undergoes metamorphosis exhibits both interspecific, as well as intraspecific variation. The phenomenon of delayed metamorphosis ensures that recruitment of adults into the population will come from a single larval year class over more than one year. An extreme case of this phenomenon was reported by Manion and Smith (1978) for *Petromyzon marinus* from Big Garlic River, Lake Superior Basin, where the 1960 year class produced metamorphosing individuals yearly over a minimum 14 year period. The exact mechanism causing a larva to transform is poorly known.

Metamorphosis lasts four to five weeks or more. At the end of metamorphosis, adults have a suctorial oral disc, the inside of which is lined with teeth, a tooth-bearing tongue-like piston, a circular median nostril, the dorsal fin or fins are higher, the branchial openings are oval with the short axis oriented along the longitudinal body axis and no longer lie in a groove, but rather, each one opens directly to the exterior, the gall bladder has disappeared, and the eyes are fully functional. Additionally, in nonparasitic species, massive destruction of oocytes through atresia occurs during metamorphosis resulting in reduced absolute fecundities relative to their parasitic counterparts. Adults (i.e. post-metamorphosis individuals) may be termed either prespawning (immature), spawning (mature) or spent. Upon achieving adulthood, lampreys, depending on the species, will lead one of a number of modes of life; hematophagous ectoparasite, scavenger, flesh-feeding predator, a mixture of blood- and flesh-feeding, or no feeding.

The breakdown in the number of species according to the types of feeding in adults has not yet been firmly established. Suffice it to say at the present time that 18 species feed as adults. Feeding adults will naturally grow to greater lengths than their larval stage while non-feeding adults will shrink in size relative to their larval stage. The 22 lamprey species that do not feed as adults are called nonparasitic and are also known collectively as brook lampreys, because they are usually found in small watercourses, never dispersing very far from where they hatched. The duration of the adult stage varies according to the mode of life: if nonparasitic, it lasts less than a year, and if parasitic (a collective word for feeding adults that encompasses a wide variety of feeding habits that includes the hematophagous ectoparasites proper in addition to scavengers and flesh-feeding predators), it can last up to two years or more. Vladykov and Follett (1958, 1965) developed a seven-level scheme for the stages of maturity in post-metamorphosis lampreys ranging from 0 for immature individuals, 1-3 for maturing individuals, 4 for prespawning individuals, 5 for spawning individuals to 6 for spent individuals. This scheme applies to both parasitic and nonparasitic species. As they approach sexual maturity, the total length of adults, whether parasitic or nonparasitic, decreases, the intestine becomes atrophied and non-functional, and the teeth become blunt. While the two dorsal fins do not touch each other even in mature adults of Geotriidae and Mordaciidae, those of Petromyzontidae (except *Ichthyomyzon* with a single dorsal fin) progressively approach each other as they become sexually mature and eventually touch at the base. Additonally, the height of the dorsal fins (or lobes in the case of *Ichthyomyzon*) increases, the bases become fleshier and the edges frayed. Secondary sexual characters include proportionally longer oral disc, prebranchial length, and tail in males and longer

trunk length in females; a urogenital papilla, which in males appears as a narrow funnel-shaped organ and in females as a trough-like organ with the trough oriented posteriorly; a downturned tail in males and an upturned tail in females; and swollen pre- and post-cloacal finfolds, best developed in females. Nest building has been described in a number of species (*Caspiomyzon wagneri*, *Ichthyomyzon castaneus*, *Lampetra aepyptera*, *L. fluviatilis*, *L. planeri*, *Lethenteron appendix*, *Petromyzon marinus*). The spawning behavior has been described in a number of species (*Caspiomyzon wagneri*, *Ichthyomyzon castaneus*, *Lampetra aepyptera*, *L. fluviatilis*, *L. planeri*, *Petromyzon marinus*). The female attaches with her oral disc to a rock at the upstream end of the nest. The male attaches to the back of her head using his oral disc and wraps his tail around her trunk region in such a way as to have each others urogenital papilla in close proximity and through muscular contraction of his body assists in the extrusion of the eggs. They vibrate vigorously for a few seconds. This results in the release of their gametes and disturbance of the substrate, which partially buries the fertilized eggs. Fertilization is external.

Historical Fisheries. Lampreys were known to the Romans of the 1st and 2nd centuries who considered them regal food. These were caught, transported, and sold alive. They were incorporated into pies or puddings. The species involved would either have been *Petromyzon marinus*, or *Lampetra fluviatilis*, or both. This tradition of royal culinary appreciation continued with English monarchs. King Henry I (c. 1068-1135), son of William the Conqueror, is said to have died from an overindulgence of lamprey while on a visit to Normandy in 1135. Either species mentioned before may have been involved. Although cases of poisoning after eating lamprey flesh and mucus, involving gastrointestinal upset, nausea, and vomiting have been reported, the etiology is not clear (Wills 1966). King John of England (c. 1166-1216) had someone sent to the continent, at Nantes, on the Loire River, Duchy of Brittany, to purchase lamprey to supplement to the great demand in England. King Henry V (c. 1387-1422), while in Normandy in 1414, likewise asked that lamprey be sent to him from Nantes. As least since the 12th century, the town of Gloucester on the Severn River had important lamprey fisheries for both *P. marinus* and *L. fluviatilis*. The town officials would show their allegiance to the crown by presenting a lamprey pie to the head of state at the coronation as well as every Christmas. The latter tradition lasted until 1836. On special occasions, such as coronations and jubilees, Gloucester still sends the monarch a lamprey pie. Queen Elizabeth II received one on the occasion of her Silver Jubilee in 1977. The method of capture was by net and the lampreys were usually eaten salted. Rondelet's (1558) "L'Histoire entière des poissons" is divided in two parts, and in each of these he describes a lamprey. In the first part, his description is that of an anadromous species which he calls in Latin, Lampetra and in French, Lamproie. The description is general and could refer to either *P. marinus* or *L. fluviatilis*. At the end of this account, he mentions that lamprey recipes are to be found in the French translation of the cookbook in Latin by Platina (1505). In the second part of his book, Rondelet (1558) mentions small lampreys called lamproions or lamprillons being fished from rivers and brooks and sold in large quantities in the southern French city of Toulouse under the name châtillons. These would have been ammocoetes as he reports them to feed on mud. He does not mention the purpose for which they are sold but it is not unreasonable to suggest that they could have been used as bait for fishing.

Conservation. Renaud (1997) summarized the conservation status of Northern Hemisphere lampreys and made some recommendations for future conservation needs. Already in the 1920s Jenkins (1925) was deploring the polluted state of rivers in England (UK) and suggesting that this was the major cause for the decline in the abundance of *Petromyzon marinus*. On the Pacific coast of the USA (from now on referred to as USA) Close *et al.* (2002) reported alarming decreases in the abundance of *Entosphenus tridentatus*: at the Winchester Dam in the Umpqua River, 46,785 were counted in 1966 and only 34 in 2001; at the Ice Harbor Dam in the Snake River, Columbia River Basin, 49,454 were counted in 1963 and only 203 in 2001. Both these cases represent a greater than 99% decrease in abundance in less than 40 yrs or roughly five generations. According to the Kentucky State Nature Preserves Commission (2004), *Ichthyomyzon gagei* is presumed to be extirpated from the state of Kentucky. In the Southern Hemisphere, a native fish strategy covering the years 2003-2013 was developed for the Murray-Darling Basin, Australia in an attempt to restore fish abundance to 60% of their pre-European settlement levels after 50 years of implementation (Anonymous, 2004). This has implications for *Mordacia mordax*, which is extirpated from Queensland and *Geotria australis*, which is rare in the lower Murray-Darling Basin (Anonymous, 2004).

Habitat. All ammocoetes, regardless of species, spend most of their larval period in the substrate of freshwater streams with only their oral hood sticking out; the mouth opening directed towards the current in order to capture food particles. After a number of years spent as a larva they undergo metamorphosis and emerge from the substrate as an adult, capable or not of feeding depending on the species. A number of parasitic species are anadromous, undertaking extensive migrations as adults to and from marine waters, and some of these have developed populations that are permanent freshwater residents. In anadromous species, the downstream migration to marine waters is for the purpose of feeding, while the upstream migration to fresh waters is for the purpose of spawning. The other parasitic species, as well as all 22 nonparasitic species, spend their entire lives in fresh water. There are reports (Gage, 1893, Lohniský, 1966; Potter *et al.*, 1968, Holčík, 1986) of adults of both parasitic and nonparasitic species (*Caspiomyzon wagneri*, *Lampetra planeri*, *Lethenteron appendix*, *Mordacia mordax*, *Petromyzon marinus*) burying in the substrate of freshwater streams.

Aging. Until relatively recently, lamprey ages were derived from length-frequency graphs by identifying modal peaks corresponding to year classes. In the last 20 yrs, ammocoetes and recently metamorphosed individuals of a few species have been aged through the counting of annual growth rings on their statoliths (either stained or unstained with oxytetracycline), a structure analogous to the teleost otoliths. Hence, *Petromyzon marinus* (Volk, 1986,

Morkert *et al.*, 1998), *Ichthyomyzon greeleyi* (Medland and Beamish, 1987), *Entosphenus tridentatus* (Beamish and Northcote, 1989), and *Lethenteron camtschaticum* (Kucheryavyi *et al.*, 2007) have been aged in this manner.

Neoteny or Paedomorphosis. Since they do not feed as adults, nonparasitic species differ from parasitic species in having shorter adult lives and by being more advanced in terms of sexual maturity at the end of metamorphosis. It is believed that they achieve the latter by prolonging their larval life by a year relative to their closest parasitic counterpart through what has been called a period of arrested growth or resting phase. Therefore, the overall lifespan of parasitic and nonparasitic species in a species pair is thought to be relatively similar. This is undoubtedly an oversimplification as some parasitic lampreys (see *P. marinus* above) have retained the ability to extend their larval stage for a considerable period. A number of authors have reported instances of neoteny or paedomorphosis in various nonparasitic lamprey species (*Entosphenus lethophagus*, *Lampetra aepyptera*, *Lethenteron zanandreai*). These cases have been reviewed and dismissed by Vladykov (1985a). The relatively advanced state of sexual maturity in recently metamorphosed individuals of those species compared to that in parasitic species is simply a reflection of the longer larval life in the former. Nonparasitic lampreys are neither neotenous (sexually mature in the larval stage without going through metamorphosis) since they undergo metamorphosis nor paedomorphic (retention of larval characteristics in the adult) since no larval characteristics are retained after metamorphosis.

Macrophthalmia. The term macrophthalmia has been used to describe the phase in the lamprey life cycle at the end of metamorphosis, when the eye is well-developed and prominent, and it extends either to the onset of adult feeding in parasitic lampreys or to the appearance of secondary sexual characters in nonparasitic lampreys. I do not find this a particularly useful term, especially since different defining criteria are used for the two modes of life; therefore, I prefer to use the word prespawning phase instead. Neira (1984) has even made a distinction between early macrophthalmia and late macrophtalmia individuals in *Mordacia lapicida*; the first having only partially developed teeth, while the second has well-developed teeth. However, for *Geotria australis*, his material only included late macrophtalmia individuals, which he described has not having well-developed teeth. The reason for the difference between the two species is not clear and reinforces my opinion to discontinue the use of this term.

Paired (Stem-Satellite) Species. A number of species, termed paired species (Zanandrea, 1959c) or stem-satellite species (Vladykov and Kott, 1979b), are very similar morphologically and differ mostly in terms of characters associated with their respective mode of life in the adult stage, namely, a feeding member and its non-feeding derivative (e.gs. *Ichthyomyzon unicuspis – I. fossor*; *Lampetra fluviatilis – L. planeri*). There are two schools of thought with regards to whether or not mode of life in the adult (i.e feeding versus non-feeding) constitutes a criterion for specific distinctiveness. There are those (Wajgel, 1884, Enequist, 1937, McPhail and Lindsey, 1970) that consider adult mode of life not to be a valid criterion for specific distinctiveness, and that the non-feeding form merely represents a reflection of food availability. The other camp (Hubbs, 1924, Hubbs and Trautman, 1937, Hardisty and Potter, 1971, Vladykov and Kott, 1979c) considers that a change in mode of life represents such a significant difference in life history to warrant specific distinctiveness. I follow the latter school since differences in size associated with post-metamorphosis feeding in one and its absence in the other preclude proper pairing (i.e. assortative mating) and ensures reproductive isolation among the two divergent life history types, as empirically demonstrated by Beamish and Neville (1992). Interestingly, Richard (Dick) J. Beamish, the first author of that paper has over a number of years published papers (Beamish 1985, Beamish and Withler 1986, Beamish *et al.* 2001) in which it is claimed that he has found evidence of a population of the nonparasitic *Lampetra richardsoni* in Morrison Creek, British Columbia, that produces both nonparasitic and parasitic segments of the population depending on conditions, which remain to be elucidated. Additionally, facultative ectoparasitism has been proposed in a few instances in two nonparasitic species, *Eudontomyzon mariae* and *Lethenteron appendix* (see those species' accounts), and this may reflect recent divergence from a parasitic ancestor. There are reported cases of paired species spawning in the same nest [*Lampetra fluviatilis* and *L. planeri* in Wales (UK), Huggins and Thompson (1970); *Ichthyomyzon unicuspis* and *I. fossor* in Michigan, Morman (1979)] and the fertilization of an individual of one life-history type by another in nature is theoretically possible since the sperm is free-swimming in fresh water for about 50 seconds (Kille, 1960). Piavis (1971) conducted some experimental crosses between *I. unicuspis* and *I. fossor* and in both cases the hybrids reached stage 17 (burrowing larva), which was the highest stage attained prior to termination of the experiment. However, while the percentage survival was 88.5% when *I. fossor* fertilized *I. unicuspis*, it was only 44.5% in the reciprocal cross. While some paired species such as *Ichthyomyzon unicuspis – I. fossor* and *Lampetra fluviatilis – L. planeri* are very close to each other morphologically and proponents of the ecological race theory have argued that members of each pair merely represent an ecological form of a single species, there is a number of nonparasitic species such as *Entosphenus hubbsi*, *Eudontomyzon hellenicus*, and *Lampetra aepyptera* that are so distinct from any extant parasitic species that they cannot be aligned with any of them. This argues for the fact that these nonparasitic species represent distinct lineages and are not simply a reflection of trophic level. However, until an unequivocal test is developed to refute one of the two hypotheses, the question will remain open. Furthermore, the two competing hypotheses need to be tested in every paired species as demonstration in one case may not apply to all cases. Espanhol *et al.* (2007) analysed sequences of three mtDNA genes (cyt *b*, ATPase 6 and 8) in the *L. fluviatilis – L. planeri* species pair from 21 wide-ranging European localities but could not conclusively rule in favor of one hypothesis over the other and suggested that perhaps more rapidly-evolving genetic markers such as microsatellites would be more appropriate to test between the two hypotheses.

Normal and Praecox Forms. Berg (1931, 1948) suggested that three anadromous species, *Caspiomyzon wagneri*, *Lampetra fluviatilis*, and *Lethenteron camtschaticum* existed in two sympatric forms, a normal form (forma typica) and what he called a praecox form that attained a smaller size as an adult, matured and spawned earlier, had a lower fecundity than the former, and can either be anadromous or a permanent freshwater resident. This phenomenon requires closer scrutiny as the difference in size at maturity and spawning periods between the normal and praecox forms may result in reproductive isolation. The triggering mechanism causing the selection of one form over another is not known. However, in a recent study of a population of *L. camtschaticum* from the Utkholok River Basin in western Kamchatka, where not two but three forms occur sympatrically; a typically anadromous form, an anadromous praecox form, and a resident form, Kucheryavyi *et al.* (2007) have proposed that the larval diet determines the life history trajectory. Their suggestion is that ammocoetes that supplement their usual diet of mainly organic detritus and algae with highly nutritious, semi-liquified, decomposing Pacific salmon carcasses become residents and cease feeding after metamorphosis, while ammocoetes that feed on organic detritus and algae only, migrate to sea. Unfortunately, this does not explain why there are normal and praecox anadromous forms, and additionally, it is unclear why the authors did not simply identify the resident form as a nonparasitic species, perhaps *Lethenteron kessleri*, which is morphologically very similar to *L. camtschaticum*. Contrary to what has been stated in Berg (1931, 1948) for other normal-praecox situations, Kucheryavyi *et al.* (2007) report that their three forms spawn synchronously. Since for any of the above species for which this phenomenon has been reported no taxonomic differences have been suggested by the authors, I have chosen here to combine length data for the putative forms within species except for the non-feeding adult stage resident form of *L. camtschaticum* reported by Kucheryavyi *et al.* (2007) for which I have offered another interpretation (see above).

Anal Fin. Lampreys do not possess an anal fin, but, as they become sexually mature, females develop a fleshy, anal fin-like fold, which should properly be called a post-cloacal finfold. However, the presence of an aberrant anal fin, supported by fin rays, has only ever been reported in two specimens, both females, of *Petromyzon marinus* by Vladykov (1973b) and Vladykov and Kott (1980a), and may represent an atavistic expression of a primitive condition.

Pheromones. Bergstedt and Seelye (1995) have shown that landlocked *Petromyzon marinus* in the Laurentian Great Lakes does not generally home to natal streams. To what extent this phenomenon also applies to anadromous *P. marinus*, or to other lamprey species, has not been investigated. It has only recently been established that stream selection for spawning purposes is based on the presence of ammocoetes and their release of a pheromone, made in part using bile acid, which is being picked up by the adults on their spawning migration through their olfactory system (Sorensen and Vrieze, 2003, Gaudron and Lucas, 2006). This is fascinating; the young lampreys are telling the preceding generation to spawn where they themselves occur, as they constitute living proof that the conditions are favorable to successful spawning. Additionally, the attraction is not species specific but applies to a wide number of lamprey species (Fine *et al.*, 2004) explaining why multiple species may be found in the same areas.

Cases of Repeat Spawning. Lampreys are semelparous (i.e. they die after spawning). Two reports (Michael, 1980, 1984) however, have claimed that one species, *Entosphenus tridentatus*, may exhibit repeat spawning, based on the capture of marked upstream migrants during two successive spawning migrations. This is taken as being an exceptional case.

Morphological Aberrations. In rare cases, morphological deviations are encountered. These include six instead of seven branchial openings on one side [2 cases in 64 adult *Eudontomyzon danfordi* examined by Renaud (1982)] or multiple tails (10 cases in 8,437 larval and one case in 3,004 adult *Petromyzon marinus* and one case in 2,726 larval *Lethenteron appendix* [reported as *Lampetra lamottei*) examined by Manion (1967)]. The 11 cases of multiple tails in larval lamprey reported by Manion (1967) involved an additional tail only, while the single case in the adult involved two supernumerary tails.

Taxonomic Characters. A number of authors (Hubbs and Trautman 1937, Vladykov 1955, Potter 1968) have proposed standard methods for making counts and measurements in adult lampreys. McPhail and Lindsey (1970) were the first to use the number of velar tentacles and their arrangement as taxonomic characters to distinguish between two species at the adult stage. Later on, Vladykov and Kott (1976d) greatly expanded the species coverage using velar tentacle characters. Vladykov (1950) was the first to develop a standard method using pigmentary characters to identify ammocoetes to species. The methodology for the taxonomic description of ammocoetes and adults followed here is essentially taken from Renaud (1982a), but see Disc Length, for example, under Morphometrics below. It is based on an extensive compilation of characters from the previous works, sometimes slightly modified, the introduction of new morphometric and pigmentary characters, and a more objective way of evaluating the degree of pigment coverage. McPhail and Lindsey (1970) have used the number of muscle grooves (myosepta) instead of myomeres (muscle blocks or bundles) as a taxonomic character. This means that their counts have values that are one or two greater than studies that use myomeres. We follow here the great majority of workers in counting myomeres.

Counts. Number of trunk myomeres: The first myomere is the one whose anterior myoseptum lies on or is posterior to the posterior edge of the 7th branchial opening and the last myomere is the one in which the lower angle of its posterior myoseptum lies at or is anterior to the anterior edge of the cloacal slit (Fig. 3). This is different from Hubbs (1924) and Neira (1984) who counted them up to the posterior edge of the cloacal slit.

Number of Oral Papillae: (also termed cirri; not to be confused with the oral cirrhi found in ammocoetes) These conical structures lie along the periphery of the oral disc,

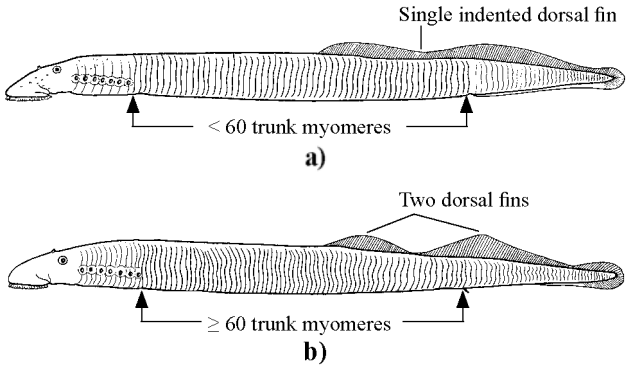

Fig. 3. Side view of an adult lamprey showing the trunk myomeres in a) a species with one dorsal fin and b) a species with two dorsal fins. The latter usually have 60 or more trunk myomeres, but there are exceptions. The same method of counting trunk myomeres applies to ammocoetes.

outside of the oral fimbriae, when the latter are present.

Number of Oral Fimbriae (also termed fringed lappets or leathery appendages): These flattened leaf–like structures lie along the periphery of the oral disc, inside of the oral papillae.

The taxonomy of lampreys is based primarily on the dentition in the adult (Fig. 4). The terminology used here in the description of dentition is that proposed by Vladykov and Follett (1967) and Potter and Hilliard (1987). When describing the various teeth on the oral disc and tongue, it is important to consider that the teeth appearing on the right side of the viewer are actually on the left side of the specimen and vice–versa. The teeth should be described in relation to the specimen and not to the viewer.

The lamprey oral disc is partitioned into four fields: one anterior, two lateral, and one posterior. The following dentition may be found on each field: anterior – marginals, anterials, and supraoral lamina; lateral – marginals, exolaterals, and endolaterals; posterior – marginals, posterials, and infraoral lamina.

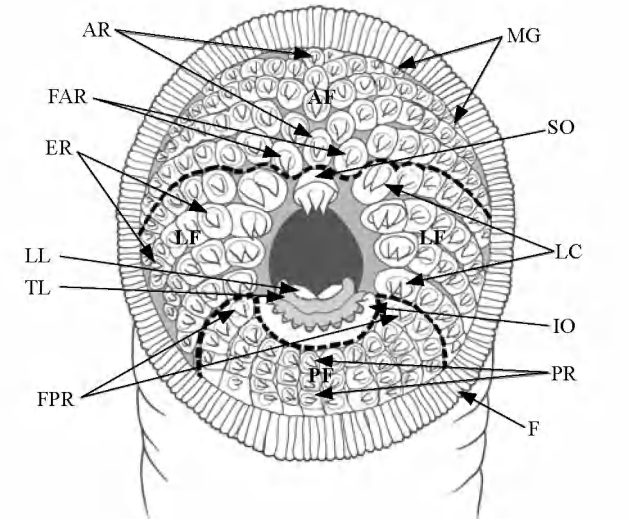

Fig. 4. Oral disc of an adult lamprey showing the dentition and other associated structures. The dotted lines delineate the various fields. After Hubbs and Potter (1971). (AF = anterior field; AR = anterial rows; ER = exolateral rows; F = oral fimbria; FAR = first anterial row; FPR = first posterial row; IO = infraoral lamina; LC = lateral circumorals or endolaterals; LF = lateral field; LL = longitudinal lingual lamina; MG = marginals; PF = posterior field; PR = posterial rows; SO = supraoral lamina; TL = tranverse lingual lamina)

A note on cusp versus tooth versus lamina. A cusp is simply a more or less pointed cap of keratin. A tooth may possess one up to four cusps. A lamina is a plate of keratin consisting of one or more teeth, each of which may possess one or more cusps. This being said, it is somewhat of a moot point whether one considers that the supraoral lamina in *Petromyzon marinus*, for example, consists of two unicuspid teeth or one bicuspid tooth.

Marginals. All lampreys possess a single row of teeth, termed marginals, lying at the margin, just inside the oral disc. Additionally, some species (*Lampetra richardsoni*; *Lethenteron meridionale* = *Lampetra aepyptera*; *Lethenteron alaskense*; *L. reissneri*) possess what has been termed supplementary marginals by Vladykov *et al.* (1975) and Vladykov and Kott (1976a, 1978a). Potter (1968) has stated that the marginal series consist of 2–3 rows of teeth in *Mordacia*. However, these authors do not offer any criterion to distinguish supplementary marginals from either exolaterals or posterials. While one could argue that teeth close to the marginal series would be considered supplementary marginals, the fact remains that teeth lying in the middle of the exolateral and/or posterial fields have been found in all of the above species. I find this situation confusing, and therefore, reject the notion of supplementary marginals, and instead, refer to these teeth either as exolaterals or posterials, as determined by the field in which they are found.

Labial teeth. This is a collective term to designate the anterial, exolateral, and posterial teeth.

Hubbs and Trautman (1937) include a marginal tooth in their count of the number of anterial rows whereas Vladykov and Follett (1967), which we follow here, exclude it. The reason for excluding marginals from the count is that these teeth are universally present in lampreys, and therefore, bring no discriminatory power to the character. Likewise, marginals are excluded from the count of the number of exolateral and posterial rows.

Rows of Anterials, Exolaterals, and Posterials. The number of rows of anterials is defined as the number of teeth along the median (straight vertical) line in the anterior field. The number of exolateral rows is defined as the number of teeth on either side of the oral disc along the median (curvilinear) line of the lateral field, excluding the endolateral tooth. Exolaterals (also called outer laterals) are invariably unicuspid. The number of rows of posterials is defined as the number of teeth along the median (straight vertical) line in the posterior field. Note, however, that there is an exception. An individual is said to possess a row of posterials, even though none of its posterials lie along the median line, if it possesses an incomplete first row of posterials (see explanation below under First Row of Posterials). As stated above, all of these counts exclude marginals.

Radial Plates. Potter (1968) used this term to describe the teeth arranged in an inner circle in *Mordacia*. They are somewhat reminiscent of the plates found in the putative

fossil lamprey *Pipiscius zangerli*. In *Geotria*, these radial plates are restricted to the posterior field (Neira, 1984). For the purpose of comparison with other species, we choose to call these anterials, lateral circumorals, or posterials based on their relative position on the disc. These plates are transitory in nature and breakdown in mature individuals to give individual teeth. This process has been termed a second metamorphosis.

First Row of Anterials. This is the row of teeth which is nearest to the supraoral lamina(e). Only the teeth that are intersected by a smooth arc linking the anteriormost lateral circumorals are counted.

First Row of Posterials. Teeth in this row, which is the one nearest to the infraoral lamina, may be present in a complete (continuous) or incomplete (discontinuous; with one or more gaps) row, or be altogether absent. Only the teeth that are intersected by a smooth arc linking the posteriormost lateral circumorals are counted. In the case of an incomplete row, even a single tooth lying along the arc is sufficient to be included in the count.

Circumoral Row. Hubbs and Trautman (1937) introduced this character in their revision of the genus *Ichthyomyzon*. It is defined as the innermost row of anterial and posterial teeth (refered to in this study as the first row of anterials and posterials, respectively) plus the endolateral teeth. This character has not gained acceptance outside of this genus. In a later appraisal of the genus, Lanteigne (1981) used the number of biscupid endolaterals only and obtained good discrimination among the three species pairs. This character has therefore been split into three: First Row of Anterials, First Row of Posterials and Number of Lateral Circumorals.

Supraoral Lamina. The characteristics recorded are the number of laminae, their shape, the number of teeth on each, their type (unicuspid, bicuspid, ...), and arrangement. Even though in some genera (e.g. *Ichthyomyzon*, *Petromyzon*), the supraoral lamina consists of a single tooth, which may be uni– or multicuspid, it is still called a lamina by convention.

Infraoral Lamina. The characteristics recorded are the number of teeth, their type, and arrangement.

Number of Lateral Circumorals on Each Side of the Oral Disc. These are called inner laterals or endolaterals by Vladykov and Follett (1967). Criteria for inclusion and exclusion of these teeth are not well defined in the literature and hence there has been some confusion as to what constitutes a lateral circumoral. These lie between or are intersected by a line drawn along the anteriormost edge of the supraoral lamina (or the two supraoral laminae in the case of *Mordacia*) and a line drawn through the apices of the two lateralmost cusps on the infraoral lamina. The endolateral formula applies to one side of the disc and gives both the number of endolaterals and their type. The first number of the formula is the type of the first endolateral, which is the one adjacent to the supraoral lamina, and the last number is the type of the last endolateral, which is adjacent to the infraoral lamina. The value of the numbers reflect the type of endolateral teeth as follows, 1 = unicuspid; 2 = bicuspid; 3 = tricuspid. Thus, an endolateral formula of 2–3–3–2 means that there are four endolaterals on one side of the disc, the first one being bicuspid, the second tricuspid, ...
The so–called tongue of lampreys is supported by the piston cartilage and is innervated by the Vth cranial nerve, the trigeminal. Three lingual laminae are present on this organ; one transverse and two longitudinal. The transverse lingual lamina acts as a rasping organ in hematophagous species and as a gouging organ in flesh–eating species.

Transverse and Longitudinal Lingual Laminae. The characteristics recorded are the shape of the lamina(e), the relative size of the teeth, their number, and type. The transverse lingual lamina may be straight, u–shaped or w–shaped, while the longitudinal lingual laminae may be straight, parentheses–shaped or j–shaped (also called hook–shaped).
The velar apparatus lies at the junction of the oesophagus (above) and the branchial cavity (below) in adults. The velar tentacles project anteriorly into the pharyngeal cavity. Velar wings, when present, are defined as one or more tentacles that are folded onto the dorsal surface of the velar apparatus (Fig. 5). In order to expose the velar apparatus without damaging other characters, two methods may be employed: a) a transverse cut on the ventral aspect of the adult lamprey down to the first branchial openings followed by a frontal cut forward up to the eye. The resulting flap when lifted forwards reveals the velar apparatus in ventral aspect or b) a partial sagittal cut is made along the dorsal aspect of the adult lamprey between the pineal organ and the first branchial opening down to the pharyngeal region. The two resulting edges are spread apart with bent needle probes to expose the dorsal aspect of the velar apparatus. The velar tentacles may be smooth, or they may bear tubercles or papillae; the latter in *Caspiomyzon wagneri* only. The tubercles or papillae are more numerous on the dorsal aspect than the ventral aspect of the tentacles.

Morphometrics (Figs. 6–9). Because lampreys lack a rigid endoskeleton, shrinkage due to initial fixation in 4–5% formalin followed by preservation in 70% ethanol can be significant. The notochord provides the main axial support, the branchial region is supported by a branchial basket made of cartilage and the head region has some cartilaginous elements, notably the annular cartilage. Because of this, differential shrinkage occurs, whereby most

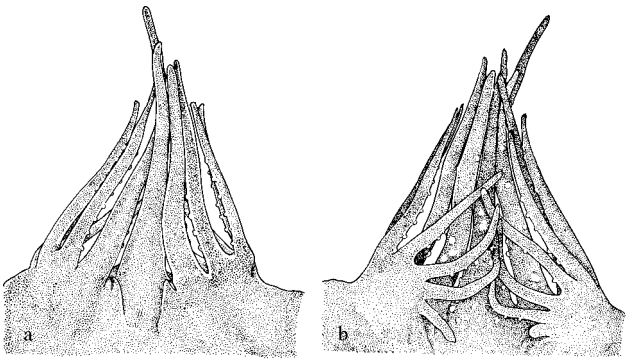

Fig. 5. Velar apparatus in an adult lamprey. a. Ventral view. b. Dorsal view. In the dorsal view can be seen lateral tentacles folded over to form "wings"; one on either side of the velar apparatus.

of the shrinkage due to preservation will happen in the oral disc, trunk, and tail areas. Shrinkage due to preservation has been estimated at 1–3% of the total length by Hubbs and Trautman (1937) and Vladykov (1949). Additionally, natural shrinkage occurs in lampreys when they go through metamorphosis and also when adults become sexually mature. In the latter case, Vladykov and Roy (1948) have determined a reduction in total length varying between 4 and 22% for *Ichthyomyzon unicuspis* kept in aquarium for periods between 2–6 months. Kan and Bond (1981) estimated the reduction in length between feeding and spawning *Entosphenus minimus* to be 13%. Beamish (1980) observed a shrinkage of 20% in the total length of *Entosphenus tridentatus* during the course of their spawning run and Renaud (1982b) found a 22.3% reduction in mean total length between prespawning and spawning *Caspiomyzon wagneri*. In the case of a nonparasitic species, *Lampetra aepyptera*, the reduction in length is less dramatic, 1.2% in males and 4.6% in females (Seversmith 1953). This means that the shortest ammocoetes are longer than the shortest newly–metamorphosed individuals and the longest mature adults are shorter than the longest immature adults. Morphometrics are typically taken on the left side of the specimen (head pointing left), using fine tip calipers and a measuring board, to the nearest 0.5 mm, and are measured as the shortest distance point to point.

Total Length (TL): from the external base of the anteriormost oral fimbria (or in the case of *Mordacia*, which lacks fimbriae, from the anteriormost internal edge of the oral disc) in adults and from the anterior edge of the upper lip in ammocoetes to the extremity of the caudal fin.

Eye Length (O): from the anterior to the posterior edge. Also called eye diameter by some.

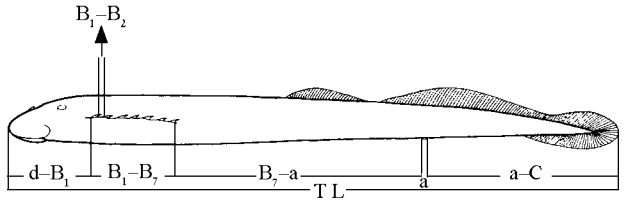

Fig. 6. Side view of larval lamprey showing various body measurements. a = cloacal slit length; a–C = tail length; B_1–B_2 = interbranchial opening distance; B_1-B_7 = branchial length; B_7–a = trunk length; d–B_1 = prebranchial length; TL = total length. After Renaud (1982a).

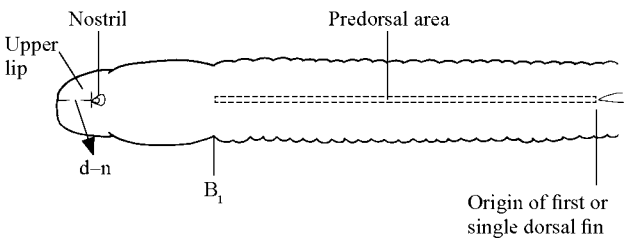

Fig. 7. Dorsal view of the predorsal region of a larval lamprey showing a measurement (d–n = prenostril length) and the limits of a pigmentary character, the predorsal area. After Renaud (1982a).

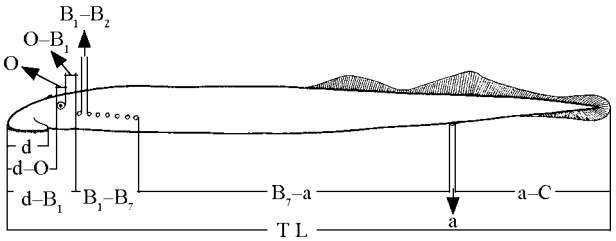

Fig. 8. Side view of adult lamprey showing various body measurements. a = cloacal slit length; a–C = tail length; B_1–B_2 = interbranchial opening distance; B_1-B_7 = branchial length; B_7–a = trunk length; d = disc length; d–B_1 = prebranchial length; d–O = snout length; O = eye length; O–B_1 = postocular length; TL = total length. After Renaud (1982a).

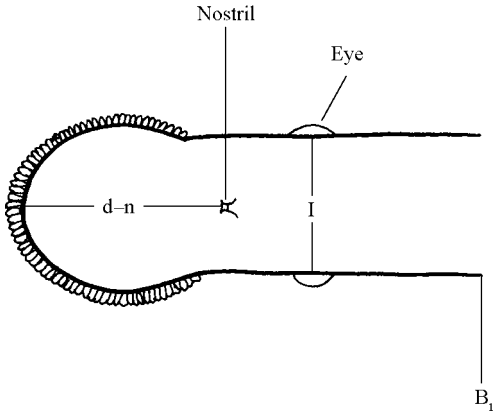

Fig. 9. Dorsal view of the head region of an adult lamprey showing two body measurements. d–n = prenostril length; I = interocular distance. After Renaud (1982a).

Snout Length (d–O): from the external base of the anteriormost oral fimbria (or in the case of *Mordacia*, which lacks fimbriae, from the anteriormost internal edge of the oral disc) to the anterior edge of the eye. Also called preorbital length or preocular length by some.

Disc Length (d): Measured with the lateral margins of the oral disc touching each other (i.e. disc closed) and taken from the external bases of the anteriormost and posteriormost oral fimbriae. This is slightly modified from Renaud (1982a) who measured up to the tip of the anteriormost oral fimbria. This follows Hubbs and Trautman (1937) and others and permits comparison with species of *Mordacia*, which do not possess oral fimbriae.

Prebranchial Length or Head Length (d–B_1): from the external base of the anteriormost oral fimbria (or in the case of *Mordacia*, which lacks fimbriae, from the anteriormost internal edge of the oral disc) in adults and from the anterior edge of the upper lip in ammocoetes to the anterior edge in adults and anterior tip in ammocoetes of the first branchial opening.

Postocular Length (O–B_1): from the posterior edge of the eye to the anterior edge of the first branchial opening.

Prenostril Length (d–n): from the external base of the anteriormost oral fimbria (or in the case of *Mordacia*, which lacks fimbriae, from the anteriormost internal edge of the oral disc) in adults and from the anterior edge of the upper lip

in ammocoetes to the anterior edge of the circular nostril in adults and to the tip of the triangular nostril in ammocoetes.

Branchial Length (B_1–B_7): from the anterior edge of the first branchial opening in adults, or anterior tip in the case of ammocoetes, to the posterior edge of the seventh branchial opening.

Interbranchial Opening Distance (B_1–B_2): Distance separating the posterior edge of the first branchial opening and the anterior edge of the second branchial opening in adults, or anterior tip in the case of ammocoetes.

Trunk Length (B_7–a): from the posterior edge of the seventh branchial opening to the anterior edge of the cloacal slit. This is different from Neira (1984) who measured to the posterior edge of the cloacal slit.

Cloacal Slit Length (a): from the anterior to the posterior edge.

Tail Length (a–C): from the posterior edge of the cloacal slit to the extremity of the caudal fin. This is different from Hubbs and Trautman (1937), Álvarez del Villar (1966), Potter (1968), Neira *et al.* (1988), Yamazaki and Goto (1997), and Kucheryavyi *et al.* (2007) who measured from the anterior edge of the cloacal slit.

Interocular Distance (I): Distance separating the dorsal edges of both eyes.

The urogenital papilla length is measured from its appearance outside of the cloacal slit to its tip.

The intestinal diameter is measured at the level of the origin of the first dorsal fin or the anterior lobe of the single dorsal fin, accordingly.

Pigmentation (Figs. 7, 10–12). Ammocoetes are notoriously difficult to identify to species. The first breakthrough in the identification of lamprey larvae is due to Vladykov (1950) who developed a pigmentation scheme to achieve this. In this seminal paper, Vladykov was able to distinguish between three species using his new characters. Vladykov (1955) further developed his scheme by specifying four classes for the degree of pigmentation; – = absent, + = weak, ++ = moderate, and +++ = strong. However, these categories remained somewhat subjective and open to variation among workers. Additionally, when referring to the branchial region, Vladykov restricted it to the lower part above the branchial groove, but it is not clear what the upper demarcation line is. Renaud (1982a) added a number of pigmentation areas and made a few modifications, such as considering the entire branchial region above the branchial groove to remove any ambiguity, calling the prebranchial blotch area of Vladykov the lower prebranchial area, adding an upper prebranchial area, and developed a semi–quantified method to evaluate more objectively the degree of pigmentation coverage as follows: – = absence to trace; + = 1% to under 25%; ++ = 25% to under 75%; +++ = 75% or more. It is important to note that it is pigmentation extent or coverage and not pigmentation intensity (i.e. darkness) or density that is considered because the amount of light exposure will either make the melanin in the melanophores expand or contract, but the melanophores themselves will remain in place delimiting the area under consideration. Pigmentation areas may be external (Figs. 7, 10–11) or internal (Fig. 12). The external ones include the upper lip (lower flap only; called lateral lip by Neira *et al.* 1988), between upper lip and cheek, cheek, subocular, upper prebranchial, lower prebranchial, upper branchial, lower branchial, ventral branchial, lower lip (called transverse lip by Neira *et al.* 1988), predorsal area, and caudal fin. The caudal fin area evaluated for pigmention is from the deepest part of the caudal fin membrane to its posterior tip. The internal ones include the pigmentation of the bulb (or middle prong) of the "tongue precursor" and the areas on either side of the elastic ridge, which roughly correspond to right-angled triangles placed as mirror images to each other. The middle prong of the tongue precursor is thought to be homologous with the transverse lingual lamina of the adult and the two lateral prongs (not shown in Fig. 12) to the longitudinal lingual laminae. In order to expose the tongue precursor without damaging other characters, the ammocoete is placed on its dorsal aspect and a longitudinal cut is made on the right side immediately inside of the lower flap of the upper lip and a transverse cut is made on the ventral aspect halfway between the lower lip edge and the first branchial opening resulting in a flap of skin that can be flipped to one side to reveal the tongue precursor. Note that a single pigmentary character is assessed according to the above method in adults; that of the caudal fin.

Body Coloration: The color description is that in the live or preserved state as indicated.

Lateral Line Neuromasts: These are bilaterally distributed as individual sensory organs on all aspects (dorsal, lateral and ventral) of the head region, on the lateral and ventral aspects of the branchial region, on the lateral aspect of the

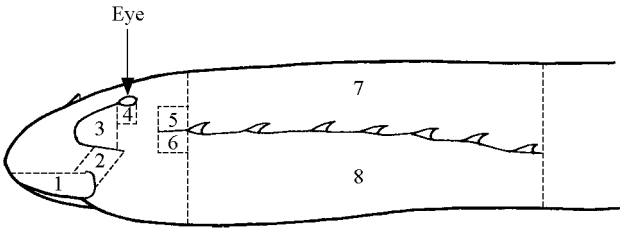

Fig. 10. Side view of the head and branchial regions of a larval lamprey showing various pigmentary areas: 1– upper lip, 2– between upper lip and cheek, 3– cheek, 4– subocular, 5– upper prebranchial, 6– lower prebranchial, 7– upper branchial, 8– lower branchial. After Renaud (1982a).

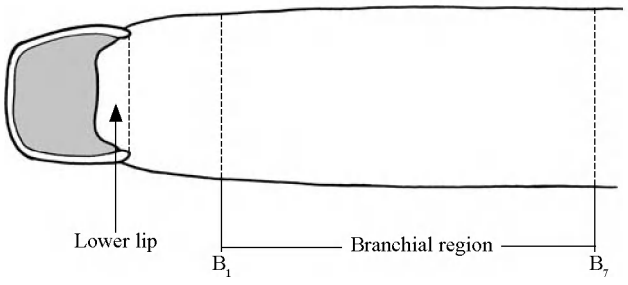

Fig. 11. Ventral view of the head and branchial regions of a larval lamprey showing the limits of two pigmentary areas; the lower lip and ventral branchial. After Renaud (1982a).

trunk region, and on the dorsal aspect of the tail region. The intensity of pigmentation is not assessed here, but simply whether they are unpigmented or darkly pigmented. While in *Ichthyomyzon* the pigmentation of neuromasts is most strikingly pronounced in ammocoetes and adults of most species or only in adults of one species (*I. fossor* being exceptional for the genus in not having pigmented neuromasts in either life stages), some lamprey species

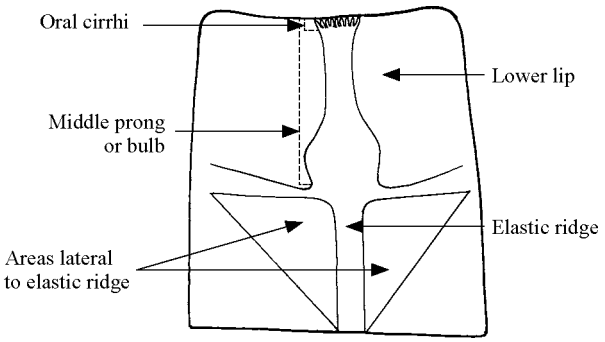

Fig. 12. Dorsal view of the tongue precursor of a larval lamprey. The two fleshy oral cirrhi–bearing prongs lateral to the middle prong or bulb have been omitted. The two pigmentary characters of interest are the middle prong and the two triangular areas lateral to the elastic ridge. After Renaud (1982a).

belonging to other genera also possess darkly pigmented lateral line organs in the adult stage (see individual species accounts below).

Caudal Fin Shape: The fin is termed spade–like if at least one of the two lobes, either the dorsal or the ventral, has a straight posterior edge. Some authors call this shape triangular or pointed. Otherwise, the fin is rounded.

Marginal Membrane Development: A more or less well–developed continuous membrane occurs along the margin of the oral disc at the interface between the oral fimbriae (or internal edge of the oral disc in *Mordacia* that lacks fimbriae) and the marginal teeth.

Repository Institutions

Despite attempts by at least two ichthyological societies at standardizing the codes of repository institutions, there remain variations. To prevent confusion, especially with regards to catalogue numbers of type material, I list below the codes used in this work.

AMS = Australian Museum, Sydney, Australia
ANSP = Academy of Natural Sciences, Philadelphia, USA
BC = University of British Columbia, Vancouver, Canada
BMNH = The Natural History Museum, London, United Kingdom (from now on referred to as UK)
CAS = California Academy of Sciences, San Francisco, USA
CMNFI (formerly NMC) = Canadian Museum of Nature, Ottawa, Canada
CU = Cornell University, Ithaca, New York, USA
CUP = Charles University, Prague, Czech Republic
LMB = Moravské Museum, Brno, Czech Republic
OS = Oregon State University, Museum of Natural History, Corvallis, USA
SNM = Slovak National Museum, Bratislava, Slovakia
UMMZ = University of Michigan, Museum of Zoology, Ann Arbor, USA
USNM = National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZISP (formerly ZIL and ZIN) = Zoological Institute of the Academy of Sciences, St. Petersburg, Russian Federation

Keys: The original intent was to provide keys to ammocoetes and adults for all species of lampreys. However, a survey of the literature quickly revealed that the ammocoetes of many of the species had either never been described or were incompletely so (specifically, *Entosphenus similis*, *Eudontomyzon morii*, *Lethenteron alaskense*, *L. camtschaticum*, *L. reissneri*, the ammocoetes of *Tetrapleurodon geminis* and *T. spadiceus* had been described together and were not distinguishable from each other, those of *Mordacia mordax* and *M praecox* are indistinguishable from each other). Additionally, Richards *et al.* (1982) proposed a new taxonomic character for ammocoetes, the pigmentation of the caudal ridge (the fleshy area overlying the notochord), but this character has so far only been examined in the four species occurring in British Columbia, Canada (*Entosphenus macrostomus*, *E. tridentatus*, *Lampetra ayresii*, and *L. richardsoni*). Therefore, it was decided that only a key to the adults and a partial key to ammocoetes would be provided. Producing a key to the ammocoetes of all of the species is one of the large studies still remaining with regards to lamprey biology.

NOTE: *Eudontomyzon hellenicus* as presented in the catalogue includes both *E. hellenicus* and *E. graecus*. The information on the latter species became available too late in the publishing process to make any changes to the species accounts or keys. However, species[1] counts in the general text of this document incorporate the new species.

[1] Reference: Renaud, C.B. and P.S. Economidis. 2010. *Eudontomyzon graecus*, a new nonparasitic lamprey from Greece (Petromyzontiformes: Petromyzontidae). Zootaxa 2477: 37–48.

1.2 Key to Lamprey Adults of the World

1a. A single indented dorsal fin . . . . . → *2*
1b. Two dorsal fins, either widely separate (in immature individuals of Northern Hemisphere lampreys or in both immature and mature individuals of Southern Hemisphere lampreys) or contiguous (in mature individuals of Northern Hemisphere lampreys) . . . . . → *3*

2a. Unpigmented lateral line neuromasts . . . . . *Ichthyomyzon fossor*
2b. Darkly pigmented lateral line neuromasts . . . . . → *9*

3a. Cloaca is anterior to or under the origin of the second dorsal fin (except in Argentinian and South Georgia Island individuals in which the cloaca is posterior to the origin of the second dorsal fin); one oral papilla on either side of the oral disc is enlarged; labial teeth spatulate . . . . . *Geotria australis*
3b. Cloaca is posterior to the origin of the second dorsal fin; no oral papillae enlarged; labial teeth either rounded or pointed . . . . . → *4*

4a. Cloaca is under the anterior half of the second dorsal fin; a single supraoral lamina; oral papillae present along the anterior edge of the oral disc; oral fimbriae present around the entire perimeter of the oral disc; eyes dorsolateral in mature adults . . . . . → *5*
4b. Cloaca is under the posterior half of the second dorsal fin; two supraoral laminae; oral papillae absent from the anterior edge of the oral disc; oral fimbriae absent; eyes dorsal in mature adults . . . . . → *6*

5a. Supraoral lamina a single tooth with 1or 2 cusps . . . . . → *7*
5b. Supraoral lamina with two teeth, either unicuspid or bicuspid, separated by a wide bridge, which may or may not bear cusps . . . . . → *8*

6a. Endolateral plates tricuspid in immature adults and unicuspid in mature adults; mature males with limited or no swelling of the gular region; trunk myomeres, 84–96 . . . . . → *18*
6b. Endolateral plates quadricuspid or pentacuspid in immature adults and unicuspid in mature adults; mature males with a large gular pouch; trunk myomeres, 78–84 . . . . . *Mordacia lapicida*

7a. Supraoral lamina with a single rounded cusp; transverse lingual lamina straight . . . . . *Caspiomyzon wagneri*
7b. Supraoral lamina with a pointed bicuspid tooth; transverse lingual lamina strongly w–shaped . *Petromyzon marinus*

8a. Exolaterals present in one or more complete rows . . . . . → *10*
8b. Exolaterals absent or only a few scattered but not forming a complete row . . . . . → *12*

9a. Endolaterals on both sides of the oral disc almost invariably unicuspid (rarely 1 or 2 are bicuspid out of 8 endolaterals in total) . . . . . *Ichthyomyzon unicuspis*
9b. Usually two or more bicuspid endolaterals out of a total of 8–10 endolaterals counting both sides of the oral disc . . . . . → *15*

10a. Infraoral lamina cusps internal to the lateralmost ones generally of two sizes . . . . . → *32*
10b. Infraoral lamina cusps internal to the lateralmost ones of a single size . . . . . → *11*

11a. Trunk myomeres, 53–63 . . . . . → *36*
11b. Trunk myomeres, 59–74 . . . . . → *20*

12a. Posterials present as a single complete row . . . . . → *13*
12b. Posterials absent, or if present, as an incomplete, and rarely, as a complete row . . . . . → *24*

13a. Infraoral lamina with usually five teeth; typically four endolaterals on each side of the oral disc . . . . . → *14*
13b. Infraoral lamina with more than five teeth; three endolaterals on each side of the oral disc . . . . . → *22*

14a. Some marginals in the lateral and anterial fields have an elongated base . . . . . *Entosphenus similis*
14b. No marginals with an elongated base . . . . . → *19*

15a. 0–8 bicuspid endolaterals; 49–56 trunk myomeres . . . . . → *16*
15b. 6–10 bicuspid endolaterals; 53–62 trunk myomeres . . . . . → *17*

16a. Disc Length/Total Length, 3.9–6.5% . . . . . *Ichthyomyzon gagei*
16b. Disc Length/Total Length, 6.3–11.6% . . . . . *Ichthyomyzon castaneus*

17a. Lateral line neuromasts on the ventral surface of the branchial region unpigmented ..... ***Ichthyomyzon greeleyi***
17b. Lateral line neuromasts on the ventral surface of the branchial region darkly pigmented ..... ***Ichthyomyzon bdellium***

18a. Adults 113–421 mm TL; mature adults 277–376 mm TL; mature males with loose skin in gular region ..... ***Mordacia mordax***
18b. Adults 102–172 mm TL; mature adults 119–160 mm TL; mature males with no swelling of the gular region ..... ***Mordacia praecox***

19a. Endolateral formula typically 2–3–3–2 ..... → ***23***
19b. Endolateral formula not typically 2–3–3–2 ..... → ***25***

20a. 3–5 teeth in first row of anterials ..... ***Eudontomyzon morii***
20b. 5–13 teeth in first row of anterials ..... → ***21***

21a. 2–4 rows of anterials ..... ***Eudontomyzon mariae***
21b. 4–7 rows of anterials ..... ***Eudontomyzon danfordi***

22a. Gular region darkly pigmented ..... ***Lethenteron appendix***
22b. Gular region unpigmented (this character state requires verification in *Lethenteron kessleri* but is definitely unpigmented in the other species below, *L. alaskense*, *L. camtschaticum*, and *L. reissneri*) ..... → ***29***

23a. Velar tentacles usually 10 or more ..... → ***26***
23b. Velar tentacles less than 10 ..... → ***30***

24a. Posterials absent ..... → ***27***
24b. Posterials present, but as an incomplete, and rarely, as a complete row ..... → ***38***

25a. Endolateral formula typically 1–1–1–1, or if a variant formula, the second or third tooth rarely tricuspid ..... ***Entosphenus hubbsi***
25b. Endolateral formula typically 2–2–2–2, or if a variant formula, the second tooth is tricuspid in 36% of cases and the third tooth is tricuspid in 15% of cases ..... ***Entosphenus lethophagus***

26a. Caudal fin rounded; Disc Length/Total Length, 4.6–9.1% ..... ***Entosphenus tridentatus***
26b. Caudal fin spade–like; Disc length/Total Length, 6.5–11.7% ..... ***Entosphenus macrostomus***

27a. Transverse lingual lamina with a median cusp only or with 5–13 cusps ..... → ***28***
27b. Transverse lingual lamina with 11–17 cusps ..... → ***31***

28a. Transverse lingual lamina with 9–13 cusps; second endolateral typically tricuspid ..... ***Lampetra planeri***
28b. Transverse lingual lamina with a median cusp only or with 5–11 cusps; second endolateral typically bicuspid ..... → ***33***

29a. Second dorsal fin unpigmented; trunk myomeres, 57–65; 38–44 anterials ..... ***Lethenteron reissneri***
29b. Second dorsal fin usually with a dark blotch; trunk myomeres, 65–77; 15–38 anterials ..... → ***34***

30a. Velar tentacles 5–9, without tubercles; parasitic ..... ***Entosphenus minimus***
30b. Velar tentacles 8–9, with tubercles; nonparasitic ..... ***Entosphenus folletti***

31a. Eye Length/Total Length, 2.3–4.3% ..... ***Lampetra ayresii***
31b. Eye Length/Total Length, 1.4–3.1% ..... ***Lampetra fluviatilis***

32a. Total Length, 180–310 mm ..... ***Tetrapleurodon spadiceus***
32b. Total Length, 106–148 mm ..... ***Tetrapleurodon geminis***

33a. Restricted to Turkey ..... ***Lampetra lanceolata***
33b. Restricted to the Pacific coasts of Canada and the USA ..... → ***37***

34a. Total Length, 110–625 mm; parasitic ..... ***Lethenteron camtschaticum***
34b. Total Length, 112–230 mm; nonparasitic ***35***

35a. 23–38 anterials; restricted to Alaska and the Northwest Territories, Canada ..... ***Lethenteron alaskense***

35b. 15–28 anterials; restricted to Siberia and perhaps Japan . . . . . ***Lethenteron kessleri***

36a. Labial teeth radially–arranged in a curvilinear fashion and completely cover all available space (i.e. pavement–like) on the oral disc fields; restricted to Greece . . . . . ***Eudontomyzon hellenicus*** [1]
36b. Labial teeth rather scattered and do not completely cover all available space on the oral disc fields; restricted to eastern USA . . . . . ***Lampetra aepyptera***

37a. Trunk myomeres, 60–67; fleshy tissues around the lingual laminae unpigmented . . . . . ***Lampetra richardsoni***
37b. Trunk myomeres, 53–58; fleshy tissues around the lingual laminae darkly pigmented . . . . . ***Lampetra pacifica***

38a. Dark blotch near the apex of the second dorsal fin; 9–15 cusps on the transverse lingual lamina . . . . . ***Lethenteron ninae***
38b. No dark blotch near the apex of the second dorsal fin; 5–7 cusps on the transverse lingual lamina . . . . . ***Lethenteron zanandreai***

1.3 Partial Key to Lamprey Ammocoetes of the World 60 mm Total Length or Greater

1a. A single slightly indented dorsal fin . . . . . → *2*
1b. Two dorsal fins (a low lying membrane not supported by fin rays may unite the two fins especially in smaller specimens) . . . . . → *3*

2a. Lateral line neuromasts darkly pigmented; trunk myomeres, 49–60 . . . . . → *4*
2b. Lateral line neuromasts unpigmented; trunk myomeres, 48–54 . . . . . → *5*

3a. Cloaca is under the origin of the second dorsal fin; caudal fin rounded . . . . . ***Geotria australis*** (Chile and Australasia)
3b. Cloaca is well posterior to the origin of the second dorsal fin; caudal fin rounded or spade–like . . . . . → *8*

4a. Trunk myomeres, 49–56 . . . . . → *6*
4b. Trunk myomeres, 55–60 . . . . . → *7*

5a. Upper branchial region heavily pigmented (+++); subocular area moderately (++) to heavily (+++) pigmented . . . . . ***Ichthyomyzon fossor***
5b. Upper branchial region moderately pigmented (++); subocular area unpigmented (–) to lightly (+) pigmented . . . . . ***Ichthyomyzon unicuspis***

6a. Subocular area unpigmented (–) to lightly (+) pigmented . . . . . ***Ichthyomyzon gagei***
6b. Subocular area moderately (++) to heavily (+++) pigmented . . . . . ***Ichthyomyzon castaneus***

7a. Subocular area unpigmented (–) to lightly (+) pigmented . . . . . ***Ichthyomyzon greeleyi***
7b. Subocular area moderately (++) pigmented . . . . . ***Ichthyomyzon bdellium***

8a. Cloaca is under the anterior half of the second dorsal fin . . . . . → *9*
8b. Cloaca is under the posterior half of the second dorsal fin . . . . . → *10*

9a. Caudal fin spade–like; trunk myomeres, 66–83 . . . . . ***Geotria australis*** (Argentina)
9b. Caudal fin rounded or spade–like; trunk myomeres, 51–74; Northern Hemisphere . . . . . → *11*

10a. Trunk myomeres, 78–83 . . . . . ***Mordacia lapicida***
10b. Trunk myomeres, 82–93 . . . . . ***Mordacia mordax*** and ***M. praecox***

11a. Trunk myomeres, 51–60 . . . . . ***Entosphenus hubbsi*** (North America), ***Lampetra aepyptera*** (North America), ***L. pacifica*** (North America), ***Lethenteron ninae*** (Asia), ***L. zanandreai*** (Europe)
11b. Trunk myomeres, 61–74 . . . . . ***Entosphenus lethophagus*** (North America), ***E. macrostomus*** (North America), ***E. tridentatus*** (Asia and North America), ***Lampetra ayresii*** (North America), ***Lethenteron appendix*** (North America), ***L. kessleri*** (Asia), ***Petromyzon marinus*** (North America, Europe, and North Africa), ***Tetrapleurodon geminis*** (Mexico), ***T. spadiceus*** (Mexico)

11c. Trunk myomeres, 53–70. . . . . ***Caspiomyzon wagneri*** (Caspian Sea Basin),
Entosphenus folletti (North America), ***E. minimus*** (North America),
Eudontomyzon danfordi (Europe), ***E. hellenicus***[1] (Greece),
E. mariae (Europe), ***Lampetra fluviatilis*** (Europe),
L. lanceolata (Turkey), ***L. planeri*** (Europe), ***L. richardsoni*** (North America)

11d. Undescribed . . . . . ***Entosphenus similis*** (North America),
Eudontomyzon morii (Asia), ***Lethenteron alaskense*** (North America),
L. camtschaticum (Eurasia), ***L. reissneri*** (Asia)

[1] *Eudontomyzon hellenicus* as presented in the catalogue includes both *E. hellenicus* and *E. graecus*. The information on the latter species became available too late in the publishing process to make any changes to the species accounts or keys.

Order PETROMYZONTIFORMES

Synonyms: Marsipobranchii; Hyperoartia Müller 1841; **Petromyzontes**

FAO Names: En — Lamprey; **Fr** — Lamproie
Local names: Neunauge **(German);** Minoga **(Russian);** Yatsume **(Japanese)**

The order Petromyzontiformes (Petromyzoniformes is an unjustified emendation) comprises 40 species grouped into three families; one in the Northern Hemisphere, Petromyzontidae, and two in the Southern Hemisphere, Geotriidae and Mordaciidae. The relationships among the three families have not yet been resolved using a cladistic approach. However, it is proposed here that Geotriidae and Mordaciidae are sister groups on the basis of two synapomorphies related to what has been termed a second metamorphosis during the transition phase from immature to mature adult; firstly, the breakdown of radial plates in the posterior field into individual cusps, and secondly, the reduction in number and hypertrophy of transverse lingual laminae cusps. The absence of both these ontogenetic changes in the Petromyzontidae is interpreted as being the plesiomorphic condition. Alternatively, Gill (1883a) had placed the Northern Hemisphere genera *Petromyzon*, *Ichthyomyzon*, *Ammocoetes* (= *Lampetra*), and *Entosphenus* with the Southern Hemisphere genera *Geotria* and *Exomegas* under the subfamily Petromyzontinae, both groups having a single supraoral lamina, while placing *Caragola* (= *Mordacia*) with two supraoral laminae in a separate subfamily Caragolinae. Silver *et al.* (2004) using the DNA sequence of a form of gonadotropin–releasing hormone have suggested that Geotriidae and Petromyzontidae have a sister–group relationship and that they are in turn sister to Mordaciidae. This had earlier been proposed by Baldwin *et al.* (1988) who looked at amino acid composition of lactate dehydrogenase. However, the above three studies inferred these relationships based on overall similarity, and therefore, they may not reflect the true phylogeny. The family Petromyzontidae comprises 36 species, the Geotridae a single species and the Mordaciidae, three.

Phylogenetic Relationships at the Generic Level: Gill *et al.* (2003) produced a cladogram of all 18 extant parasitic species (*Caspiomyzon wagneri*, the inferred scavenger was included in with the parasitic species) of the order using morphological characters (Fig. 13). Docker *et al.* (1999) examined the relationships within the Northern Hemisphere genus *Lampetra sensu lato*, that included 11 species here considered in the genera *Lampetra sensu stricto* (2 parasitic and 2 nonparasitic species), *Entosphenus* (3 parasitic and 2 nonparasitic species), and *Lethenteron* (1 parasitic and 1 nonparasitic species) using molecular characters. However, whereas the former is a cladistic treatment, the latter study is phenetic and it may not reflect the true phylogeny. It is nevertheless interesting to note that the relationships amongst the seven species in common in those two studies were remarkably similar, in that *Petromyzon* was sister to *Entosphenus–Lethenteron–Lampetra*, with *Entosphenus* in turn sister to *Lethenteron–Lampetra*. The only difference was in the placement of *Lampetra ayresii*, where it was sister to *Lampetra fluviatilis* in Gill *et al.* (2003), whereas it was sister to a group comprising *Lethenteron camtschaticum* (as *Lampetra japonica*) and *Lampetra fluviatilis*, thereby rendering the genus polyphyletic, in Docker *et al.* (1999). In addition to the single apomorphy to support the monophyly of the *Entosphenus–Lethenteron–Eudontomyzon–Lampetra* clade, as revealed by Gill *et al.* (2003), Monette and Renaud (2005) added another apomorphy, a two–lumen gular pouch. A comprehensive phylogenetic study that includes both the parasitic and the nonparasitic species has yet to be made. However, the majority of workers (Hubbs, 1924, Zanandrea, 1961) believe that the nonparasitic mode of life represents the derived condition as the buccal glands of those that have been investigated still secrete an anticoagulant and cytolytic agents (lamphredin) despite not needing them. Zanandrea (1961) hypothesized a step–wise evolutionary process in which an anadromous parasitic ancestor became landlocked, feeding exclusively in a freshwater environment as an adult, and later, this adult feeding phase was completely abandoned, resulting in a nonparasitic lamprey. The evolution of a nonparasitic mode of life is thought to have occurred repeatedly throughout the order. Piavis *et al.* (1970) are alone in suggesting that parasitic species evolved from nonparasitic species.

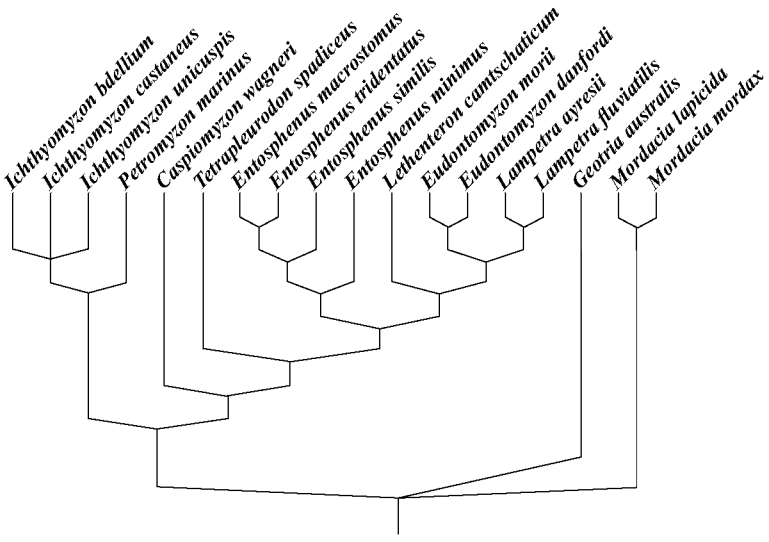

Fig. 13. Cladogram of the parasitic lamprey species, with representatives from all of the recognized lamprey genera, resulting from an analysis of morphological characters. After Gill *et al.* (2003) and Monette and Renaud (2005).

Family GEOTRIIDAE

Fig. 14

Synonyms: Geotriidae Jordan 1923: 83.

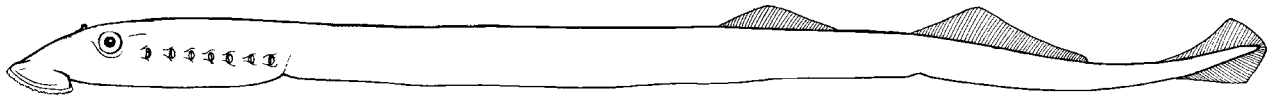

Fig. 14. Side view of *Geotria australis* prespawning adult. After Neira (1984).

This is a monogeneric family restricted to the Southern Hemisphere. Two dorsal fins. Second dorsal fin confluent with caudal fin in ammocoetes. Cloaca anterior to or under the origin of the second dorsal fin (except in ammocoetes and adults from Argentina where it is located under the anterior half of the second dorsal fin). Midgut of ammocoete possesses two diverticula. Oral papillae present along the anterior and lateral edges of the oral disc, but absent from the posterior edge. One oral papilla on either side of the oral disc is enlarged. Oral fimbriae present around the entire perimeter of the oral disc. One wide supraoral lamina with 4 unicuspid teeth (two pointed central ones flanked by broad lateral flanges). Labial teeth spatulate and radially–arranged in a curvilinear fashion completely covering all fields of the oral disc. The single row of ridge–like radial plates found in the posterior field of the oral disc in prespawning (immature) adults break down into multiple rows of individual unicuspid teeth in spawning (mature) adults. The transverse lingual lamina also undergoes a dramatic transformation from recently metamorphosed individuals (three unicuspid teeth, the median one enlarged) to feeding adults (three unicuspid teeth, the lateral ones greatly enlarged) to mature adults (two unicuspid teeth). Eyes dorsolateral in immature and mature adults. Two dorsal fins separate in immature and mature adults. Second dorsal fin separate from the caudal fin in immature and mature adults. Spawning males have a large pendulous gular pouch that extends from immediately posterior to the oral disc to the first or second branchial opening. In spawning females, the gular pouch is much less developed. Additionally, the oral disc in spawning specimens is greatly expanded laterally and appears broadly triangular when opened. Two buccal glands.

Genus *Geotria* Gray 1851

Synonyms: ***Geotria*** Gray 1851: 142; ***Velasia*** Gray 1851: 143; ***Thysanochilus*** Philippi 1857: 268; ***Chilopterus*** Philippi 1858: 308; ***Yarra*** de Castelnau 1872: 231 (based on an ammocoete; type species: ***Yarra Singularis*** de Castelnau 1872 by monotypy); ***Neomordacia*** de Castelnau 1872: 232 (based on a recently metamorphosed adult; type species: ***Neomordacia howittii*** de Castelnau 1872 by monotypy); ***Exomegas*** Gill 1883: 522, 524 (based on a feeding–phase *Geotria*; type species: ***Petromyzon macrostomus*** Burmeister 1868); ***Macrophthalmia*** Plate 1897: 137

This is a monotypic genus (one parasitic species but see Taxonomic Remarks under the *Geotria australis* species account) restricted to the Southern Hemisphere. The generic characters are those of the family (see above). The taxonomy has been reviewed by Potter and Strahan (1968). The type species is *Geotria australis* Gray 1851.

Geotria australis Gray 1851

Figs. 15–17

Synonyms: ***Geotria australis*** Gray 1851: 142, pl. 2 (holotype: 480 mm TL; type locality: Inkar pinki River (= Onkaparinga River), south of Adelaide, South Australia, but according to de Castelnau (1872) it is Brighton Beach, Hobson's Bay, near Melbourne, Victoria, Australia); ***Velasia chilensis*** Gray 1851: 143, pl. 1, fig. 4 (holotype: adult, 380 mm TL; type locality: Chile, in fresh water); ***Thysanochilus valdivianus*** Philippi 1857: 268 (Chile); ***Ammocoetes caeruleus*** Philippi 1858: 306-307 (holotype: 76 mm TL ammocoete, Chile); ***Petromyzon Fonki*** Philippi 1865: 109 (Chile); ***Petromyzon macrostomus*** Burmeister 1868: XXXVI (holotype: 400 mm TL; type locality: near Buenos Aires, Argentina); ***Geotria allporti*** Günther 1872: 675, pl. LXX (holotype: 330 mm TL according to original description, but 350 mm TL according to Regan (1911); Australia: Tasmania, in fresh water); ***Yarra Singularis*** de Castelnau 1872: 231 (holotype: ammocoete, 111 mm TL (originally) re-measured in 2003 as 107 mm TL, MNHN A–7542; type locality: in brackish water, lower Yarra River, Victoria, Australia); ***Neomordacia howittii*** de Castelnau 1872 (holotype: recently metamorphosed adult of undetermined sex, 80 mm TL, MNHN A–7543; type locality: Cape Schanck, Victoria, Australia); ***Velasia stenostomus*** Ogilby 1896: 409-418 (468 mm TL; type locality: Tasmania, Australia); ***Macrophthalmia chilensis*** Plate 1897: 137–141 (Chile); ***Geotria saccifera*** Regan 1911: 196–197 (holotype: 420 mm TL; type locality: Otago Peninsula, New Zealand)

Taxonomic Remarks: Neira *et al.* (1988) showed that ammocoetes of an Argentinian population were morphologically distinct from ammocoetes of both Chilean and Australasian (mainland Australia, Tasmania, and New Zealand) populations of the species. Additionally, they stated that adults from Argentina and from South Georgia Island had the cloaca positioned well posterior to the origin of the second dorsal fin rather than aligned immediately under its origin as in Chilean and Australasian populations. Perhaps, therefore, the Argentinian and South Georgian Island population represents a distinct species and this question merits closer scrutiny.

FAO Name: En — Pouched Lamprey; **Fr** — Lamproie saccifère
Local Names: Piharau, Kanakana **(Māori)**

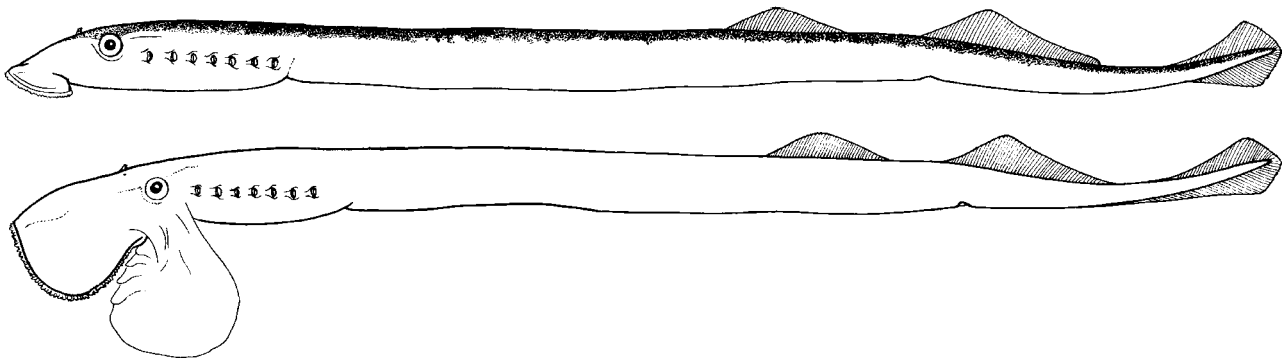

Fig. 15. Side views of *Geotria australis* prespawning adult (above) and spawning male with gular pouch (below). After Neira (1984).

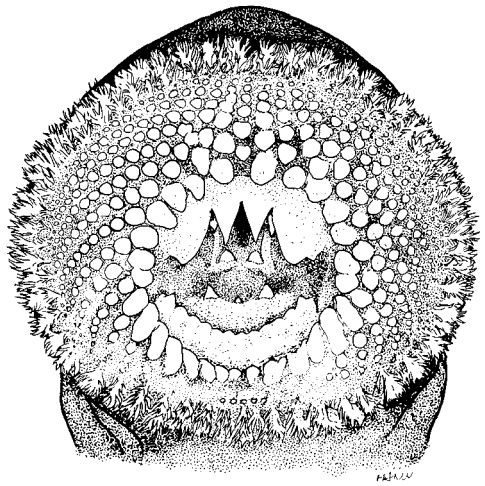

Fig. 16. Oral disc of *Geotria australis*.

Diagnostic Features: Ammocoetes: Maximum size attained, 111 mm TL. Body proportions, as percentage of TL [based on 1,516 specimens measuring 11–108 mm TL; values are approximate because they are derived from graphs since they were not stated explicitly in the text in Neira *et al.* (1988)]: prebranchial length, 6.2–12.9; branchial length, [as low as 9.7 according to Neira (1984)] 10.8–17.4; trunk length, 55.9–60.8 [52.5–77.1 according to Neira (1984)]; tail length, 12.0–25.6. Trunk myomeres, 66–83. Body coloration unrecorded. Lateral line neuromast pigmentation unrecorded. A number of distinctive characters have been found (Neira *et al.* 1988) between ammocoetes from Argentina, Chile, and Australasia, and therefore, these three groups will be treated separately. Argentina: cloaca under the anterior half of the second dorsal fin; distinct notch between the confluent second dorsal and caudal fins; caudal fin spade–like; pigmentation: upper lip, –; subocular, –; upper prebranchial, –; lower prebranchial, –; upper branchial, + or ++; lower branchial, –; caudal fin, ++ or +++. Chile: cloaca under the origin of the second dorsal fin; second dorsal and caudal fins smoothly confluent; caudal fin rounded; pigmentation: upper lip, +++; subocular, +++; upper prebranchial, +++; lower prebranchial, +++; upper branchial, ++ or +++; lower branchial, –; caudal fin, –. Australasia: cloaca under the origin of the second dorsal fin; second dorsal and caudal fins smoothly confluent; caudal fin rounded; pigmentation: upper lip, +++; subocular, –; upper prebranchial, +++; lower prebranchial, +++; upper branchial, ++ or +++; lower branchial, +; caudal fin, –.

Metamorphosing Ammocoetes: 76–112 mm TL.

Adults: 76–570 mm TL. Body proportions, as percentage of TL (based on 17 specimens measuring 90–570 mm TL): prebranchial length, 8.3–20.2; branchial length, 7.9–11.8; trunk length, 47.6–61.5; tail length, 16.1–31.1; eye length unrecorded; disc length unrecorded. The urogenital papilla is not prominent in mature adults. Trunk myomeres, 70–78. Dentition: supraoral lamina, 4 unicuspid teeth (two pointed central ones flanked by broad lateral flanges); infraoral lamina, 9–15 unicuspid teeth; 8–9 unicuspid endolaterals on each side; 5–7 rows of anterials; first row of anterials, 1–4 unicuspid teeth; 6–8 rows of exolaterals on each side; 1 row of posterials in feeding phase adults consisting of 12 radial plates that may also be flanked on each side by two unicuspid teeth and in spawning adults about 3 rows, the first one consisting of 9 unicuspid teeth; transverse lingual lamina, 3 unicuspid teeth, the median one enlarged in recently metamorphosed individuals, 3 unicuspid teeth the lateral ones greatly enlarged in feeding individuals and 2 unicuspid teeth in mature individuals; longitudinal lingual laminae each with 4 unicuspid teeth. Velar tentacles, 23–40. Body coloration (live), in prespawning adults, dorsal surface dark with a pair of longitudinal blue–green stripes running along the dorso–lateral

aspect, ventral surface silvery. Spawning adults are dark blue on the dorsal surface and light blue on the ventral surface. Lateral line neuromasts darkly pigmented. Caudal fin pigmentation unrecorded. Caudal fin shape, rounded. Oral fimbriae, 55–65. Oral papillae, 16–19.

Habitat and Biology: Anadromous. Ammocoetes and adults are found in rivers and lakes. Metamorphosing ammocoetes are found at the mouths of rivers. In the sea, adults may be found in surface waters.
In Australia, larval life is reported to last 3.25–4.25 yrs. In Chile, metamorphosis occurs between August and March, while in Australia, it starts at the end of January, beginning of February. Young adults migrate out of Argentinian and Chilean rivers into marine waters during austral winter (June–September). Adults parasitic, feeding at sea. The duration of the marine feeding phase is not known but is thought to be quite long. Adults are preyed upon extensively by two species of albatrosses (black–browed and grey–headed) in surface waters around South Georgia Island. It has been estimated that these two bird species yearly consume 100,000 and 1,800,000 adult lampreys, respectively. The marine migration between Argentina and South Georgia Island is at least 1,750 km one way. The spawning migration is believed to last 15–16 months during which the lampreys do not feed. In Chile, the mature adults reach continental waters during the austral summer months (January–March). On mainland Australia the spawning run may be several hundred kilometres up the Murray River. The spawning behavior has not been described. Stones with a volume of 144 mL, equivalent in size to a tennis ball, can be transported by adults using their oral disc. Fecundity, 48,004 to 68,212 eggs/female. In two Tasmanian rivers (North Esk and Derwent), where they co–occur with ammocoetes of *Mordacia mordax*, those of *Geotria australis* are 3–8 times less abundant.

Geographic Distribution (Fig. 17): Australia: Donnelly, Brunswick, Denmark, Swan, Warren, Bow, and Kalgan rivers, Western Australia; Gulf St. Vincent, Port, Torrens, Onkaparinga, and Murray rivers, and The Coorong, South Australia; Glenelg, Moyne, Merri, Curdies, Yarra, Tarwin, and Albert rivers, Gippsland lakes Victoria and King, Victoria; Dundas, Hellyer, Plenty, Russell, Ringarooma, Swan, Forth, Great Forester, Triabunna, North Esk, Derwent, Browns, and Huon rivers, and Bruny Island, Tasmania; New Zealand: Okuti River; Chile: Andalién, Biobío, Carampangue, Malleco, Picoiquén, Huequén, Purén, Claro, Mehuín, Calle–Calle, Valdivia, Toma Galeones, Santo Domingo, Maullín, Curilelfu, and Donguil rivers, and Lake Risopatron; Argentina: Limay River; and the Falkland and South Georgia islands.

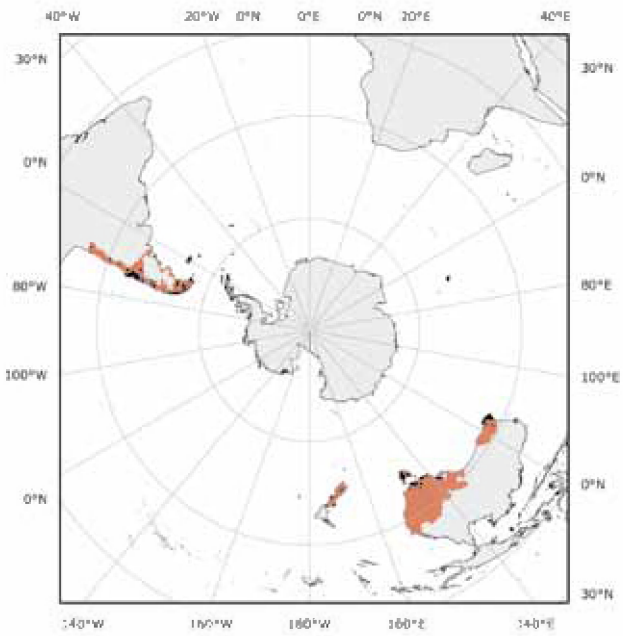

Fig. 17. Geographic distribution of *Geotria australis*.

Interest to Fisheries: In New Zealand, the Maori use the Pouched Lamprey at the beginning of their upstream migration for human consumption and ceremonial purposes (McDowall, 1990). These are caught using weirs built along river edges or collected by hand as they are making their way up the rocky face of falls. They are then dried for human consumption.

References: Burmeister (1868), Cook *et al.* (1990), de Castelnau (1872), Gill *et al.* (2003), Gray (1851), Günther (1872), Hubbs and Potter (1971), Ivanova–Berg (1968), Khidir and Renaud (2003), Lahille (1915), Lethbridge and Potter (1979), Maskell (1929), McDowall (1990), Neira (1984), Neira *et al.* (1988), Ogilby (1896), Plate (1897), Philippi (1857, 1858, 1865), Potter (1968), Potter and Hilliard (1986), Potter and Strahan (1968), Potter and Welsch (1997), Potter *et al.* (1979, 1980, 1983), Regan (1911), Strahan (1959)

Family MORDACIIDAE

Fig. 18

Synonyms: Caragolinae Gill 1883; **Mordaciidae** Gill 1893

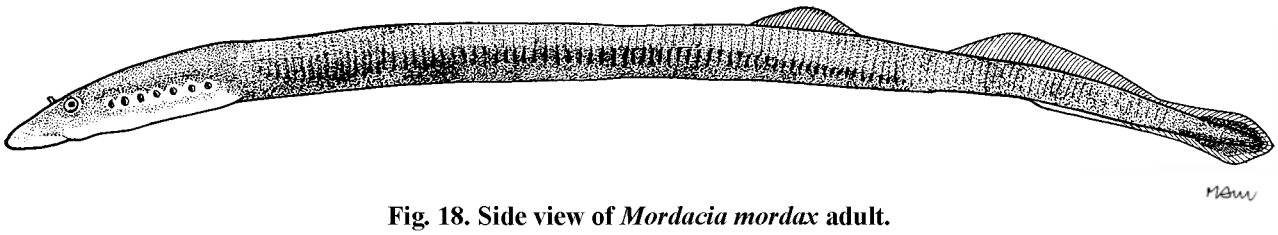

Fig. 18. Side view of *Mordacia mordax* adult.

This family comprises one genus that is restricted to the Southern Hemisphere. Two dorsal fins. Second dorsal fin confluent with caudal fin in ammocoetes. Cloaca under the posterior half of the second dorsal fin in ammocoetes and adults. Midgut of ammocoetes (in *Mordacia lapicida* and *M. mordax*) possesses one diverticulum. Oral papillae absent from the anterior as well as the posterior edges of the oral disc, but present along the lateral edges. All oral papillae of uniform size. Oral fimbriae absent. Two triangular and tricuspid supraoral laminae. The multicuspid radial plates found in the anterior, lateral and posterior fields of the oral disc in prespawning (immature) adults break down and leave only individual unicuspid teeth in spawning (mature) adults. Labial teeth pointed. Transverse lingual lamina w-shaped in prespawning individuals and, at least in *M. lapicida*, undergoes a dramatic change to only two greatly enlarged unicuspid teeth in spawning individuals. Eyes dorsolateral in immature adults and dorsal in mature adults. Two dorsal fins separate in immature and mature adults (in *M. lapicida* and *M praecox*). Second dorsal fin either connected to or separate (at least in some individuals of *M. mordax*) from the caudal fin in adults. Three buccal glands. According to Potter (1968), *M. mordax – M. praecox* constitute a species pair.

Genus *Mordacia* Gray 1851

Synonyms: ***Mordacia*** Gray 1851: 143 [original description; type species: *Petromyzon mordax* Richardson 1846 by subsequent designation of the first revisor (Günther 1870)]; ***Caragola*** Gray 1851: 143 (type species: *Caragola lapicida* Gray 1851 by monotypy)

This genus comprises three species (two parasitic and one nonparasitic) that are restricted to the Southern Hemisphere. The generic characters are those of the family (see above). The taxonomy has been reviewed by Potter and Strahan (1968). The type species is *Petromyzon mordax* Richardson 1846.

Mordacia lapicida (Gray 1851) **Figs. 19–21**

Synonyms: ***Caragola lapicida*** Gray 1851: 143 (type locality: Bay of Valparaiso, Chile); ***Petromyzon Anwandteri*** Philippi 1863: 207 (Chile); ***Petromyzon acutidens*** Philippi 1865: 107 (Chile)

FAO Names: En — Chilean Lamprey; **Fr** — Lamproie du Chili

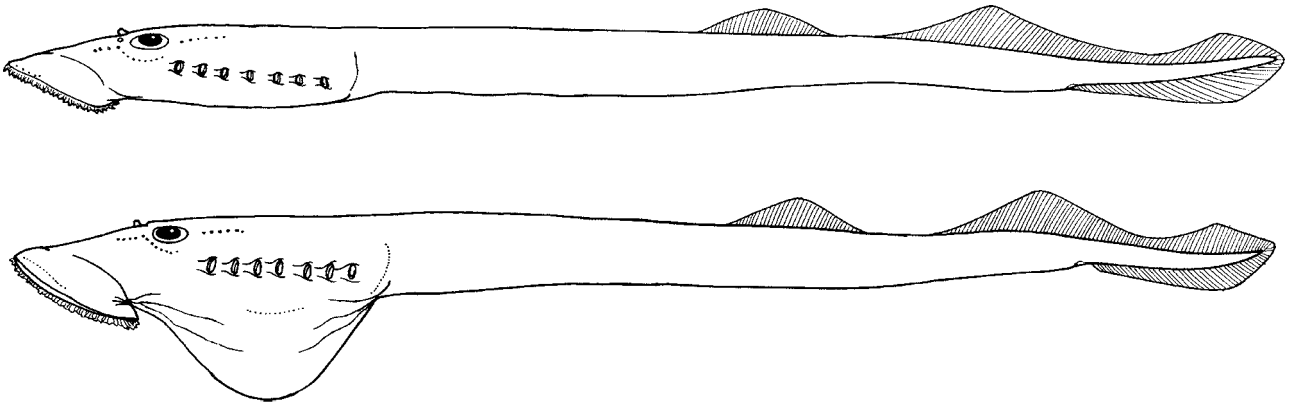

Fig. 19. Side views of *Mordacia lapicida* prespawning adult (above) and spawning male with gular pouch (below). After Neira (1984).

Diagnostic Features: Ammocoetes: Maximum size attained, 154 mm TL. Body proportions, as percentage of TL [based on about 100 specimens measuring 36.0–138.0 mm TL; values are approximate because they are derived from graphs since they were not stated explicitly in the text in Neira *et al.* (1988)]: prebranchial length, [as low as 7.3 according to Neira (1984)] 7.7–11.1; branchial length, 11.6–14.4 [10.3–15.5 according to Neira (1984)]; trunk length, 58.2–63.2 [as high as 63.6 according to Neira (1984)]; tail length, [as low as 14.5 according to Neira (1984)] 15.6–20.8. Trunk myomeres,

73–83. Body coloration unrecorded. Pigmentation: upper lip, +++; subocular, +++; upper prebranchial, +++; lower prebranchial, +++; upper branchial, +++; lower branchial, –; caudal fin, +++. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded or spade–like. Second dorsal and caudal fins smoothly confluent.

Metamorphosing Ammocoetes: 110–150 mm TL.

Adults: 111–540 mm TL. Body proportions, as percentage of TL (based on 39 specimens measuring 111–313 mm TL): prebranchial length, 8.0–17.0; branchial length, 8.3–12.1; trunk length, 57.8–77.1; tail length, 13.8–19.0; eye length unrecorded; disc length unrecorded. Mature males have a large gular pouch that extends from immediately posterior of the oral disc to the end of the branchial region. The urogenital papilla length, as a percentage of branchial length, in spawning males unrecorded. Trunk myomeres, 78–84. Dentition: supraoral lamina, two triangular supraoral laminae each with three unicuspid teeth, one per apex; infraoral lamina, 9–13 unicuspid teeth of various size in immature individuals and divided into three tricuspid plates with, in each case, the median cusp largest in spawning individuals; 7 endolateral plates on either side each bearing 3–5 unicuspid teeth in prespawning individuals, usually 4–5; endolateral formula, typically 3–3–4–4–4–4–3 or 4–4–4–5–5–4–3 or 5 endolaterals as individual unicuspid teeth on either side in spawning individuals; 1–2 rows of anterials; first row of anterials consisting of 4 tricuspid radial plates in recently transformed individuals, of 2 tricuspid flanked on either side by 1 quadricuspid radial plate in feeding phase individuals and of 6 unicuspid teeth in spawning individuals; 1 row of exolaterals on each side; 1 row of posterials; first row of posterials, 10–12 tricuspid (sometimes quadricuspid) plates in prespawning individuals and 12 unicuspid teeth in spawning individuals; transverse lingual lamina, w–shaped, with numerous unicuspid teeth in prespawning individuals and with only 2 greatly enlarged lateral unicuspid teeth in spawning individuals; longitudinal lingual laminae, each with 9–15 unicuspid teeth. Velar tentacles number unrecorded. Body coloration unrecorded. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation, pigmented but extent of coverage not determined. Caudal fin shape, spade–like. Oral papillae number unrecorded.

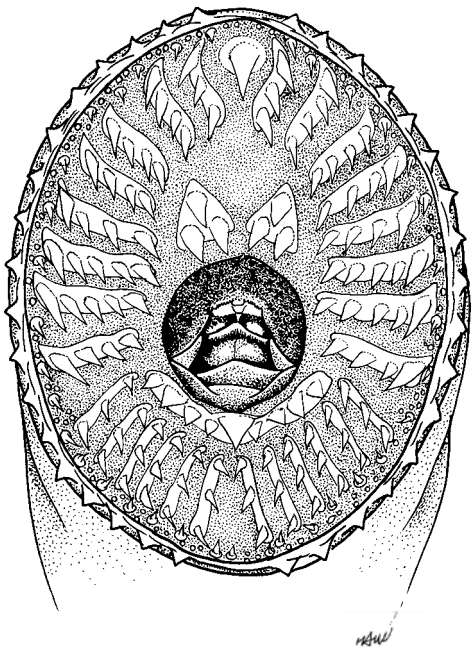

Fig. 20. Oral disc of *Mordacia lapicida*. After Neira (1984).

Habitat and Biology: Anadromous. Ammocoetes and adults are found in rivers. Ammocoetes occur in substrates of fine sand with abundant organic detritus along the river banks.

Metamorphosis occurs between August and March and recently metamorphosed adults enter marine waters during austral winter (June–August) at about 143 mm TL. Adults parasitic in marine waters. Mature adults occur in continental marine waters between September and December. The spawning behavior has not been described.

Geographic Distribution (Fig. 21): Chile: Aconcagua, Ñuble, Andalién, Biobío, Renaico, Toltén, Claro, Mehuín, Donguil, Calle–Calle, Llanquihue, Tucapel, and San Juan rivers.

Interest to Fisheries: None

References: de Buen (1961), Eigenmann (1927), Fowler (1940), Gray (1851), Günther (1870), Neira (1984), Neira *et al.* (1988), Philippi (1863, 1865), Plate (1902), Potter *et al.* (1968), Potter and Strahan (1968), Strahan (1960)

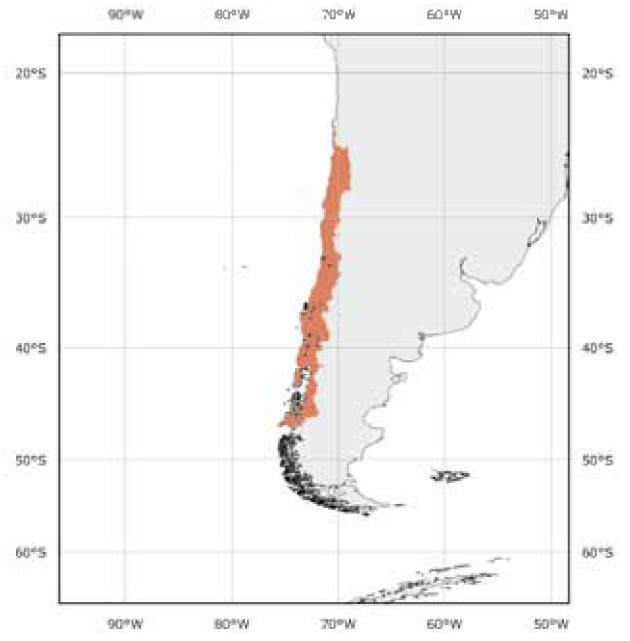

Fig. 21. Geographic distribution of *Mordacia lapicida*.

Mordacia mordax (Richardson 1846) Figs. 22–24

Synonyms: ***Petromyzon mordax*** Richardson 1846: 62, pl. 38, figs. 3–6 [holotype: adult, 267 mm TL; type locality: seas of Van Diemen's Land (= Tasmania), Australia]; ***Mordacia mordax*** Gray 1851: 144 (new combination)

FAO Name: En — Australian Lamprey, Short–headed Lamprey; **Fr** — Lamproie australienne

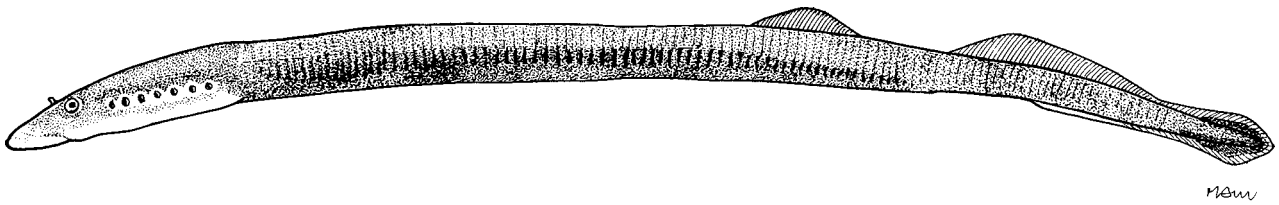

Fig. 22. Side view of *Mordacia mordax* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, 151 mm TL. Body proportions, as percentage of TL [based on about 230 specimens measuring 22.0–138.0 mm TL; values are approximate because they are derived from graphs since they were not stated explicitly in the text in Neira *et al.* (1988)]: prebranchial length, 6.1–11.3; branchial length, 10.0–16.4; trunk length, 61.0–67.5; tail length, 11.4–18.6. Trunk myomeres, 82–93. Body coloration unrecorded. Pigmentation: upper lip, +; subocular, +++; upper prebranchial, ++; lower prebranchial, +; upper branchial, ++ or +++; lower branchial, –; caudal fin, –. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like. Distinct notch between the confluent second dorsal and caudal fins.
Metamorphosing Ammocoetes: 120–150 mm TL.
Adults: 113–432 mm TL. Body wet weight of 50 individuals 339–421 mm TL, 35.1–72.0 g. Body proportions, as percentage of TL (based on 125 prespawning specimens measuring 113–421 mm TL): prebranchial length, 8.5–11.3; branchial length, 7.1–9.8; trunk length, 60.4–68.3; tail length, 14.4–20.1; eye length, 1.1–1.7; disc length, 4.9–6.6. Body proportions, as percentage of TL (based on eight spawning males measuring 277–376 mm TL): prebranchial length, 11.4–16.6; branchial length, 8.8–10.1; trunk length, 60.1–65.3; tail length, 13.3–15.7; disc length, 8.1–11.2. Mature males have some loose skin in the gular region. The urogenital papilla is not prominent in mature adults. Trunk myomeres, 84–96. Dentition: two triangular supraoral laminae each with three unicuspid teeth, one per apex; infraoral lamina, 7–9 unicuspid teeth of various size (these teeth become greatly enlarged with sexual maturation); 5–7 endolateral plates on either side each bearing 2–3 unicuspid teeth, usually 3; endolateral formula, typically 2–3–3–3–3–3 in immature individuals and 5–7 individual cusps on either side in mature individuals; 1 row of anterials; first row of anterials, 2 unicuspid teeth plus 1–2 bicuspid teeth or 3 unicuspid teeth flanked on either side by 1 bicuspid tooth; 1 row of exolaterals on each side; 1 row of posterials; first row of posterials, 12–14 posterial plates, the 2–4 lateralmost tricuspid and the internal ones bicuspid in immature individuals and 12–14 unicuspid teeth in mature individuals; transverse lingual lamina w–shaped, with 29 unicuspid teeth, the median one and the two subterminal ones slightly enlarged; longitudinal lingual laminae interrupted j–shaped, each with an undetermined number of unicuspid teeth. Velar tentacles, 3–4, smooth. Body coloration (live) of immature adults brownish gray on dorsal surface and silvery on ventral surface. Lateral line neuromasts darkly pigmented. Caudal fin pigmentation, ++. Caudal fin shape, spade–like. Oral papillae, 25–45.

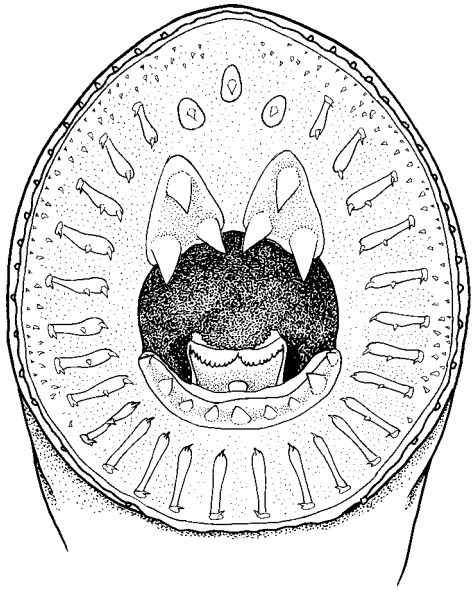

Fig. 23. Oral disc of *Mordacia mordax*. After Potter *et al.* (1968).

Habitat and Biology: Anadromous. Both ammocoetes and adults, when the latter are not feeding or migrating, burrow in the sandy substrate of lakes, creeks, and rivers.
The larval life is 3.5 yrs. Metamorphosis starts at the end of February beginning of March. In the Gippsland Lakes region of Victoria, adults spend about five months (austral summer and autumn) feeding in the lakes, and then go to sea (austral

winter) where they spend about 18 months feeding before returning to fresh water. There is perhaps a permanent freshwater resident population in Lake Wellington, the freshest of the three lakes. Adults parasitic on fishes (*Acanthopagrus butcheri*, *Aldrichetta forsteri*, and introduced *Salmo trutta* in lakes of varying salinity and *Thyrsites atun* at sea). The ascent of rivers occurs from July to January on mainland Australia, with the peak of the spawning migration occurring between September and November. During the spawning migration, adults burrow in the substrate of rivers during the day and migrate upstream during the night. On mainland Australia the spawning run is known to reach Torrumbarry fishway, over 1,600 km up the Murray River. The spawning behavior has not been described. Fecundity, 3,789–13,372 eggs/female. Egg diameter in spawning–run adults from Dandenong Creek in September, 0.38 mm, while that in spawning–run adults from Derwent River in January, 0.55 mm. In two Tasmanian rivers (North Esk and Derwent), where they co–occur with ammocoetes of *Geotria australis*, those of *Mordacia mordax* are 3–8 times more abundant.

Geographic Distribution (Fig. 24): Australia: Gulf St. Vincent, Gawler, South Para, Port, Torrens, Onkaparinga, and Murray rivers, and The Coorong, South Australia; Dandenong, Graceburn, and Maribyrnong creeks, Bunyip, Glenelg, Merri, Aire, Werribee, Yarra, Lang Lang, Bass, and Tarwin rivers, Gippsland lakes Wellington, Victoria, and King, Victoria; Walla, Towamba, Tuross, Moruya, and Hawkesbury rivers, New South Wales; North Esk, George, Triabunna, Saltwater, Derwent, Browns, Huon, Ouse, Ringarooma, Russell, and Swan rivers, and Maria Island, Tasmania.

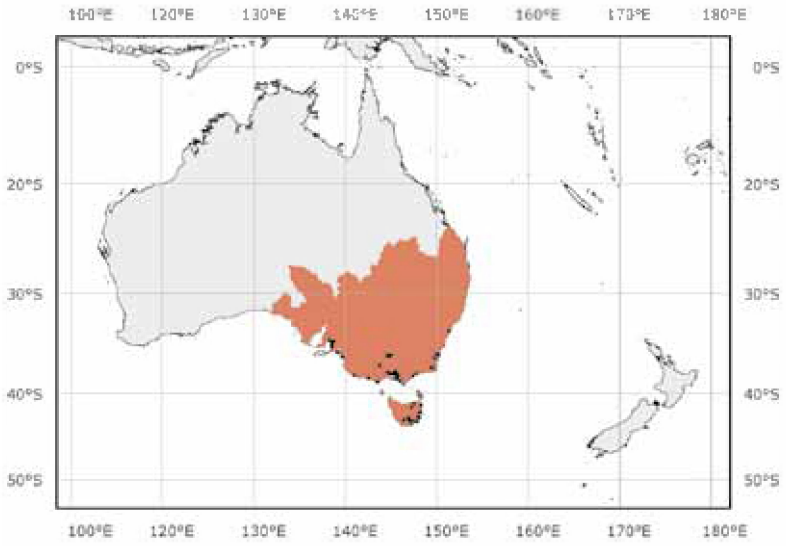

Fig. 24. Geographic distribution of *Mordacia mordax*.

Interest to Fisheries: This species parasitizes fishes of commercial importance in lakes of varying salinity (*Acanthopagrus butcheri* and *Aldrichetta forsteri*) and marine waters (*Thyrsites atun*) in southeastern Australia. De Castelnau (1872) states that the adults from the lower Yarra River, Victoria, are considered good food.

References: Anonymous (2004), de Castelnau (1872), Gill *et al.* (2003), Gray (1851), Hughes and Potter (1969), Khidir and Renaud (2003), Neira *et al.* (1988), Ogilby (1896), Potter (1968, 1970), Potter and Strahan (1968), Potter *et al.* (1968, 1995), Richardson (1846), Strahan (1960)

Mordacia praecox Potter 1968

Figs. 25–27

Synonyms: ***Mordacia praecox*** Potter 1968: 260 (holotype: male, 147 mm TL, AMS IB.7936; type locality: Moruya River, southern New South Wales, Australia)

FAO Name: No common name has been coined for this species other than the general term nonparasitic lamprey. Australian Brook Lamprey is therefore proposed as the English common name and lamproie de ruisseau australienne for the French common name.

Fig. 25. Side view of *Mordacia praecox* adult, about 140 mm TL, July 1967. After Potter (1968).

Diagnostic Features: Ammocoetes: No study has specifically described ammocoetes of this species. Based on the general statement in Potter (1968) and Potter *et al.* (1968) that ammocoetes of *M. mordax* are indistinguishable from those of *M. praecox*, the reader is advised to refer to the description of ammocoetes of *M. mordax* above.
Metamorphosing Ammocoetes: lengths unrecorded.

Adults: 102–172 mm TL. Body wet weight of a 147 mm TL individual was 3.2 g. Body proportions, as percentage of TL (based on 20 specimens measuring 119–160 mm TL): prebranchial length, 9.4–12.6; branchial length, 8.2–9.9; trunk length, 59.6–64.2; tail length, 16.5–20.4; eye length, 1.3–1.5; disc length, 5.4–8.4. No gular pouch develops. The urogenital papilla is not prominent in mature adults. Trunk myomeres, 85–93. Dentition: two triangular supraoral laminae each with three unicuspid teeth, one per apex (exceptionally, four unicuspid teeth per supraoral lamina). Infraoral lamina, 9–10 unicuspid teeth of various size (these teeth become greatly enlarged with sexual maturation); 5–6 endolaterals on each side; endolateral formula, typically 2–2–3–3–4–3 or 2–2–3–3–4–4 in immature individuals and 1–1–1–1–1 or 1–1–1–1–1–1 in mature individuals; 1 row of anterials; first row of anterials, 2 unicuspid teeth flanked on either side by one bicuspid tooth in immature individuals and 4 unicuspid teeth in mature individuals; 1–2 rows of exolaterals on each side; 1 row of posterials; first row of posterials, 16 posterial plates, the three lateralmost tricuspid and the internal ones bicuspid in immature individuals and 13 unicuspid teeth in mature individuals; transverse lingual lamina w–shaped with numerous unicuspid teeth of various size, the middle apex one being intermediate in size and the two bottom apex ones being largest, while the rest are small; longitudinal lingual laminae hook–shaped each with an undetermined number of unicuspid teeth. Velar tentacle number unrecorded. Body coloration (live) of mature adults with dark blue dorsal surface, occasionally with a green tinge, ventral surface of males mottled gray and ventral surface of females yellowish. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation, ++. Caudal fin shape, spade–like. Oral papillae, 33–48.

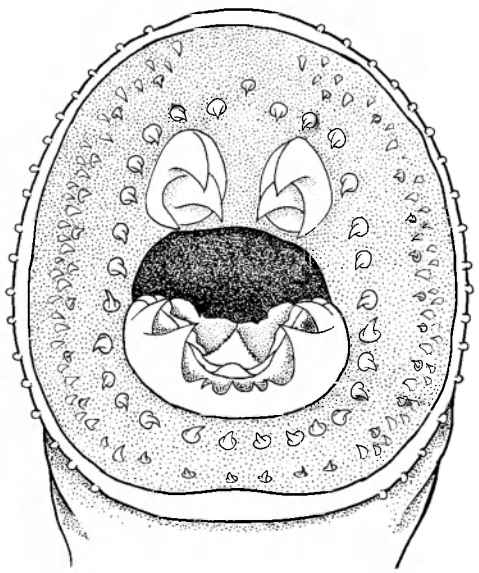

Fig. 26. Oral disc of *Mordacia praecox*. After Potter (1968).

Habitat and Biology: Freshwater. Adults nonparasitic. Metamorphosis occurs in October and November. Sexual maturity becomes apparent in April, about 5–6 months after metamorphosis. The spawning behavior has not been described, but spawning is believed to occur between August and October. Fecundity, 326–675 eggs/female. Egg diameter in sexually mature adults in July, 0.7 mm.

Geographic Distribution (Fig. 27): Australia: Moruya and Tuross rivers, New South Wales.

Interest to Fisheries: None

References: Hughes and Potter (1969), Potter (1968, 1970), Potter and Strahan (1968), Potter *et al.* (1968)

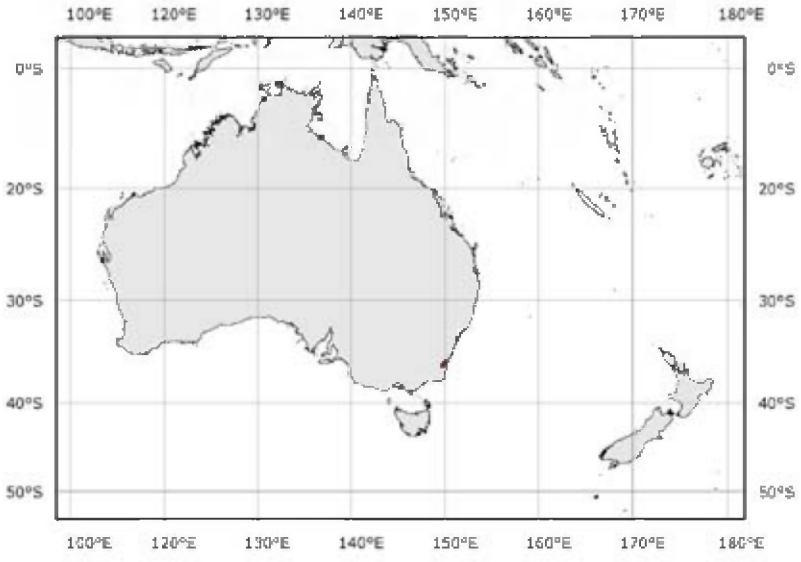

Fig. 27. Geographic distribution of *Mordacia praecox*.

Family PETROMYZONTIDAE

Fig. 28

Synonyms: Pétromyzides Risso 1827; **Petromyzonidae** Bonaparte 1832 (an unjustified emendation); **Suctorii** Kirtland 1838: 170

Renaud (1997) recognized 34 species grouped into eight genera in this family collectively known as the Northern Hemisphere

lampreys. Two other species, *Lethenteron ninae* Naseka *et al.* (2009) and *Eudontomyzon graecus* Renaud and Economidis (2010) have since been added, bringing the total to 36. The number of genera within this family has been the subject of debate. Whereas Vladykov and Kott (1979b), which is followed here, suggested eight (*Caspiomyzon*, *Ichthyomyzon*, *Petromyzon*, *Lampetra*, *Entosphenus*, *Eudontomyzon*, *Lethenteron*, and *Tetrapleurodon*), Bailey (1980) suggested that four were sufficient, accepting the first three and lumping the rest into *Lampetra*. His basis for lumping the five genera into

Fig. 28. Side view of *Petromyzon marinus* adult.

one was their possession of a wide supraoral lamina. Before carrying out such an action, it seems advisable to wait until a full cladistic treatment of the family is completed, especially in light of the statement by Bailey (1980) that the relationships among the lumped taxa within *Lampetra* was not well understood. Vladykov (1972) and Vladykov and Kott (1979c) proposed three subfamilies: Petromyzoninae (comprising *Petromyzon*, *Caspiomyzon*, *Ichthyomyzon*), Entospheninae (*Entosphenus* and *Tetrapleurodon*), and Lampetrinae (*Lampetra*, *Lethenteron*, *Eudontomyzon*). The first two are paraphyletic while the last is monophyletic according to the cladistic analysis of Gill *et al.* (2003). One (genus *Ichthyomyzon*) or two (all other genera) dorsal fins. Cloaca under the anterior half of the second dorsal fin. Midgut of ammocoetes (at least in *Entosphenus tridentatus*, *Lampetra fluviatilis*, and *Petromyzon marinus*) does not possess a diverticulum. Oral papillae present along the anterior and lateral edges of the oral disc, but absent from the posterior edge. All oral papillae of uniform size. Oral fimbriae present around the entire perimeter of the oral disc. One supraoral lamina. Labial teeth either pointed or rounded. Eyes dorsolateral in immature and mature adults. In the genera with two dorsal fins, these are separate in immature and contiguous in mature adults. Second dorsal fin/posterior lobe of the single dorsal fin confluent with (= continuous with) the caudal fin in ammocoetes as well as in immature and mature adults. One pair of kidney–shaped buccal glands. Gular pouch, when present, small, never extending past the posterior edge of the eye. *Petromyzon* Linnaeus 1758 is the type genus.

Genus *Caspiomyzon* Berg 1906

Synonyms: ***Caspiomyzon*** Berg 1906: 173; ***Agnathomyzon*** Gratzianow 1907:18; ***Haploglossa*** Gratzianow 1907: 18 (as new subgenus)

This is a monotypic genus (one scavenger species) endemic to the Caspian Sea Basin. Two dorsal fins. Teeth are rounded. Supraoral lamina narrow. Labial teeth radially–arranged in a curvilinear fashion and completely covering all fields of the oral disc. Transverse lingual lamina straight, the median tooth not enlarged. Velar tentacles possess papillae and a median tentacle is present. The type species is *Petromyzon Wagneri* Kessler 1870. Creaser and Hubbs (1922) treated *Caspiomyzon* as a subgenus of *Petromyzon* but this is not supported by the cladogram produced by Gill *et al.* (2003), which shows *Ichthyomyzon–Petromyzon* as a monophyletic group distinct from *Caspiomyzon* and the rest of the Northern Hemisphere species.

Caspiomyzon wagneri (Kessler 1870) **Figs. 29–31**

Synonyms: ***Petromyzon Wagneri*** Kessler 1870: 207–214, Pl. 3, figs. 4–5 (3 syntypes: 290–330 mm TL, ZISP 31; type locality: Volga River near Saratov and Kazan, Russian Federation); ***Agnathomyzon wagneri*** Gratzianow 1907: 18 (new combination);
Agnathomyzon (Haploglossa) caspicus Gratzianow 1907: 18; ***Petromyzon (Caspiomyzon) wagneri*** Creaser and Hubbs (1922): 2, 5 (new combination)

Taxonomic Remarks: Berg (1931) suggested that this species consists of two races; a normal form (forma typica) and a smaller praecox form.

FAO Name: En — Caspian Lamprey, Volga Lamprey; **Fr** — Lamproie caspienne

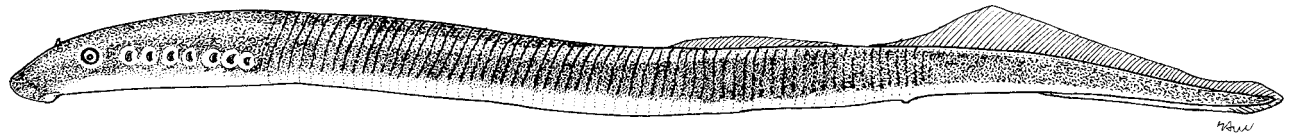

Fig. 29. Side view of *Caspiomyzon wagneri* adult. After Askerov *et al.* (2001).

Diagnostic Features: Ammocoetes: Maximum size attained, 130 mm TL. Body proportions, as percentage of TL (based on 300 specimens measuring 25–125 mm TL): prebranchial length, 5.4–6.6; branchial length, 11.1–12.3; trunk length, 54.9-55.9; tail length, 24.8–27.1. Trunk myomeres, 53–68. Body coloration light gray. Pigmentation of various body regions has not been studied. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like.
Metamorphosing Ammocoetes: 80–110 mm TL.
Adults: 190–553 mm TL. Maximum body wet weight, 206 g. Body proportions, as percentage of TL (based on 129 specimens measuring 305–530 mm TL): prebranchial length, 8.7–12.1; branchial length, 7.7–11.0; trunk length, 43.6–57.6 (derived by deduction; represents a maximum possible range); tail length, 26.0–33.0; eye length, 0.8–2.2; disc length, 2.4-4.5. The intestinal diameter in prespawning individuals has a mean of 2.7 mm and in spawning individuals a mean of 1.4 mm. The urogenital papilla length, as a percentage of branchial length, in five spawning males measuring 301–344 mm TL, 14.3-21.2. Trunk myomeres, 63–66. Dentition: supraoral lamina, one unicuspid (sometimes bicuspid) tooth; infraoral lamina, 4–6, usually 5, unicuspid teeth, but sometimes the lateralmost ones are bicuspid; 4 endolaterals on each side; endolateral formula, typically 1–1–1–1; 3–5 rows of anterials; first row of anterials, 3 unicuspid teeth; 8 rows of exolaterals on each side; 3 rows of posterials; first row of posterials, 11 unicuspid teeth; transverse lingual lamina straight, 5–8 unicuspid teeth, the median one not enlarged; longitudinal lingual laminae with undetermined number of unicuspid teeth. Velar tentacles, 3, long and bearing papillae. Body coloration in prespawning adults, dark gray on dorsal and lateral aspects and silvery white ventrally. Spawning adults are black on dorsal and lateral aspects and gray with dark oval spots ventrally. The color of eggs in prespawning females is light gray or yellow, while in spawning females it is bluish–green. Lateral line neuromasts unpigmented. Caudal fin pigmentation unrecorded. Caudal fin shape, spade–like. Oral fimbriae, 93–115. Oral papillae, 24–31.

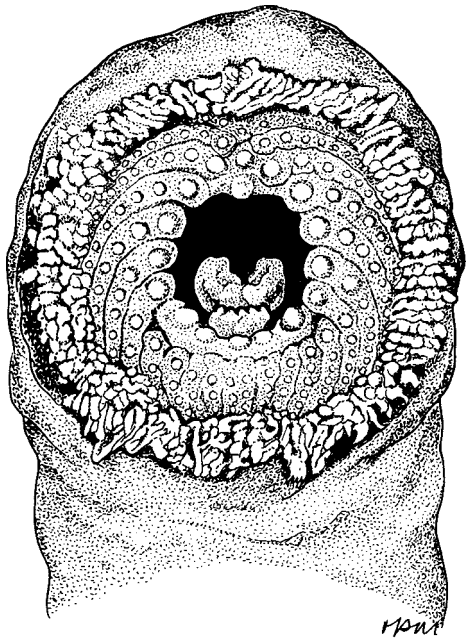

Fig. 30. Oral disc of *Caspiomyzon wagneri*. After a drawing by Paul I. Voevodine [418 mm TL, NMC (= CMNFI) 1980–926, Volga River, near Nikol'skoye, Russian Federation, Jan. 1957, V.S. Tanassiytchuk].

Habitat and Biology: Anadromous. Ammocoetes burrow 1–2 cm deep in substrates containing sand, clay, and detritus, in areas with slow current, and at water depths between 0.3 and 22 m. They may also be found on the surface of the substrate among macrophytes and submerged wood. Metamorphosing individuals occur in areas with faster current, devoid of macrophytes, and at greater water depths. Adults are found in rivers and marine waters. In the Volga River delta, adults may be found in shallow lakes in the flood plain (il'men in Russian).
Larval life is 3 years in the Volga River Basin and 2–4 years in the Kura River Basin. Ammocoetes feed on diatoms and detritus. Their feeding activity is highest in the summer and lowest in the winter. Metamorphosis begins in mid–July in the Volga River (Russian Federation), at the end of August and beginning of September in the Kura River (Azerbaijan), and it occurs in October in Iran (Islamic Republic of). Metamorphosing ammocoetes do not feed. The adult life is at least 17 months. The feeding habits of adults have been the subject of much speculation. Their teeth are blunt, yet their intestine remains functional and they grow considerably post–metamorphosis (Berg, 1931). Vladykov and Kott (1979c) suggested that they might feed on demersal fish eggs or on some invertebrates. Renaud (1982b) found juvenile acanthocephalans (*Corynosoma* sp.) in their intestine and suggested that they feed on amphipods since the latter serve as an intermediate host. Holčík (1986) proposed that these acanthocephalans could have been acquired through feeding on decaying fishes that had been infected.

On the basis of this indirect evidence, Renaud (1997) classified the adult feeding habits as those of a scavenger. Adult lamprey on their spawning run will attach, particularly in the opercular region, to likewise upstream–migrating winter form of brown sea trout (*Salmo trutta caspius*). Prespawning adults in the Kama River, Russian Federation, serve as a host for unionid glochidia, which attach to its gills. According to Berg (1931), two adult forms or races exist; a normal form (370–553 mm TL) and a praecox form (190–310 mm TL). The spawning run up the Kura and Volga rivers is nocturnal and it occurs between November and February in the former and mid–September and March in the latter. Upstream migrants swim near the surface on dark nights and close to the bottom of the river on moonlit nights. During the day, they stay among stones on the bottom. The distance traveled can be as much as 1,500 km for the larger individuals. Swimming speed varies from 2–16 km per day. At the beginning of the migration, the fat content of an adult individual can be as high as 34% by body weight and at the end, on the spawning grounds, as low as 1–2% by body weight. Spawning occurs between mid–March and mid–July over sandy and rocky substrate, at water temperatures between 15–23 °C. The spawning grounds are distributed along the entire courses of the Volga and Kura rivers from their estuaries to their upper reaches historically, and to their man–made reservoirs presently. Upon arrival at the spawning grounds, adults at first either conceal themselves amongst stones or burrow into the substrate, and later, swim and periodically break the water's surface with their heads. Redds are constructed by both sexes in sand and gravel substrates, usually in shallow waters. Fecundity, 14,000–60,000 eggs/female. Ammocoetes hatch 8–10 days after fertilization at lengths of 3.3–4.2 mm. Three to four days after hatching, the yolk sac is almost completely absorbed.

Geographic Distribution (Fig. 31): Caspian Sea Basin in the Russian Federation (Volga River Basin: Volga, Kama, Vyatka, Sura, Penza, and Oka rivers; Ural River Basin: Ural River; Terek River Basin: Terek River), Kazakhstan (Ural River), Azerbaijan (Kura River Basin: Kura and Araks rivers), and Iran (Islamic Republic of) (Sefid River Basin: Sefid River).

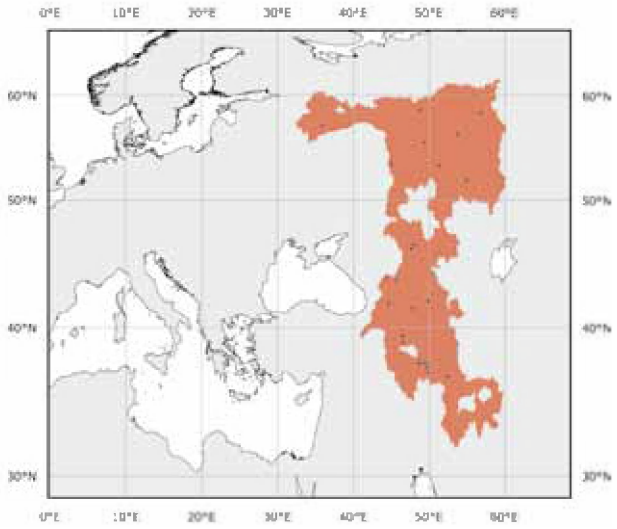

Fig. 31. Geographic distribution of *Caspiomyzon wagneri*.

Interest to Fisheries: Berg (1948) reported on two fisheries for this species; one in the lower Volga River, Russian Federation, and the other in the Kura River, Azerbaijan. The Volga River fishery was carried out in both the spring and autumn, with over 75% of the catch occurring in autumn. Between 1910 and 1913 inclusively, from 16,900,000 to 33,400,000 Caspian Lamprey were harvested annually. For the Kura River fishery, catches compiled in five–year increments between 1881 and 1935, varied from a low of 11,000 lamprey for the period 1891–1895 to a high of 612,000 lamprey for the period 1911–1915. Annual catches for the years 1936 and 1937 were respectively, 213,000 and 304,000 lamprey. The lipid content is 30.3% of the body weight. Prior to 1868, the catch was dried and used as a substitute for candles, and after 1868, it was harvested as food for humans. The caloric value for Caspian Lamprey is 3.4 kcal/g wet weight. According to Holčík (1986), water regulation projects on the Volga and Kura rivers have had such deleterious effects on the abundance of Caspian Lamprey, preventing access to areas above the Volgograd and Mingechaur reservoirs, respectively, that it is no longer considered a commercially important species. There are reports of intoxication through eating this species (Halstead 1967).

References: Askerov *et al.* (2001), Berg (1931, 1948), Creaser and Hubbs (1922), Gill *et al.* (2003), Gratzianow (1907), Halstead (1967), Holčík (1986), Kessler (1870), Khidir and Renaud (2003), Kott *et al.* (1988), Renaud (1982b, 1997), Vladykov and Kott (1976d, 1979c)

Genus *Entosphenus* Gill 1862

Synonyms: ***Entosphenus*** Gill 1862: 331 (waters of western North America).

This genus comprises seven species (4 parasitic and 3 nonparasitic); six of them occur in western North America and one species, *Entosphenus tridentatus*, also occurs on the Asian side. Two dorsal fins. Supraoral lamina with two unicuspid teeth separated by a wide bridge, which usually bears a smaller median unicuspid tooth. Labial teeth radially–arranged in a curvilinear fashion only in the anterior field. Exolaterals absent but one or two on each side of the oral disc may be present in *E. similis*. A single row of posterials. Transverse lingual lamina weakly w–shaped with median cusp only slightly enlarged. Velar tentacles possess tubercles and a median tentacle is present. The type species is *Petromyzon tridentatus* Gairdner in Richardson 1836. Hubbs and Potter (1971) treated *Entosphenus* as a subgenus of *Lampetra*.

Entosphenus folletti Vladykov and Kott 1976

Figs. 32–34

Synonyms: ***Entosphenus folletti*** Vladykov and Kott 1976: 975, figs. 1–3 [holotype: male, 228 mm TL, NMC (= CMNFI) 1975–1549; type locality: Willow and Boles creeks, near Clear Lake Reservoir, Klamath River Basin, Modoc County, California, USA]

FAO Names: En — Northern California Brook Lamprey; **Fr** — Lamproie de ruisseau de Californie septentrionale

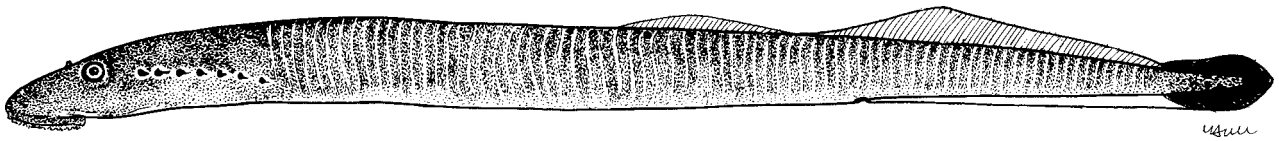

Fig. 32. Side view of *Entosphenus folletti*, prespawning male, 228 mm TL, holotype, NMC (= CMNFI) 1975–1549, Willow and Boles creeks, near Clear Lake Reservoir, Klamath River Basin, Modoc County, California, USA, Aug. 1972, California Fish and Game. After Vladykov and Kott (1976c).

Diagnostic Features: Ammocoetes: Maximum size attained should be at least 228 mm TL judging by the size of the adults, but the largest recorded 153 mm TL. Body proportions, as percentage of TL (based on 25 specimens measuring 78-153 mm TL): prebranchial length, 6.1–9.0; branchial length, 10.1–13.7; trunk length, 47.0–52.4; tail length, 30.5–35.2. Trunk myomeres, 56–65. Body coloration unrecorded. Pigmentation: upper lip, ++ (20% of specimens) or +++ (80%); subocular, ++ (8%) or +++ (92%); lower prebranchial, ++ (12%) or +++ (88%); upper branchial, ++ (88%) or +++ (12%); lower branchial, –; caudal fin, ++ (32%) or +++ (68%); tongue precursor bulb, + or ++; along elastic ridge of tongue precursor, +++. Lateral line neuromasts unpigmented. Caudal fin shape, spade–like.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 176–228 mm TL. Body proportions, as percentage of TL (based on six specimens measuring 186–228 mm TL): prebranchial length, 12.3–14.5; branchial length, 9.2–10.6; trunk length, 42.7–48.6; tail length, 28.4–32.7; eye length, 1.7–2.3; disc length, 6.6–7.8. The urogenital papilla length, as a percentage of branchial length, in one spawning male measuring 210 mm TL, 5.7. Trunk myomeres, 61-65. Dentition: supraoral lamina, 3 unicuspid teeth, the median one smaller than the lateral ones; infraoral lamina, 5 unicuspid teeth; 4 endolaterals on each side; endolateral formula, typically 2–3–3–2, the fourth endolateral can also be unicuspid; 1–2 rows of anterials; first row of anterials, 2 unicuspid teeth; exolaterals absent; 1 row of posterials with 13–18 teeth, of which 0–4 are bicuspid and the rest unicuspid (some of these teeth may be embedded in the oral mucosa); transverse lingual lamina, 14-20 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae teeth are too poorly developed to be counted. Velar tentacles, 8–9, with tubercles. The median tentacle is about the same size as the lateral ones immediately next to it. Body coloration (preserved), dark brown on dorsal, lateral, and ventral aspects. Lateral line neuromasts darkly pigmented. Second dorsal fin pigmentation, +++. Caudal fin pigmentation, +++. Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae, 13.

Habitat and Biology: Freshwater; in creeks and rivers. Adults nonparasitic.

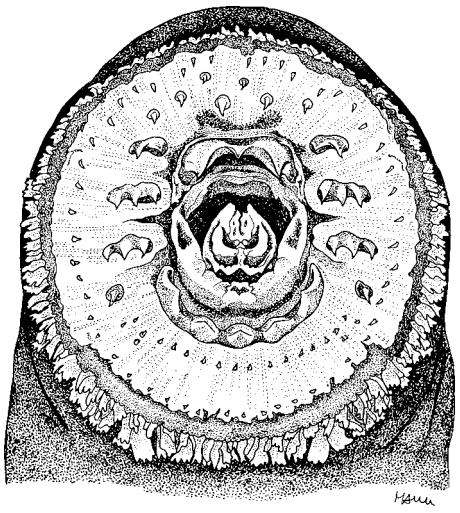

Fig. 33. Oral disc of *Entosphenus folletti*. After a drawing by Susan Laurie–Bourque [206.5 mm TL, paratype, NMC (= CMNFI) 1986–805, Lost River, Klamath River Basin, Modoc County, California, USA, 14 April 1954, M.H. Coots].

Geographic Distribution (Fig. 34): USA: Klamath River Basin (Willow and Boles creeks, Fall Creek, and Lost River, California).

Interest to Fisheries: None

References: Hubbs (1971), Kott *et al.* (1988), Vladykov and Kott (1976c, 1976d, 1979c)

Fig. 34. Geographic distribution of *Entosphenus folletti.*

Entosphenus hubbsi Vladykov and Kott 1976

Figs. 35–37

Synonyms: ***Entosphenus hubbsi*** Vladykov and Kott 1976: 60–61, figs. 1–2 (holotype: male, 131 mm TL, CAS 35987; type locality: Friant–Kern Canal, east of Delano, Kern County, California, USA)

FAO Names: En — Kern Brook Lamprey, Central California Brook Lamprey; **Fr** — Lamproie de ruisseau de Californie centrale

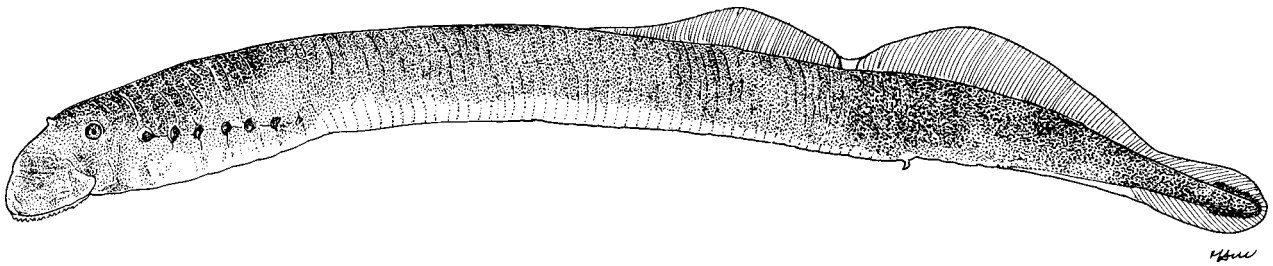

Fig. 35. Side view of *Entosphenus hubbsi*, spawning male, 110 mm TL, Merced River, California, USA. After Vladykov and Kott (1984).

Diagnostic Features: Ammocoetes: Maximum size attained, 160 mm TL. Body proportions, as percentage of TL (based on two specimens measuring 100–160 mm TL): prebranchial length, 6.9–9.0; branchial length, 10.6–12.0; trunk length, 49.0-54.4; tail length, 29.0–30.6. Trunk myomeres, 53–57. Body coloration unrecorded. Pigmentation: upper prebranchial, –; lower prebranchial, +; upper branchial, ++; lower branchial, –; caudal fin, ++; tongue precursor bulb, strongly pigmented (more so than in *E. folletti*); along elastic ridge of tongue precursor, strongly pigmented. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 81–142 mm TL. Body proportions, as percentage of TL (based on 127 specimens measuring 81–142 mm TL): prebranchial length, 7.8–14.4; branchial length, 8.5–12.8; trunk length, 44.6–56.9; tail length, 24.3–30.8; eye length, 0.8-2.8; disc length, 3.7–8.7. The urogenital papilla length, as a percentage of branchial length, in nine spawning males

measuring 106–124 mm TL, 8.3–16.7. Trunk myomeres, 50–57. Dentition: supraoral lamina, 2 unicuspid teeth, rarely 3; infraoral lamina, 4–7 unicuspid teeth, usually 5; 4 endolaterals on each side, rarely 3 (Note: The photograph of the oral disc of the holotype in the original description, fig. 1, shows only 3 endolaterals on each side); endolateral formula, typically 1–1–1–1, the first endolateral may also be bicuspid, the second and third endolaterals bi– or tricuspid, and the fourth bicuspid, however, no endolateral formula of 2–3–3–2 was encountered in 40 individuals examined; 2 row of anterials, 3–9 unicuspid teeth in total, three of these in the first row; exolaterals absent; 1 row of posterials, 8–12 unicuspid teeth in a continuous (complete) row or discontinuous (incomplete) row of only six unicuspid teeth; transverse lingual lamina, cusps too poorly developed to count, however, the median one not enlarged; longitudinal lingual laminae, cusps too poorly developed to count. Velar tentacles, 3–5, with tubercles. The median velar tentacle is shorter than the lateral ones immediately next to it. There are no velar wings. Body coloration (preserved), gray–brown on dorsal and lateral aspects, whitish on ventral aspect. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation, +. Caudal fin shape, rounded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater. Both the larval and adult stages were originally collected from the Friant–Kern Canal, which is 85% concrete lined and has a discharge greater than 57 m^3/sec; an artificial habitat. Occurs in the Merced River, which should be considered typical habitat.
Adults nonparasitic.

Geographic Distribution (Fig. 37): USA: California (San Joaquin River Basin: Merced River and Friant–Kern Canal, the latter connects Kern River to the San Joaquin River).

Interest to Fisheries: None

References: Kott *et al.* (1988), Vladykov and Kott (1976b, 1976d, 1979c, 1984)

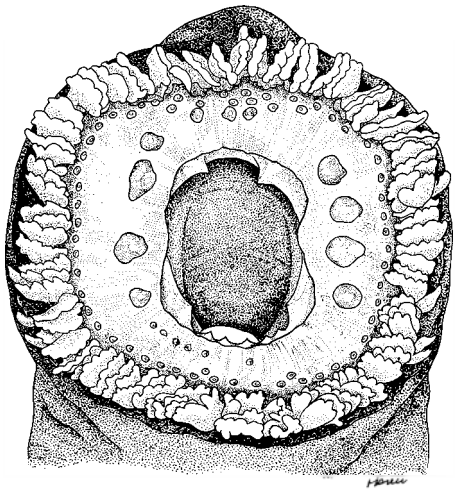

Fig. 36. Oral disc of *Entosphenus hubbsi*. After a drawing by Susan Laurie–Bourque [113 mm TL, NMC (= CMNFI) 1986–821, Merced River, near Merced Falls, San Joaquin River Basin, Merced County, California, USA, Feb.–March 1977, R. Menchen].

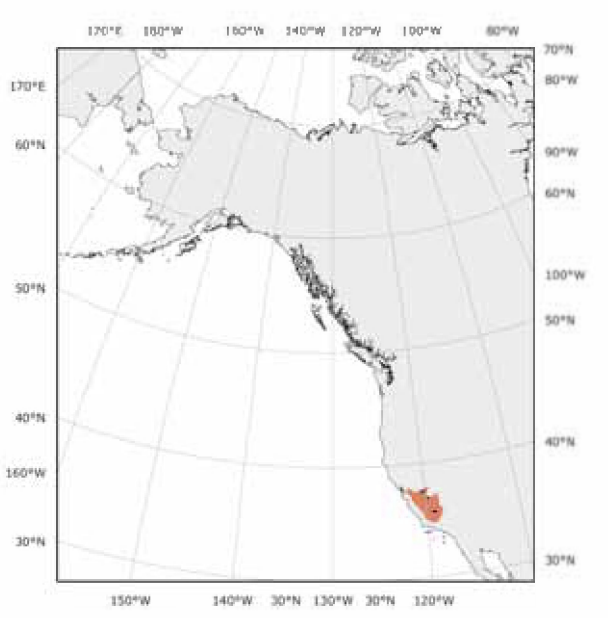

Fig. 37. Geographic distribution of *Entosphenus hubbsi*.

Entosphenus lethophagus (Hubbs 1971) Figs. 38–40

Synonyms: *Lampetra lethophaga* Hubbs 1971: 126–127, 130, fig. 1A–B, tables 3–6, 8 (holotype: male, 128 mm TL, UMMZ 130648; type locality: headwaters of Fall River, a tributary to Pit River, Shasta County, California, USA)

FAO Names: En — Pit–Klamath Brook Lamprey; **Fr** — Lamproie de ruisseau du bassin Pit–Klamath

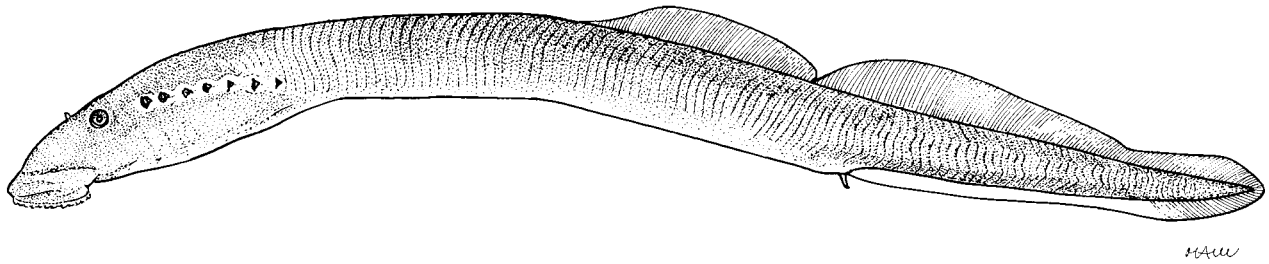

Fig. 38. Side view of *Entosphenus lethophagus,* spawning male, 154 mm TL, OS 2856, Crooked Creek, Klamath County, Oregon, USA, 13 March 1970, Oregon Game Commission. After Hubbs (1971).

Diagnostic Features: Ammocoetes: Maximum size attained, 187 mm TL. Body proportions, as percentage of TL (based on 12 specimens measuring 92–187 mm TL): prebranchial length, 6.1–8.0; branchial length, 9.4–11.5; trunk length, 48.0–52.7; tail length, 27.7–34.6. Trunk myomeres, 61–66. Body coloration unrecorded. Pigmentation: upper lip, ++ or +++; subocular, +++ (100% of specimens); lower prebranchial, +++ (100%); upper branchial, ++ (17%) or +++ (83%); caudal fin, + (8%) or ++ (42%) or +++ (50%); tongue precursor bulb, –; along elastic ridge of tongue precursor, ++. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 124–184 mm TL. Body proportions, as percentage of TL (based on ten specimens measuring 126–184 mm TL): prebranchial length, 8.2–13.3; branchial length, 8.4–10.8; trunk length, 43.4–51.6; tail length, 28.8–35.3; eye length, 1.6–3.2; disc length, 4.1–6.1. The urogenital papilla length, as a percentage of branchial length, in a spawning male measuring 129 mm TL, 16.0. Trunk myomeres, 58–73. Dentition: supraoral lamina, 2–3 unicuspid teeth, usually 3; infraoral lamina, 5–7 unicuspid teeth; 4 endolaterals on each side; endolateral formula, typically 2–2–2–2 or 2–3–3–2, the first and fourth endolaterals may also rarely be unicuspid; 2–3 rows of anterials (not all shown on Fig. 39 because hidden from view by folding of anterior part of oral disc); first row of anterials, 1 or 5 unicuspid teeth; exolaterals absent; 1 row of posterials with 10–17 teeth, of which 0–12 are bicuspid and the rest unicuspid; transverse lingual lamina, 15–20 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae each with undetermined number of unicuspid teeth. Velar tentacles, 5–12, with tubercles. Median tentacle shorter than the lateral ones immediately next to it. Body coloration (preserved), ventral aspect whitish. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation unrecorded. Caudal fin shape unrecorded. Oral fimbriae number unrecorded. Oral papillae, 5–26.

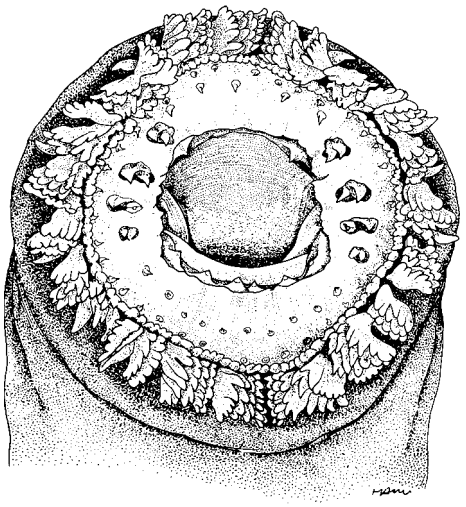

Fig. 39. Oral disc of *Entosphenus lethophagus.* After a drawing by Susan Laurie–Bourque [124 mm TL, NMC (= CMNFI) 1986–733, Crooked Creek, Klamath County, Oregon, USA, 8 Feb. 1957].

Habitat and Biology: Freshwater; in creeks and rivers.
Adults nonparasitic. Adults from Crooked Creek, Oregon are sexually mature in mid–March.

Geographic Distribution (Fig. 40): USA: Klamath River Basin in Oregon (Sprague River and Crooked Creek at the Klamath Fish Hatchery) and Pit River Basin in California (Fall and Pit rivers and Crystal Lake Hatchery).

Interest to Fisheries: None

References: Bond and Kan (1973), Hubbs (1971), Kott *et al.* (1988), Lorion *et al.* (2000), Vladykov and Kott (1976c, 1976d, 1979c)

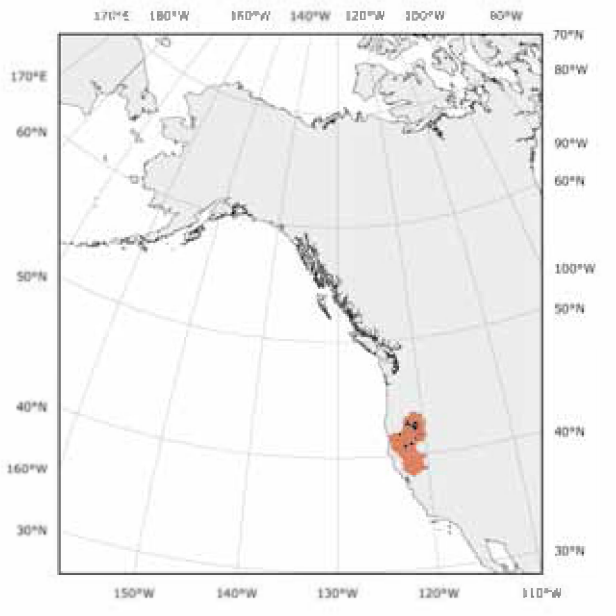

Fig. 40. Geographic distribution of *Entosphenus lethophagus*.

Entosphenus macrostomus (Beamish 1982) — Figs. 41–43

Synonyms: ***Lampetra macrostoma*** Beamish 1982: 737–740, figs. 1A, B, D, F, 2A, C, E [holotype: immature male, 228 mm TL before preservation and 221 mm TL after preservation, NMC (= CMNFI) 1981–1219; type locality: Lake Cowichan, 48°52'36"N 124°17'0"W, Vancouver Island, British Columbia, Canada]

FAO Names: En — Vancouver Lamprey (Although this is the official common name following Nelson *et al.* (2004), it should really be Vancouver Island Lamprey to prevent confusion with the city of Vancouver, which occurs on the mainland); **Fr** — Lamproie de l'île de Vancouver

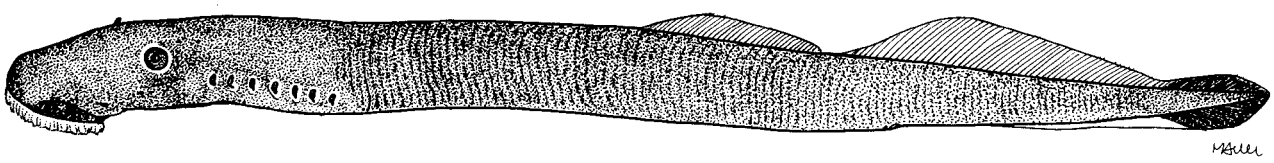

Fig. 41. Side view of *Entosphenus macrostomus*. After a photograph by Brian W. Coad [immature male, 221 mm TL, holotype, NMC (= CMNFI) 1981–1219, Lake Cowichan, Vancouver Island, British Columbia, Canada, 14 Nov. 1980, M. Smith].

Diagnostic Features: Ammocoetes: Maximum size attained, 170 mm TL. Body proportions, as percentage of TL (based on 16 specimens for which the size range was not stated, but presumably was 100–170 mm TL, because this was the range given for the larger ammocoetes in the original description of the species): prebranchial length, 7.6–10.7; branchial length, 12.8–15.7; trunk length, 45.5–51.4; tail length, 28.3–33.1. Trunk myomeres, mean of 66.1, but range not given. Body coloration unrecorded. Pigmentation: lower prebranchial, +++; upper branchial, ++; lower branchial, –; caudal fin, ++; tongue precursor bulb, –; along elastic ridge of tongue precursor, – or +. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like or rounded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 118–273 mm TL. Body wet weigth of a 221 mm TL individual, 19.8 g. Body proportions, as percentage of TL (based on 112 specimens measuring 118–273 mm TL): prebranchial length, 14.3–17.6; branchial length, 9.4–12.6;

trunk length, 37.5–48.2; tail length, 20.9–31.7; eye length, 2.2–3.5; disc length, 6.5–11.7. Trunk myomeres, 59–70. Dentition: marginals, 54–67; supraoral lamina, 3, rarely 4 unicuspid teeth, the median one smaller than the lateral ones; infraoral lamina, 5–6 unicuspid teeth; 4 endolaterals on each side; endolateral formula, typically 2–3–3–2; 2 rows of anterials; first row of anterials, 3 unicuspid teeth; exolaterals absent; 1 row of posterials, 14–21 teeth, 2–3 lateralmost on each side bicuspid and the internal ones unicuspid; transverse lingual lamina, 13–20 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae parentheses–shaped and each with 17–27 unicuspid teeth. Velar tentacles, 11–15 with wings. Body coloration (preserved), uniformly dark, almost black. Lateral line neuromasts darkly pigmented. Caudal fin pigmentation, +++. Caudal fin shape, spade–like. Oral fimbriae, 117. Oral papillae, 17.

Habitat and Biology: Freshwater, in lakes and in the inlets to them. Ammocoetes and recently metamorphosed individuals are mostly found along the edges of lakes. Ammocoetes are found in the silt substrate of two lakes and of inlet streams within 100 m of the lakes.
Adult life span believed to be at least two years. Adults parasitic on fishes (*Oncorhynchus clarkii* and *O. kisutch*) in freshwater lakes throughout the year. Wounds produced known to penetrate deeply into the musculature or even reach the body cavity of hosts. Up to three adults have been recorded attached to a host. Adults are known experimentally to be able to survive in salt water, but apparently remain in fresh water despite the absence of barriers preventing access to the sea. Adults in spawning readiness collected from shallow gravel bars between 1 June and 23 August.

Geographic Distribution (Fig. 43): Canada: Lake Cowichan and Mesachie Lake, Vancouver Island, British Columbia.

Interest to Fisheries: Between 50 and 80% of fishes, mostly salmonids, in Lake Cowichan and Mesachie Lake show evidence of attacks from this lamprey, and based on the severity of the wounds inflicted, an estimated 15% of these attacks would probably result in the death of the host.

References: Beamish (1982, 2001), Carl (1953), Gill *et al.* (2003), Khidir and Renaud (2003), Mayden *et al.* (1992), Page and Burr (1991)

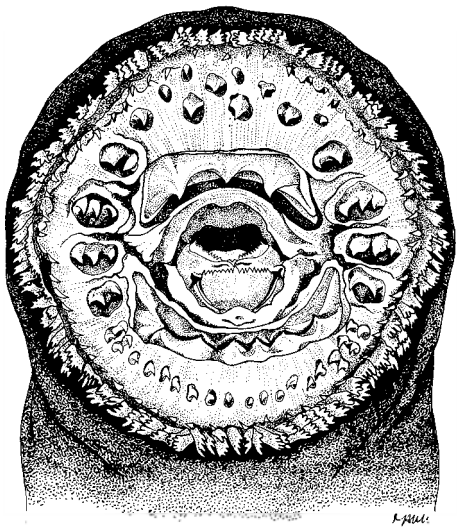

Fig. 42. Oral disc of *Entosphenus macrostomus*. After a drawing by Susan Laurie–Bourque [221 mm TL, holotype, NMC (= CMNFI) 1981–1219, Lake Cowichan, Vancouver Island, British Columbia, Canada, 14 Nov. 1980, M. Smith].

Fig. 43. Geographic distribution of *Entosphenus macrostomus*.

Entosphenus minimus (Bond and Kan 1973) **Figs. 44–46**

Synonyms: ***Lampetra (Entosphenus) minima*** Bond and Kan 1973: 569–570, fig. 1 (holotype: male, 93 mm TL, USNM 353919, formerly OS 3180; type locality: Miller Lake, Oregon, USA)

FAO Names: En — Miller Lake Lamprey; **Fr** — Lamproie du lac Miller

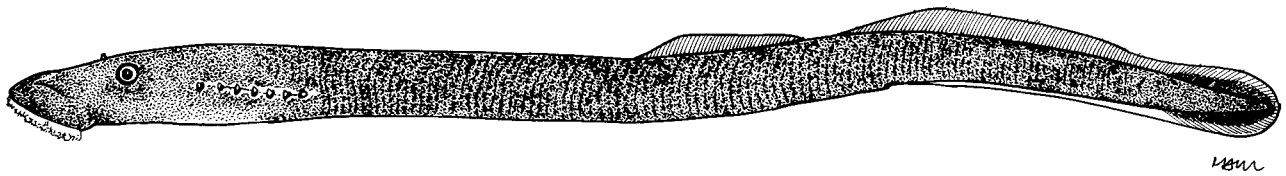

Fig. 44. Side view of *Entosphenus minimus*. After a photograph by Brian W. Coad [adult male, 107.5 mm TL, NMC (= CMNFI) 1986–728, Miller Lake, Deschutes County, Oregon, USA].

Diagnostic Features: Ammocoetes: Maximum size attained, 141 mm TL. Body proportions, as percentage of TL (based on 102 specimens measuring 37–111 mm TL): prebranchial length, 6.8–11.1; branchial length, 11.7–17.5; trunk length, 47.5–53.3; tail length, 23.7–31.4. Trunk myomeres, 59–66. Body coloration (preserved) uniformly yellowish brown. Pigmentation: upper lip, +; subocular, +++; lower prebranchial, +++ (100% of specimens); upper branchial, +++ (100%); caudal fin, +++ (100%); tongue precursor bulb, –; along elastic ridge of tongue precursor, +++. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 72–145 mm TL. Body proportions, as percentage of TL (based on 58 specimens measuring 80–145 mm TL): prebranchial length, 11.0–17.0; branchial length, 8.9–12.2; trunk length, 40.3–49.1; tail length, 27.0–34.6; eye length, 2.1–3.3; disc length, 5.0–8.6. The height of the second dorsal fin, as a percentage of TL, is significantly greater in mature (4.4–6.1) versus immature adults (2.2–4.2). The urogenital papilla length, as a percentage of branchial length, in 12 spawning males measuring 78–100 mm TL, 10.0–18.8. Trunk myomeres, 59–66. Dentition: supraoral lamina, 2–3 unicuspid teeth, usually 3, the median one smaller than the lateral ones; infraoral lamina, 5 unicuspid teeth; 4 endolaterals on each side; endolateral formula, typically 2–3–3–2; 2 rows of anterials; first row of anterials, 3 unicuspid teeth; exolaterals absent; single row of posterials, 11–19, usually with the outermost 1–3 posterials on either side bicuspid and the internal ones unicuspid, however, 0–16 can be bicuspid; transverse lingual lamina, 17–29 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae each with 18–25 unicuspid teeth. Velar tentacles, 5–9, without tubercles. Wings consisting of a single short tentacle on either side. Median tentacle shorter than the lateral ones immediately next to it. Body coloration (preserved) in adults is darker on the upper surface and paler on the lower surface with immature adults being yellowish brown, and with mature and spent adults being brownish purple. Lateral line neuromasts unpigmented. Caudal fin pigmentation, ++. Caudal fin shape, spade–like or rounded. Oral fimbriae, 86–101. Oral papillae, 7–17.

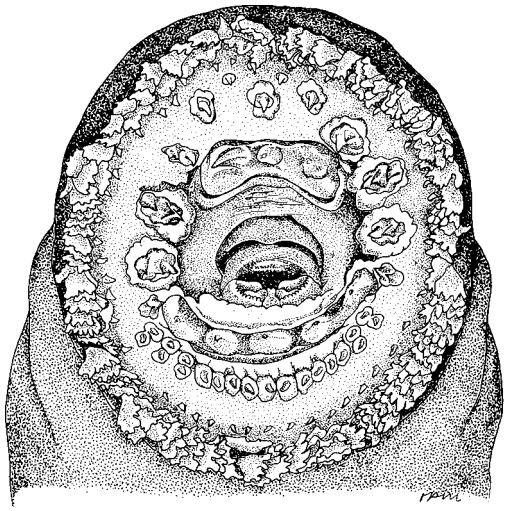

Fig. 45. Oral disc of *Entosphenus minimus*. After a drawing by Susan Laurie–Bourque [107.5 mm TL, NMC (= CMNFI) 1986–728, Miller Lake, Deschutes County, Oregon, USA].

Habitat and Biology: Freshwater; in the upper reaches of rivers at an elevation of 1,402–2,134 m. Ammocoetes are associated with substrates of organic detritus at water depths up to 1 m. Spawning has been observed both in lake and in stream habitats.
Life span approximately 36 months; about 30 months as an ammocoete and 6 months as an adult. Metamorphosis occurs in the fall. Adults parasitic on fishes (native *Gila bicolor*, *Rhinichthys osculus klamathensis*, and introduced *Salvelinus fontinalis*, *Salmo trutta*) usually measuring much less than 150 mm TL. Because of the small size of the hosts and the deep nature of the wounds inflicted, most attacks likely result in the death of the fish being attacked. Also reported to be scavengers and cannibals. Adults apparently do not feed more than a few months. Spawning migration is very limited.

Adults build redds about 10 cm wide by 3 cm deep, at a water depth of about 30 cm. The redds consist of gravel and sand. Spawning period between 17 July and 20 August in Miller Lake and 10 June in Sycan River; in the latter case, spawning occurred during mid–morning at a water temperature of 12 °C. Fecundity, 503–727 eggs/female. Adults die after spawning.

Geographic Distribution (Fig. 46): USA: Endemic to the upper Klamath River Basin (Miller, Evening, Jack, and Long creeks, and upper reaches of the Williamson and Sycan rivers), Oregon. Formerly in Miller Lake (see under Interest to Fisheries).

Interest to Fisheries: The species was extirpated from Miller Lake through poisoning in 1958 because of its parasitism of planted trout fingerlings.

References: Bond and Kan (1973), Gill *et al.* (2003), Kan and Bond (1981), Khidir and Renaud (2003), Kott *et al.* (1988), Lorion *et al.* (2000), Vladykov and Kott (1976c, 1976d, 1979a, 1979c)

Fig. 46. Geographic distribution of *Entosphenus minimus*.

Entosphenus similis Vladykov and Kott 1979

Figs. 47–49

Synonyms: ***Entosphenus similis*** Vladykov and Kott 1979: 809–810, figs. 1–2 [holotype: female, 212 mm TL, NMC (= CMNFI) 1975–1550; type locality: Klamath River, California, USA]

FAO Names: En — Klamath Lamprey, Klamath River Lamprey; **Fr** — Lamproie de la rivière Klamath

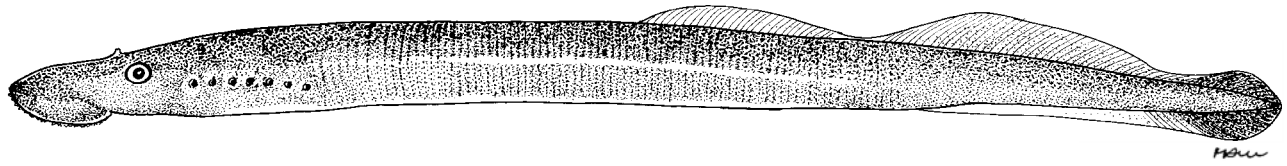

Fig. 47. Side view of *Entosphenus similis* adult.

Diagnostic Features: Ammocoetes: The ammocoetes have not been studied.
Metamorphosing Ammocoetes: The metamorphosing ammocoetes have not been studied.
Adults: 136–269 mm TL. Body proportions, as percentage of TL (based on 29 specimens measuring 136–269 mm TL): prebranchial length, 13.0–16.4; branchial length, 8.2–11.8; trunk length, 42.5–52.0; tail length, 27.0–34.9; eye length, 1.4–2.7; disc length, 7.8–10.5. The intestinal diameter in feeding individuals is 4.5 mm. Trunk myomeres, 58–65. Dentition: the marginals in the anterior and lateral fields are of two different sizes, small and with an elongated base, while those in the posterior field are small; exceptionally, one or two of these elongate marginals on each side lie in the middle of the lateral fields and therefore qualify as exolaterals (see fig. 4a in Vladykov and Kott 1979a); supraoral lamina, 3 unicuspid teeth, the median one smaller than the lateral ones; infraoral lamina, 5–6 unicuspid teeth, predominantly 5; 4 endolaterals on each side, rarely 3 on one side; endolateral formula, typically 2–3–3–2, the second endolateral may also be uni–, bi– or quadricuspid, the third endolateral may also be quadricuspid, and the fourth endolateral may be absent, but if present, also be uni–, bi– or quadricuspid; 2 rows of anterials; first row of anterials, 4–5 unicuspid teeth; exolaterals not present as rows

but 1 or 2 on each side may be present; 1 row of posterials with 16–20 teeth, of which 0–15 are bicuspid and the rest unicuspid; transverse lingual lamina, 20–29 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae each with 24–33 unicuspid teeth. Velar tentacles, 7–9, with tubercles and wings consisting of a very short tentacle on either side. Median tentacle shorter than the lateral ones immediately next to it. Body coloration (preserved), dark brown on dorsal, lateral, and ventral aspects. Lateral line neuromasts darkly pigmented. Caudal fin pigmentation, +++. Second dorsal fin pigmentation, +++. Caudal fin shape, spade–like. Oral fimbriae, 98–111. Oral papillae, 12–20.

Habitat and Biology: Freshwater, in rivers and lakes. Adults parasitic on fishes.

Geographic Distribution (Fig. 49): USA: Klamath River Basin in Oregon (Upper Klamath Lake) and California (Klamath River).

Interest to Fisheries: Known to feed on fishes perhaps of commercial importance, but these were not identified.

References: Khidir and Renaud (2003), Vladykov and Kott (1979a, 1979c)

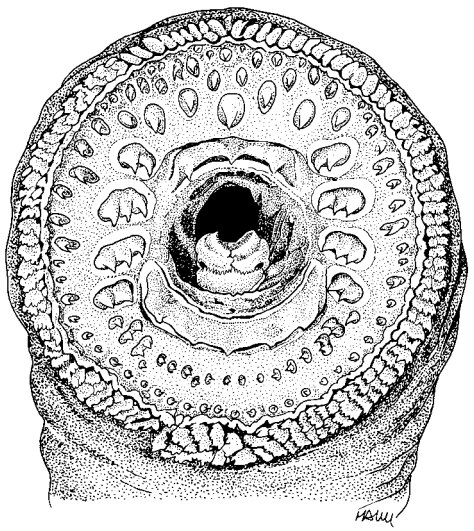

Fig. 48. Oral disc of *Entosphenus similis*. After a drawing by Paul I. Voevodine [male, 260 mm TL, NMC (= CMNFI) 1986–1027, Klamath River, California, USA, Spring 1953].

Fig. 49. Geographic distribution of *Entosphenus similis*.

Entosphenus tridentatus Gairdner in Richardson 1836 — Figs. 50–52

Synonyms: ***Petromyzon tridentatus*** Gairdner in Richardson 1836: 293 (559 mm TL; type locality: falls of the Walamet River, known today as the Willamette River, Columbia River Basin, Washington (almost certainly Oregon, USA); ***Petromyzon ciliatus*** Ayres 1855: (610 mm TL; type locality: San Francisco Bay, California, USA); ?***Ammocoetes cibarius*** Girard 1858: 383–384 (holotype: metamorphosing ammocoete of 102 mm TL originally, but with tail now missing, USNM 981, recatalogued as USNM 6176; type locality: Fort Steilacoom, Puget Sound, Washington); ?***Petromyzon lividus*** Girard 1858: (381 mm TL; type locality: Wahlahmath River, known today as the Willamette River, Columbia River Basin, Oregon, USA); ?***Petromyzon astori*** Girard 1858: (178 mm TL; type locality: Astoria, Oregon, USA)

Taxonomic Remarks: The landlocked population in the Sprague River, Klamath River Basin, Oregon, appears distinctive from other conspecifics in a number of characters and would benefit from a closer examination. For example, four of the five specimens from the Sprague River examined by Vladykov and Kott (1979a) did not possess wings on their velar apparatus and had counts between 7–10 tentacles, while typically, *E. tridentatus* possesses wings and 11–18 tentacles. Hubbs (1924) suggested that the population in Goose Lake, Oregon (the lake also straddles California) represented a separate but unnamed race. This requires further investigation.

FAO Names: En — Pacific Lamprey, Three–toothed Lamprey; **Fr** — Lamproie du Pacifique; **Sp** — Lamprea del Pacífico
Local names: Ksuyas, Asum **(Sahaptin, North American First Nation's language)**

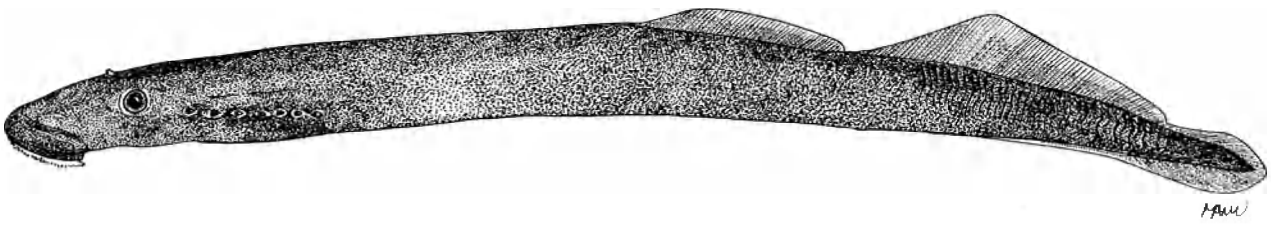

Fig. 50. Side view of *Entosphenus tridentatus*. After a photograph by Brian W. Coad [prespawning male, 261.5 mm TL, NMC (= CMNFI) 1986–761, Stamp River, British Columbia, Canada].

Diagnostic Features: Ammocoetes: Maximum size attained, 144 mm TL. Body proportions, as percentage of TL (based on 50 specimens measuring 81–144 mm TL): prebranchial length, 6.3–9.3; branchial length, 9.0–14.1; trunk length, 48.1–53.5; tail length, 27.1–32.4. Trunk myomeres, 67–70. Body coloration unrecorded. Pigmentation: upper lip, + (4% of specimens) or ++ (60%) or +++ (36%); subocular, – (4%) or + (48%) or ++ (40%) or +++ (8%); lower prebranchial, – (28%) or + (40%) or ++ (28%) or +++ (4%); upper branchial, + (84%) or ++ (16%); caudal fin, ++ (28%) or +++ (72%); tongue precursor bulb, –; along elastic ridge of tongue precursor, – or +. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like.

Metamorphosing Ammocoetes: lengths unrecorded.

Adults: 96–800 mm TL. Specimens 380–620 mm TL weigh 120–510 g wet weight. Body proportions, as percentage of TL (based on 274 specimens measuring 96–716 mm TL): prebranchial length, 9.8–18.0; branchial length, 7.8–12.6; trunk length, 40.3–54.0; tail length, 23.6–34.9; eye length, 1.3–4.5; disc length, 4.6–9.1. The urogenital papilla length, as a percentage of branchial length, in two spawning males measuring 211–217 mm TL, 12.0–12.5. Trunk myomeres, 60–71 [57–74, according to Creaser and Hubbs (1922) and as high as 78 according to Renaud (2008)]. Dentition: marginals, 48–62; supraoral lamina, 3 unicuspid teeth, the median one being smaller; infraoral lamina, 5–6 unicuspid teeth, predominantly 5; 4 endolaterals on each side; endolateral formula, typically 2–3–3–2, the first endolateral rarely unicuspid and the second and third endolaterals rarely bicuspid; 2 rows of anterials; first row of anterials, either 1 or 5 unicuspid teeth; exolaterals absent; 1 row of posterials, 12–21 teeth, of which 0–5 may be bicuspid and the remainder unicuspid; transverse lingual lamina, 14–23 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae parentheses–shaped, each with 20–27 unicuspid teeth [50–63 according to McPhail and Lindsey (1970)]. Velar tentacles, 10–18, with tubercles; the dorsal wings may each consist of up to 5–6 long tentacles that reach the median tentacle. Median tentacle about the same length as the lateral ones immediately next to it. Four of five specimens from the Sprague River did not possess wings and had 7–10 tentacles. Body coloration (preserved), dorsal, lateral, and ventral aspects bluish gray in older individuals and ventral aspect either dark gray or almost white in recently metamorphosed individuals. Lateral line neuromasts unpigmented or darkly pigmented. Caudal fin pigmentation, +++. Caudal fin shape, rounded or spade–like. Oral fimbriae, 94–105. Oral papillae, 12–18.

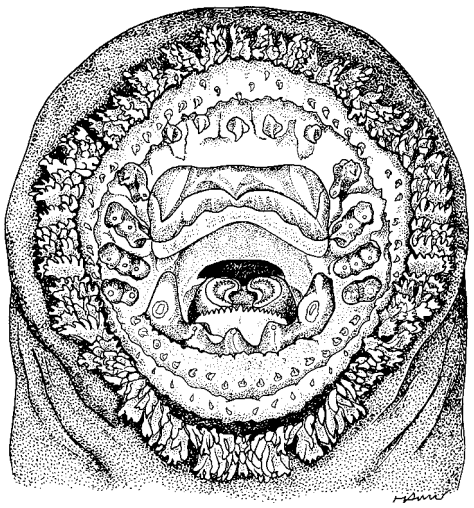

Fig. 51. Oral disc of *Entosphenus tridentatus*. After a drawing by Susan Laurie–Bourque [284 mm TL, NMC (= CMNFI) 1986–761, Stamp River, British Columbia, Canada].

Habitat and Biology: Anadromous, but also a number of permanent freshwater resident populations (Cultus Lake, British Columbia; Sprague River, Klamath River Basin, Oregon). In marine waters, adults mostly inhabit the mesopelagic zone down to 800 m depth and have been documented as far as 117 km off the coast of Oregon. In fresh waters, ammocoetes and adults inhabit lakes, rivers, and creeks. Ammocoetes occur in soft sediments in shallow areas along stream banks. Larval life is 4–6 yrs. Newly–hatched ammocoetes emerging from their nest are preyed upon by *Oncorhynchus kisutch* fry. Metamorphosis occurs between July and November. Migration to the sea begins in the fall and extends until the spring depending on whether the populations are coastal (former) or further inland (latter). Young outmigrating adults are preyed upon by *Ptychocheilus oregonensis* and introduced *Ictalurus punctatus* in the Snake River. Three gull species and one tern species feed on downstream migrants in the Columbia River. Great Blue Heron feed on adults in the San Francisco Bay area, California. Three pinnipeds, California and Steller sea lions and Pacific Harbor Seal, feed heavily on adults in the Rogue River, Oregon. Mink feed on adults in the Skeena River, British Columbia. In marine waters, adults are parasitic on a wide variety of fishes (*Oncorhynchus gorbuscha*, *O. kisutch*, *O. mykiss*, *O. nerka*, *O. tshawytscha*, *Gadus macrocephalus*, *Theragra chalcogramma*, *Merluccius productus*, *Ophiodon elongatus*, *Anoplopoma fimbria*, *Hippoglossus stenolepis*, *Reinhardtius hippoglossoides*, *Atheresthes evermanni*, *A. stomias*, *Sebastes alutus*, *S. aleutianus*, and *S. reedi*) and whales (*Balaenoptera borealis*, *B. physalus*, *Megaptera novaeangliae*, and *Physeter macrocephalus*). Adults are found in the Strait of Georgia from December to mid–June. The duration of the feeding phase at sea has been estimated at 20–42 months. In British Columbia, return to fresh water begins as early as April and is completed by September. In the Columbia River, prior to the completion of the Grand Coulee Dam in 1941, spawning migrations of 800 km up to Kettle Falls, Washington occurred. In order to cross barriers such as falls, they use their suctorial disc to attach to the vertical surfaces and slowly make their way up. In British Columbia spawning is in June to the end of July, while in Oregon, it begins in May at water temperatures of 10–15 °C and continues through July. Fecundity, 98,300–238,400 eggs/female in Oregon populations from Clear, Trout, and Cow creeks, respectively, in the John Day, Molalla, and Umpqua river basins. Death of spawners follows 3–36 days after spawning. Eggs are eaten by *Oncorhynchus mykiss* and *Rhinichthys osculus* in the Umatilla River, Oregon.

Geographic Distribution (Fig. 52): Pacific Ocean Basin: Canada (Strait of Georgia, Cowichan, Nicola, Oyster, Qualicum, Skeena, Stamp and Fraser rivers, Haslam and Robertson creeks, and Babine and Cultus lakes, British Columbia); USA (Norton Sound, Alaska; Puget Sound and Snake River, Washington; Snake River, Idaho; Columbia, John Day, Sprague, Umatilla, Umpqua, Rogue, and Willamette rivers, and Clear, Cow, Milk, and Trout creeks, Oregon; Goose Lake, Oregon/California; San Francisco Bay, Merced, Trinity, and Tuolumne rivers, Carr, Cottonwood, Coyote, Deer, Mill, Salt, Sespe, and Tracy creeks, California); México (off Clarión Island, Revillagigedo Archipelago and Baja California); Japan (off Kushiro, Hokkaidō Island; Naka River Basin: Arakawa, Hoki, Maki, Naka, and Yusaka rivers, Honshu Island). The population in Clear Lake, California (Moyle 1976) and that of Elsie Lake Basin, British Columbia (Beamish and Northcote 1989) no longer exist. In the latter case, the direct cause of disappearance was the building between 1957 and 1959 of five dams on the outlet and in the area immediately surrounding Elsie Lake, on Vancouver Island, preventing access to the sea.

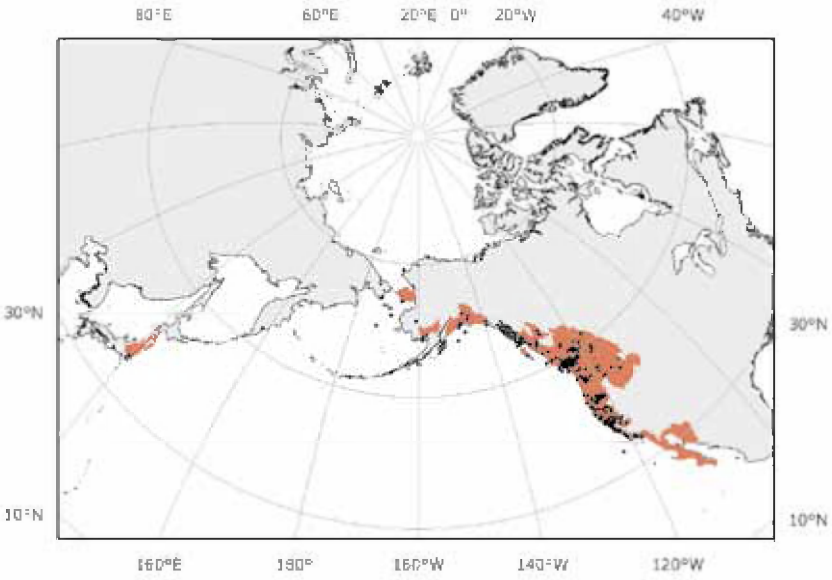

Fig. 52. Geographic distribution of *Entosphenus tridentatus*.

Interest to Fisheries: The Native American tribes of the mid–Columbia River Plateau have an ongoing tradition dating back hundreds of years of harvesting Pacific Lamprey, which they call ksuyas or asum. The adults are caught either by hand or dipnet in areas where they congregate prior to spawning. They are prepared for human consumption either by drying or roasting. Caloric values for Pacific Lamprey range from 5.9 to 6.3 kcal/g wet weight. Their oil is also extracted and used for medicinal purposes. Ammocoetes are used as bait for introduced *Micropterus dolomieu* in the John Day River, Oregon. In 1812, Americans of European descent obtained Pacific Lamprey from the Umatilla tribe of Oregon for the purposes of consumption. In the early 1900s, fur trappers utilized Pacific Lamprey as bait for coyotes. A fishery for adult lamprey has existed at Willamette Falls on the Willamette River, Oregon at least since 1913. That year, 24.5 metric tons were harvested and ground into fishmeal for young hatchery salmon. Between 1943 and 1949, 740 metric tons in total were harvested and used for vitamin oil, food for livestock, poultry, and fishmeal. In 1994, about 1.8 metric tons were exported to Europe for human consumption. The North Carolina Biological Supply House regularly collects adults from this locality for use as teaching material.

References: Ackerman (1997), Ayres (1855b), Barnhart (1937), Beamish (1980, 1982), Beamish and Northcote (1989), Beamish and Williams (1976), Bond and Kan (1973), Chase (2001), Close *et al.* (2002), Creaser and Hubbs (1922), Farlinger and Beamish (1984), Fukutomi *et al.* (2002), Gill *et al.* (2003), Girard (1858), Hubbs (1924, 1967), Kan (1975), Khidir and Renaud (2003), Kott *et al.* (1988), Lorion *et al.* (2000), McPhail and Lindsey (1970), Mecklenburg *et al.* (2002), Miller and Lea (1972), Morris (1975), Moyle (1976), Pletcher (1963), Renaud (2008), Richardson (1836), Roffe and Mate (1984), Ruiz–Campos and González–Guzmán (1996), Ruiz–Campos *et al.* (2000), Vladykov and Follett (1958), Vladykov and Kott (1976b, 1976c, 1976d, 1979a, 1979c, 1984), Vogt (1988), Wolf and Jones (1989)

Genus *Eudontomyzon* Regan 1911

Synonyms: ***Eudontomyzon*** Regan 1911: 194, 200–201 (Romania: Transylvania; type species: ***Eudontomyzon danfordi*** Regan 1911, by monotypy)

This genus was revised by Renaud (1982a) and comprises five species (2 parasitic and 3 nonparasitic). Four species occur in Europe and one species, *Eudontomyzon morii*, is endemic to Asia. Two dorsal fins. Supraoral lamina with two teeth separated by a wide bridge, which may occasionally bear one or more unicuspid teeth. Labial teeth villiform (except in *E. hellenicus* and *E. graecus* where they are pavement–like), radially–arranged in a curvilinear fashion and present on all fields of the oral disc (rarely, however, posterials are absent in *E. mariae*) but not necessarily fully occupying all available space. Transverse lingual lamina u–shaped and with an enlarged median cusp.Velar tentacles with tubercles and a median tentacle is present. The type species is *Eudontomyzon danfordi* Regan 1911. Creaser and Hubbs (1922) treated *Eudontomyzon* as a subgenus of *Petromyzon* and Berg (1931) treated it as a subgenus of *Lampetra*. The former view is not supported by the cladogram produced by Gill *et al.* (2003) but the latter interpretation is consistent with Gill *et al.* (2003). Bănărescu (1969) suggested that *Eudontomyzon* originated in Siberia and dispersed to Europe and East Asia, subsequently becoming extirpated from Siberia during glaciation.

Eudontomyzon danfordi Regan 1911 **Figs. 53–55**

Synonyms: ***Eudontomyzon danfordi*** Regan 1911: 200–201 [six syntypes: adults, 120–220 mm TL, BMNH 1951.5.22.1–5 and NMC (= CMNFI) 1986–717; type locality: Transylvania, Romania; type species by monotypy]; ***Lampetra Bergi*** Vladykov 1925: 251–252 (Subcarpathian Ukraine); ***Lampetra (Eudontomyzon) gracilis*** Kux 1965: 294 (holotype: adult male, 211 mm TL, LMB 1247/7; type locality: Topl'a River, Lukov, Slovakia)

FAO Names: En — Carpathian Lamprey; **Fr** — Lamproie carpathique
Local names: Chişcar or Cicar **(Romanian)**; Vladykov (1931) lists 24 common names for the small region of Subcarpathian Ukraine alone. The common name of Hungarian Lamprey coined by Berg (1931) is inappropriate because the species does not occur in Hungarian waters.

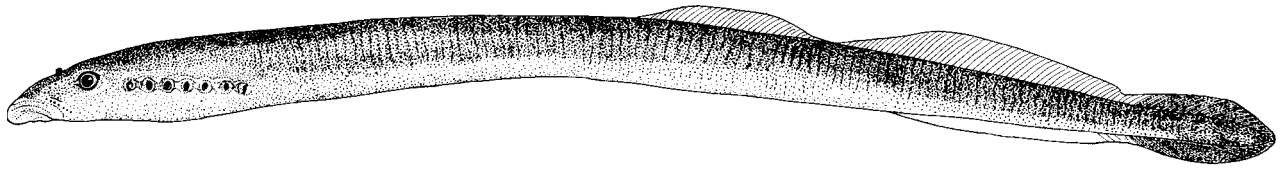

Fig. 53. Side view of *Eudontomyzon danfordi*. After a photograph by Sallai Zoltán [adult].

Diagnostic Features: Ammocoetes: Maximum size attained, 211 mm TL. Body wet weight of 321 individuals 21.5–208 mm TL, 0.02–14.29 g. Body proportions, as percentage of TL (based on 190 specimens measuring 50–208 mm TL): prebranchial length, 5.8–10.3; branchial length, 10.2–14.7; trunk length, 48.1–58.9; tail length, 22.2–32.7; cloacal slit length, 0.5–2.4; prenostril length, 1.8–4.0. Trunk myomeres, 58–70. Body coloration unrecorded. Pigmentation: upper lip, – (36% of specimens), + (45%), ++ (18%) or +++ (1%); between upper lip and cheek, ++ (4%) or +++ (96%); cheek, – (2%), + (2%), ++ (26%) or +++ (70%); subocular, – (78%), + (12%), ++ (4%) or +++ (5%); upper prebranchial, – (22%), + (27%), ++ (22%) or +++ (30%); lower prebranchial, – (28%), + (41%), ++ (23%) or +++ (8%); upper branchial, – (1%), + (1%), ++ (71%) or +++ (28%); lower branchial, – (93%) or + (7%); ventral branchial, – (77%), + (22%) or ++ (1%); lower lip, – (35%), + (40%), ++ (20%) or +++ (4%); caudal fin, – (1%), + (68%), ++ (28%) or +++ (3%); predorsal, – (34%), + (41%), ++ (20%) or +++ (5%); tongue precursor bulb, – (75%) or + (25%); along elastic ridge of tongue precursor, – (25%), + (50%), or +++

(25%). Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like (99%) or rounded (1%).
Metamorphosing Ammocoetes: 134–175 mm TL.
Adults: 120–300 mm TL. Body wet weight of 48 individuals 140–241 mm TL, 2.66–21.65 g. Body proportions, as percentage of TL (based on 60–66 specimens measuring 140–241 mm TL): prebranchial length, 7.8–13.5; branchial length, 8.6–11.4; trunk length, 42.9–52.5; tail length, 25.6–32.3; cloacal slit length, 0.6–1.7; eye length, 1.0–2.1; disc length, 2.8–7.5; prenostril length, 4.1–8.3; snout length, 4.8–9.3; postocular length, 2.2–3.5. Intestine diameter, 0.3–5.0 mm. The urogenital papilla length, as a percentage of branchial length, in a spawning male measuring 180 mm TL, 16.2. Trunk myomeres, 59–68. Dentition: Most labial teeth are villiform; supraoral lamina, 2 unicuspid teeth; infraoral lamina, 7–12 teeth, the lateralmost sometimes bicuspid while the rest are unicuspid; usually 3 endolaterals on one side (96%), but 4 (3%) and 2 (1%) also found; endolateral formula, typically 1–2–2 (59%) and 2–2–2 (23%), but also 1–2–1 (9%), and 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; 4–7 rows of anterials; first row of anterials, 6–13 unicuspid teeth; 2–5 rows of exolaterals; 2–4 rows of posterials; first row of posterials, 15–28 unicuspid teeth; transverse lingual lamina, 9–15 unicuspid teeth, the median one enlarged; longitudinal lingual laminae each with 10–17 usually unicuspid teeth, rarely, one may be bicuspid. Velar tentacles, 7–16, with tubercles; dorsal wings consisting of 2–6 tentacles usually present on either side, not reaching the median tentacle. Body coloration (live) gray blue on the head and dorsal aspect, gray towards pink on lateral aspects and white on the ventral aspect. Lateral line neuromasts unpigmented. Caudal fin pigmentation, – (20%), + (4%), ++ (12%), +++ (64%). Caudal fin shape, spade–like. Oral fimbriae, 90–115. Oral papillae, 15–25.

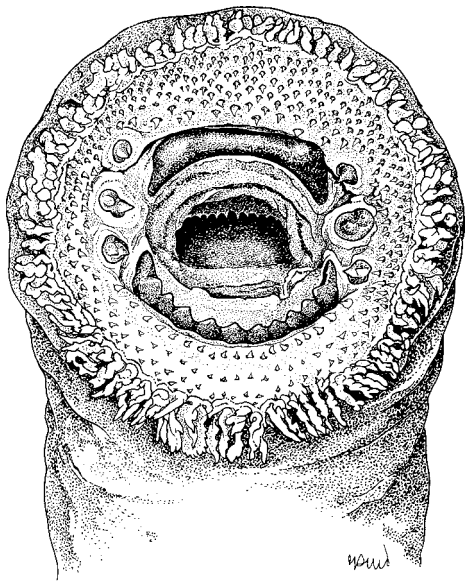

Fig. 54. Oral disc of *Eudontomyzon danfordi*. After a drawing by Paul I. Voevodine.

Habitat and Biology: Freshwater, in brooks and rivers. In Slovakia, it occurs in the submountainous zone at altitudes between 465 and 550 m and in Subcarpathian Ukraine it is found almost exclusively above 250 m.
Larvae live 4+ – 5+ years. Metamorphosis occurs between the end of July to October. Adults live 17–19 months, feeding only during the first year. Adults parasitic/scavenger on various fishes (*Barbus barbus*, *B. petenyi*, *Squalius cephalus*, *Barbatula barbatula*, *Cottus gobio*, *C. poecilopus*). The spawning period varies with location. Dead and spent adults have been found in April and May in Subcarpathian Ukraine, whereas in Romania, spawning is said to take place from the end of May into June in Iara Brook, Transylvania and between the end of June and the beginning of July in Bistra Mărului Brook, Banat. Fecundity, 7,500–10,300 eggs/female.

Geographic Distribution (Fig. 55): Black Sea Basin: Tisa River Basin (Hornád, Okna, and Topl'a rivers, and Ulička Brook, Slovakia; Apshitsa, Borzhava, Kusva, Latorica, Rika, Sopurka, Tereshova, Tereblya, Tisa, and Uh rivers, Ukraine; Arieş, Bega, Bistriţa, Crişul Alb, Crişul Negru, Crişul Repede, Drăgan, Mureşul, Someşul, Someşul Cald, Someşul Mare, Someşul Mic, Someşul Rece, Strei, Vida, and Vişeu rivers and Agirbici, Anies, Bistra, Capus, Cormaia, Gudea–Mare, Gudea–Unita, Gurghiu, Iara, Lapusna, Moneasa, Răcătău, Rastolita, Risca, Sălăuta, Sebeşul, Toplita, and Zebrac brooks, Romania) and Timiş River Basin (Timiş River and Birzava, Bistra Mărului, and Sucu brooks, Romania).

Interest to Fisheries: In certain regions of Romania, local people consume (presumably adults of) this species and fishermen also use it (presumably the ammocoetes) as live bait. The feeding phase adults inflict serious damage to trout in Romanian hatcheries.

Fig. 55. Geographic distribution of *Eudontomyzon danfordi*.

References: Berg (1931), Chappuis (1939), Creaser and Hubbs (1922), Gill *et al.* (2003), Hardisty (1964), Khidir and Renaud (2003), Kott *et al.* (1988), Kux (1965), Regan (1911), Renaud (1982a), Renaud and Holčík (1986, 1988), Salewski *et al.* (1995), Vladykov (1925, 1927, 1931), Vladykov and Kott (1976d), Vladykov *et al.* (1982), Zanandrea (1959a)

Eudontomyzon hellenicus Vladykov, Renaud, Kott, and Economidis 1982 — Figs. 56–58

Synonyms: ***Eudontomyzon hellenicus*** Vladykov, Renaud, Kott, and Economidis 1982: 2898, figs. 1, 2c, 3a [holotype: male, 96 mm TL, NMC (= CMNFI) 1977–1773; type locality: Kefalárion Brook, near Kefalárion, Central Macedonia Periphery, 41°04'N 24°16'E, Strymon River Basin, Greece]

Taxonomic Remarks: Recently (Renaud and Economidis 2010) it was found that *Eudontomyzon hellenicus* is restricted to the Strymon River Basin, Aegean Sea Basin and that the *Eudontomyzon* species found in the Loúros River Basin, Ionian Sea Basin, in fact is a different and new species, *E. graecus*. Reference: Renaud, C.B. and P.S. Economidis. 2010. *Eudontomyzon graecus*, a new nonparasitic lamprey from Greece (Petromyzontiformes: Petromyzontidae). Zootaxa 2477: 37–48.

FAO Names: En — Greek Brook Lamprey; **Fr** — Lamproie de ruisseau grecque

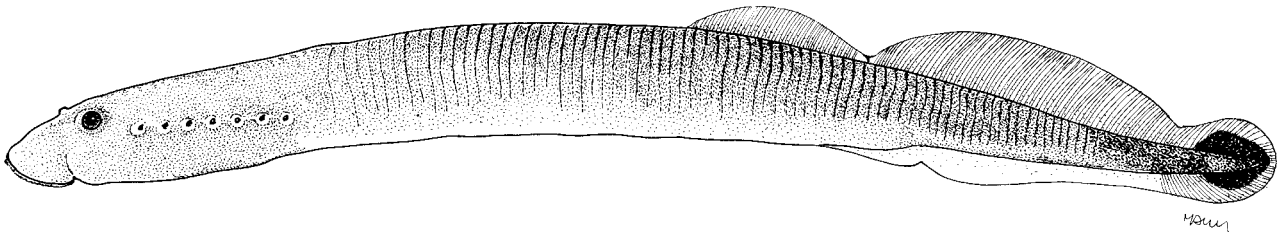

Fig. 56. Side view of *Eudontomyzon hellenicus*, spawning female, 105 mm TL, paratype, NMC (= CMNFI) 1977–1753, Kefalárion Brook, near Kefalárion, Strymon River Basin, Greece, 19 May 1977, P.S. Economidis, A.I. Sinis, and V.D. Vladykov. After Renaud (1982a).

Diagnostic Features: Ammocoetes: Maximum size attained, 189 mm TL. Body proportions, as percentage of TL (based on 237 specimens measuring 33–189 mm TL): prebranchial length, 6.6–13.6; branchial length, 10.9–16.2; trunk length, 46.8–55.4; tail length, 21.2–31.7; cloacal slit length, 0.7–1.8; prenostril length, 1.9–4.6. Trunk myomeres, 53–63. Pigmentation: upper lip, + (12% of specimens), ++ (78%) or +++ (9%); between upper lip and cheek, – (4%), + (21%), ++ (40%) or +++ (36%); cheek, + (4%), ++ (24%) or +++ (72%); subocular, – (34%), + (27%), ++ (10%) or +++ (29%); upper prebranchial, – (63%), + (33%), ++ (4%) or +++ (1%); lower prebranchial, – (83%), + (16%) or ++ (2%); upper branchial, + (3%), ++ (94%) or +++ (2%); lower branchial, – (48%), + (51%) or ++ (1%); ventral branchial, – (28%) or + (72%); lower lip, + (8%), ++ (45%) or +++ (47%); caudal fin, + (1%), ++ (86%) or +++ (13%); predorsal, – (4%), + (16%), ++ (32%) or +++ (48%); tongue precursor bulb, – (54%) or + (46%); along elastic ridge of tongue precursor, – (36%), + and ++ (18% each) or +++ (27%). Lateral line neuromasts unpigmented. Caudal fin shape, rounded (only 2 of 218 ammocoetes had a spade–like caudal fin).

Metamorphosing Ammocoetes: 113.5–156.5 mm TL.

Adults: 95.5–158.5 mm TL. Body proportions, as percentage of TL (based on 66 specimens measuring 95.5–158.5 mm TL): prebranchial length, 8.4–13.1; branchial length, 9.5–12.4; trunk length, 46.4–54.7; tail length, 26.2–33.0; cloacal slit length, 0.6–2.0; eye length, 1.3–2.1; disc length,

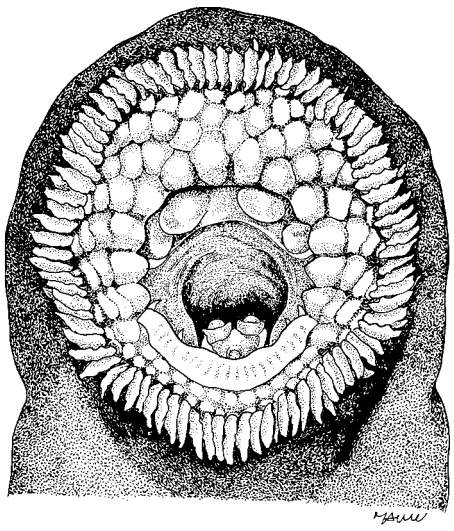

Fig. 57. Oral disc of *Eudontomyzon hellenicus*. After a drawing by Susan Laurie–Bourque [118 mm TL, CMNFI 1994–7, Kefalárion Brook, near Kefalárion, Strymon River Basin, Greece, 18 Jan. 1980, P.S. Economidis and A.I. Sinis].

2.9–7.3; prenostril length, 3.6–7.3; snout length, 4.4–8.9; postocular length, 2.3–3.8. The intestinal diameter, <0.5–1.0 mm. The urogenital papilla length, as a percentage of branchial length, in eight spawning males measuring 96–133 mm TL, 3.3–9.1. Trunk myomeres, 53–63. Dentition: All labial teeth are pavement–like; supraoral lamina, 2 teeth, usually unicuspid, but one or both may be bicuspid; infraoral lamina, 7–11 teeth; typically 3 endolateral teeth on each side, but 4 teeth also occur (6 cases out of 96); endolateral formula, typically 2–2–2, but variant formulae occur in 25% of cases and each of the teeth can be either uni–, bi–, or tricuspid; 3–4 rows of anterials; first row of anterials, 4–8 teeth; 2–6 rows of exolaterals on each side; 1–4 rows of posterials; first row of posterials, 10–15 teeth; transverse lingual lamina with a greatly enlarged median tooth but no lateral teeth; longitudinal lingual laminae without teeth. Additonally, 9 of 66 adults possessed 1–2 accessory unicuspid teeth inside the ring formed by the supraoral and infraoral laminae and the endolateral teeth. Velar tentacles, 2–5. Body coloration (preserved) in mature adults is gray on the upper surface and flanks and light brown on the lower surface. Lateral line neuromasts unpigmented. Caudal fin pigmentation, + (2% of specimens), ++ (19%) or +++ (79%). Caudal fin shape, rounded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater, in 25–75 cm deep, clear, fairly fast–flowing watercourses with gravelly substrate, some rocks and aquatic vegetation. Also found in mud, especially among the roots of aquatic vegetation.
Ammocoetes feed on green algae. Metamorphosis occurs between October and January. Adults nonparasitic and are believed to live only 3–4 months. The spawning period is believed to be between January and May.

Geographic Distribution (Fig. 58): Strymon River Basin (Ayannis, Kefalárion, and Milopótamos brooks) and Loúros River Basin (Loúros River and Filippiás Brook), Greece.

Interest to Fisheries: None

References: Kott *et al.* (1988), Renaud (1982a), Renaud (1986), Vladykov *et al.* (1982)

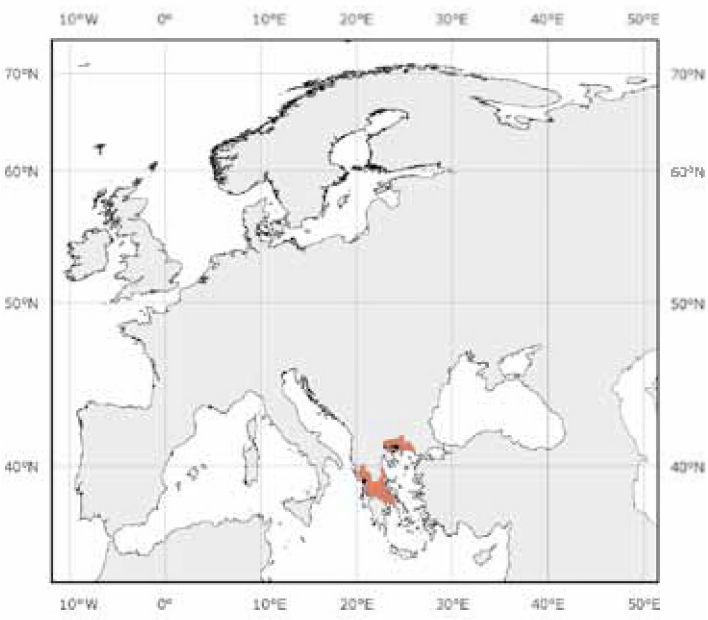

Fig. 58. Geographic distribution of *Eudontomyzon hellenicus*.

Eudontomyzon mariae (Berg 1931) Figs. 59–61

Synonyms: ***Lampetra mariae*** Berg 1931: 94–96, pl. I, fig. 3, pl. IV, fig. 1 (36 syntypes: spawning adults, 161–206 mm TL, ZISP 23124; six of these, 171–183.5 mm TL, CMNFI 1986–718; type locality: Kharkiv River, near Kharkiv, 50°0'N 36°15'E, Don River Basin, Ukraine); ***Eudontomyzon danfordi vladykovi*** Oliva and Zanandrea 1959: 2–4 [holotype: spent female, 150 mm TL, CUP 4525, from the original type locality of Danube River at Čilistovo, near Bratilsava, Slovakia was so damaged that a neotype, an adult male, 150 mm TL, SNM 41858, from the new type locality of Hraničný Kriváň Brook, Slovakia was designated by Holčík (1963)]; ***Eudontomyzon vladykovi stankokaramani*** Karaman 1974: 1–4, fig. 2, tables 1–6 (holotype: adult male, 150 mm TL, presumed lost, type locality: Istočka River and Rastavički Brook, Beli Drim River Basin, near Peć, Serbia)

Taxonomic Remarks: Rembiszewski (1968) reported on three adult hybrids between *E. mariae* and *Lampetra planeri* in the Jeziorka River, Poland. Holčík and Šorić (2004) have recently elevated *E. stankokaramani*, but I prefer to leave it in synonymy until a more comprehensive study of the variation in the velar tentacle morphology of the wide–ranging *E. mariae* has been undertaken. Based on the facts that *E. mariae* exhibits a broad geographic distribution (Adriatic, Aegean, Baltic, and Black sea basins) with clear disjunctions and wide variation in a number of taxonomic characters, Renaud (1982a) suggested that *E. mariae* may consist of a number of subspecies. However, the lack of sufficient adult specimens from across the range to elucidate this question remains a problem. Additionally, the lampreys from the Kuban' River Basin require a re–evaluation (N.G. Bogutskaya, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, pers. comm., 2007).

FAO Names: En — Ukrainian Brook Lamprey; **Fr** — Lamproie de ruisseau ukrainienne
Local names: Chişcar, Cicar, or Ţipari **(Romanian)**

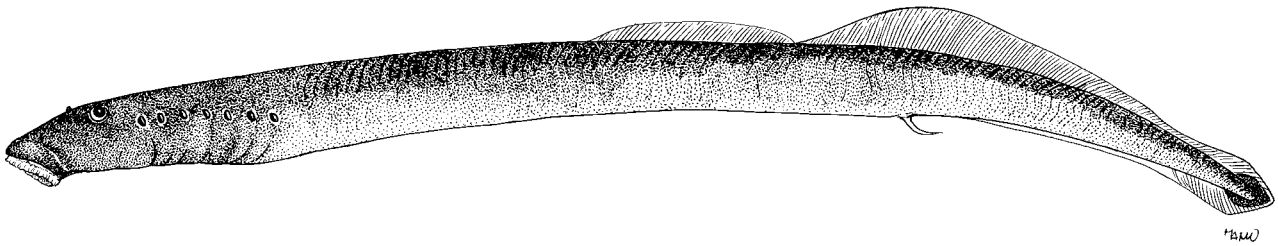

Fig. 59. Side view of *Eudontomyzon mariae.* After a photograph by Brian W. Coad [spawning male, 147.5 mm TL, NMC (= CMNFI) 1986–896, Jeziorka River, Vistula River Basin, Poland, J.M. Rembiszewski].

Diagnostic Features: Ammocoetes: Maximum size attained, 230 mm TL, but perhaps can exceed 250 mm TL based on the maximum total length recorded for metamorphosing ammocoetes. Body wet weight of 174 individuals 34–212 mm TL, 0.07–15.17 g. Body proportions, as percentage of TL (based on 174 specimens measuring 34–212 mm TL): prebranchial length, 5.3–11.8; branchial length, 9.4–20.5; trunk length, 50.0–58.0; tail length, 17.6–30.8; cloacal slit length, > 0.0–1.6; prenostril length, 1.8–4.5. Trunk myomeres, 58–70. Body coloration (live and preserved for up to 3 yrs), with mottling. Pigmentation: upper lip, – (61% of specimens), + (35%), or ++ (4%); between upper lip and cheek, + (1%), ++ (8%) or +++ (91%); cheek, + (5%), ++ (58%) or +++ (36%); subocular, – (91%), + (2%), ++ (3%) or +++ (4%); upper prebranchial, – (34%), + (24%), ++ (25%) or +++ (17%); lower prebranchial, – (53%), + (28%), ++ (14%) or +++ (5%); upper branchial, + (2%), ++ (79%) or +++ (18%); lower branchial, – (91%), + (6%), ++ (2%) or +++ (1%); ventral branchial, – (92%), + (5%) or ++ (2%); lower lip, – (69%), + (22%) or ++ (9%); caudal fin, – 2%), + (11%), ++ (40%) or +++ (46%); predorsal, – (17%), + (38%), ++ (21%) or +++ (25%); tongue precursor bulb, –; along elastic ridge of tongue precursor, –. Tongue precursor shape, bulbous. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like (only 2 of 166 ammocoetes had a rounded caudal fin).

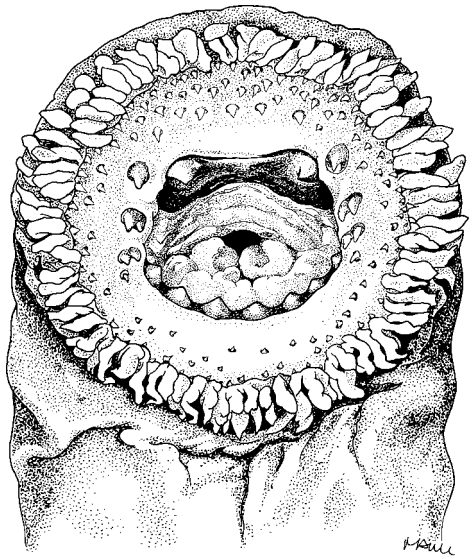

Fig. 60. Oral disc of *Eudontomyzon mariae.* After a drawing by Paul I. Voevodine.

Metamorphosing Ammocoetes: 150–250 mm TL.
Adults: 120–222 mm TL. Body wet weight of 37 individuals 131–195 mm TL, 3.61–12.69 g. Body proportions, as percentage of TL (based on 39 specimens measuring 123–195 mm TL): prebranchial length, 6.9–12.1; branchial length, 8.5–12.3; trunk length, 44.9–54.4; tail length, 24.3–31.3; cloacal slit length, 0.4–2.2; eye length, 0.7–2.1; disc length, 2.2–5.8; prenostril length, 2.5–6.5; snout length, 2.7–7.6; postocular length, 2.4–3.7. The urogenital papilla length, as a percentage of branchial length, in eight spawning males measuring 143.5–184 mm TL, 25.0–38.6. Trunk myomeres, 60–73. Dentition: Most labial teeth are villiform; supraoral lamina, usually only 2 unicuspid teeth, but in less than 10% of cases, 1–3 small unicuspid teeth may also be found on the bridge; infraoral lamina, 5–10 usually unicuspid teeth, but 1–2 lateralmost teeth may be bicuspid; usually 3 endolaterals on each side (83%), but 4 (11%), 1 (4%), and 2 (2%) also found; endolateral formula, typically 1–2–2 (26%), 1–2–1 (22%), 2–2–1 (13%), 2–2–2 (11%), but also 1–1–1, 2–2–3, 1–1–2–2 (each 6%), 2, 1–1–2–1 (each 4%), 1–2, 1–2–2–2 (each 2%) – Naseka *et al.* (2009) reported the following additional formulae from the syntypic series, including a count of 5 endolaterals: 1–1–2, 1–3–1, 2–1–1, 2–3–2, 1–2–2–1, 2–1–2–2, 1–1–2–1–1; 2–5 rows of anterials; first row of anterials, 5–10 unicuspid teeth, exceptionally, one lateralmost tooth may be bicuspid; 1–4 rows of exolaterals; rows of posterials, 0–3 (absent in 10% of individuals only); first row of posterials, either complete (continuous) with 12–20 unicuspid teeth (62% of individuals) or incomplete (discontinuous) with 1–12 unicuspid teeth (38% of individuals) or entirely absent (very rarely) – Naseka *et al.* (2009) reported the following additional counts from the syntypic series: complete row with 10 unicuspid and 1 bicuspid teeth; incomplete row with 13–17 unicuspid teeth and with 4 unicuspid and one bicuspid teeth; transverse lingual lamina, 3–7 unicuspid teeth, the median one enlarged (in 79% of individuals, the median cusp is both higher and wider, while in 21% of individuals it is wider, but not noticeably higher, than the flanking cusps); longitudinal lingual laminae each with 5–11 unicuspid teeth. Velar tentacles, 7–12, with tubercles. Body coloration unrecorded. No dark blotch near the apex of

the second dorsal fin. Lateral line neuromasts unpigmented or darkly pigmented, at least on the ventral aspect. Caudal fin pigmentation, – (7%), + (3%), ++ (13%), +++ (77%). Caudal fin shape, spade–like (97% of individuals), rarely rounded. Oral fimbriae, 88–98. Oral papillae number unrecorded.

Habitat and Biology: Freshwater, in brooks, rivers, and lakes.
Metamorphosis occurs in September in Poland and Slovakia and in July in the Ukraine. Adults nonparasitic. However, rare cases of ectoparasitism have been reported in Jelešná Brook, Slovakia and the Prut River, Ukraine. Adults are preyed upon by *Esox lucius*. Spawing occurs in late April – early May in the Ukraine. Fecundity, 1,950–7,106 eggs/female.

Geographic Distribution (Fig. 61): Baltic Sea Basin – Vistula River Basin: Jeziorka, Skawa, and Wilga rivers and Rudawa Brook, Poland; Neman River Basin: Berezyna, Isloch, and Peretut' rivers, Belarus; Black Sea Basin – Dnepr River Basin: Iput, Ratomka, Svisloch', and Volma rivers, Belarus and Desna, Dnepr, Goryn, Irpen', Perga, Sozh, Teterev, and Uzh rivers, Ukraine; Don River Basin: Don River and Ilovlya River Basin, Russian Federation and Donets, Kharkiv, and Lopanj rivers, Ukraine; Dnestr River Basin: Strwiąż River, Poland and Dnestr River, Moldova river; Danube River Basin: Drava and Mur rivers, Austria and Argeş, Bratia, and Republic of Moldova rivers and Suceava Brook, Romania and Biela Orava, Danube, Hron, Ipel', Rudava, and Turiec rivers, Hraničný Kriváň, Jelešná, and Mutnianka brooks, Slovakia and Sava River, Slovenia and Prut and Siret rivers, Ukraine; Kuban' River Basin: Il' River, Russian Federation and rivers west of the Caucasus in the Russian Federation and Georgia flowing directly into the Black Sea; Caspian Sea Basin – Volga River Basin: Sura and Elan'–Kadada rivers, Russian Federation; Adriatic Sea Basin – Lake Ohrid, The former Yugoslav Republic of Macedonia; Beli Drim River Basin: Istočka River, Bistrica and Rastavički brooks, Serbia; Aegean Sea Basin – Vardar River, The former Yugoslav Republic of Macedonia.

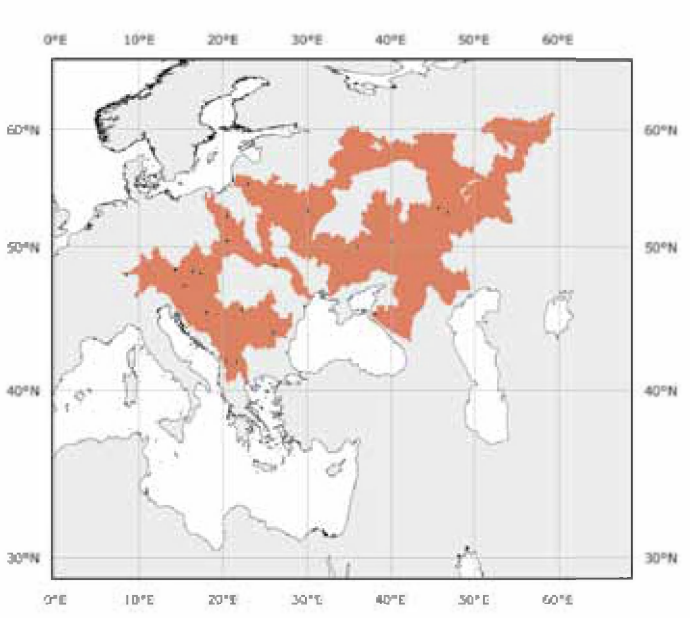

Fig. 61. Geographic distribution of *Eudontomyzon mariae*.

Interest to Fisheries: None

References: Balon and Holčík (1964), Belyĭ (1966), Berg (1931), Hankó (1922), Holčík (1963, 2003), Holčík and Delić (2000), Holčík and Šorić (2004), Karaman (1974), Kott *et al.* (1988), Levin (2001), Levin and Holčík (2006), Naseka *et al.* (2009), Oliva and Hensel (1962), Oliva and Zanandrea (1959a), Rembiszewski (1968), Renaud (1982a), Vladykov and Kott (1976d, 1979c), Wajgel (1884), Zhukov (1969)

Eudontomyzon morii (Berg 1931) Figs. 62–64

Synonyms: ***Lampetra morii*** Berg 1931: 97, pl. V, fig. 1 [four syntypes: adults, 153–165 mm TL, ZISP 23145; one of these measuring 171 mm TL, longer than the reported range given in Berg (1931), CMNFI 1986–757; type locality: upper Yalu River, near Ko–sui–in, approx. 40°42'N 128°7'E, Democratic People's Republic of Korea]

FAO Names: En — Korean Lamprey (Manchurian Lamprey, the original common name given by Berg (1931), no longer reflects common usage for the region's name); **Fr** — Lamproie coréene

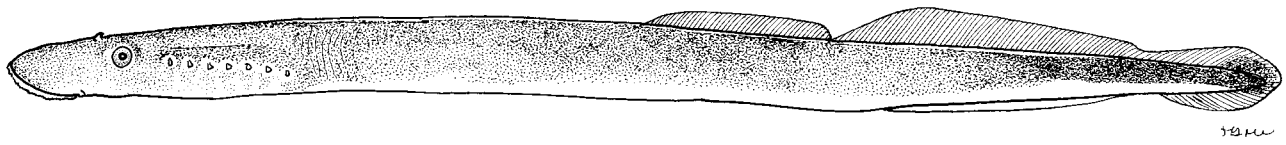

Fig. 62. Side view of *Eudontomyzon morii*, prespawning female, 196 mm TL, NMC (= CMNFI) 1980–930, upper Yalu River, near Changbai, Jilin Province, People's Republic of China, July 1975. After Renaud (1982a).

Diagnostic Features: Ammocoetes: The ammocoetes have not been studied.
Metamorphosing ammocoetes: lengths unrecorded.
Adults: 153–290 mm TL. Body wet weight of individuals 172.5–211.5 mm TL, 6.3–10.3 g. Body proportions, as percentage of TL (based on four specimens measuring 171-211.5 mm TL): prebranchial length, 11.7–13.0; branchial length, 8.7–10.2; trunk length, 47.0–47.5; tail length, 29.8-30.4; cloacal slit length, 1.2–1.7; eye length, 1.2–1.7; disc length, 6.1–7.2; prenostril length, 6.7–7.5; snout length, 7.6–8.7; postocular length, 2.8–3.1. Intestinal diameter, 3–4 mm. Trunk myomeres, 68–74. Dentition: Most labial teeth are villiform; supraoral lamina, 2 unicuspid teeth; infraoral lamina, 6–10 teeth, the lateralmost tooth on each side usually bicuspid, the internal ones unicuspid; 3 endolaterals on each side; endolateral formula, typically 2–2–2 (75%), but also 1–1–1 (25%); 3 rows of anterials; first row of anterials, 3–5 unicuspid teeth; 1–2 rows of exolaterals; 1 row of posterials; first (and only) row of posterials, 19–24 unicuspid teeth; transverse lingual lamina, 13–19 unicuspid teeth, the median one enlarged; longitudinal lingual laminae each with 14–15 unicuspid teeth. Velar tentacles, 9, with wings made up of two tentacles on each side. Body coloration unrecorded. Lateral line neuromasts unpigmented. Caudal fin pigmentation, ++ (50%), +++ (50%). Caudal fin shape, spade–like. Oral fimbriae, 95–100. Oral papillae, 16–22.

Habitat and Biology: Freshwater.
Adults parasitic on various fishes (*Sarcocheilichthys soldatovi*, *Rhynchocypris percnurus*, *Pseudogobio esocinus*, *Carassius auratus*, *Barbatula toni*, *Cobitis taenia*). Fecundity, 14,000–20,000 eggs/female.

Geographic Distribution (Fig. 64): Upper Yalu River Basin: Yalu River, People's Republic of China and Democratic People's Republic of Korea.

Interest to Fisheries: None

References: Berg (1931), Gill *et al.* (2003), Khidir and Renaud (2003), Ma and Yu (1959), Renaud (1982a), Vladykov and Kott (1979c)

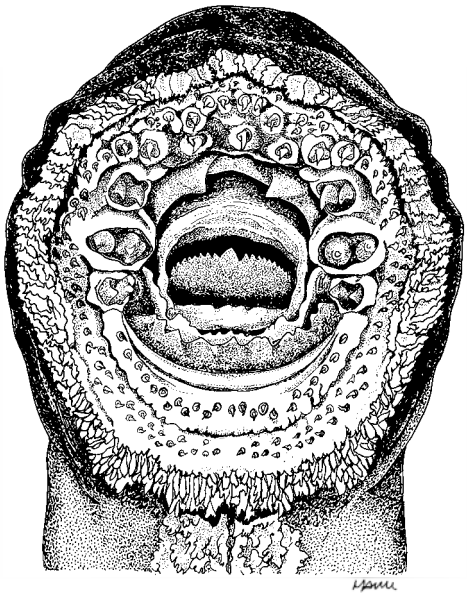

Fig. 63. Oral disc of *Eudontomyzon morii*. After a drawing by Susan Laurie-Bourque [212 mm TL, NMC (= CMNFI) 1980–930, upper Yalu River, near Changbai, Jilin Province, People's Republic of China, July 1975].

Fig. 64. Geographic distribution of *Eudontomyzon morii*.

Genus *Ichthyomyzon* Girard 1858

Synonyms: ***Ichthyomyzon*** Girard 1858: 381 [original description; type species: ***Petromyzon argenteus*** Kirtland 1838 (by subsequent designation Jordan 1882) = ***Ichthyomyzon bdellium*** (Jordan 1885)]; ***Scolecosoma*** Girard, 1858: 384 (based on unidentified ammocoetes of ***Ichthyomyzon***); ***Reighardina*** Creaser and Hubbs 1922: 4 (type species: ***Ichthyomyzon fossor*** Reighard and Cummins, 1916 by subsequent designation)

This genus was revised by Hubbs and Trautman (1937) and comprises six species (three parasitic and three nonparasitic) restricted to fresh waters in Canada and the USA. The main diagnostic feature is the presence of a single indented dorsal fin consisting of a lower anterior lobe and a higher posterior lobe. Supraoral lamina a single, usually multicuspid tooth. Labial teeth radially–arranged in a curvilinear fashion and completely covering all fields of the oral disc. Transverse lingual lamina varies from straight to strongly w–shaped but with the median cusp never enlarged. Velar tentacles are smooth and a median tentacle is absent. According to Hubbs and Trautman (1937), the six species are arranged as pairs, each containing a parasitic species and a nonparasitic derivative, respectively, as follows: *Ichthyomyzon bdellium – I. greeleyi*; *I. castaneus – I. gagei*; *I. unicuspis – I. fossor*. The revisionary work of Hubbs and Trautman (1937) dealt only with the adults. Lanteigne (1981) conducted a comprehensive morphological study of the larvae of the six species. Hubbs and Trautman (1937) suggested that *Ichthyomyzon* was the nearest relative of *Petromyzon* and the cladistic analysis by Gill *et al.* (2003) corroborates their sister group relationship. The type species is *Ichthyomyzon bdellium* (Jordan, 1885).

Ichthyomyzon bdellium (Jordan 1885) **Figs. 65–67**

Synonyms: ***Petromyzon bdellium*** Jordan 1885: 792 [Replacement name for ***Petromyzon argenteus*** Kirtland 1838, a name preoccupied by Bloch 1795, a synonym of ***Lampetra fluviatilis*** (Linnaeus 1758)]. According to Hubbs and Trautman (1937), Kirtland's type for *P. argenteus*, measuring 279 mm TL, has been lost; type locality: Big Miami (probably Great Miami River), Ohio River Basin, Ohio, USA)

Taxonomic Remarks: Hubbs and Trautman (1937) suggested that one adult specimen from the lower part of the Scioto River, Ohio River Basin, Ohio, might be a hybrid between *I. bdellium* and *I. unicuspis*.

FAO Names: En — Ohio Lamprey; **Fr** — Lamproie de l'Ohio

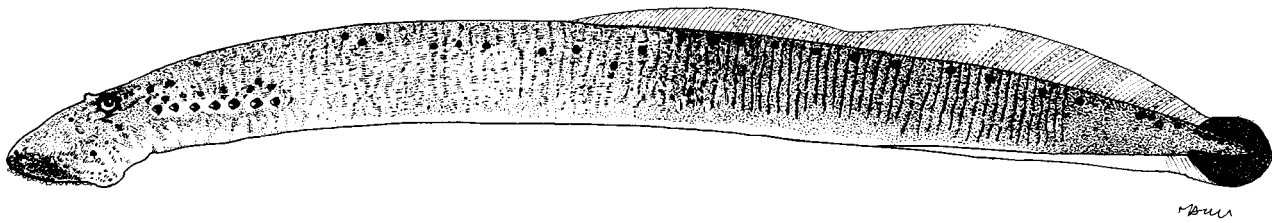

Fig. 65. Side view of *Ichthyomyzon bdellium* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, 169 mm TL. Body proportions, as percentage of TL (based on 35 specimens measuring 110–169 mm TL): prebranchial length, 5.7–8.2; branchial length, 8.8–11.8; trunk length, 53.0–62.6; tail length, 22.7–30.0. Trunk myomeres, 55–59. Pigmentation: upper lip, ++ (69% of specimens) or +++ (31%); subocular, – (6%), + (6%) or ++ (89%); upper branchial, +++ (100%); caudal fin, ++ (86%) or +++ (14%). Lateral line neuromasts darkly pigmented at least by 162 mm TL. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: 137 mm TL.
Adults: 117–279 mm TL. Body proportions, as percentage of TL (based on 51 specimens measuring 125–259 mm TL): prebranchial length, 10.4–14.0; branchial length, 7.6–10.6 [as high as 10.7 according to Hubbs and Trautman (1937)]; trunk length, 47.3–54.3; tail length, 25.1–31.2 [as low as 21.4 according to Hubbs and Trautman (1937)]; eye length, 1.1-1.8 [as low as 0.6 according to Hubbs and Trautman (1937)]; disc length, 6.9–9.5 [as low as 6.2 according to Hubbs and Trautman (1937)]. The urogenital papilla length, as a percentage of branchial length, in ten spawning males measuring 117–247 mm TL, 8.7–16.0. Trunk myomeres, 53–62. Dentition: supraoral lamina, 2–3 teeth (if 3, the median one shortest); infraoral lamina, 5–11 teeth; typically 4 endolateral teeth on each side, but 5 teeth also occur; 7–10, mode

of 8, bicuspid endolaterals in total, the other endolaterals, if any, unicuspid; 3–4 rows of anterials, usually 3; first row of anterials, 3 teeth, all unicuspid; 4–8 rows of exolaterals on each side, usually 6; 2 rows of posterials; first row of posterials, 8–9, all unicuspid; transverse lingual lamina moderately to strongly w–shaped, with numerous cusps; longitudinal lingual laminae, number of teeth unrecorded. Velar tentacles, 2–3, smooth. Body coloration (live), slate gray dorsal aspect and silvery gray lateral and ventral aspects. Lateral line neuromasts darkly pigmented, although they may be unpigmented in recently transformed adults. Caudal fin pigmentation, +++. Caudal fin shape, rounded. Oral fimbriae, 103–144. Oral papillae, 20–32.

Habitat and Biology: Freshwater. Ammocoetes and spawning adults inhabit brooks and small rivers, while feeding adults inhabit medium–sized to large rivers.
Adults are parasitic on fishes (introduced *Cyprinus carpio* and native *Moxostoma carinatum*, *M. erythrurum*, *Sander vitreus*).

Geographic Distribution (Fig. 67): USA: Wabash River Basin, Illinois and Indiana; Ohio River Basin, Kentucky, Ohio, Pennsylvania, New York, and West Virginia; Tennessee–Cumberland River Basin, Alabama, Kentucky, North Carolina, Tennessee, and Virginia.

Interest to Fisheries: None

References: Daniels *et al.* (2006), Hubbs and Trautman (1937), Jordan (1885), Khidir and Renaud (2003), Kirtland (1838, 1840), Kott *et al.* (1988), Lanteigne (1981), Vladykov and Kott (1976d)

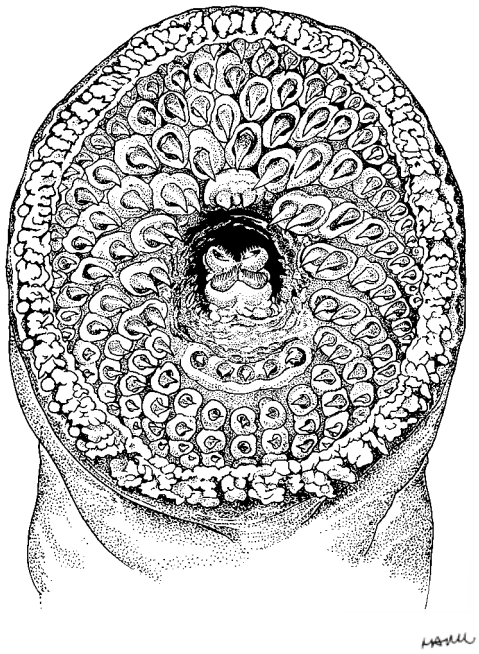

Fig. 66. Oral disc of *Ichthyomyzon bdellium*. After a drawing by Paul I. Voevodine.

Fig. 67. Geographic distribution of *Ichthyomyzon bdellium*.

Ichthyomyzon castaneus Girard 1858 — Figs. 68–70

Synonyms: ***Ichthyomyzon castaneus*** Girard 1858: 381 [holotype: male, 248 mm TL, USNM 979; type locality: Galena, Minnesota, USA, but Hubbs and Trautman (1937) believe the state to be Illinois rather than Minnesota]; ***Ichthyomyzon hirudo*** Girard, 1858: 382 (holotype: unsexed adult, 125 mm TL, USNM 980; type locality: Arkansas River, Fort Smith, Arkansas, USA)

Taxonomic Remarks: Hubbs and Trautman (1937) suggested that one adult specimen from Green Bay, near Gladstone, Lake Michigan Basin, might be a hybrid between *I. castaneus* and *I. unicuspis* and Starrett *et al.* (1960) suggested that an adult specimen from the Mississippi River, at Moline, Illinois might be a hybrid between *I. castaneus* and *I. unicuspis*.

FAO Names: En — Chestnut Lamprey, Western Lamprey (The latter name was proposed by Hubbs and Trautman (1937), but it was rejected by Chute *et al.* (1948) in favor of the former name.); **Fr** — Lamproie brune

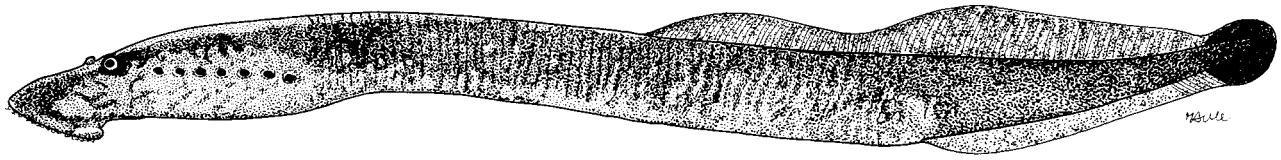

Fig. 68. Side view of *Ichthyomyzon castaneus*. After a photograph by William Pflieger [adult].

Diagnostic Features: Ammocoetes: Maximum size attained, 165 mm TL. Body proportions, as percentage of TL (based on 22 specimens measuring 75–165 mm TL): prebranchial length, 6.4–8.3; branchial length, 8.9–12.4; trunk length, 52.0–56.6; tail length, 25.0–30.3. Trunk myomeres, 50–56. Pigmentation: upper lip, ++ (50% of specimens) or +++ (50%); subocular, + (4%), ++ (77%) or +++ (18%); upper branchial, +++ (100%); caudal fin, ++ (96%) or +++ (4%). Lateral line neuromasts darkly pigmented at least by 94 mm TL. Caudal fin shape, rounded.

Metamorphosing Ammocoetes: 94–165 mm TL.

Adults: 85–363 mm TL. Body proportions, as percentage of TL (based on 36 specimens measuring 89–261 mm TL): prebranchial length, 11.5–15.5; branchial length, 8.4–10.3 [as high as 11.4 according to Hubbs and Trautman (1937) and a range of 7.3–12.6 according to Starrett *et al.* (1960)]; trunk length, 44.4–52.9; tail length, 23.9–34.4; eye length, 0.8–2.4; disc length, 8.5–11.6 [as low as 5.4 according to Starrett *et al.* (1960) and 6.3 according to Hubbs and Trautman (1937)]. The urogenital papilla length, as a percentage of branchial length, in a spawning male 183 mm TL, 5.3. Trunk myomeres, 49–56 [as high as 58 according to Starrett *et al.* (1960)]. Dentition: supraoral lamina, 1–4 teeth (as high as 5 according to Starrett *et al.* (1960)], usually 2–3; infraoral lamina, 6–11 teeth [as high as 13 according to Starrett *et al.* (1960)]; typically 4 endolateral teeth on each side, but 5 teeth also occur; 1–8, mode of 6, bicuspid endolaterals in total, the other endolaterals, if any, unicuspid; 2–4 rows of anterials [as high as 5 according to Starrett *et al.* (1960)], usually 4; first row of anterials, 3 teeth; 4–9 rows of exolaterals on each side [as high as 10 according to Starrett *et al.* (1960)], usually 6–7; 2–3 rows of posterials; first row of posterials, 8–11 usually unicuspid teeth, but one lateralmost may be bicuspid; crest of transverse lingual lamina variable, linear or weakly w–shaped to rarely strongly w–shaped, with numerous cusps, the median one not enlarged; longitudinal lingual laminae number of teeth unrecorded. Additonally, one accessory tooth is occasionally developed inside the ring formed by the supraoral and infraoral laminae and the endolateral teeth. Velar tentacles, 2, smooth. Body coloration (preserved) in adults grading from darker on the upper surface to paler on the lower surface; lateral aspects sometimes mottled; spent adults blue–black.

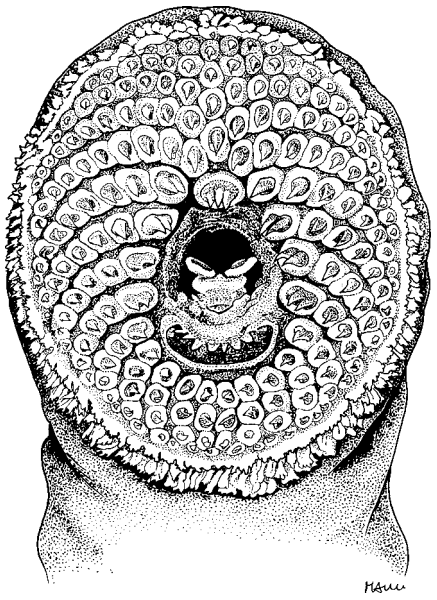

Fig. 69. Oral disc of *Ichthyomyzon castaneus*. After a drawing by Paul I. Voevodine [167 mm TL, NMC (= CMNFI) 1996–19, Sac River, Missouri, USA, 20–23 May 1951].

Lateral line neuromasts darkly pigmented beginning around 150 mm TL. Caudal fin pigmentation, +++. Caudal fin shape, rounded. Oral fimbriae, 90–126. Oral papillae, 15–30.

Habitat and Biology: Freshwater. Ammocoetes more commonly found in firm, relatively stable, sand–silt substrate, in areas with current. Adults occur in still to swift water, clear to brown–tinged, over rocky and weedy substrates, to a maximum depth of 20 m. The usual habitat is large to medium–sized rivers with summer flows 0.8–31 m^3/s and summer water temperatures 15.5–22 °C. It can also occur in small to large lakes. Generally associated with warmwater habitats and tolerant of variation in terms of discharge, water temperature, and substrate. Spawning adults only found in streams. Metamorphosis occurs in October, in Michigan. Adults parasitic on fishes (introduced *Cyprinus carpio* and native *Catostomus commersonii*, *Ictiobus* sp., *Moxostoma* sp., *Esox lucius*, *Salvelinus fontinalis*). Reported scavenging on *Catostomus* sp. In Manitoba, spawning behavior has been observed on 11–12 June at a water temperature of 16.5 °C and current velocity about 1 m/s. In Michigan, the spawning period is from 28 May to 25 June, at water temperatures between 15.6–22.2 °C, with peak spawning activity in early June. Nests (up to 6.2 m X 1 m X 0.05 m) are built with stones 3.5–5 cm in diameter in streams having 6.5–43 m width, 38–90 cm depth, and 1.1–54 m^3/s flow. Up to four spawning lampreys have been found in a nest in Michigan and about 50 in Manitoba. Eggs are elliptical with long axis 0.64 mm and short axis 0.56 mm on average. Eggs are preyed upon by *Luxilus cornutus*. There are reported occurrences in Michigan of communal spawning of Chestnut Lamprey with Sea Lamprey (Pine, Platte, and Muskegon rivers) and of Chestnut Lamprey with Sea Lamprey and American Brook Lamprey (Betsie River).

Geographic Distribution (Fig. 70): Canada and USA: Qu'Appelle River, Saskatchewan; lakes Manitoba and Winnipeg, Assiniboine, Rat, and Red rivers, Manitoba; Lake of the Woods, Chippewa, Mad, and St. Lawrence rivers, Ontario; Brewery Creek and St. Lawrence River, Québec; Red River of the North, North Dakota and Minnesota; Lake Michigan Basin, Wisconsin, Michigan (Betsie, Pine, Platte, and Muskegon rivers) and Indiana; Lake Huron Basin, Michigan; Mississippi River Basin, Minnesota, Wisconsin, Iowa, Illinois, Indiana, Kentucky, Tennessee, Alabama, Kansas, Missouri (Sac River), Oklahoma, Texas, Arkansas (Arkansas River), Mississippi, and Louisiana; Trinity River Basin, Texas; Sabine River Basin, Texas; Bogue Chitto River Basin, Louisiana; Pearl River Basin, Mississippi; Mobile River Basin, Mississippi and Alabama; Alabama River Basin, Georgia.

Fig. 70. Geographic distribution of *Ichthyomyzon castaneus*.

Interest to Fisheries: In the Laurentian Great Lakes Basin, it has presumably been negatively affected by control measures directed towards *Petromyzon marinus*, except for the chemosterilization of males which affects only the latter species (see that particular species' account).

References: Case (1970), Chute *et al.* (1948), Cochran *et al.* (2003), Girard (1858), Hall (1963), Hubbs and Trautman (1937), Khidir and Renaud (2003), Kott *et al.* (1988), Lanteigne (1981), Mayden *et al.* (1989), Moore and Kernodle (1965), Morman (1979), Neave (2004), Renaud and de Ville (2000), Renaud *et al.* (1996), Starrett *et al.* (1960), Vladykov and Kott (1976d)

Ichthyomyzon fossor Reighard and Cummins 1916 — Figs. 71–73

Synonyms: ***Ichthyomyzon fossor*** Reighard and Cummins 1916: 1–3, 5 (table), pl. 1, fig. 1, pl. 2, figs. 1–2 (holotype: male, 121 mm TL, UMMZ 107045, formerly UMMZ 48377; type locality: Mill Creek, Huron River Basin, Lake Erie Basin, west of Ann Arbor, Washtenaw Co., Michigan, USA)

FAO Names: En — Northern Brook Lamprey; **Fr** — Lamproie du nord, lamproie de ruisseau septentrionale

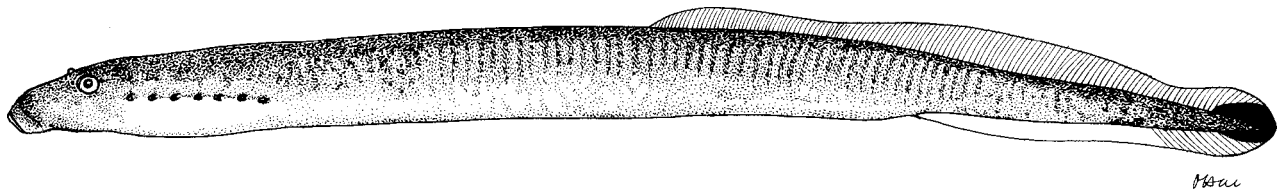

Fig. 71. Side view of *Ichthyomyzon fossor*. After a photograph by John Lyons [adult].

Diagnostic Features: Ammocoetes: Maximum size attained should be at least 182 mm TL judging by the size of the metamorphosing ammocoetes. Body proportions, as percentage of TL (based on 73 specimens measuring 68–167 mm TL): prebranchial length, 6.3–9.6; branchial length, 9.9–13.4; trunk length, 48.3–55.6; tail length, 24.0-31.9. Trunk myomeres, 48–53. Pigmentation: upper lip, ++ (77% of specimens) or +++ (23%); subocular, + (22), ++ (74%) or +++ (4%); upper branchial, ++ (8%) or +++ (92%); lower branchial – (100%); caudal fin, + (30%), ++ (67%) or +++ (3%). Lateral line neuromasts unpigmented. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: 84–182 mm TL.
Adults: 86–166 mm TL. Body proportions, as percentage of TL (based on 59 specimens measuring 98–158 mm TL): prebranchial length, 7.4–9.9; branchial length, 8.7–11.3 [as high as 11.9 according to Hubbs and Trautman (1937)]; trunk length, 46.7–54.6; tail length, 27.7–33.7; eye length, 1.1–2.0 [as low as 1.0 according to Hubbs and Trautman (1937)]; disc length, 4.0–6.4 [as low as 3.6 according to Hubbs and Trautman (1937)]. The urogenital papilla length, as a percentage of branchial length, in 25 spawning males measuring 99–149.5 mm TL, 6.7–21.7. Trunk myomeres, 47–58. Dentition: supraoral lamina, 1–4 unicuspid teeth, usually 2; infraoral lamina, 6–11 teeth, usually unicuspid but one may be bicuspid; 4 endolateral teeth on each side; 0–1, strong mode of 0, bicuspid endolaterals in total, the other endolaterals unicuspid; 1–3 rows of anterials; first row of anterials, 3 unicuspid teeth; 1–5 rows of exolaterals on each side, usually 3–4; 2–3 rows of posterials; first row of posterials, 10–11 unicuspid teeth; crest of transverse lingual lamina strongly w–shaped and with either indistinct or about 20 small cusps, the median one not enlarged; longitudinal lingual laminae with 17 cusps each. Marginal membrane vestigial. A small gular pouch is present in both males and females. Velar tentacles, 1–2, smooth. Body coloration (preserved) in adults darker (grayish brown) on the dorsal and upper lateral aspects and lighter (pale gray or silvery white) on the lower lateral and ventral aspects, giving a distinctly bicolored appearance. Lateral line neuromasts unpigmented. Caudal fin pigmentation, ++ or +++. Caudal fin shape, rounded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

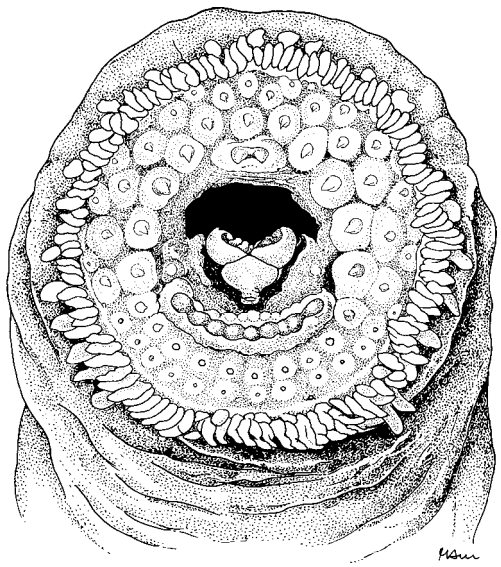

Fig. 72. Oral disc of *Ichthyomyzon fossor*. After a drawing by Paul I. Voevodine.

Habitat and Biology: Freshwater. Generally associated with warmwater habitats and tolerant of variation in terms of discharge, water temperature, and substrate. Mainly inhabits warmwater, isolated segments of moderate–sized to large streams with summer flows 0.03–31 m^3/s, summer water temperatures 14–25.6 °C, and predominant substrates being either sand or sand with gravel.
Metamorphosis occurs in late August to September, in Michigan and extends to early October in Québec. Adults nonparasitic. Adults live less than 6 months. In Michigan, the spawning period is from 13 May to 6 July, at water temperatures

between 12.8–23.3 °C, with peak spawning activity in late May to mid–June. In Québec, spawning occurs in May, at water temperatures between 12.8–17.2 °C, peaking at temperatures between 13.3–15.6 °C. Nests are usually in the open and are poorly defined, but have also been found downstream of large stones 18–36 cm in diameter, or on a patch of gravel downstream of a submerged log. The nests are found in streams having 3.5–8 m width, 10–61 cm depth, and 0.1–0.6 m^3/s flow. Up to 13 spawning lampreys have been found in a nest. There are reported occurrences in Michigan of communal spawning of Northern Brook Lamprey with Silver Lamprey (Pine River), and of Northern Brook Lamprey with Sea Lamprey (Devils River). Fecundity, 1,200 eggs/female. During spawning, adults preyed upon by *Ambloplites rupestris*.

Geographic Distribution (Fig. 73): Canada and USA: Lake Winnipeg Basin, Manitoba; Lake Superior Basin, Ontario, Michigan, and Wisconsin; Lake Michigan Basin, Indiana, Michigan, and Wisconsin; Lake Huron Basin, Ontario and Michigan (Devils and Pine rivers); Lake Erie Basin, Ontario, Michigan, New York, Ohio, and Pennsylvania; Mississippi River Basin, Illinois, Kentucky, Missouri, Ohio, and Wisconsin; Gatineau River and St. Lawrence River Basin, Québec.

Fig. 73. Geographic distribution of *Ichthyomyzon fossor*.

Interest to Fisheries: In the Laurentian Great Lakes Basin, it has been negatively affected by control measures directed towards *Petromyzon marinus*, except for the chemosterilization of males, which affects only the latter species (see that particular species' account) (Schuldt and Goold, 1980). Vladykov (1949) reported that in the province of Québec, Canada, fishermen use ammocoetes as bait for sportfishes.

References: Comtois *et al.* (2004), Hubbs and Trautman (1937), Jyrkkanen and Wright (1979), Kott (1971), Kott *et al.* (1988), Lanteigne (1981, 1988), Leach (1939, 1940), Morman (1979), Neave (2004), Reighard and Cummins (1916), Schuldt and Goold (1980), Vladykov (1949), Vladykov and Kott (1976d, 1979c)

Ichthyomyzon gagei Hubbs and Trautman 1937

Figs. 74–76

Synonyms: ***Ichthyomyzon gagei*** Hubbs and Trautman 1937: 80, 82–86, pl. I, fig. E, pl. II, fig. F (holotype: male in spawning condition, 103 mm TL, UMMZ 107042; type locality: brook, 0.4 km south of Dry Prong, Grant Parish, Louisiana, USA; presumably a secondary tributary to Little River, Red River Basin, Louisiana)

FAO Names: En — Southern Brook Lamprey; **Fr** — Lamproie de ruisseau méridionale

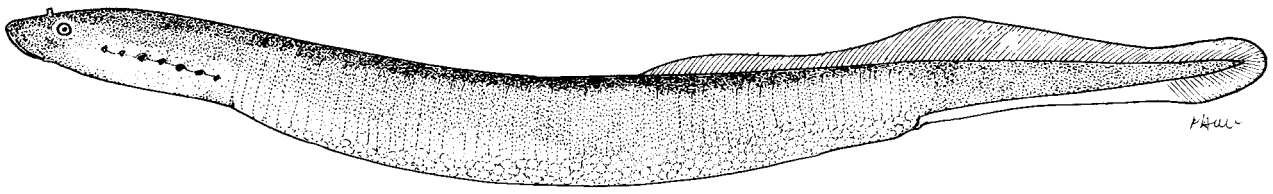

Fig. 74. Side view of *Ichthyomyzon gagei*. After a photograph by John Brill [adult female, from Louisiana].

Diagnostic Features: Ammocoetes: Maximum size attained, 150 mm TL. Body proportions, as percentage of TL (based on 95 specimens measuring 56–150 mm TL): prebranchial length, 5.9–9.3; branchial length, 10.1–13.8; trunk length, 50.5–57.7; tail length, 24.2–31.2. Trunk myomeres, 49–56, with a strong mode of 52. Pigmentation: upper lip, ++ (93% of specimens) or +++ (7%); subocular, – (19%), + (70%) or ++ (12%); upper branchial, +++ (100%); caudal fin, + (45%) or ++ (55%). Lateral line neuromasts darkly pigmented at least by 122 mm TL. Caudal fin shape unrecorded.
Metamorphosing Ammocoetes: lengths unrecorded.

Adults: 86–129 mm TL. Body proportions, as percentage of TL (based on 35 specimens measuring 86–129 mm TL): prebranchial length, 8.3–11.2; branchial length, 8.3–11.1; trunk length, 47.0–56.0; tail length, 25.6–33.3; eye length, 1.3–2.1 [as low as 1.1 according to Hubbs and Trautman (1937)]; disc length, 3.9–6.5 [as low as 3.8 according to Hubbs and Trautman (1937)]. The urogenital papilla length, as a percentage of branchial length, in six spawning males measuring 92–111 mm TL, 22.7–33.3. Trunk myomeres, 50–56, with a strong mode at 53. Dentition: supraoral lamina, 2–4 teeth, usually 2; infraoral lamina, 5–10 unicuspid teeth, usually 8–9; 4–5 endolaterals on each side; 0–8 bicuspid endolaterals in total, the other endolaterals, unicuspid; 3–4 rows of anterials; first row of anterials, 3 unicuspid teeth; 3–4 rows of exolaterals on each side; 2 rows of posterials; first row of posterials, 9 unicuspid teeth; crest of transverse lingual lamina linear to weakly w–shaped, with no apparent cusps; longitudinal lingual laminae each with undetermined number of unicuspid teeth. Velar tentacle number unrecorded. Body coloration (preserved) distinctly bicolored, with the dorsal aspect dark and the ventral aspect light. Lateral line neuromasts darkly pigmented. Caudal fin pigmentation unrecorded. Caudal fin shape, rounded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater. Inhabits creeks and small rivers.
Adults nonparasitic. Average fecundities varied from 713–2,448 eggs/female among 19 localities across the distributional range.

Geographic Distribution (Fig. 76): USA: Missouri River Basin, Missouri; Lower Mississippi River Basin, Mississippi; Arkansas–Red–White River Basin, Arkansas, Louisiana, Missouri, and Oklahoma; Tennessee–Cumberland River Basin, Alabama, Kentucky [presumed extirpated according to the Kentucky State Nature Preserves Commission (2004)], and Tennessee; Eastern Gulf of Mexico drainage, Alabama (Choctafaula Creek), Georgia, Florida, and Mississippi; Western Gulf of Mexico drainage, Louisiana and Texas.

Interest to Fisheries: None

References: Beamish *et al.* (1994), Hubbs and Trautman (1937), Kentucky State Nature Preserves Commission (2004), Kott *et al.* (1988), Lanteigne (1981)

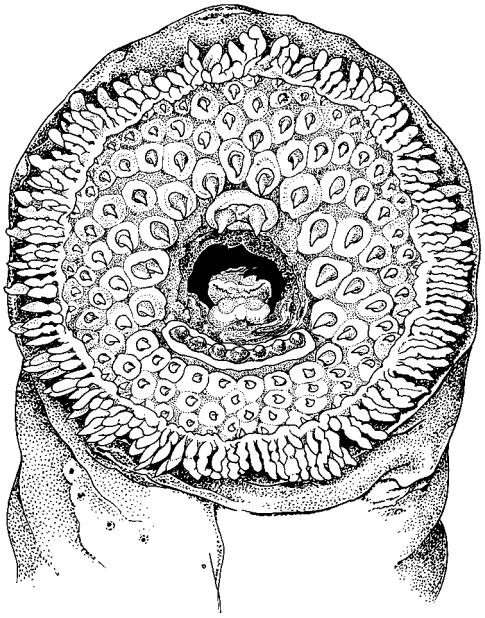

Fig. 75. Oral disc of *Ichthyomyzon gagei*. After a drawing by Paul I. Voevodine [119 mm TL, NMC (= CMNFI) 1996–22, Choctafaula Creek, Alabama, USA, 1 May 1948, J.S. Dendy and Ichthyology class].

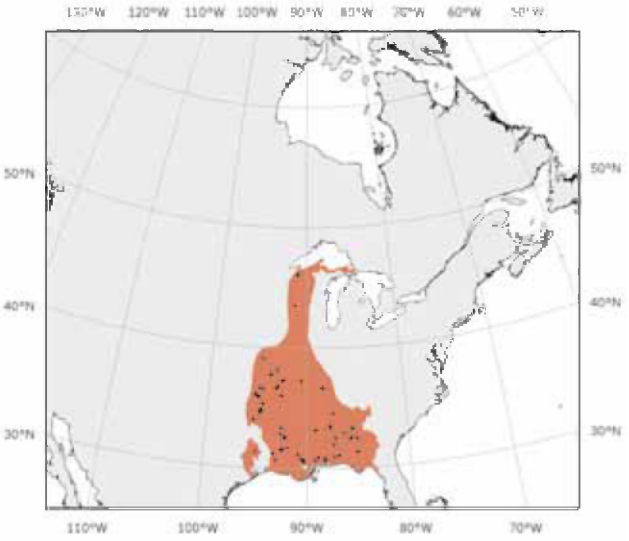

Fig. 76. Geographic distribution of *Ichthyomyzon gagei*.

Ichthyomyzon greeleyi Hubbs and Trautman 1937

Figs. 77–79

Synonyms: ***Ichthyomyzon greeleyi*** Hubbs and Trautman 1937: 93–98, pl. I, fig. F, pl. II, fig. H (holotype: female in spawning condition, 105 mm TL, UMMZ 92317; type locality: French Creek, a tributary to Allegheny River, 1.6 km east of Wattsburg, Erie County, Pennsylvania, USA); ***Ichthyomyzon hubbsi*** Raney 1952: 93–98, pl. I (holotype: adult male, 107.5 mm TL, CU 20324; type locality: Nottely River, Hiwassee River Basin, Tennessee River Basin, Union County, Georgia, USA)

FAO Names: En — Mountain Brook Lamprey, Allegheny Brook Lamprey; **Fr** — Lamproie de ruisseau d'Allegheny

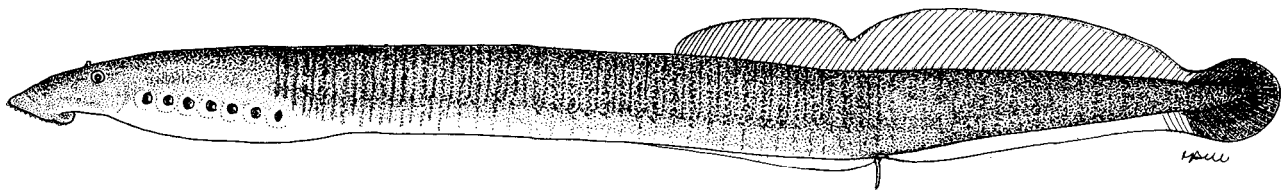

Fig. 77. Side view of *Ichthyomyzon greeleyi*, spawning male.

Diagnostic Features: Ammocoetes: Maximum size attained, 160 mm TL. Body proportions, as percentage of TL (based on 26 specimens measuring 110–160 mm TL): prebranchial length, 6.7–7.7; branchial length, 9.6–11.4; trunk length, 54.4–57.8; tail length, 24.5–29.2. Trunk myomeres, 55–60, with a strong mode of 58. Body coloration unrecorded. Pigmentation: upper lip, ++ (100% of specimens); subocular, – (8%), + (73%) or ++ (19%); upper branchial, +++ (100%); caudal fin, ++ (96%) or +++ (4%). Lateral line neuromasts darkly pigmented at least by 153 mm TL. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 105–165 mm TL. Body proportions, as percentage of TL (based on 48 specimens measuring 110–165 mm TL): prebranchial length, 8.1–11.5; branchial length, 8.9–10.6 [8.8–11.0 according to Hubbs and Trautman (1937)]; trunk length, 46.6–55.0; tail length, 25.7–33.9 [as low as 24.5 according to Hubbs and Trautman (1937)]; eye length, 0.9–1.8; disc length, 4.0–7.9. The urogenital papilla length, as a percentage of branchial length, in 23 spawning males measuring 108–156 mm TL, 16.0–28.6. Trunk myomeres, 55–62, with strong modes of 57–59. Dentition: supraoral lamina, 2–4 teeth, usually 3 (if 3, the median one shortest); infraoral lamina, 7–12 unicuspid teeth; 4–5 endolaterals on each side; 6–10 bicuspid endolaterals in total, the other endolaterals, if any, unicuspid; 4 rows of anterials; first row of anterials, 3 unicuspid teeth; 4–5 rows of exolaterals on each side; 2–3 rows of posterials; first row of posterials, 10–11 unicuspid teeth; crest of the transverse lingual lamina strongly w–shaped, with numerous cusps; longitudinal lingual laminae each with undetermined number of unicuspid teeth. Velar tentacles, 2–4, smooth. Body coloration (preserved), dark slate or brown color on the dorsal and lateral surfaces contrasting sharply with the light yellow ventral surface. Pineal region is light yellow. Spent individuals are dark blue on the back and sides and bluish white below. Lateral line neuromasts darkly pigmented at least by 143 mm TL. Caudal fin pigmentation, +++. Caudal fin shape, rounded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

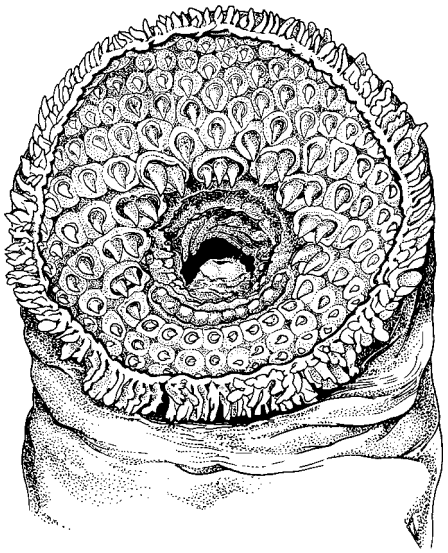

Fig. 78. Oral disc of *Ichthyomyzon greeleyi*. After a drawing by Paul I. Voevodine [128 mm TL, paratype, UMMZ 108111, Little Neshannock Creek, Ohio River Basin, Pennsylvania, USA, 26 May 1935, E.C. Raney].

Habitat and Biology: Freshwater. Found in large to small creeks.
Adults nonparasitic. Spawning period at the end of May in Pennsylvania. Spawning occurs in watercourses with swift current and large stones. Adults preyed upon by *Necturus maculosus*.

Geographic Distribution (Fig. 79): USA: Ohio River Basin, Kentucky, Ohio, Pennsylvania (French and Little Neshannock creeks), New York, and West Virginia; Tennessee–Cumberland River Basin, Alabama, Georgia (Nottely River), Kentucky, Tennessee, and Virginia.

Interest to Fisheries: None

References: Daniels *et al.* (2006), Etnier and Starnes (1993), Hubbs and Trautman (1937), Kott *et al.* (1988), Lanteigne (1981), Medland and Beamish (1987), Raney (1952), Vladykov and Kott (1976d)

Fig. 79. Geographic distribution of *Ichthyomyzon greeleyi*.

Ichthyomyzon unicuspis Hubbs and Trautman 1937

Figs. 80–82

Synonyms: ***Ichthyomyzon unicuspis*** Greene 1935: 21 [Wisconsin, nomen nudum according to Hubbs and Trautman (1937: 56)]; ***Ichthyomyzon unicuspis*** Hubbs and Trautman 1937: 53–65, pl. I, fig. A, pl. II, figs. A–B (holotype: male in spawning condition, 319 mm TL, UMMZ 107040; type locality: Swan Creek, Maumee River Basin, Toledo, Ohio, USA)

Taxonomic Remarks: Hubbs and Trautman (1937) suggested that one adult specimen from Green Bay, near Gladstone, Lake Michigan Basin, might be a hybrid between *I. unicuspis* and *I. castaneus* and another from the Scioto River, Ohio River Basin, might be a hybrid between *I. unicuspis* and *I. bdellium*. Starrett *et al.* (1960) suggested that an adult specimen from the Mississippi River, at Moline, Illinois might be a hybrid between *I. castaneus* and *I. unicuspis*.

FAO Names: En — Silver lamprey, Northern Lamprey (The latter name was proposed by Hubbs and Trautman (1937), but it was rejected by Chute *et al.* (1948) in favor of the former name.); **Fr** — Lamproie argentée

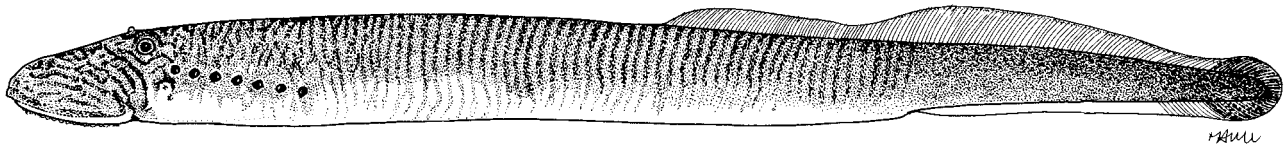

Fig. 80. Side view of *Ichthyomyzon unicuspis*. After a photograph by John Lyons [adult].

Diagnostic Features: Ammocoetes: Maximum size attained, 138 mm TL. Body proportions, as percentage of TL (based on 72 specimens measuring 73–138 mm TL): prebranchial length, 6.5–8.7; branchial length, 9.3–12.8; trunk length, 50.0–54.5; tail length, 26.2–32.6. Trunk myomeres, 48–54, with high modal counts of 51–53. Body coloration unrecorded. Pigmentation: upper lip, ++ (100% of specimens); subocular, – (36%) or + (64%); upper branchial, ++ (97%) or +++ (3%); caudal fin, + (25%) or +++ (75%). Lateral line neuromasts unpigmented. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: 91–155 mm TL.
Adults: 85–392 mm TL and wet weight 34–133 g for individuals 250–392 mm TL. Body proportions, as percentage of TL (based on 43 specimens measuring 85–270 mm TL): prebranchial length, 11.4–15.9; branchial length, 8.7–10.8 [8.0–12.2 according to Hubbs and Trautman (1937)]; trunk length, 42.4–49.2; tail length, 26.8–32.6 [25.8–35.0 according to Hubbs and Trautman (1937)]; eye length, 1.1–2.5 [as low as 0.7 according to Hubbs and Trautman (1937)]; disc length, 7.9–12.4 [as low as 5.9 according to Hubbs and Trautman (1937)]. The urogenital papilla length, as a percentage of branchial length, in

seven spawning males measuring 185–279 mm TL, 5.3–7.7. Trunk myomeres, 47–55 [up to 57 according to Starrett *et al.* (1960)]. Dentition: supraoral lamina, 1–4 unicuspid teeth, but usually 2; infraoral lamina, 5–12 unicuspid teeth, usually 7–8; 3–6 endolaterals on each side, usually 4; endolateral formula, typically 1–1–1–1; 0–2 bicuspid endolaterals in total, usually 0, the other endolaterals unicuspid; 2–4 rows of anterials; first row of anterials, 1–3 unicuspid teeth; 5–8 rows of exolaterals on each side [as few as 4 according to Starrett *et al.* (1960)]; 3 rows of posterials; first row of posterials, 8–10 unicuspid teeth; crest of transverse lingual lamina moderately to strongly w–shaped, rarely weakly w–shaped, with about 35 short unicuspid teeth, the median one not enlarged; longitudinal lingual laminae each with 33-40 unicuspid teeth. Well–developed marginal membrane. Velar tentacles, 2–6, smooth. Body coloration (live) a light yellow tan and (preserved) usually yellowish, darker on the dorsal surface, gradually becoming lighter towards the ventral surface with mottling of these shades on the sides; occasionally grayish. Spent individuals blue–back. Lateral line neuromasts darkly pigmented at least by 146 mm TL. Caudal fin pigmentation, +++. Caudal fin shape, rounded. Oral fimbriae, 81–108. Oral papillae, 15–25.

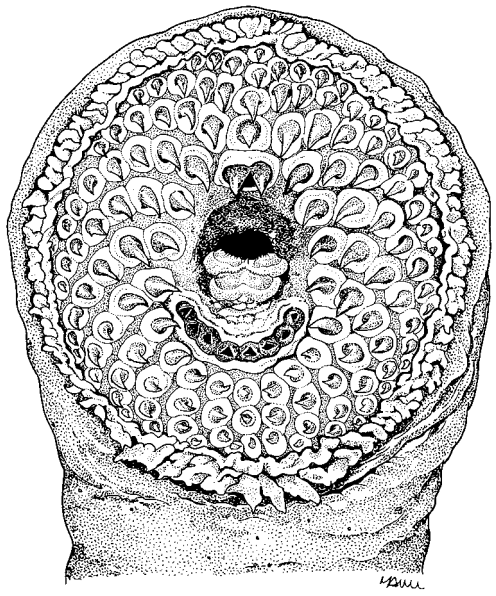

Fig. 81. Oral disc of *Ichthyomyzon unicuspis*. After a drawing by Paul I. Voevodine [male, 177.5 mm TL, NMC (= CMNFI) 1986–1028, Manitoba, Canada].

Habitat and Biology: Freshwater. Generally associated with warmwater habitats and tolerant of variation in terms of discharge (summer flows 0.06–34 m^3/s), water temperature, and substrate. Occurs principally in the mainstems of large streams. It can also occur in small to large lakes. In Lake Huron, has been collected at depths between 26 and 31 m. Spawning adults are found in streams or lakes. Metamorphosis occurs in November, in Michigan. Duration of adult stage 12–13 months in Québec. Adults parasitic on fishes (*Acipenser fulvescens*, *A. oxyrinchus*, *Polyodon spathula*, *Catostomus catostomus*, *C. commersonii*, *Ictiobus niger*, *Ameiurus nebulosus*, *Esox lucius*, *E. masquinongy*, *Coregonus clupeaformis*, *Salvelinus namaycush*, *Morone saxatilis*, *Ambloplites rupestris*). Up to 61 individuals were attached to a single *Acipenser fulvescens*. In Ohio, the spawning period is from 26 April to 2 June. In Michigan, the spawning period is from 23 May to 26 June, at water temperatures between 12.8–22.8 °C, with peak spawning activity in early June. Nests are built in streams having 3.5–30 m width, 10-61 cm depth, and 0.1–4.2 m^3/s flow. A nest can be 30–cm in diameter, open on the downstream side, 8–15 cm deep, and it can also contain sticks and twigs. Up to ten spawning lampreys have been found in a nest. Fecundity, 10,800 eggs/female. Spawning occurs during daylight hours and into dusk. There are reported occurrences in Michigan of communal spawning of Silver Lamprey with Northern Brook Lamprey (Pine River), of Silver Lamprey with Sea Lamprey (Carp Lake, Devils, East Au Gres, and Rifle rivers), and of Silver Lamprey, with Sea Lamprey, and American Brook Lamprey (Carp Lake River).

Geographic Distribution (Fig. 82): Canada and USA: Hudson Bay Basin, Manitoba, Ontario, and Minnesota; Lake Superior Basin, Ontario, Michigan, and Wisconsin; Lake Michigan Basin, Illinois, Michigan (Carp Lake River), and Wisconsin; Lake Huron Basin, Ontario and Michigan (Devils, East Au Gres, Pine, and Rifle rivers); Lake St. Clair, Ontario; Detroit and St. Clair rivers, Michigan; Lake Erie Basin, Ontario, Michigan, New York, and Ohio (Swan Creek); Lake Ontario Basin, Ontario and New York; St. Lawrence River Basin, Ontario, Québec, New York, and Vermont; Ohio River Basin, Kentucky, Illinois, Indiana, Ohio, Pennsylvania, and West Virginia; Missouri River Basin, Missouri, Nebraska, and South Dakota; Upper Mississippi River Basin, Illinois, Iowa, Minnesota, Missouri, and Wisconsin; Tennessee–Cumberland River Basin, Tennessee; Lower Mississippi River Basin, Mississippi.

Fig. 82. Geographic distribution of *Ichthyomyzon unicuspis*.

Interest to Fisheries: In the Laurentian Great Lakes Basin, it has been negatively affected by control measures directed towards *Petromyzon marinus*, except for the chemosterilization of males, which affects only the latter species (see that particular species' account) (Schuldt and Goold 1980).

References: Chute *et al.* (1948), Cochran and Marks (1995), Cochran *et al.* (2003), Comtois *et al.* (2004), Choudhury and Dick (1993), Greene (1935), Hubbs and Trautman (1937), Khidir and Renaud (2003), Kott (1971), Kott *et al.* (1988), Lanteigne (1981), Manion and Hanson (1980), Morman (1979), Neave (2004), Renaud (2002), Roy (1973), Schuldt and Goold (1980), Starrett *et al.* (1960), Vladykov (1949, 1985b), Vladykov and Kott (1976d), Vladykov and Roy (1948).

Genus *Lampetra* Bonnaterre 1788

Synonyms: ***Lampetra*** Bonnaterre 1788: li, 1

According to Rondelet (1558) the genus name is derived from the Latin lambendis petris, which means to suck rocks. This genus comprises seven species (2 parasitic and 5 nonparasitic). Three species are endemic to Eurasia (*Lampetra fluviatilis*, *L. lanceolata*, and *L. planeri*) and four are endemic to North America (*L. aepyptera*, *L. ayresii*, *L. pacifica*, and *L. richardsoni*). Two dorsal fins. Supraoral lamina with two teeth separated by a wide bridge. Labial teeth radially–arranged in a curvilinear fashion only in the anterior field. Exolaterals and posterials are absent except in *Lampetra aepyptera* where both are present and in *L. lanceolata* where one case of one posterial was recorded and *L. richardsoni* where one case of two posterials was recorded. Transverse lingual lamina u–shaped and with an enlarged median cusp. Velar tentacles with tubercles and a median tentacle is present. The type species is *Lampetra fluviatilis* (Linnaeus 1758). *L. fluviatilis* – *L. planeri* are said to constitute a paired species.

Lampetra aepyptera (Abbott 1860) **Figs. 83–85**

Synonyms: ***Ammocoetes aepyptera*** Abbott 1860: 327–328 [holotype: adult about 140 mm TL, ANSP 354; type locality: Ohio River, near Portland (not Portsmouth), Ohio, USA]; ***Lethenteron meridionale*** Vladykov, Kott, and Pharand–Coad 1975: 11–13, figs. 1–3 [holotype: adult male, 104 mm TL, NMC (= CMNFI) 1974–249; type locality: Blue Springs Creek, Tennessee River Basin, Tennessee, USA]

Taxonomic Remarks: The taxonomic position of this species is uncertain. It is provisionally placed in the genus *Lampetra* but further study may show that it should more appropriately be placed in the genus *Okkelbergia* Creaser and Hubbs 1922. It is the only species in the genus that possesses both exolateral and posterial teeth.

FAO Names: En — Least Brook Lamprey; **Fr** — Petite lamproie de ruisseau

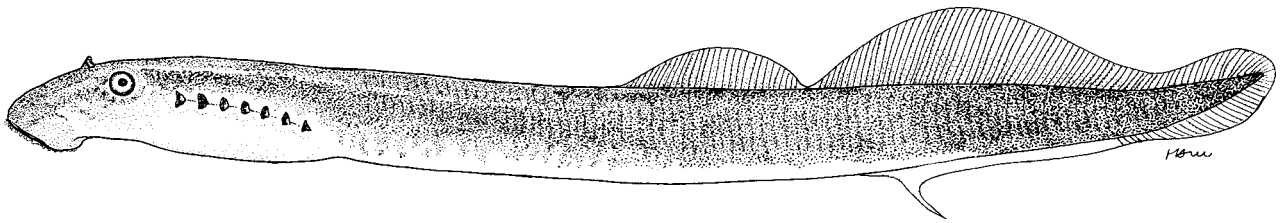

Fig. 83. Side view of *Lampetra aepyptera*, spawning male.

Diagnostic Features: Ammocoetes: Maximum size recorded, 135 mm TL, but presumably can attain greater lengths as adults have been recorded to 178 mm TL. Body proportions, as percentage of TL (based on 44 specimens measuring 100-130 mm TL): prebranchial length, 5.2 (estimated mean); branchial length, 10.8–15.4; trunk length, 50.3–56.2; tail length, 26.5–30.8. Trunk myomeres, 51–60. Body coloration unrecorded. Pigmentation: upper lip, +; cheek, +++; subocular, –; lower prebranchial, ++; upper branchial, ++; lower branchial, –; caudal fin, +; tongue precursor bulb, ++; along elastic ridge of tongue precursor, ++. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: 86–114 mm TL.

Adults: 75–178 mm TL and wet weight 0.9–3.0 g for individuals 82–120 mm TL. Body proportions, as percentage of TL (based on 166 specimens measuring 75–165 mm TL): prebranchial length, 6.9–13.0; branchial length, 8.4–12.8; trunk length, 42.8–57.3; tail length, 23.4–35.0; eye length, 0.9–2.1; disc length, 2.8–6.7. The urogenital papilla length, as a percentage of branchial length, in 71 spawning males measuring 102–146 mm TL, 23.1–60.0. Trunk myomeres, 53–62. Dentition: marginals, 63–67; supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–13 unicuspid teeth; 3–4 endolaterals on each side; endolateral formula, 2–1–2 with variations, including 1–1–1, 2–3–2 and 2–3–3; 2 rows of anterials; first row of anterials, 4–5 unicuspid teeth (some teeth may even be found on the anterior field between the supraoral lamina and the first row of anterials; see fig. 84); 1–2 row of exolaterals on each side; 0–1 row of posterials; first row of posterials, when present, may be complete (13% of individuals) or incomplete (87%) with 1–22 unicuspid teeth; transverse lingual lamina, undetermined number of unicuspid teeth, the median one of undetermined size; longitudinal lingual laminae each with an undetermined number of unicuspid teeth. Velar tentacles, 3–5, with tubercles. Body coloration (live) of spawning individuals, dorsal aspect mottled gray–brown and ventral aspect light silvery–yellow. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation, darkly pigmented, but the extent of coverage has not been reported. Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae, 12–20.

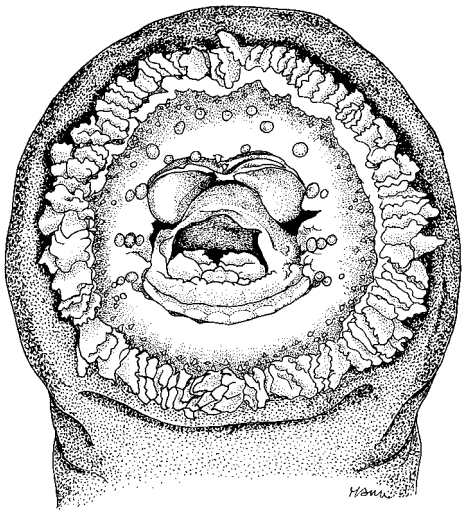

Fig. 84. Oral disc of *Lampetra aepyptera*. After a drawing by Susan Laurie–Bourque [spawning male, 130.5 mm TL, NMC (= CMNFI) 1986–818, tributary of Clear Creek, Hocking River Basin, Ohio, USA, 13 April 1975, T. Cavender].

Habitat and Biology: Freshwater, in streams and lakes. In Delaware, occurs in small streams with relatively slow current, usually 0.03 m/s or less, with water temperatures throughout the year 4.0–19.0 °C, dissolved oxygen 5.6–14.0 ppm, and pH 6.0–7.3. In Kentucky, occurs in small to medium size, clear creeks with sand–gravel substrate, either among debris (adults) or in mud banks with silt deposits (ammocoetes).

Larval period varies from 2.5 to at least 5.4 yrs. Metamorphosis in early September and maybe even mid– to late August. In Maryland, metamorphosis has been reported as late as February. Adults nonparasitic. Fecundity, 572–3,816 eggs/female and relative fecundity, 373–687 eggs/g body weight. Egg diameter, 0.66–1.36 mm. In Delaware, spawning occurs at the end of March at a water temperature of 13.8 °C, dissolved oxygen 11.6 ppm, and pH 6.6. In Maryland, spawning occurs from 10 April to 10 May when the water reaches 16 °C. Both sexes participate in nest building. Stones up to 2.5 cm in diameter are moved using their oral disc. Nests are circular or oval, 15–22 cm in diameter and about 7 cm deep. They are built in streams 4.5–6.3 m wide and 15–41 cm deep with a substrate of sand and fine gravel. From 2–15 lampreys share a nest. Up to two males will spawn with one female. Average size at hatching, 3.4 mm TL. Modal length at age 1 is 27–28 mm TL and at age 2 is 50 mm TL. Most growth occurs during the spring season, intermediate growth in summer and fall and very little during winter. In Kentucky, mean length at age 1 is 39 mm TL, at age 2 is 65 mm TL, and at age 3 is 89 mm TL.

Geographic Distribution (Fig. 85): USA: Delaware (Cheasapeake Bay Basin), Maryland (Chesapeake Bay Basin, North, Patuxent, and Potomac river basins, Lake Chambers), Virginia (Rappahannock River Basin), North Carolina (Neuse River Basin), Kentucky, Ohio (Ohio River Basin), Tennessee (Tennessee River Basin), Georgia, Alabama, and Mississippi (Tombigbee and Pascagoula river basins).

Interest to Fisheries: None

References: Abbott (1860), Cook (1952), Creaser and Hubbs (1922), Kott *et al.* (1988), Raney (1941), Rohde *et al.* (1976), Seversmith (1953), Vladykov (1950), Vladykov and Kott (1976d, 1979c), Vladykov *et al.* (1975), Walsh and Burr (1981)

Fig. 85. Geographic distribution of *Lampetra aepyptera*.

Lampetra ayresii (Günther 1870) Figs. 86–88

Synonyms: ***Petromyzon plumbeus*** Ayres 1855: 2 (preoccupied by *P. Plumbeus* Shaw 1804: 263. Ayres's holotype, an adult 121 mm TL, USNM 977, was destroyed; type locality: San Francisco Bay, California, USA); ***?Ammocoetes cibarius*** Girard 1858: 383–384 (holotype: metamorphosing ammocoete of 102 mm TL originally but with tail now missing, USNM 981, recatalogued as USNM 6176; type locality: Fort Steilacoom, Puget Sound, Washington); ***Petromyzon ayresii*** Günther 1870: 505 (Replacement name for *P. plumbeus* Ayres 1855. Neotype: female, 147 mm TL, CAS 25935; San Francisco Bay at Point Richmond, 35°54'35"N 122°23'12"W, Contra Costa County, California, USA)

Taxonomic Remarks: The specific identity of *Ammocoetes cibarius* Girard 1858 cannot be established with certainty and could be either *Lampetra ayresii* or *Entosphenus tridentatus* (see that species' account). The population from Morrison Creek, British Columbia and named *Lampetra richardsoni* var. *marifuga* (meaning to shun the sea) by Beamish and Withler (1986) fed parasitically under laboratory conditions. Another interpretation would be therefore to call it a permanent freshwater resident population of *L. ayresii* as suggested by Renaud (1997) and as it is treated here.

FAO Names: En — River Lamprey (Although this is the official common name following Nelson *et al.* (2004), it should really be the Western River Lamprey, first proposed by Miller and Lea (1972). This would distinguish it from the European River Lamprey, *Lampetra fluviatilis*, a Linnaean species that certainly has a greater claim, by virtue of original usage, to being called River Lamprey than the latter does); **Fr** — Lamproie de rivière de l'ouest

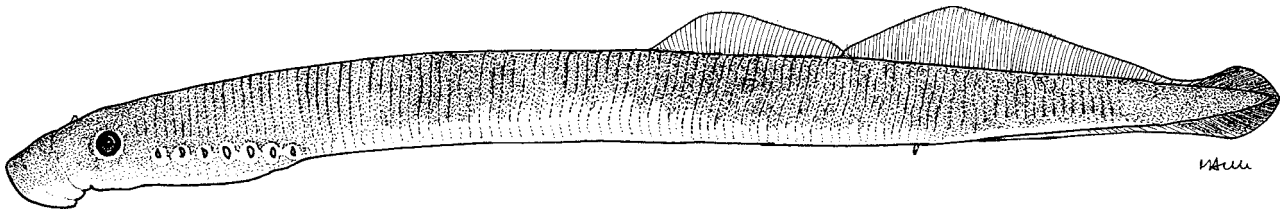

Fig. 86. Side view of *Lampetra ayresii*, spawning male, 194 mm TL, Sacramento River, near Meridian, Sutter County, California, USA, 28–29 April 1954, E.D. Bailey. After Vladykov and Follett (1958).

Diagnostic Features: Ammocoetes: Maximum size attained, 172 mm TL. Body proportions, as percentage of TL (based on 12 specimens measuring 102–172 mm TL): prebranchial length, 5.9–8.3; branchial length, 9.6–11.8; trunk length, 51.7–55.0; tail length, 26.5–28.9. Trunk myomeres, 65–70. Body coloration unrecorded. Pigmentation: upper lip, – (100% of specimens); subocular, – (100%); upper prebranchial – (100%); lower prebranchial, – (100%); upper branchial, ++ (100%); caudal fin, ++ (100%); tongue precursor bulb, – (100%); along elastic ridge of tongue precursor, – (100%). Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 114–311 mm TL. Body wet weight in individuals 175–230 mm TL, 20–24 g. Body proportions, as percentage of TL (based on 68 specimens measuring 117–311 mm TL): prebranchial length, 10.9–14.1; branchial length, 7.8–11.8; trunk length, 45.9–55.9; tail length, 24.4–29.5; eye length, 2.3–4.3; disc length, 4.7–7.2. The urogenital papilla length, as a percentage of branchial length, in two spawning males measuring 174–187 mm TL, 10.3–12.5. Trunk myomeres, 60–71. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 7–10 teeth, the lateralmost often bicuspid, the others unicuspid; 3 endolaterals on each side; endolateral formula, typically 2–3–2, very rarely 2–2–2; 3 rows of anterials; first row of anterials, 4 unicuspid teeth; exolaterals absent; posterials absent; transverse lingual lamina, 12–17 unicuspid teeth, the median one greatly enlarged; longitudinal lingual laminae each with 9–12 unicuspid teeth. Velar tentacles, 3–5, with tubercles. Body

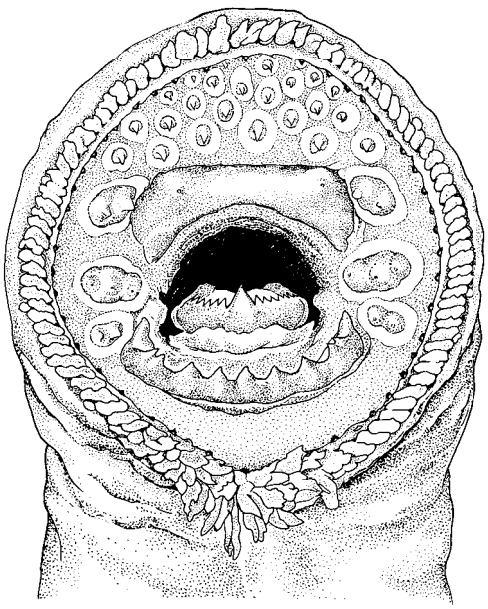

Fig. 87. Oral disc of *Lampetra ayresii*. After a drawing by Paul I. Voevodine [female, 147 mm TL, neotype, CAS 25935, San Francisco Bay at Point Richmond, California, USA, 7 Feb. 1954, W.I. Follett and B. Yacorzynski].

coloration in marine waters (live), lead gray on dorsal and upper lateral aspects, silvery on the lateral aspect, and white on the ventral aspect. Body coloration (preserved), dorsal and lateral aspects brownish gray and ventral aspect whitish. Lateral line neuromasts unpigmented. Caudal fin pigmentation, ++ or +++. Caudal fin shape, spade–like or rounded. Oral fimbriae, 88–117. Oral papillae, 12–18.

Habitat and Biology: Anadromous. A permanent freshwater resident population is believed to occur in Morrison Creek, British Columbia. In marine waters, they inhabit surface waters. In fresh waters, they occur in lakes, rivers, and creeks. Adults predatory on fishes (*Clupea pallasii*, *Oncorhynchus kisutch*, *O. nerka*, *O. tshawytscha*). They leave rivers to enter the sea in late spring or early summer, where they actively feed throughout the summer, and return to the rivers in the fall. Adults at sea are preyed upon by *Ophiodon elongatus* and in the Columbia River estuary to a small extent by Brandt's cormorant. In the Sacramento River, California, the spawning season is thought to be from late April into May. Fecundity, 11,398–37,288 eggs/female. Egg diameter, 0.6–0.7 mm.

Geographic Distribution (Fig. 88): Pacific Ocean Basin in Canada and the USA: Morrison Creek and Skeena and Fraser rivers and Strait of Georgia (British Columbia); Taku River and Lynn Canal (Alaska); Duwamish River estuary, Puyallup River, Lake Washington, and Lake Sammamish (Washington); Yaquina Bay and Columbia River (Oregon); Mill Creek, Sacramento, Middle, and San Joaquin rivers, and San Pablo and San Francisco bays (California).

Interest to Fisheries: Beamish and Williams (1976) have estimated that this lamprey kills between 60 and 600 million young *Clupea pallasii* and *Oncorhynchus* spp. per year in the Strait of Georgia. They also kill young *Oncorhynchus kisutch* and *O. nerka* in rivers and lakes, respectively.

References: Ayres (1855a), Beamish (1980, 1985), Beamish and Williams (1976), Beamish and Withler (1986), Bean (1887), Couch and Lance (2004), Günther (1870), Khidir and Renaud (2003), Kott *et al.* (1988), Miller and Lea (1972), Roos *et al.* (1973), Vladykov and Follett (1958), Vladykov and Kott (1976d)

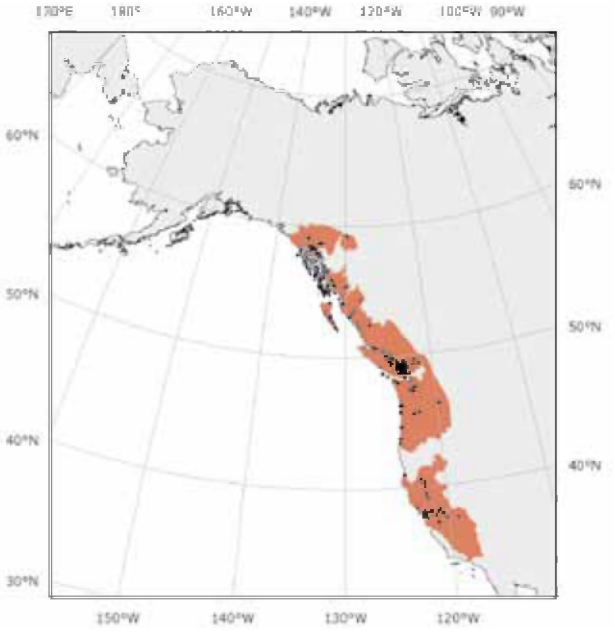

Fig. 88. Geographic distribution of *Lampetra ayresii*.

Lampetra fluviatilis (Linnaeus 1758) Figs. 89–91

Synonyms: ***Petromyzon fluviatilis*** Linnaeus 1758: 230 (type locality: European rivers); ***Petromyzon argenteus*** Bloch 1795: 74, pl. 415, fig. 2; ***Lampetra fluviatilis*** Gray 1851: 140 (new combination); ***Petromyzon Omalii*** Van Beneden 1857: 549, 551–554, figs. 1–3 [three syntypes: prespawning adults, 206.5–224.5 mm TL, MNHN 4161 (note, however, that the original description reports a length of only 160 mm); type locality: coastal waters of Belgium]; ***Lampetra opisthodon*** Gratzianow 1907: 18 (type: adult, 287 mm TL; type locality: St. Petersburg, Russian Federation)

Taxonomic Remarks: Berg (1931) suggested that this species consists of two races; a normal form (*forma typica*) and a smaller praecox form. The praecox form has been reported from the Neva River and Lake Ladoga in the Russian Federation and the Severn River in England (UK).

FAO Names: En — European River Lamprey; **Fr** — Lamproie de rivière européene, lamproie fluviatile européene
Local name: Lampern **(English);** Flußneunauge **(German)**

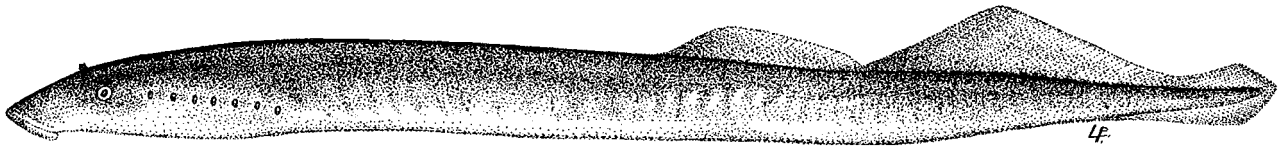

Fig. 89. Side view of *Lampetra fluviatilis* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, 145 mm TL. Body proportions, as percentage of TL (based on 20 specimens measuring 100–145 mm TL): prebranchial length, 6.8–9.3 [as low as 6.1 according to Potter and Osborne (1975)]; branchial length, 11.1–13.2; trunk length, 49.0–53.8; tail length, 25.2–28.5 [as high as 29.7 according to Potter and Osborne (1975)]. Trunk myomeres, 58–66. Body coloration unrecorded. Pigmentation: upper lip, – (100% of specimens); subocular, ++ (80%) or +++ (20%); lower prebranchial, – (90%) or + or ++ (5% each); upper branchial, + (100%); caudal fin, – or + (combined total 100%). Dark pigment is found on the tongue precursor bulb and along its elastic ridge. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: 80–130 mm TL.
Adults: 86–492 mm TL. Body wet weight in individuals 180–492 mm TL, 30–150 g. Body proportions, as percentage of TL (based on 48 specimens measuring 108–386 mm TL): prebranchial length, 10.0–12.9; branchial length, 7.9–10.8 [as high as 11.3 according to Zanandrea (1959b)]; trunk length, 46.2–54.3; tail length, 24.1–30.3; eye length, 1.4–3.1; disc length, 4.6–6.7 [as high as 7.0 according to Zanandrea (1959b)]. The urogenital papilla length, as a percentage of branchial length, in 19 spawning males measuring 197–283 mm TL, 15.9–37.5. Trunk myomeres, 58–66. Dentition: marginals, 70–95; supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–9 either all unicuspid teeth or, more frequently, the lateralmost are bicuspid and the internal ones unicuspid (Van Beneden (1857) reported 10 unicuspid teeth for *Petromyzon Omalii* but the three syntypes at the MNHN had either 5 or 7 teeth with the lateralmost in all cases bicuspid); 3 endolaterals on each side; endolateral formula, typically 2–3–2, rarely 1–3–2 or 2–3–1; 1–2 rows of anterials; first row of anterials, 4–7 unicuspid teeth; exolaterals absent; posterials absent; transverse lingual lamina, 8–18, usually 12–14, unicuspid teeth, the median one enlarged; longitudinal lingual laminae straight or parentheses–shaped and each with 9–13 unicuspid teeth. Marginal membrane present. Velar tentacles, 4–10, with tubercles; no velar wings. Body coloration in recently metamorphosed individuals silvery; in preserved upstream migrants, bluish brown or lead gray on the dorsal aspect tending towards silvery on the lateral aspects and whitish or yellowish on ventral aspect. Early upstream spawning migrants returning from the sea have a bronze sheen. Dorsal fins of maturing individuals may have a purplish tint. Iris is golden yellow. Body coloration in the landlocked population in Lake Ladoga is completely black. Lateral line neuromasts unpigmented or darkly pigmented. Caudal fin pigmentation, – in young adults and +++ in spawning individuals. Caudal fin shape, spade–like. Oral fimbriae, 84–112. Oral papillae, 11–20.

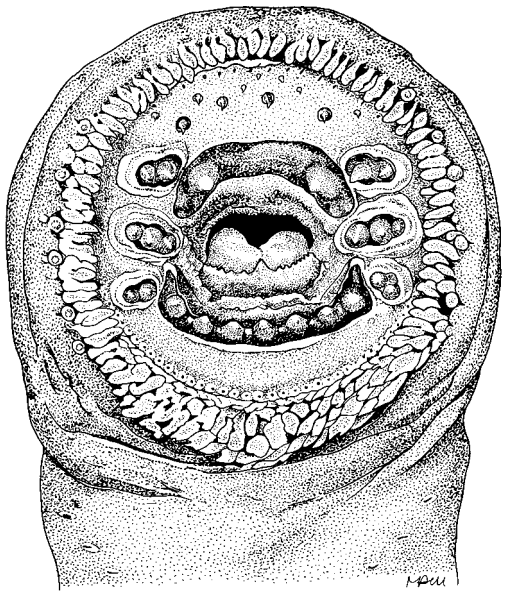

Fig. 90. Oral disc of *Lampetra fluviatilis*. After a drawing by Paul I. Voevodine [male, 295.5 mm TL (originally measured 308 mm TL), NMC (= CMNFI) 1986–1026, Severn River, England (UK), E.W. Baxter].

Habitat and Biology: Anadromous, but some populations are permanent freshwater residents (e.g. Lough Neagh, Northern Ireland (UK); Loch Lomond, Scotland (UK); lakes Ladoga and Onega, Russian Federation). In fresh waters, in rivers, brooks, and lakes.
Adults predatory on marine fishes (*Clupea harengus*, *Gadus morhua*, *Sprattus sprattus*) from the end of July to October, as well as anadromous (*Coregonus autumnalis*) and freshwater fishes (*Coregonus clupeoides*). Trematodes and cestodes have been found in the intestine of prespawning adults at sea. Spawning migration upriver (Vistula and Neman rivers) begins near the end of September in the Baltic Sea Basin. In tributaries to the Gulf of Finland (Narva, Neva, and Luga rivers), upstream spawning migrations occur twice yearly; once in summer–fall and once in spring. In the upper Rhine River, the spawning season is February to April; in England (UK) from April to May; and in the lower Neva River, Russian Federation, from early June to early July. Fecundity is highly variable and ranges from 650 to 42,500 eggs/female; 10,000–16,000 eggs/female in Lake Ladoga. Communal spawning in the same redd by *L. fluviatilis* and *L. planeri* has been reported in the River Tywi Basin, Wales (UK), in April, at a water temperature of 11 °C. Both species participated in constructing a redd about 23 cm in diameter and 5–8 cm deep, consisting of pebbles, gravel and coarse sand.

Geographic Distribution (Fig. 91): Finland, Sweden (Dalälven and Lule Alv rivers); Ireland; Northern Ireland (UK) (Lough Neagh); Scotland (UK) (Loch Lomond); Wales (UK) (River Tywi Basin); England (UK) (Bela, Crake, Severn, Teme, Thames, and Trent rivers); The Netherlands (North Sea Basin: Maas River); Belgium (North Sea Basin: Schelde River Basin: Grande Nèthe River); France (Atlantic Sea Basin: Garonne and Dordogne rivers; Mediterranean Sea Basin: Rhône River); Denmark (North Sea Basin: Varde River); Germany (North Sea Basin: Elbe and Rhine rivers); Poland (Baltic Sea Basin: Vistula River); Russian Federation (Baltic Sea Basin: Neman (shared with Lithuania), Narva (shared with Estonia), Luga,

Lemenka, and Neva rivers, lakes Ladoga and Onega); Czech Republic (Elbe River Basin: brook in the Vltava River Basin); Italy (Mediterranean Sea Basin: Arno and Tiber rivers, Gulf of Gaeta); Portugal.

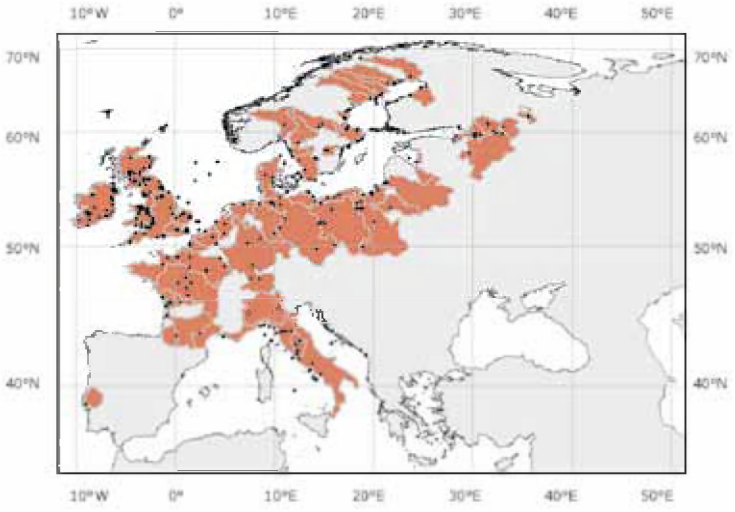

Fig. 91. Geographic distribution of *Lampetra fluviatilis*.

Interest to Fisheries: Fisheries exist in England (UK), Finland, France, and the Russian Federation. In the 19th century, up to 450,000 adults yearly were used by the English fishing fleet as bait in the fisheries for *Gadus morhua* and *Psetta maxima*. In Finland, the catch in 1983 was 2.3–2.4 million individuals (about 100 t) for a value of $800,000 US. There are reports of intoxication through eating this species (Halstead 1967). I have eaten several meals of adults of *L. fluviatilis* without any ill effect. These were collected from the Neva River, Russian Federation during the month of October 1993 and 2009. The animals were de–slimed, their heads and branchial regions removed, the rest of the body covered in sunflower flour, and cooked in sunflower oil.

References: Bahr (1933), Berg (1931, 1948), Bonnaterre (1788), Dill (1990), Gill *et al.* (2003), Goodwin *et al.* (2006), Hagelin and Steffner (1958), Halstead (1967), Hardisty (1986b), Huggins and Thompson (1970), Khidir and Renaud (2003), Kott *et al.* (1988), Legendre (1962), Potter and Osborne (1975), Salewski *et al.* (1995), Van Beneden (1857), Vladykov (1949), Vladykov and Follett (1958), Vladykov and Kott (1976d, 1979c), Zanandrea (1959b)

Lampetra lanceolata Kux and Steiner 1972 — Figs. 92–94

Synonyms: ***Lampetra lanceolata*** Kux and Steiner 1972: 377–381, figs. 1–3, 6, 10 (holotype: adult male, 137 mm TL, LMB 2077/2; type locality: 200 m upstream of the mouth of the Iyidere River, Trabzon, Turkey)

Taxonomic Remarks: In the original description of this species, Kux and Steiner (1972) measured in *L. lanceolata* two new morphological characters; the distance between the end of notochord and the tip of the caudal fin and the depth of the caudal fin, which they respectively compared with *Lampetra planeri* and *Eudontomyzon mariae*, and claimed that they were diagnostic. The taxonomic usefulness of these characters is difficult to evaluate because they have not been used in other lampreys. Other standard morphometrics such as the disc and tail lengths were not measured. A redescription of *L. lanceolata* is needed. For the purposes of this catalogue, I have supplemented below the incomplete original description with my observations of four topotypic specimens; three ammocoetes, 84–143 mm TL (CMNFI 1986–914) and one adult, 124 mm TL (CMNFI 1986–913, a paratype).

FAO Names: En — Turkish Brook Lamprey; **Fr** — Lamproie de ruisseau turque

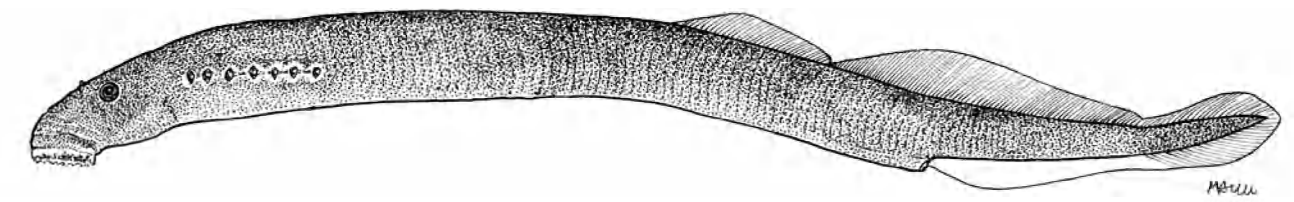

Fig. 92. Side view of *Lampetra lanceolata*. After a photograph by Brian W. Coad [spawning female, 124 mm TL, paratype, NMC (= CMNFI) 1986–913, mouth of Iyidere River, Trabzon, Turkey, 20 April 1969, H.M. Steiner].

Diagnostic Features: Ammocoetes: Maximum size attained, 143 mm TL. Body proportions, as percentage of TL (based on three specimens measuring 84–143 mm TL): prebranchial length, 7.3–8.3; branchial length, 11.5–13.1; trunk length, 50.6–52.8; tail length, 25.9–28.0. Trunk myomeres, 55–62. Body coloration (preserved), dorsal and upper lateral aspects brownish, lower lateral and ventral aspects lighter. Pigmentation: upper lip, – or +; between upper lip and cheek, +++;

cheek, –; subocular, –; upper prebranchial, –; lower prebranchial, –; upper branchial, + or ++; lower branchial, –; ventral branchial, –; lower lip, –; caudal fin, +; predorsal, +++; tongue precursor bulb, –; along elastic ridge of tongue precursor, ++. Lateral line neuromasts unpigmented. Caudal fin shape, rounded.

Metamorphosing Ammocoetes: lengths unrecorded.

Adults: 115–140.5 mm TL. Body proportions, as percentage of TL (based on the holotype and two paratypes measuring 115–137 mm TL or on a single paratype 124 mm TL; if the latter case then a single value is given): prebranchial length, 11.1–11.7; branchial length, 10.2–10.9; trunk length, 46.7–51.6; tail length, 29.0; eye length, 2.0–2.3; disc length, 5.2. The urogenital papilla length, as a percentage of branchial length, in spawning males, undetermined. Trunk myomeres, 58–64. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–6 unicuspid teeth; 3 endolaterals on each side; endolateral formula, typically 2–2–2; 1–2 rows of anterials; first row of anterials, 9 unicuspid teeth; exolaterals absent; posterials absent except for one very small cusp on the right side; transverse lingual lamina, one low but wide–based median cusp with no flanking lateral teeth; longitudinal lingual laminae condition undetermined.Velar tentacles, 5 with tubercles. The median tentacle is shorter than the lateral ones immediately next to it. Body coloration in mature individuals (preserved), dorsal and upper lateral aspects grayish brown, lower lateral and ventral aspects yellowish. Lateral line neuromasts unpigmented. Caudal fin pigmentation, –. Caudal fin shape, spade–like. Oral fimbriae, 124 (estimate based on number counted on right side times two because left side damaged). Oral papillae, about 23 (estimate based on number counted on right side times two because left side damaged).

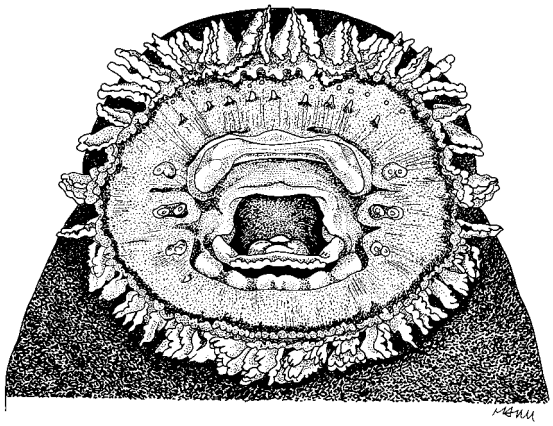

Fig. 93. Oral disc of *Lampetra lanceolata*. After a drawing by Susan Laurie–Bourque [124 mm TL, paratype, NMC (= CMNFI) 1986–913, mouth of Iyidere River, Trabzon, Turkey, 20 April 1969, H.M. Steiner].

Habitat and Biology: Freshwater. The Iyidere River, Turkey is 5 m above sea level. Ammocoetes are found in a mixture of coarse sand and organic detritus near the river banks overgrown by riparian vegetation.

Adults nonparasitic. Spawning was observed over a rocky substrate on 20 April at 200 m upstream of the mouth of the Iyidere River, Turkey. The water depth was 0.3 m and the stream width was 1.5 m.

Geographic Distribution (Fig. 94): Turkey: Iyidere River.

Interest to Fisheries: None

References: Kux and Steiner (1972), Vladykov and Kott (1979c)

Fig. 94. Geographic distribution of *Lampetra lanceolata*.

Lampetra pacifica Vladykov 1973 **Figs. 95–97**

Synonyms: ***Lampetra pacifica*** Vladykov 1973: 206, figs. 1–2, 5 [holotype: male, 175 mm TL, NMC (= CMNFI) 1971–769; type locality: Clackamas River, Columbia River Basin, near Estacada, Oregon, USA]

Taxonomic Remarks: This species may be a synonym of *L. richardsoni*, the lower number of trunk myomeres in the former reflecting a latidutinal cline. This requires further investigation.

FAO Names: En — Pacific Brook Lamprey; **Fr** — Lamproie de ruisseau du Pacifique

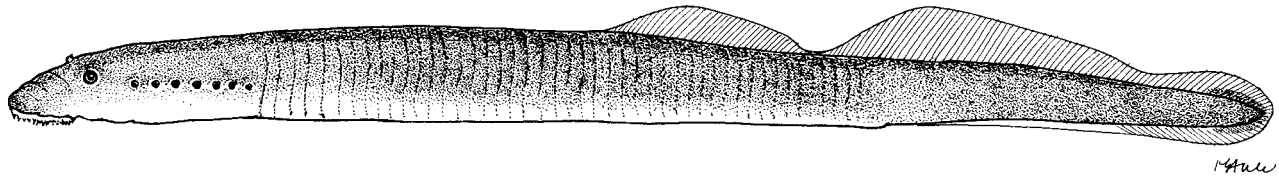

Fig. 95. Side view of *Lampetra pacifica*, prespawning male, 173 mm TL (originally 175 mm TL), holotype, NMC (= CMNFI) 1971–769, Clackamas River, Columbia River Basin, near Estacada, Oregon, USA, 9 April 1964, W.H. Staut. After Vladykov (1973).

Diagnostic Features: Ammocoetes: Maximum size attained should be at least 175 mm TL judging by the size of the adults, but the largest recorded 148 mm TL. Body proportions, as percentage of TL (based on mean values of four samples totaling 41 specimens measuring 75–143 mm TL): prebranchial length, 7.1–8.8; branchial length, 11.5–13.1; trunk length, 49.5–52.6; tail length, 27.5–28.2. Trunk myomeres, 52–57. Body coloration unrecorded. Pigmentation: upper lip, + (80% of specimens); subocular, – (29%) or + (44%) but the ammocoete in fig. 8 of the original description shows +++; lower prebranchial, – (33%) or + (60%) but the ammocoete in fig. 8 of the original description shows ++; upper branchial, ++ (% not known); caudal fin, + (84%); tongue precursor bulb, – or + (both 47%) or ++ (7%). Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded.

Metamorphosing Ammocoetes: 110–160 mm TL.

Adults: 98–175 mm TL. Body proportions, as percentage of TL (based on 39 specimens measuring 98–173 mm TL): prebranchial length, 8.9–12.8; branchial length, 8.9–11.3; trunk length, 44.7–53.5; tail length, 24.3–35.0; eye length, 1.4–3.0; disc length, 4.1–7.2. The urogenital papilla length, as a percentage of branchial length, in ten spawning males measuring 112–133 mm TL, 17.8–36.4. Trunk myomeres, 53–58. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 6–9 unicuspid teeth, usually 8; usually 3 endolaterals on each side, occasionally 2 on one side; endolateral formulae highly variable with the first two teeth 1–3 and the third 1–2; 1–2 rows of anterials; first row of anterials, 6 unicuspid teeth (in spawning specimens, the teeth in the anterior field may be lost); exolaterals absent; posterials absent; transverse lingual lamina, undetermined number of minute unicuspid teeth on either side of an enlarged median one; longitudinal lingual laminae cusps too small to count. Velar tentacles, 3–6, with tubercles. Body coloration (preserved), dark gray on dorsal and lateral aspects, whitish on ventral aspect. Lateral line neuromasts unpigmented. Caudal fin pigmentation, + (in prespawning individuals) or +++ (in spawning individuals). Fleshy tissues around the lingual laminae darkly pigmented. Caudal fin shape, rounded. Oral fimbriae, 83 (holotype). Oral papillae number unrecorded.

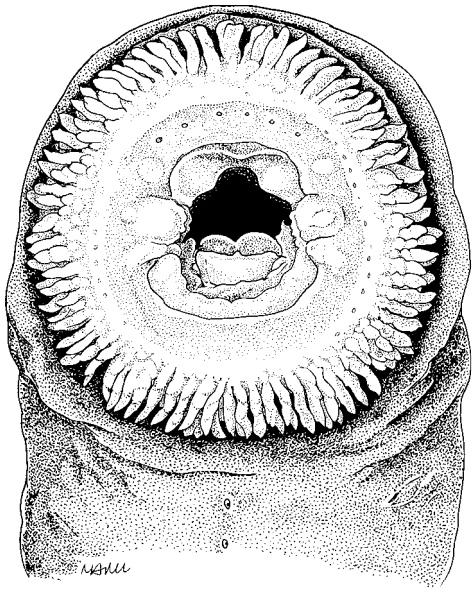

Fig. 96. Oral disc of *Lampetra pacifica*. After a drawing by Paul I. Voevodine [prespawning male, 173 mm TL (originally 175 mm TL), holotype, NMC (= CMNFI) 1971–769, Clackamas River, Columbia River Basin, near Estacada, Oregon, USA, 9 April 1964, W.H. Staut].

Habitat and Biology: Freshwater; creeks and rivers. Metamorphosis occurs in October in Oregon and California. Adults nonparasitic. Based on the dates of collection of spawning individuals in the original description, the spawning period probably occurs between mid–April and August in Oregon, while in California spawning probably occurs between the end of April and the beginning of May.

Geographic Distribution (Fig. 97): Oregon (Columbia River Basin: Clackamas and Willamette rivers and Crystal Springs Creek) and California [Sacramento River Basin: Friant–Kern Canal (artificially linked to the Sacramento River Basin), San Joaquin River, and Mill, Big Chico, and Putah creeks] (USA).

Interest to Fisheries: None

References: Kott *et al.* (1988), Vladykov (1973a), Vladykov and Kott (1976b, 1976d, 1979c)

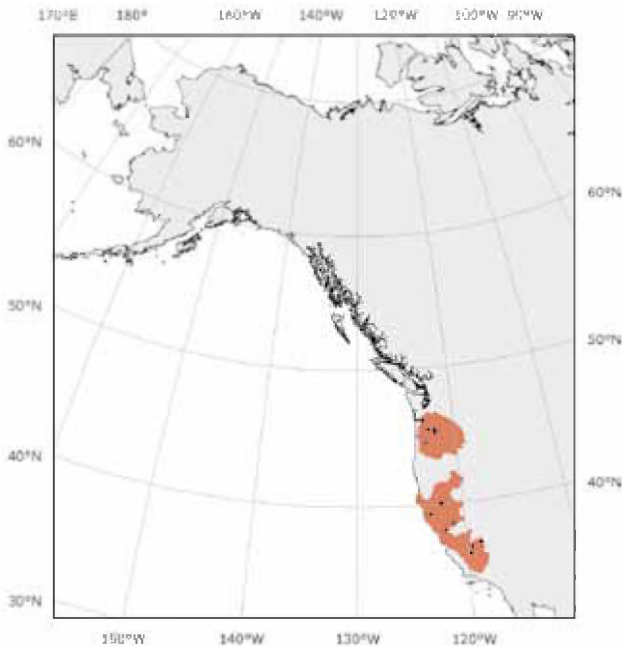

Fig. 97. Geographic distribution of *Lampetra pacifica*.

Lampetra planeri (Bloch 1784) — Figs. 98–100

Synonyms: ***Petromyzon planeri*** Bloch 1784: 47 (type locality: brooks of Thuringia, Germany); ***Petromyzon niger*** Lacepède 1802: 666–668, pl. 15, fig. 2; ***Petromyzon bicolor*** Shaw 1804: 263

Taxonomic Remarks: Rembiszewski (1968) reported on three adult hybrids between *L. planeri* and *Eudontomyzon mariae* in the Jeziorka River, Poland.

FAO Names: En — European Brook Lamprey; **Fr** — Lamproie de ruisseau européene, lamproie de Planer
Local name: Bachneunauge **(German)**

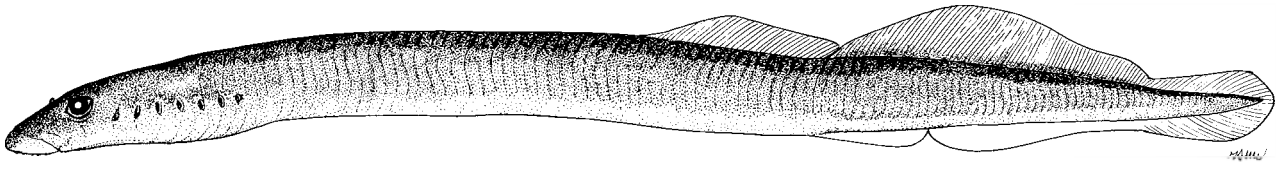

Fig. 98. Side view of *Lampetra planeri*. After a photograph by Brian W. Coad [spawning female, 127 mm TL, NMC (= CMNFI) 1986–833, Židovka Brook, Elbe River Basin, Czech Republic].

Diagnostic Features: Ammocoetes: Maximum size attained, 177 mm TL. Body proportions, as percentage of TL (based on 23 specimens measuring 123–177 mm TL): prebranchial length, 7.0–8.2; branchial length, 9.0–11.6; trunk length, 50.3–55.2; tail length, 25.0–28.6. Trunk myomeres, 58–64. Body coloration, dorsal and upper lateral aspects brownish, lower lateral and ventral aspects lighter. Pigmentation: upper lip, – (100% of specimens); subocular, – (percentage not known); lower prebranchial, – (72%) or + or ++ (14% each); upper branchial, + (95%) or ++ (5%); caudal fin, – (98%) or + (2%). Additionally, the lower lip and the ventral branchial region are both unpigmented (–). Lateral line neuromasts unpigmented. Caudal fin shape, spade–like.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 86–170 mm TL. Body proportions, as percentage of TL (based on 16 specimens measuring 106–133 mm TL): prebranchial length, 10.9–12.6; branchial length, 7.5–9.9; trunk length, 44.4–53.3; tail length, 25.4–31.4; eye length, 2.3–2.9; disc length, 5.2–7.0. The urogenital papilla length, as a percentage of branchial length, in ten spawning males measuring 111–140 mm TL, 21.4–52.6. Trunk myomeres, 60–65. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 7–9 teeth, usually all unicuspid, but occasionally one lateralmost bicuspid; 3 endolaterals on each side; endolateral

formula, typically 2–3–2; 2 rows of anterials; first row of anterials, 9 unicuspid teeth; exolaterals absent; posterials absent; transverse lingual lamina, 9–13 unicuspid teeth, the median one enlarged; longitudinal lingual laminae each with about 9 unicuspid teeth. Velar tentacles, 4–6, with tubercles. Body coloration (preserved), dorsal and lateral aspects grayish, ventral surface whitish, dorsal fins and caudal fin yellowish. Some specimens display a prominent dark blotch at the apex of the second dorsal fin. The iris is yellow. Lateral line neuromasts unpigmented. Caudal fin pigmentation, unpigmented except for spawning individuals in which it is "weakly peppered". Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater; in rivers and brooks. Larval life is 5+ to 6+ years, with the smaller individuals of the latter year class delaying metamorphosis by one year. Metamorphosis occurs in September in the Czech Republic. Duration of the life cycle is believed to last 6 years on average. Adults nonparasitic. Communal spawning in the same redd by *L. fluviatilis* and *L. planeri* has been reported in the River Tywi Basin, Wales (UK), in April, at a water temperature of 11 °C. Both species participated in constructing a redd about 23 cm in diameter and 5–8 cm deep, consisting of pebbles, gravel, and coarse sand. In the river Yeo, England (UK), peak spawning activity varies between 26 March and 24 April when water temperatures reach 10-11 °C. As the spawning season progresses, male:female ratios shift from 3.54:1 to 1.60:1. In the Czech Republic, both sexes participate in the redd construction in shady areas of streams that are 1–8 m in width and a few centimeters to 0.8 m in depth. Spawning occurs between 1 and 17 June at water currents 1–4 m/s and water temperatures 10–16 °C. Sexually mature adults have been observed burrowing in fine sand.

Geographic Distribution (Fig. 100): Sweden (Delaven River), England (UK) (Brue, Chess, Teme, and Yeo rivers), Wales (UK) (River Tywi Basin), France (Allier, Auzon, Loire, and Morge rivers), Germany, Czech Republic (Elbe River Basin (Zdobnice River, Bělěc and Židovka brooks) and Morava River Basin), Poland (Odra River and Vistula River Basin: Jeziorka River), Romania, Russian Federation, Italy (Dese River), and Spain

Interest to Fisheries: None

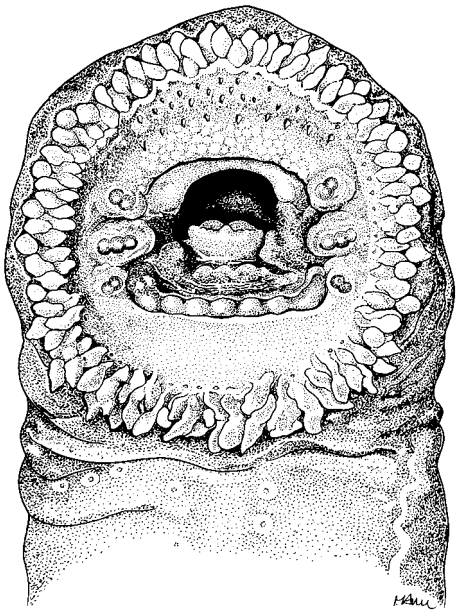

Fig. 99. Oral disc of *Lampetra planeri*. After a drawing by Paul I. Voevodine [spawning male, 120 mm TL, Allier River, Loire River Basin, France].

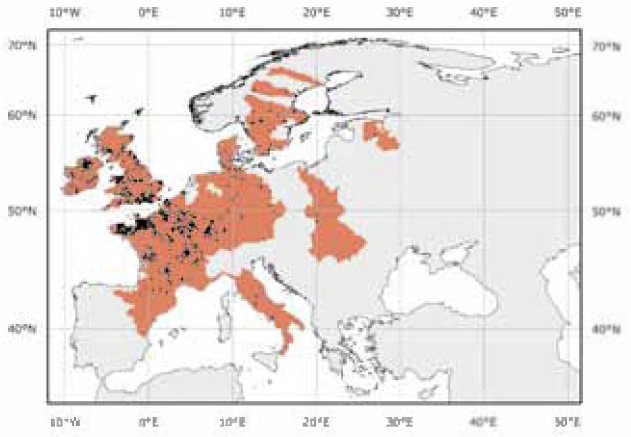

Fig. 100. Geographic distribution of *Lampetra planeri*.

References: Hardisty (1961), Huggins and Thompson (1970), Lohniský (1966), Kott *et al.* (1988), Vladykov (1955), Vladykov and Follett (1965), Vladykov and Kott (1976d), Rembiszewski (1968)

Lampetra richardsoni Vladykov and Follett 1965

Figs. 101–103

Synonyms: ***Lampetra richardsoni*** Vladykov and Follett 1965: 142, figs. 3, 5 [holotype: male, 154 mm TL, NMC (= CMNFI) 1964–57; type locality: Smith Creek, Cultus Lake Basin, British Columbia, Canada]

FAO Names: En — Western Brook Lamprey; **Fr** — Lamproie de ruisseau occidentale

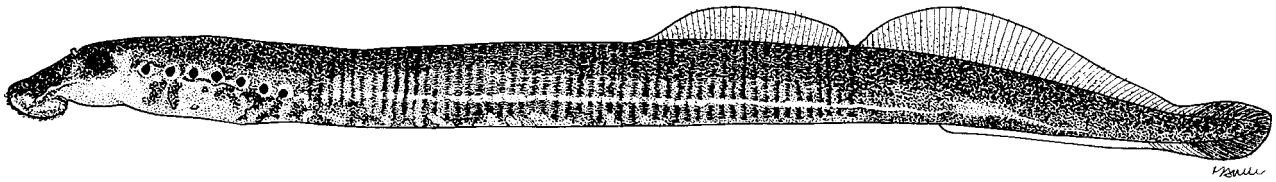

Fig. 101. Side view of *Lampetra richardsoni* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, 175 mm TL. Body proportions, as percentage of TL (based on 72 specimens measuring 29–175 mm TL): prebranchial length, 5.5–13.8; branchial length, 8.7–17.2; trunk length, 46.7–55.5; tail length, 20.2–28.0. Trunk myomeres, 57–65. Body coloration unrecorded. Pigmentation: upper lip, + (4% of specimens) or ++ (87%) or +++ (9%); subocular, + (2%) or ++ (11%) or +++ (87%); lower prebranchial + (9%) or ++ (40%) or +++ (51%); upper branchial, + (9%) or ++ (21%) or +++ (70%); lower branchial, + (% not known); caudal fin, + (21%) or ++ (55%) or +++ (23%); tongue precursor bulb, – (71%) or + (24%) or ++ (6%). Lateral line neuromast pigmentation unrecorded. Caudal fin shape, rounded or spade–like.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 80–154 mm TL. Body proportions, as percentage of TL (based on 45 specimens measuring 101–154 mm TL): prebranchial length, 10.4–14.0; branchial length, 8.3–10.8; trunk length, 44.7–53.1; tail length, 25.2–30.4; eye length, 2.0–2.7; disc length, 4.1–7.9. The urogenital papilla length, as a percentage of branchial length, in 26 spawning males measuring 122–151 mm TL, 17.6–30.8. Trunk myomeres, 60–67. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 7–10, usually 7 unicuspid teeth; 3 endolaterals on each side; endolateral formula, typically 1–2–1 (15 cases), 2–2–1 (12), or 2–2–2 (10), and rarely 2–3–2 (5) and 2–3–1 (1); 2 rows of anterials; first row of anterials, 4–6 unicuspid teeth; exolaterals absent; posterials usually absent (However, one specimen in Vladykov (1973a: fig. 6) has one unicuspid tooth at either end of the posterior field); transverse lingual lamina, 5–11 unicuspid teeth, the median one enlarged or only the median enlarged tooth is present; longitudinal lingual laminae cusps too small to count. Velar tentacles, 5–6, with tubercles. Body coloration (preserved), dorsal and lateral aspects grayish, ventral surface whitish. Lateral line neuromasts unpigmented. Caudal fin pigmentation, +++. Fleshy tissues around the lingual laminae unpigmented. Caudal fin shape, rounded or spade–like. Oral fimbriae, 93. Oral papillae number unrecorded.

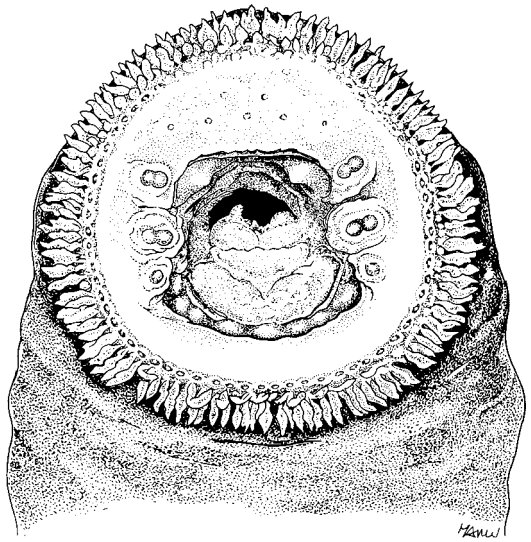

Fig. 102. Oral disc of *Lampetra richardsoni*. After a drawing by Paul I. Voevodine [prespawning male, 154 mm TL, holotype, NMC (= CMNFI) 1964–57, Smith Creek, Cultus Lake Basin, British Columbia, Canada, 30 May 1942, G.C. Carl[.

Habitat and Biology: Freshwater; in lakes, creeks, and rivers.
Adults nonparasitic. Spawning period in early May in British Columbia as evidenced by spent females being collected on 8 May. Spawning occurs in redds and fertilized eggs collected on 8 May hatched in about 28 days at water temperatures between 10–12 °C. Eggs are greenish.

Geographic Distribution (Fig. 103): Canada (Holmes Creek, Smith Creek, and Millstone River, British Columbia) and USA (Washington Creek, North Creek, Evans Creek, Matthews Creek, Clover Creek, Yakima River, Chehalis River, Steel Lake and Ames Lake, Washington and creek tributary to Umpqua River, Oregon).

Interest to Fisheries: In the state of Washington, in the early 1900s, ammocoetes were sold at $1.50 to $1.75 US per dozen to use as bait for sportfishes (Schultz, 1930).

References: Carl (1953), Kott *et al.* (1988), Schultz (1930), Vladykov (1973a), Vladykov and Follett (1965), Vladykov and Kott (1976d, 1979c)

Fig. 103. Geographic distribution of *Lampetra richardsoni*.

Genus *Lethenteron* Creaser and Hubbs 1922

Synonyms: ***Lethenteron*** Creaser and Hubbs 1922: 3 (proposed as a subgenus of *Entosphenus*)

This genus comprises seven species (one parasitic and six nonparasitic). Of the six nonparasitic species, two are endemic to North America (*Lethenteron alaskense* and *L. appendix*), three are endemic to Asia (*L. kessleri*, *L. ninae*, and *L. reissneri*), and one is endemic to Europe (*L. zanandreai*). The parasitic species, *Lethenteron camtschaticum*, is very widespread, occurring in Eurasia and North America. Two dorsal fins. Supraoral lamina with two teeth separated by a wide bridge, which occasionally bears 1–2 teeth in some species. Labial teeth radially–arranged in a curvilinear fashion only in the anterior field. Exolaterals absent or if present, only one or two per lateral field, not a complete row, except rarely in *L. alaskense*, *L. reissneri*, and *L. zanandreai*. A single row of posterials, rarely absent. Transverse lingual lamina u-shaped with a greatly enlarged median cusp. Velar tentacles with tubercles and a median tentacle is present. The type species is *Petromyzon appendix* DeKay 1842.

Lethenteron alaskense Vladykov and Kott 1978

Figs. 104–106

Synonyms: ***Lethenteron alaskense*** Vladykov and Kott 1978: 7–9, figs. 1–3 [holotype: male, 164 mm TL, NMC (= CMNFI) 1976–614; type locality: West Creek, a tributary to Brooks Lake, Alaska]

FAO Names: En — Alaskan Brook Lamprey, Darktail Lamprey; **Fr** — Lamproie de ruisseau d'Alaska

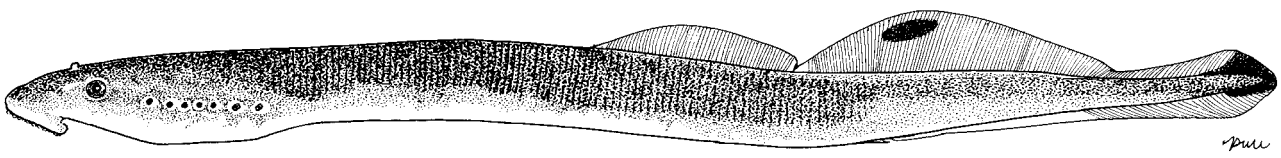

Fig. 104. Side view of *Lethenteron alaskense*, spawning male, 164 mm TL, holotype, NMC (= CMNFI) 1976-614, West Creek, a tributary to Brooks Lake, Alaska, USA, 11 June 1964, W. Heard. After Vladykov and Kott (1978a).

Diagnostic Features: Ammocoetes: The ammocoetes have not been studied.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 122–188 mm TL. Body proportions, as percentage of TL (based on 68 specimens measuring 122–188 mm TL): prebranchial length, 9.3–14.9; branchial length, 8.7-11.6; trunk length, 45.4–53.5; tail length, 25.7–33.5; eye length, 1.7–3.2; disc length, 3.8–7.3. The urogenital papilla length, as a percentage of branchial length, in a 141 mm TL spawning male, 26.9. The shape of the second dorsal fin in spawning males is arch–like and in females triangular. Trunk myomeres, 66–72. Dentition: supraoral lamina, 2 unicuspid teeth (1 of 34 specimens had 2 additional small unicuspid teeth on the bridge); infraoral lamina, 6–11 teeth, the lateralmost one on each side unicuspid or bicuspid and the internal ones unicuspid; 3 endolaterals on each side; endolateral formula, 2–2–2; 3 rows of anterials; first row of anterials, 3–5 unicuspid teeth; total number of anterials, 23–38 unicuspid teeth; exolaterals absent or one or two unicuspid exolaterals present in each lateral field (Note: The holotype of *L. alaskense* possesses one exolateral tooth in each lateral field.), exceptionally, one complete row of exolaterals on each side; single row of posterials, 17–24 unicuspid teeth; transverse lingual lamina, 9–15 unicuspid teeth, the median one greatly enlarged; longitudinal lingual laminae each with 6–13 unicuspid teeth. Velar tentacles, 5–7, with tubercles and with the single median tentacle shorter than the lateral tentacles immediately next to it. Body coloration (preserved) in mature adults is gray brown on the upper surface and flanks and whitish on the lower surface. Lateral line neuromasts unpigmented. Gular region unpigmented (2 of 64 specimens had weak pigmentation). Second dorsal fin with a dark blotch near the apex (4 of 64 specimens did not have a blotch). Caudal fin pigmentation, + (17% of specimens), ++ (36%) or +++ (46%). Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae, 18.

Habitat and Biology: Freshwater, in creeks and rivers. Adults nonparasitic. Spawning period between 11 June and 25 September in Naknek River Basin, Alaska. Fecundity, 2,188–3,477 eggs/female. Egg length, 0.9 mm.

Geographic Distribution (Fig. 106): West Creek and Brooks River, Naknek River Basin and Chatanika River, Yukon River Basin, Alaska (USA) and Martin River, Mackenzie River Basin, Northwest Territories (Canada).

Interest to Fisheries: None

References: Heard (1966), Kott *et al.* (1988), Mecklenburg *et al.* (2002), Vladykov and Kott (1978a, 1979c), Vladykov *et al.* (1980)

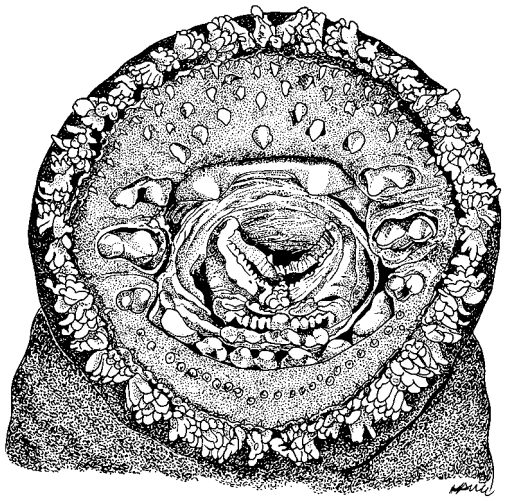

Fig. 105. Oral disc of *Lethenteron alaskense*. After a drawing by Susan Laurie–Bourque [185 mm TL, paratype, NMC (= CMNFI) 1976–614A, West Creek, a tributary to Brooks Lake, Alaska, USA, 11 June 1964, W. Heard].

Fig. 106. Geographic distribution of *Lethenteron alaskense*.

Lethenteron appendix (DeKay 1842) **Figs. 107–109**

Synonyms: ***?Petromyzon lamottenii*** Lesueur 1827: 5–6, pl. 3 (type locality: Lamotte mine, Missouri, USA); ***Petromyzon appendix*** DeKay 1842: 381–382, pl. 64, fig. 211 (type locality: DeKay received material from Mr. Joseph Mauran of Providence, Rhode Island, but this does not necessarily indicate the place of origin of the material. DeKay also mentioned receiving material from the Hudson River and this is more likely the type locality.); ***?Lampetra wilderi*** Gage in Jordan and Evermann 1896: 13 (type locality: Cayuga Lake, New York, USA)

Taxonomic Remarks: This species' nomenclatural history is very complex and over the years authors have used a variety of names for it (see Creaser and Hubbs, 1922, Hubbs and Trautman, 1937, Chute *et al.*, 1948, Bailey, 1980, Vladykov and Kott, 1982a, 1982b). The specific name used here reflects a stable use over the last 25 years or so.

FAO Names: En — American Brook Lamprey; **Fr** — Lamproie de l'est, lamproie de ruisseau américaine

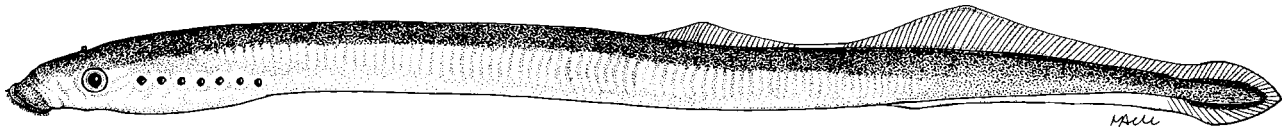

Fig. 107. Side view of *Lethenteron appendix*. After a photograph by John Lyons [adult].

Diagnostic Features: Ammocoetes: Maximum size attained, 240 mm TL. Body proportions, as percentage of TL (based on 19 specimens measuring 100–143 mm TL): prebranchial length, 5.0 (estimated mean); branchial length, 12.6–14.4; trunk length, 51.0–53.7; tail length, 27.7–31.6. Trunk myomeres, 63–71. Body coloration unrecorded. Pigmentation: upper lip, +; cheek, ++; subocular, –; upper prebranchial, –; lower prebranchial, –; upper branchial, ++; lower branchial, –; caudal fin, + or ++; tongue precursor bulb, ++; along elastic ridge of tongue precursor, +. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, spade–like.

Metamorphosing Ammocoetes: 154–181 mm TL.

Adults: 103–217 (exceptionally, 260–354, see under Biology below) mm TL and wet weight 2.8–16.2 g. Body proportions, as percentage of TL (based on 329 specimens measuring 103–217 mm TL): prebranchial length, 10.4–13.7; branchial length, 9.0–11.9; trunk length, 46.7–53.5; tail length, 24.0–32.3; eye length, 1.2–2.6; disc length, 3.2–6.0. The urogenital papilla length, as a percentage of branchial length, in 44 spawning males measuring 146–214 mm TL, 4.5–16.7. Trunk myomeres, 64–74. Dentition: supraoral lamina, 2 unicuspid teeth, but occasionally a third small cusp is present on the bridge; infraoral lamina, 6–10 unicuspid teeth; 3 endolaterals on each side; endolateral formula, typically 2–2–2; 3 rows of anterials; first row of anterials, 4–6 unicuspid teeth; exolaterals usually absent, but Kott (1974) reported on the presence of one or two exolaterals, on either or both lateral fields in 21% of specimens examined; single row of posterials with 20 unicuspid teeth; transverse lingual lamina u–shaped with 15 unicuspid teeth, the median one greatly enlarged; longitudinal lingual laminae each with 5–8 unicuspid teeth. Marginal membrane vestigial. A small gular pouch occurs in males. Velar tentacles, 5–9, with tubercles. Body coloration (preserved), uniformly slate brown on the dorsal aspect, progressively paler on the lateral aspects, and much paler on the ventral aspect. Lateral line neuromasts darkly pigmented, at least the ventral ones. Gular region darkly pigmented. Second dorsal fin with a dark blotch near the apex (38% of individuals) or not (62%). Caudal fin pigmentation, + (44% of specimens), ++ (26%) or +++ (30%). Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae, 18–35.

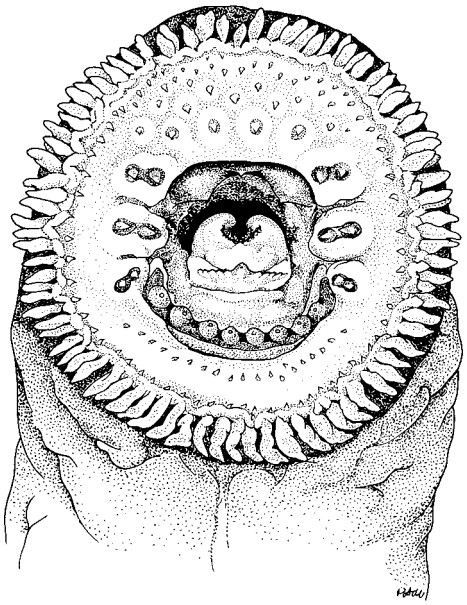

Fig. 108. Oral disc of *Lethenteron appendix*. After a drawing by Paul I. Voevodine.

Habitat and Biology: Freshwater. Mainly associated with stable, high quality, coldwater habitats. Ammocoetes and adults are most abundant in clear, permanent, unpolluted, pool–riffle streams where sand–gravel substrates predominate and

summer flows are 0.3–4,400 m^3/s and summer water temperatures 14–22.5 °C. In Michigan, ammocoetes have been reported in lentic habitats up to 450 m from the presumed originating stream, at water depths 1–16 m, where substrates vary from sand–silt, with or without detritus, to gravel–rubble–sand. Spawning adults can be found in streams or lakes. Larval life lasts 4.5 yrs or more based on length–frequency analysis. Diet of ammocoetes is organic detritus, diatoms (11 genera), and desmids (one genus). Metamorphosis occurs between mid–August and October in Tennessee. Adults nonparasitic. Duration of adult life is about six months. However, three reports (Manion and Purvis, 1971, Vladykov and Kott, 1980a, Cochran, 1997) of seven adults measuring 260–354 mm TL, exceeding the maximum reported larval length of 240 mm TL, have been interpreted as an indication in this species of facultative feeding, either parasitically or perhaps on fish eggs or organic detritus, in the adult stage. Between metamorphosis and spawning it spends most of its time hidden under stones. In Michigan, the spawning period is from 20 April to 26 June, at water temperatures between 6.7–20.6 °C, with peak spawning activity in early May. In Québec, peak spawning activity occurs at a water temperature of 17 °C. In Tennessee, the spawning period is in March and in Delaware, it is from 28 March to 4 April, at water temperatures between 6.8–12.0 °C. Nests are built in streams with gravel and cobble substrates having 1.5–18 m width, 15–61 cm depth, and 0.1-5.2 m^3/s flow. A typical nest is 16 cm in diameter. Up to 14 spawning lampreys have been found in a nest. The sex ratio is usually 1:1 and there are no significant differences in the length and weight of spawning males and females. Fecundity, 1,327–5,185 eggs/female and relative fecundity, 274–531 eggs/g body weight. Egg diameter, 0.94–1.19 mm. Eggs are spherical, adhesive, and demersal with color from pale yellow to light green. Hatching occurs 2–3 weeks after fertilization. Average length at hatching, 2.6 mm TL. Mean length at age 1 is 38 mm TL. There are reported occurrences in Michigan of communal spawning of American Brook Lamprey with Sea Lamprey (Carp Lake, Pine, and Pentwater rivers), of American Brook Lamprey with Chestnut Lamprey and Sea Lamprey (Betsie River), and of American Brook Lamprey with Silver Lamprey and Sea Lamprey (Carp Lake).

Geographic Distribution (Fig. 109): Canada and USA: Lake Superior Basin, Michigan; Lake Michigan Basin, Michigan (Carp Lake, Betsie, Pine, and Pentwater rivers) and Indiana; Lake Huron Basin, Michigan; Lake Erie Basin, Ontario and Michigan; Lake Ontario Basin, Ontario and New York; Mississippi River Basin, Minnesota, Missouri, Pennsylvania, Kentucky, Tennessee, and Alabama; St. Lawrence River Basin, Québec and New York; Atlantic Slope basins, New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Delaware, Maryland, and Virginia.

Fig. 109. Geographic distribution of *Lethenteron appendix*.

Interest to Fisheries: In the Laurentian Great Lakes Basin, it has been negatively affected by control measures directed towards *Petromyzon marinus*, except for the chemosterilization of males, which affects only the latter species (see that particular species' account) (Schuldt and Goold, 1980). Vladykov (1949) reported that in the province of Québec, Canada, ammocoetes were at the time extensively sold at $0.50 to $1.00 Canadian per dozen as bait for sportfishes.

References: Beamish and Lowartz (1996), Burr and Warren (1986), Chute *et al.* (1948), Cochran (1997), Comtois *et al.* (2004), DeKay (1842), Gage (1893), Jordan and Evermann (1896), Kott (1971, 1974), Kott *et al.* (1988), Lesueur (1827), Manion and Purvis (1971), Morman (1979), Mundahl and Sagan (2005), Mundahl *et al.* (2005), Rohde (1980), Rohde *et al.* (1976), Schuldt and Goold (1980), Seagle and Nagel (1982), Vladykov (1949, 1950), Vladykov and Kott (1976d, 1978a, 1979c, 1980a)

Lethenteron camtschaticum (Tilesius 1811) Figs. 110–112

Synonyms: ***Petromyzon marinus Camtschaticus*** Tilesius 1811: 240–246, pl. 9 (type locality: marine waters off Petropavlosk Kamchatskiy, Kamchatka, Russian Federation); ***Petromyzon lumbricalis*** Pallas 1814: 69–70, pl. 10, fig. 1; ***Petromyzon fluvialis*** Richardson 1823: 705; ***Petromyzon Japonicus*** von Martens 1868: 3, pl. 1, fig. 2; ***Ammocoetes aureus*** Bean 1881: 159; ***Lampetra japonica septentrionalis*** Berg 1931: 100–102, pl. V, fig. 4 (10 syntypes: adults, 284–377 mm TL, ZISP 12159; type locality: Onega River at Podporozhye, Russian Federation)

Taxonomic Remarks: Berg (1931) recognized three subspecies, *japonica*, *septentrionalis*, and *kessleri* under what he called *Lampetra japonica*. The first two are treated here together under *Lethenteron camtschaticum*, while *Lethenteron kessleri* is recognized here as a distinct species (see that species' account). Further study is required to determine whether the *japonica* and *septentrionalis* taxa represent distinct species. Additionally, Berg (1931) suggested that the subspecies *septentrionalis* consists of two races; a normal form (forma typica) and a smaller praecox form.

FAO Names: En — Arctic Lamprey; **Fr** — Lamproie arctique
Local names: Kawayatsume **(Japanese)**; Nû–mug–û–shûk **(Alaskan native language)**

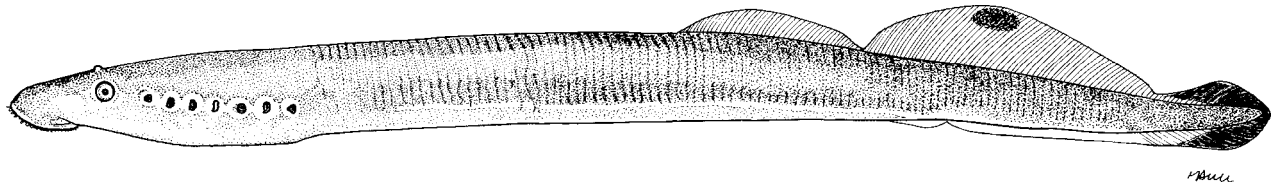

Fig. 110. Side view of *Lethenteron camtschaticum* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, approximately 220 mm TL. Wet weight of individuals 7–180 mm TL, 0.1–6.9 g. Body proportions, as percentage of TL (based on 400 specimens measuring 7–180 mm TL, with an average of 76 mm; however, because the sample included individuals that were so small, the ranges for body proportions are very wide and not strictly comparable with other species, and therefore, I have included in parentheses the average values; additionally, these data are taken from Kucheryavyi *et al.* (2007) and may include some larval *L. kessleri*): prebranchial length, 4.9–22.1 (8.4); branchial length, 7.0–43.0 (15.4); trunk length, 17.5–61.1 (46.8); tail length, 18.9–79.6 (31.7). Trunk myomere number unrecorded. Body coloration unrecorded. Pigmentation of the various body regions unrecorded. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.

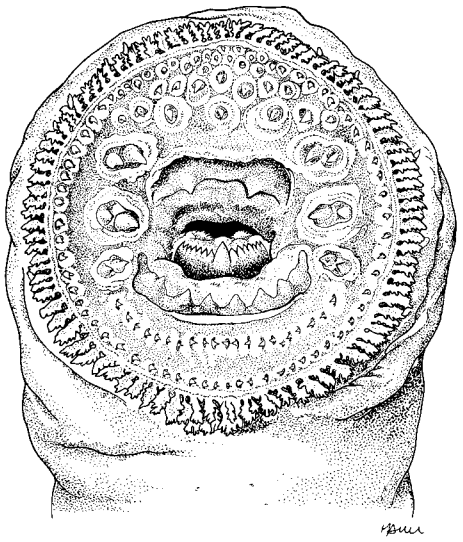

Fig. 111. Oral disc of *Lethenteron camtschaticum*. After a drawing by Paul I. Voevodine [female, 496 mm TL, Hokkaidō Island at Fukagawa, Japan, 11 Oct. 1948, S. Sato].

Metamorphosing Ammocoetes: approximately 140–184 mm TL (The latter number represents an average length).

Adults: 110–625 mm TL. Wet weight of individuals 145–350 mm TL, 3.2–87.7 g. Body proportions, as percentage of TL (based on 63 specimens measuring 130–460 mm TL): prebranchial length, 9.4–14.6 [7.3–21.3 according to Kucheryavyi *et al.* (2007)]; branchial length, 7.8–11.1 [as high as 20.8 according to Kucheryavyi *et al.* (2007)]; trunk length, 46.5–55.7 [21.9–56.3 according to Kucheryavyi *et al.* (2007)]; tail length, 24.6–30.8; eye length, 0.7–3.7; disc length, 4.5–7.7. The intestinal diameter can reach up to 13 mm. The urogenital papilla length, as a percentage of branchial length, in six spawning males measuring 339–401 mm TL, 14.6–19.5. Trunk myomeres, 65–77 [Kucheryavyi *et al.* (2007) reported counts of 63–85 for 19 downstream migrants and 55–79 for 87 anadromous individuals from Utkholok River Basin, Kamchatka]. Dentition: supraoral lamina, 2 unicuspid, rarely bicuspid, teeth; infraoral lamina, 6–10 teeth, usually 8 [as few as 5 according to Kucheryavyi *et al.* (2007)], the lateralmost tooth on either end usually bicuspid, the internal ones unicuspid; usually 3, rarely 4 endolaterals on each side; endolateral formula typically 2–2–2 with variant formulae, 2–2–1, 2–2–2–2, 2–2–2–1; 3 rows of anterials; first row of anterials, 3 unicuspid teeth; total number of anterials, 20–33 teeth [5–43 according to Kucheryavyi *et al.* (2007) and as low as 11 according to Iwata *et al.* (1985), which may be due to regional effects, but this requires further investigation]; exolaterals absent; single row of posterials, 12–28 teeth; transverse lingual lamina, 13–18 teeth, the median one greatly enlarged; longitudinal lingual laminae each with 10–14 teeth. Velar tentacles, 5–7, with tubercles and with the single median tentacle shorter than the lateral tentacles immediately next to it, and with dorsal velar wings on either side, each consisting of a single tentacle. Body coloration (live) of recently transformed adults brown on dorsal and lateral aspects and silvery on ventral aspect, while upstream spawning migrants have a yellowish olive dorsal aspect, becoming lighter on the lateral aspects, and dull yellowish on the ventral aspect. Lateral line neuromasts unpigmented. Gular region unpigmented. Second dorsal fin with a dark blotch near the apex. Caudal fin pigmentation, + (29% of specimens), ++ (57%) or +++ (14%). Caudal fin shape, spade–like. Oral fimbriae, 87–112. Oral papillae, 12–22.

Habitat and Biology: Anadromous. The Great Slave Lake Basin population is believed to be a permanent freshwater resident population. In fresh waters, occurs in rivers and lakes. Ammocoetes occur along river banks in silty–muddy substrate where current is slight. Spawning occurs on pebble–sand substrate.
Larval period lasts four years. Age classes range in total length approximately as follows: 0+ up to 35 mm; 1+ 30–65 mm; 2+ 60–155 mm; 3+ 150–220 mm. They tend to disperse downstream as they age. Mean densities in the Hay River, Northwest Territories, have been estimated at 137 ammocoetes/m^2. Larvae feed mainly on organic detritus and algae. Ammocoetes are preyed upon by fishes (*Lota lota*, *Esox lucius*, and *Sander vitreus*). Metamorphosis begins in late summer (mid–August) and continues through the winter in Great Slave Lake Basin, Northwest Territories, Canada and recently metamorphosed adults enter the lake in May to July. Downstream movement of recently metamorphosed adults towards the sea begins in late May and ends in July in Kamchatka. Adults parasitic on various fishes in both fresh (*Catostomus catostomus*, *Coregonus artedi*, *C. clupeaformis*, *Salvelinus namaycush*, *Stenodus leucichthys*) and marine waters. The site of attachment is usually below the lateral line and anterior to the pelvic fins. Adults are preyed upon by fishes (*Esox lucius*) and birds (gulls). Spawning adults ascend rivers in Japan between October and January, while this occurs between the end of May and June in Utkholok River Basin, Kamchatka, and between the end of November and the end of April in the Yukon River, Alaska. The spawning migration distance up the Yukon River exceeds 1,600 km. Both sexes participate in the building of the oval–shaped redd. Spawning occurs in June in Utkholok River Basin, Kamchatka, from April to July in Japan and mid June – early July in Great Slave Lake Basin, Canada. Fecundity, 9,790–29,780 eggs/female in Great Slave Lake Basin (believed to be a permanent freshwater resident population), 12,272–34,586 eggs/female in an anadromous population from Kamchatka, and 62,936–119,180 eggs/female in anadromous populations from rivers in Japan. In the latter case, the long diameter of the eggs varies from 0.85 to 1.23 mm and the short diameter from 0.75 to 1.14 mm. The eggs are dark blue and adhesive. When they emerge from the egg after about a one–month incubation period, larvae measure about 7 mm total length. Adult life is about two years.

Geographic Distribution (Fig. 112): Varanger Fiord and Pasvik River, Norway; White Sea Basin, Barents Sea Basin to the Pechora River, Arctic Ocean Basin and its rivers from the Ob' (Kara Sea Basin) to the Kolyma (East Siberian Sea Basin), Anadyr territory, Utkholok River and its tributary Kolkavayam River (Kamchatka Peninsula), Iturup and Sakhalin islands, Amur and Suchan rivers, Russian Federation; Mutan River (Sungari River Basin), Tumen River, People's Republic of China; to the southern extremity of the Korean Peninsula; Toufutsu Lake and Assabu, Ishikari, Mukawa, Ohno, Ryukei, and Saru rivers (Hokkaidō Island) and Mogami and Shinano rivers (Honshū Island), Japan; Kenai Peninsula, Brooks Lake, Brooks and Naknek rivers (Naknek River Basin), Nushagak and Yukon rivers, Bering Sea at St. Lawrence Island and Bering Strait, Alaska, USA; Beaufort Sea, between Point Barrow, Alaska, USA and Anderson River, Canada; Yukon River, Mackenzie River Basin (Mackenzie River, Artillery Lake, and Great Slave Lake, and its tributaries Hay and Slave rivers), and Anderson River, Canada.

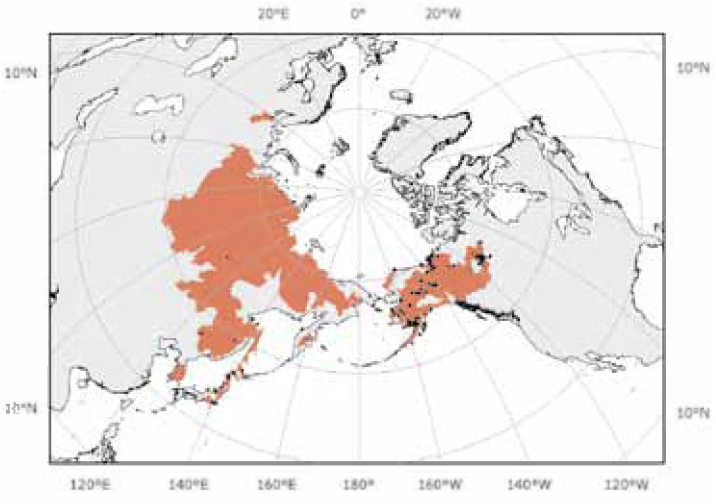

Fig. 112. Geographic distribution of *Lethenteron camtschaticum*.

Interest to Fisheries: Around 1879 it was of great importance for native peoples along the Yukon River at Russian Mission and Anvik, Alaska, where they would catch upstream spawning migrants by the dozens through the ice using long multi–forked poles or dipnets (Turner, 1886, Nelson, 1887). The oil in the lamprey would be rendered through boiling in water and used for human food or in lamps as a substitute for seal oil. Recently, there has been an interest in starting a commercial fishery for upstream migrants targeting the Asian market in the USA and abroad in addition to the traditional subsistence harvest. The 2003 quota was set at 20,000 kg. The taste has been compared to that of sardine because of the high lipid content that can reach 38% of the body weight. In Japan, in the Shinano River estuary, upstream spawning migrants are caught between October and January using large handnets; in 1959, daily catches varied from a few dozen to over 1,000 lampreys (Honma 1960). In winter, lampreys are caught at the same place but using a gang of about ten bell–shaped leather fishing traps that is laid in a string along the river floor (Honma, 1960). The lampreys are served in a number of different ways in restaurants, and in salt–dried form are highly valued as a medicine against night blindness (Honma, 1960).

References: Bean (1881), Berg (1931, 1948), Cheng *et al.* (1993), Heard (1966), Hensel (1963), Honma (1960), Iwata *et al.* (1985), Khidir and Renaud (2003), Kott *et al.* (1988), Kottelat (1997), Kucheryavyi *et al.* (2007), Nelson (1887), Nursall and Buchwald (1972), Okada (1955), Pallas (1814), Richardson (1823), Sidorov and Pichugin (2005), Tilesius (1811), Turner (1886), Vladykov and Kott (1976d, 1978a), von Martens (1868), Yamazaki *et al.* (2001)

Lethenteron kessleri (Anikin 1905) Figs. 113–115

Synonyms: ***Petromyzon kessleri*** Anikin 1905: 10 (type locality: Tom' and Kirgizka rivers near Tomsk, Ob' River Basin, western Siberia, Russian Federation); ***?Lethenteron matsubarai*** Vladykov and Kott 1978: (holotype: 150 mm TL, BC 77–71; type locality: Shokotsu River, Hokkaidō Island, Japan)

Taxonomic Remarks: Iwata *et al.* (1985) synonymized *Lethenteron matsubarai* Vladykov and Kott 1978 with *L. kessleri* (Anikin 1905). However, while they examined the holotype of the former, they did not compare it with material of *L. kessleri* from the type locality (Tom' and Kirgizka rivers near Tomsk, Russian Federation), but rather with material from Hokkaidō Island, Japan. Their action is provisionally accepted here with the caveat that further studies with appropriate comparative material are required. Of particular note is the fact that material examined by Iwata *et al.* (1985) did not possess a dark blotch on the second dorsal fin, as in *L. matsubarai*, while material examined by Poltorykhina (1971, 1974) from the Irtysh River Basin, part of the Ob' River Basin to which the Tom' and Kirgizka rivers belong, possessed a dark blotch. It is not clear whether the 100–165 mm TL non–feeding adult stage resident form on Kamchatka, and identified by Kucheryavyi *et al.* (2007) as *L. camtschaticum*, refers instead to *L. kessleri*.
Yamazaki *et al.* (2006) suggested that *L. kessleri* was a junior synonym of *L. reissneri* based on their examination of trunk myomeres, allozymes, and mtDNA genes CO I and cyt *b* in larval material from the type localities. This needs to be corroborated with the examination of adult material.

FAO Names: En — Siberian Lamprey; **Fr** — Lamproie de Sibérie

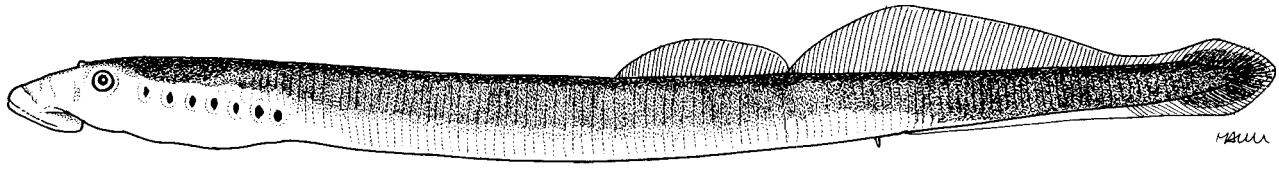

Fig. 113. Side view of *Lethenteron kessleri* spawning male. After Iwata *et al.* (1985).

Diagnostic Features: Ammocoetes: Maximum size attained, at least 218 mm TL. Body proportions, as percentage of TL (based on 50 specimens measuring a mean of 218 mm TL; the values given below represent a mean): prebranchial length, 5.7; branchial length, 9.8; trunk length, 54.4 (derived by deduction); tail length, 30.1. Trunk myomeres, 67–71. Body coloration unrecorded. Pigmentation of the various body regions unrecorded. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.
Metamorphosing Ammocoetes: 225–233 mm TL (This is a range of means).
Adults: 112–230 mm TL. Body proportions, as percentage of TL (based on 300 specimens measuring 153–230 mm TL; the values given below represent ranges of means based on samples of 50 specimens): prebranchial length, 11.2-12.0; branchial length, 9.5–9.6 (8.9–11.9 absolute range according to Iwata *et al.* (1985) based on 97 specimens 112–184 mm TL); trunk length, 48.8 (derived by deduction); tail length, 29.1–30.9; eye length, 2.1–2.2; disc length, 5.6–6.0. The intestinal diameter is less than 1.0 mm. The urogenital papilla length, as a percentage of branchial length, in three spawning males measuring 147–169 mm TL, 5.9–10.0 [5.8–34.7 according to Iwata *et al.* (1985) based on 23 spawning males 121–160 mm TL]. Trunk myomeres, 65–73 [57–78 in resident *L. camtschaticum* form *sensu* Kucheryavyi *et al.* (2007)]. Dentition: supraoral lamina, 2 unicuspid teeth, rarely 3; infraoral lamina, 5–10 teeth, usually 6–8, the lateralmost unicuspid or bicuspid [one or both rarely unicuspid in resident *L. camtschaticum*

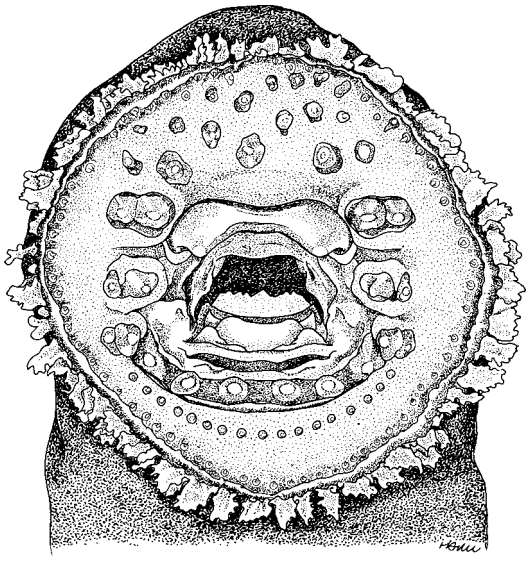

Fig. 114. Oral disc of *Lethenteron kessleri*. After a drawing by Susan Laurie–Bourque [based on a paratype of *Lethenteron matsubarai*, male, 164 mm TL, NMC (= CMNFI) 1984–274, Shokotsu River, Hokkaidō Island, Japan, 1950–1952, T. Hikita].

form *sensu* Kucheryavyi *et al.* (2007)] and occasionally some of the internal ones also bicuspid, the rest unicuspid; 3 endolaterals on each side; endolateral formula, typically 2–2–2, variant formulae, 2–2–1 and 2–1–2 [also 2–2–2–2 in resident *L. camtschaticum* form *sensu* Kucheryavyi *et al.* (2007)]; 2 rows of anterials; first row of anterials, 3–5 unicuspid teeth; total number of anterials, 15–28 unicuspid teeth [8–30 in resident *L. camtschaticum* form *sensu* Kucheryavyi *et al.* (2007)]; exolaterals usually absent, but if present, only 1 unicuspid tooth per lateral field; single row of posterials consisting of 16–25 unicuspid teeth [as low as 12 in resident *L. camtschaticum* form *sensu* Kucheryavyi *et al.* (2007)], sometimes completely absent; transverse lingual lamina, numerous unicuspid teeth, the median one enlarged; longitudinal lingual laminae parentheses–shaped, each with numerous unicuspid teeth. Velar tentacles, 7. Body coloration (live), brownish on dorsal and lateral aspects and whitish on the ventral aspect. Lateral line neuromast pigmentation unrecorded. Gular region pigmentation unrecorded. Second dorsal fin with a dark blotch near the apex; however, specimens from Japan do not have a dark blotch. Caudal fin pigmentation, – (rarely) or +++ (usually). Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater, in rivers, brooks, and lakes. Ammocoetes live in oozy substrate. Metamorphosing ammocoetes are mostly found in areas with abundant aquatic vegetation at the mouth of small streams.
Larval life lasts 6+ yrs. Ammocoetes feed on detritus and unicellular algae. Onset of metamorphosis is at the end of July beginning of August and is complete at the end of October to the middle of November. The population in the upper Irtysh River Basin is apparently unique among lampreys in that it continues to feed during metamorphosis gradually switching from a detritus and unicellular algae diet to an exclusively unicellular algae diet. This would explain the fact that the maximum total length of the metamorphosing ammocoete exceeds the maximum total length of the ammocoete; mean of 233 mm in the former versus 218 in the latter. Unicellular algae consumed include Cyanophyceae (*Oscillatoria*), Chlorophyceae (*Spirogyra*, *Chlorella*), and Diatomeae (*Fragilaria*, *Pinnularia*). This phenomenon is particularly interesting as it implies that the metamorphosing ammocoetes must switch from a filter–feeding mode to a grazing mode of feeding, since, during the process of metamorphosis, the oral cirrhi are lost. The grazing may be achieved possibly with the help of the lingual laminae and the action of the piston cartilage. Adults are nonparasitic. Spawning period in Japan in early May. Fecundity, 1,387–2,125 eggs/female in Japan, with long diameter of eggs varying from 1.12 to 1.22 mm and the short diameter from 0.91 to 1.11 mm. Kucheryavyi *et al.* (2007) reported a fecundity of 468–3,441 eggs/female in non–feeding adult stage resident *L. camtschaticum* (= *L. kessleri*?) on Kamchatka.

Geographic Distribution (Fig. 115): Russian Federation: Tom', Kirgizka, and Yenisei rivers, Kolyma and Anadyr river basins; Kazakhstan: Upper Irtysh River Basin (Irtysh, Ul'ba, and Cheremshanka rivers); Japan: Toufutsu Lake, Abira, Assabu, Atsuma, Barou, Betsubetsu, Bettouga, Chashikotsu, Chitose, Ichani, Mukawa, Nishikitappu, Saru, Shiraoi, Shizunai, Shokotsu, and Yuuchi rivers, Hokkaidō Island.

Interest to Fisheries: None

References: Anikin (1905), Berg (1931, 1948), Iwata *et al.* (1985), Kott *et al.* (1988), Kucheryavyi *et al.* (2007), Poltorykhina (1971, 1974), Sidorov and Pichugin (2005), Vladykov and Kott (1978b), Yamazaki *et al.* (2001, 2006)

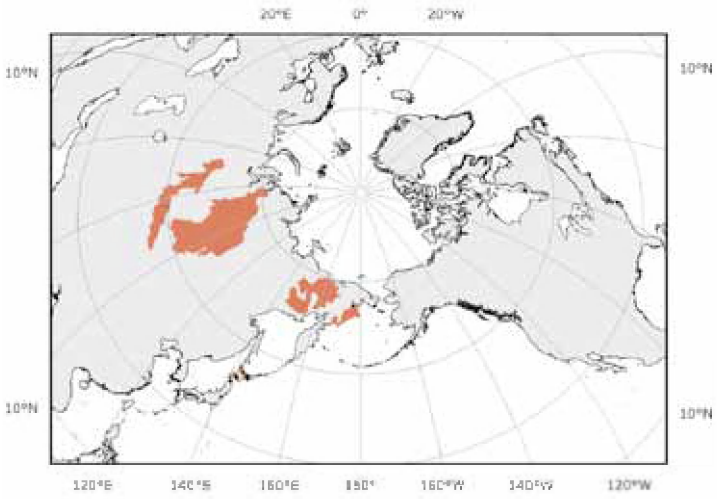

Fig. 115. Geographic distribution of *Lethenteron kessleri*.

Lethenteron ninae Naseka, Tuniyev, and Renaud 2009 **Figs. 116–118**

Synonyms: ***Lethenteron ninae*** Naseka, Tuniyev, and Renaud 2009: 18, 20, figs. 2, 3a, 4a, 5, 6, 7a, 8, Table 3 (holotype: adult female, 164 mm TL, ZISP 54431; type locality: Shakhe River at Khartsyz, Sochi District, 43° 48' 35" N 39° 36' 54" E, Black Sea Basin, Russian Federation)

FAO Names: En — Western Transcaucasian Brook Lamprey; **Fr** — Lamproie de ruisseau de la Transcaucasie occidentale

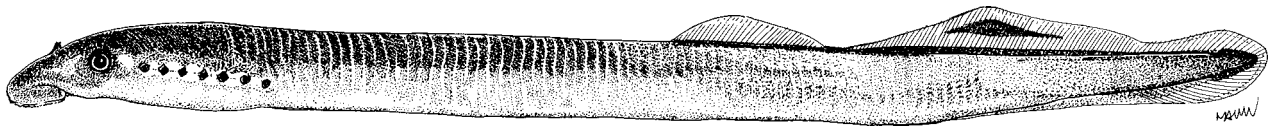

Fig. 116. Side view of *Lethenteron ninae* adult, 162.5 mm TL, paratype, ZISP 54435, Mokva River, Black Sea Basin, Abkhazia, Georgia, 24 Sept. 2007, S.B. Tuniyev. After Naseka *et al.* (2009).

Diagnostic Features: Ammocoetes: Maximum size known 148 mm TL. However, presumably attain greater lengths than 166 mm TL, the longest recorded length of the adults. Body proportions, as percentage of TL (based on nine specimens measuring 90–142 mm TL): prebranchial length, 7.0–7.9; branchial length, 12.5–13.7; trunk length, 50.4–54.0; tail length, 25.1–28.7. Trunk myomeres, 56–60. Pigmentation: upper lip, + (11% of specimens), ++ (22%), +++ (67%); cheek, ++ (33%), +++ (67%); subocular, – (22%), + (11%), ++ (33%), +++ (33%); upper prebranchial, +++ (100%); lower prebranchial, + (33%), ++ (67%); upper branchial, ++ (33%), +++ (67%); lower branchial, – (100%); ventral branchial, – (89%), + (11%); caudal fin, + (100%); tongue precursor bulb, –; along elastic ridge of tongue precursor, +. Lateral line neuromasts unpigmented. Tongue precursor bulb shape triangular. Caudal fin shape, rounded or spade–like. Body coloration (live and freshly preserved) is gray on the dorsal aspect and lighter on the ventral aspect and without mottling.

Metamorphosing ammocoetes: Size unrecorded.

Adults: 130.6–166 mm TL. Body proportions, as percentage of TL (based on 12 recently metamorphosed specimens measuring 130.6–166 mm TL): prebranchial length, 8.7-13.1; branchial length, 9.6–10.9; trunk length, 50.1–53.6; tail length, 25.7–29.2; eye length, 1.4–2.0; disc length, 3.8–5.2; prenostril length, 4.0–6.0; snout length, 4.8–6.9; postocular length, 2.7–3.6. Trunk myomeres, 58–62. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–7 mostly unicuspid teeth, but 1–2 may be bicuspid; 3 endolateral teeth on each side; endolateral formula, typically 2–2–2, but 2–3–2 (20% of cases) and 2–2–3 (15%) also occur; 1–2 rows of anterials; first row of anterials, 5–7 unicuspid teeth; exolaterals absent; first posterial row absent (27% of cases) or present in a single incomplete row consisting of 3–7 mostly unicuspid teeth, but 1–2 may be bicuspid; transverse lingual lamina, 9–15 unicuspid teeth, the median one greatly enlarged; longitudinal lingual laminae straight, each with 5–9 unicuspid teeth. Velar tentacles, 7; the median one shorter than the adjacent lateral ones and the tentacles have tubercles on their dorsal aspect. There are no velar wings. Body coloration (live and freshly preserved) is gray on the dorsal aspect and lighter on the ventral aspect and without mottling. Dark blotch near apex of second dorsal fin. Lateral line neuromasts darkly pigmented on the ventral surface and prebranchial region in some individuals but unpigmented in others. Caudal fin pigmentation, + or ++. Caudal fin shape, rounded or spade–like. Oral fimbriae, 69–99. Oral papillae number unrecorded.

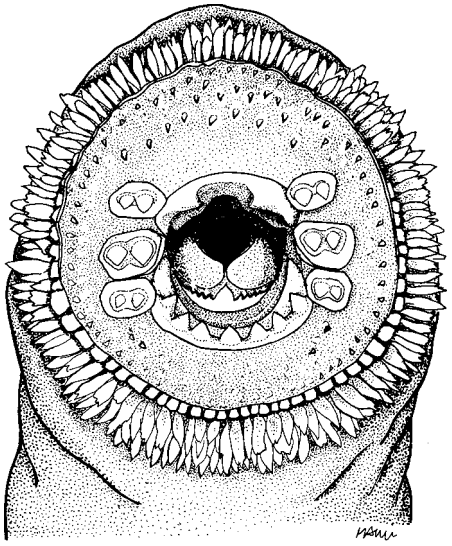

Fig. 117. Oral disc of *Lethenteron ninae*, female, 163.8 mm TL, holotype, ZISP 54431, Shakhe River at Khartsyz, Black Sea Basin, Sochi District, Russian Federation, 27 Sept. 2007, S.B. Tuniyev. After Naseka *et al.* (2009).

Habitat and Biology: Freshwater. Ammocoetes live in silt, sand or fine pebble substrate in the middle and lower sections of rivers where the current is absent or slow, at water depths of 10–50 cm, among submerged plants (*Rumex acetosella*, *Polygonum* sp., *Juncus* sp.). Adults are also found in the same general habitat as both life stages are commonly caught together.

Metamorphosis is believed to occur prior to mid–September when fully metamorphosed individuals were first caught. Adults are nonparasitic. The spawning period is undetermined.

Geographic Distribution (Fig. 118): Black Sea Basin: Shakhe and Mzymta rivers, and Chakhtsutsyr Brook, Russian Federation; Bzyb' and Mokva rivers, Abkhazia, Georgia.

Interest to Fisheries: None

Reference: Naseka *et al.* (2009)

Fig. 118. Geographic distribution of *Lethenteron ninae*.

Lethenteron reissneri (Dybowski 1869) Figs. 119–121

Synonyms: ***Petromyzon Reissneri*** Dybowski 1869: 958 (type locality: Onon and Ingoda rivers, Amur River Basin, Russian Federation)

Taxonomic Remarks: This taxon requires a revision in light of papers by Yamazaki and Goto (1998) and Yamazaki *et al.* (1999, 2003). They report on two morphologically indistinguishable but genetically divergent forms based on protein electrophoresis as well as mitochondrial DNA evidence. These cryptic species, refered to in Yamazaki *et al.* (2003, 2006) as *Lethenteron* sp. N(orthern) and *L.* sp. S(outhern), are partly sympatric on Honshū Island, Japan (Makino, Shou–gawa, and Ushiwatari rivers). They consider the two forms to be distinct undescribed species. The relationships between these two forms and either *L. reissneri* or *L. kessleri* is not clear. For the purposes of this catalog however, and pending such a revision, they are treated together here under *L. reissneri* since they had been treated as such in Yamazaki *et al.* (2001). More recent work by Yamazaki *et al.* (2006) shows that *Lethenteron* sp. N belongs in a monophyletic group with *L. camtschaticum*, *L. kessleri*, and *L. reissneri*, while *L.* sp. S forms a distinct clade based on both partial sequences of mtDNA genes, CO I (1009 bp) and cyt *b* (384 bp). However, all the material used in these analyses was larval and the results need to be corroborated with adult material.

FAO Names: En — Far Eastern Brook Lamprey; **Fr** — Lamproie de ruisseau de l'Extrême–Orient
Local name: Sunayatsume (Japanese)

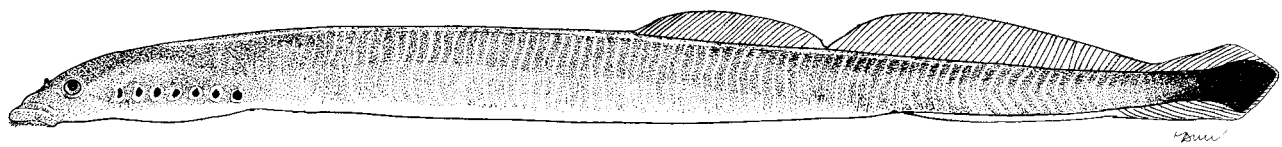

Fig. 119. Side view of *Lethenteron reissneri* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, at least 202 mm TL judging by the maximum total length attained by adults. Body proportions, as percentage of TL (based on 75 sympatric specimens of the northern and southern forms on Honshū Island, Japan measuring 59.7–145.4 mm TL): prebranchial length, 6.0–10.1; branchial length, 9.8–14.0; trunk length, 49.3–56.8; tail length, 22.9–30.9. Trunk myomeres, 51–60. Body coloration unrecorded. Pigmentation of various body regions unrecorded. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 111–202 mm TL. Body proportions, as percentage of TL (based on 19 specimens measuring 116–172 mm TL): prebranchial length, 10.3–12.3; branchial length, 9.6–13.3 (as low as 9.5 according to Iwata *et al.*, 1985); trunk length, 46.0-54.2; tail length, 25.0–31.6; eye length, 1.2–2.4; disc length, 4.7–6.4. The urogenital papilla length, as a percentage

of branchial length, in three spawning males measuring 143–154 mm TL, 26.7–48.8 [16.4–67.8 according to Iwata *et al.* (1985) based on 21 spawning males 111–154 mm TL]. Trunk myomeres, 57–65. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 6–11 unicuspid teeth; 3 endolaterals on each side; endolateral formula, typically 2–2–2; 1–2 rows of anterials; first row of anterials, 4–5 unicuspid teeth; total number of anterials, 38–44 unicuspid teeth according to Vladykov and Kott (1978a), however, one of the specimens that they identified in their publication as this species was used here for the drawing of the oral disc (fig. 120) and it only shows 13 unicuspid anterials; usually one exolateral present on one or both sides, exceptionally, one complete row of exolaterals on each side; single row of posterials consisting of 19–27 unicuspid teeth; transverse lingual lamina, 13 unicuspid teeth, the median one greatly enlarged; longitudinal lingual laminae each with 7–8 unicuspid teeth. Velar tentacles, 7, with tubercles, the median tentacle shorter than the lateral ones immediately next to it. Body coloration unrecorded. Lateral line neuromasts unpigmented. Gular region unpigmented. Second dorsal fin unpigmented. Caudal fin pigmentation, + (33%) or +++ (67%). Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater. Occurs in rivers, brooks, ponds, and lakes.
Adults nonparasitic. Spawning period in Japan is from mid to late May. Fecundity, 495–2,942 eggs/female in Japan, with the long diameter of eggs varying from 0.98 to 1.37 mm and the short diameter from 0.86 to 1.25 mm.

Geographic Distribution (Fig. 121): Russian Federation: Onon and Ingoda rivers (Amur River Basin), Tym' River (Sakhalin Island); Japan: Lake Biwa, Honshū Island and Ohnuma and Touru lakes, Hyotan Pond, Ashiribetsu, Atsunai, Butokamabetsu, Charo, Chitose, Futoro, Hekiriji, Kamekawa, Kikonai, Kotodo, Monbetsu, Moshosanbetsu, Ohno, Onbetsu, Osatsu, Rukotsu, Ruuomansorappchi, Ryukei, Shiriuchi, Shokanbetsu, Toubetsu, and Utabetsu rivers, Hokkaidō Island.

Interest to Fisheries: None

References: Dybowski (1869), Iwata *et al.* (1985), Kott *et al.* (1988), Okada (1955), Vladykov and Kott (1976d, 1978a, 1979c), Yamazaki and Goto (1997, 1998), Yamazaki *et al.* (1999, 2001, 2003, 2006)

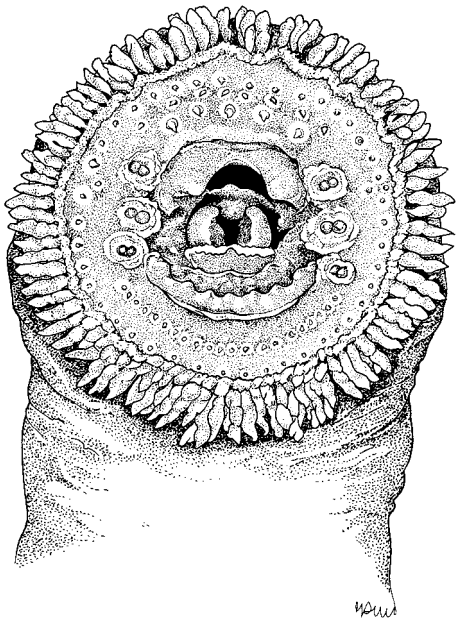

Fig. 120. Oral disc of *Lethenteron reissneri*. After a drawing by Paul I. Voevodine [NMC (= CMNFI) 1986–843, Osawa, Hokkaidō Island, Japan, 10 May 1936, S. Sato].

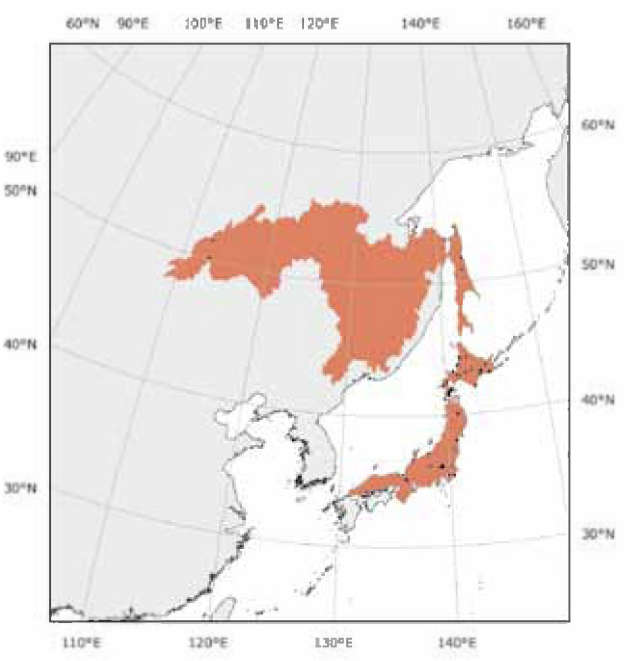

Fig. 121. Geographic distribution of *Lethenteron reissneri*.

Lethenteron zanandreai (Vladykov 1955) Figs. 122–124

Synonyms: ***Lampetra zanandreai*** Vladykov 1955: 216, pl. 1, table 2 (holotype: male, 131 mm TL, originally kept in the Provincial Department of Fisheries, Québec, Canada, and later transferred to NMC (= CMNFI) 1986–1; type locality: Guà di Lonigo River, Adige River Basin, Vicenza, Italy)

Taxonomic Remarks: In the original description, Vladykov (1955: 218) stated that "mandibular labials (= posterials) are lacking". However, examination of two topotypic paratypes [NMC (= CMNFI) 1986–1A] revealed the presence of two posterials in one and five posterials in the other. Furthermore, one of these also possessed four exolaterals in a row next to the marginal row on either side of the oral disc, while the other had none. It would seem therefore advisable to provisionally place this species in *Lethenteron* even though this genus by definition should not possess exolaterals.

FAO Names: En — Lombardy Brook Lamprey; **Fr** — Lamproie de ruisseau de Lombardie

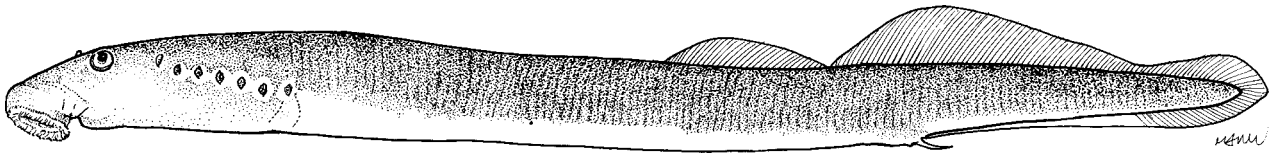

Fig. 122. Side view of *Lethenteron zanandreai*, male, 131 mm TL, holotype, NMC (= CMNFI) 1986–1, Guà di Lonigo River, Adige River Basin, Vicenza, Italy, 19 April 1953, G. Zanandrea. After Vladykov (1955).

Diagnostic Features: Ammocoetes: Maximum size attained, 158 mm TL. Body proportions, as percentage of TL (based on 24 specimens measuring 91–158 mm TL): prebranchial length, 7.6–9.3; branchial length, 11.8-13.8; trunk length, 50.5–54.4; tail length, 23.3–28.5. Trunk myomeres, 52–56. Body coloration unrecorded. Pigmentation: upper lip, – (11% of specimens) or + (68%) or ++ (21%); lower prebranchial, – (4%) or + (7%) or ++ (29%) or +++ (61%); upper branchial, + (43%) or ++ (46%) or +++ (11%); caudal fin, + (36%) or ++ (57%) or +++ (7%). Additionally, the lower lip (++) and the ventral branchial region (+ or ++) are pigmented. Lateral line neuromasts unpigmented. Caudal fin shape, rounded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 118–156 mm TL. Body proportions, as percentage of TL (based on 19 specimens measuring 118–156 mm TL): prebranchial length, 10.2–13.7; branchial length, 9.3–11.9; trunk length, 45.5–52.6; tail length, 24.0–28.7; eye length, 1.6–2.5; disc length, 4.6–6.9. The urogenital papilla length, as a percentage of branchial length, in six spawning males measuring 128–139 mm TL, 23.5–40.0. Trunk myomeres, 54–60. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–8 unicuspid teeth, usually 7; three endolaterals on each side; endolateral formula, typically 2–3–2 (2–2–2 in the holotype); 2 rows of anterials; first row of anterials, 4 unicuspid teeth; 0–1 row of exolaterals on each side; single incomplete row of posterials with 2–5 unicuspid teeth (2 in the holotype); transverse lingual lamina, 5–7 unicuspid teeth, the median one enlarged; longitudinal lingual laminae each with about 6 or 7 unicuspid teeth. Velar tentacles, 3–5, with tubercles. Body coloration (preserved), dorsal and lateral aspects grayish, ventral surface whitish, dorsal fins and caudal fin yellowish. No dark blotch near the apex of the second dorsal fin. Lateral line neuromasts unpigmented. Caudal fin pigmentation unrecorded. Caudal fin shape, spade–like. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

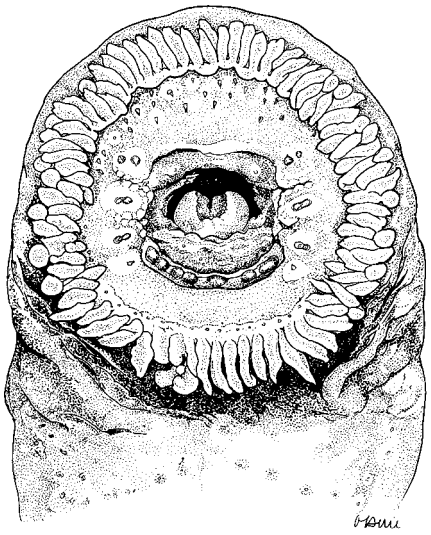

Fig. 123. Oral disc of *Lethenteron zanandreai*. After a drawing by Paul I. Voevodine [male, 131 mm TL, holotype, NMC (= CMNFI) 1986–1, Guà di Lonigo River, Adige River Basin, Vicenza, Italy, 19 April 1953, G. Zanandrea].

Habitat and Biology: Freshwater.
Adults nonparasitic.

Geographic Distribution (Fig. 124): Italy (Adige River Basin: Guà di Lonigo River and Po River Basin: Ticino River) and Croatia.

Interest to Fisheries: None

References: Holčík and Mrakovčić (1997), Kott *et al.* (1988), Naseka *et al.* (2009), Vladykov (1955), Vladykov and Kott (1976d, 1979c)

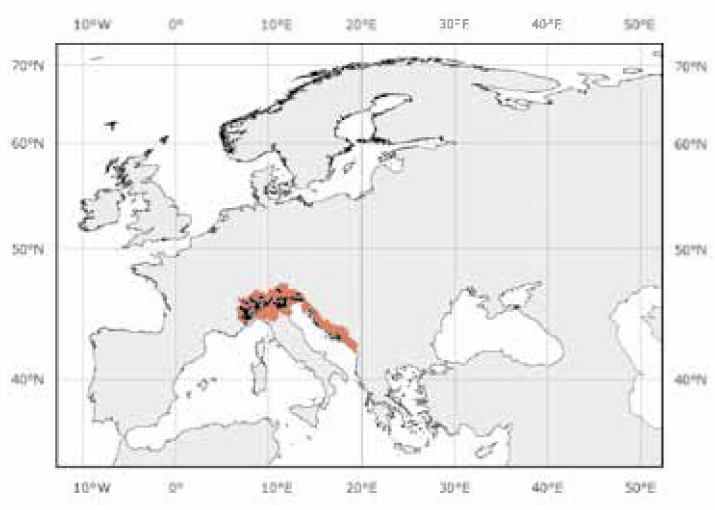

Fig. 124. Geographic distribution of *Lethenteron zanandreai*.

Genus *Petromyzon* Linnaeus 1758

Synonyms: ***Petromyzon*** Linnaeus 1758: 230; ***Bathymyzon*** (as subgenus) Gill 1883: 253–254 [based on an adult with obsolescent supraoral and infraoral laminae; ***Petromyzon*** (***Bathymyzon***) ***Bairdii*** Gill 1883 type species by monotypy]; ***Oceanomyzon*** Fowler 1908: 461 (***Oceanomyzon wilsoni*** Fowler 1908 type species by monotypy)

This is a monotypic genus (one parasitic species) with a widespread distribution, occurring in North America, Europe, and North Africa. Two dorsal fins. Supraoral lamina a single bicuspid tooth. Labial teeth radially–arranged in a curvilinear fashion and completely covering all fields of the oral disc. Transverse lingual lamina strongly w–shaped, the median tooth not enlarged. Velar tentacles are smooth and a median tentacle is usually absent. The type species is *Petromyzon marinus* Linnaeus 1758.

Petromyzon marinus Linnaeus 1758

Figs. 125–127

Synonyms: ***Petromyzon marinus*** Linnaeus 1758: 230 (type locality: European seas); ***Petromyzon Americanus*** Lesueur 1818: 383 (type locality: Philadelphia, presumably in the Delaware River); ***Petromyzon nigricans*** Lesueur 1818: 385; ***?Ammocoetes bicolor*** Lesueur 1818: 386–387 (type locality: Connecticut River, Massachusetts); ***Petromyzon marinus dorsatus*** Wilder in Jordan and Gilbert 1883: 869 (type locality: Cayuga Lake, New York, USA); ***Petromyzon*** (***Bathymyzon***) ***Bairdii*** Gill 1883: 253–254 (holotype: adult with obsolescent supraoral and infraoral laminae, USNM 33311, type locality: Atlantic Ocean, off New Jersey, USA, 40°02'00"N 68°50'30"W, US Fish Commission Steamer Albatross station 2048, 31 July 1883, 1000 m depth); ***Oceanomyzon wilsoni*** Fowler 1908: 461–464 (holotype: adult with damaged tail, ANSP 375, type locality: Atlantic Ocean)

FAO Names: En — Sea Lamprey (anadromous or landlocked), Lake Lamprey (landlocked form only); **Fr** — Lamproie marine

Fig. 125. Side view of *Petromyzon marinus* adult.

Diagnostic Features: Ammocoetes: Maximum size attained, 156 mm TL (but presumably at least 167 mm TL, the length attained by metamorphosing ammocoetes). Body proportions, as percentage of TL (based on 123 specimens measuring 60–129 mm TL; the values given below represent ranges of means based on six groups of samples as follows: 11 and 21 specimens 60–90 mm TL, 39 and 21 specimens 90–99 mm TL, and 10 and 21 specimens 120–129 mm TL): prebranchial length, 6.9–9.2; branchial length, 12.1–14.5; trunk length, 52.3–53.1; tail length, 23.4–28.8. Trunk myomeres, 67–74. Body coloration unrecorded. Pigmentation: upper lip, ++ or +++; cheek, +++; subocular, +++; upper prebranchial, ++ or +++; lower prebranchial, +; upper branchial, ++ or +++; lower branchial, –; caudal fin, ++ or +++; tongue precursor bulb, – ; along elastic ridge of tongue precursor, +. Lateral line neuromast pigmentation unrecorded. Caudal fin shape, typically rounded, rarely spade–like.

Metamorphosing Ammocoetes: 136–167 mm TL.

Adults: 114–1,200 mm TL. Body wet weight of the 1,200 mm TL individual was 2.3 kg. Maximum size attained by landlocked populations in the Laurentian Great Lakes, 600 mm TL. Body proportions, as percentage of TL (based on a variable number of specimens and sizes as indicated after the ranges): prebranchial length, 9.2–16.0 (in 46 specimens 192–827.5 mm TL); branchial length, 8.1–16.0 (in 46 specimens 192–827.5 mm TL); trunk length, 45.6–58.5 (in 42 specimens 256–827.5 mm TL); tail length, 22.0–42.2 (in 46 specimens 192–827.5 mm TL); eye length, 0.8–3.6 (in 49 specimens 135–827.5 mm TL); disc length, 4.5–9.3 (in 58 specimens 135–835 mm TL); snout length, 6.5–10.9 (in 41 specimens 256–827.5 mm TL). The urogenital papilla length, as a percentage of branchial length, in seven spawning males measuring 385–492 mm TL, 9.5–13.0. Spawning males develop a rope–like dorsal ridge ahead of the first dorsal fin and extending to the level of the posterior part of the branchial region, and hence, are sometimes called corded males. Trunk myomeres, 67–74. Dentition: supraoral lamina, 1 bicuspid tooth; infraoral lamina, 6–10 unicuspid teeth, the lateralmost sometimes bicuspid; 4 endolaterals on each side; endolateral formula, typically 2–2–2–2; 3 rows of anterials; first row of anterials, 1 unicuspid tooth; 5–7 rows of exolaterals on each side; 3 rows of posterials; first row of posterials, 10 unicuspid teeth; transverse lingual lamina strongly w–shaped, with 12–14 cusps, the median one not enlarged; longitudinal lingual laminae j–shaped, each with 12–14 cusps. Moderately well–developed marginal membrane. Velar tentacles, 2–3, smooth. Body coloration (preserved), newly–transformed individuals 135–175 mm TL have their colour grading from gray–bluish dorsally to silvery white ventrally while in individuals 450 mm TL or more the dorsal and lateral aspects become mottled and the ventral aspect remains uniformly pale. The iris is golden yellow. Lateral line neuromasts unpigmented or darkly pigmented. Caudal fin pigmentation, +++. Caudal fin shape, spade–like. Oral fimbriae, 114–150. Oral papillae, 24–33.

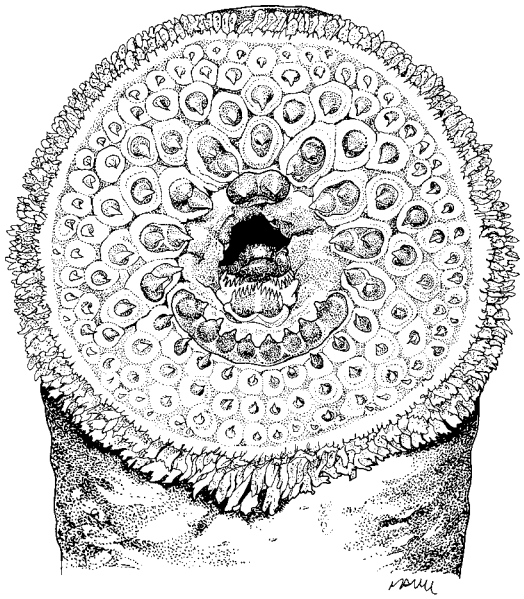

Fig. 126. Oral disc of *Petromyzon marinus*. After a drawing by Paul I. Voevodine [total length not known, but disc length is 47 mm, CMNFI 1995–22, St. Lawrence River at Saint–Vallier, Québec, Canada, May 1949, M. Labrecque].

Habitat and Biology: Some populations are permanent freshwater residents [Laurentian Great Lakes, Finger Lakes (Lake Cayuga), Lake Champlain], while others are anadromous. Occupies a wide range of streams and habitats. Larvae are found in streams with summer flows 0.03–4,400 m^3/s and summer water temperatures 10–26.1 °C. Relatively abundant in cool, pool–riffle streams with sand–gravel substrate, high water quality and stable flows, but is also tolerant of fluctuating flows. In Michigan, ammocoetes have been reported in lentic habitats up to 450 m from the presumed originating stream, at water depths 1–16 m, where substrates vary from sand–silt, with or without detritus, to gravel–rubble–sand. Feeding adults of permanent freshwater populations can be found in small to large lakes and large rivers and, in the case of anadromous populations, in small to large rivers and in the ocean. In the ocean, it occurs both pelagically and benthically, possibly to a depth of 4,099 m. Spawning adults can be found in creeks or lake inlets.

Duration of larval life is usually a minimum 5 yrs, but has been reported as short as 2 yrs and as long as 19 or more yrs. Duration of adult life in anadromous populations approximately two years. Metamorphosis occurs in July–October, but has been reported as early as April, in Michigan. In fresh waters, adults are parasitic on fishes (*Coregonus johannae*, *C. nigripinnis*, *C. zenithicus*, *Oncorhynchus mykiss*, *Salvelinus namaycush*) and in the sea, they are parasitic on fishes (*Cetorhinus maximus*, *Acipenser oxyrinchus*, *Alosa sapidissima*, *Clupea harengus*, *Salmo salar*, *Gadus morhua*, *Urophycis chuss*, *Scomber scombrus*) and marine mammals. Multiple attachments can occur (e.g., 3 on *Cetorhinus maximus*, 2–3 on *Urophycis chuss*). Adults are preyed upon by *Lamna nasus* in northwestern Atlantic waters. Feeding migrations in landlocked parasitic adults in the Laurentian Great Lakes can reach 628 km. In Michigan, the spawning period is from 27 May to 2 September, at water temperatures between 11.1–26.1 °C, with peak spawning activity in late

May to mid–June. In Ontario, nest building occurs from 4 to 21 June at water temperatures 18–23 °C. In Québec and New York streams spawning also occurs in June, but in New York lakes spawning is from the end of May to the beginning of July. Nests are built in streams having 1.5–43 m width, 15–90 cm depth, and 0.01–54 m^3/s flow. Up to ten spawning lampreys have been found in a nest. Fecundity, 43,997–101,932 [up to 108,000 according to Gage (1928)] eggs/female in landlocked populations and 151,836–304,832 eggs/female in anadromous populations. There are reported occurrences in Michigan of communal spawning of Sea Lamprey with Chestnut Lamprey (Pine, Platte, and Muskegon rivers), of Sea Lamprey with Northern Brook Lamprey (Devils River), of Sea Lamprey with Silver Lamprey (Carp Lake, Devils, East Au Gres, and Rifle rivers), of Sea Lamprey with American Brook Lamprey (Carp Lake, Pine and Pentwater rivers), of Sea Lamprey with American Brook Lamprey and Chestnut Lamprey (Betsie River), and of Sea Lamprey with American Brook Lamprey and Silver Lamprey (Carp Lake).

Geographic Distribution (Fig. 127): East and West North Atlantic Ocean – Canada and USA: Lake Superior Basin, Ontario, Michigan; Lake Michigan Basin, Wisconsin, Michigan (Carp Lake, Betsie, Muskegon, Pentwater, Pine, and Platte rivers), Illinois, and Indiana; Lake Huron Basin, Ontario, Michigan (Devils, East Au Gres, and Rifle rivers); Lake Erie Basin, Ontario, New York, Ohio, Michigan; Lake Ontario Basin, Ontario, New York; St. Lawrence River Basin (Québec, New York, Vermont) and along the eastern coast of Canada (Newfoundland-Labrador but only in the Newfoundland part, Québec, New Brunswick, and Nova Scotia) and the USA (New Hampshire, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Delaware, South Carolina, Florida) from Newfoundland down to Florida and into the Gulf of Mexico; west coast of Greenland; Iceland; European coast from Scandinavia (northern Norway) down into the Baltic Sea (Poland, Lithuania, Latvia, Estonia, Russian Federation, Finland), along the coasts of England (UK) (Severn River), France, and Portugal, and then down into the Mediterranean Sea (Spain, France, Italy) to the Adriatic Sea (Italy, Croatia, Bosnia and Herzegovina, Montenegro), and along the North African coast (Morocco, Algeria, Tunisia).

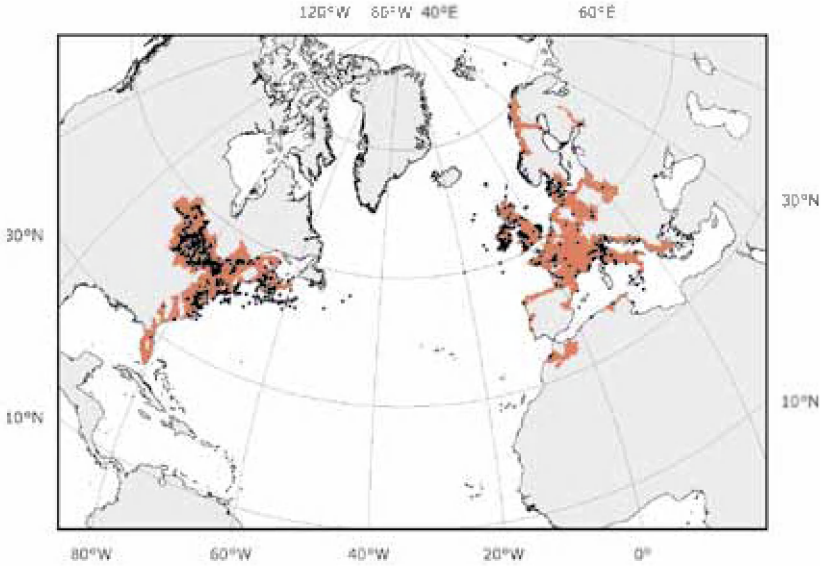

Fig. 127. Geographic distribution of *Petromyzon marinus*.

Interest to Fisheries: Invaded the upper Laurentian Great Lakes (Huron–Michigan–Superior) in the late 1930s, where it contributed to some extent to the collapse of the Lake Trout and various cisco (*Coregonus johannae*, *C. nigripinnis*, and *C. zenithicus*) fisheries. The fishes that did not die directly from the lamprey attacks or indirectly from secondary fungal infection had reduced market value because of the unsightly wounds. Splake, a fast–growing hybrid between Brook Trout and Lake Trout was developed specifically in response to the effect of Sea Lamprey on Lake Trout. Overfishing was also a major consideration in the demise of Lake Trout populations and Gilbertson (1992) has suggested that another contributing factor would be the extreme sensitivity of eggs and sac fry of this species to a persistent dioxin–like PCB isomer that was probably present in the Great Lakes by the 1930s and resulted in its reduced reproductive success. Sea Lamprey has been targeted by control measures in the Laurentian Great Lakes' Basin that include lampricide treatments (3–trifluoromethyl–4–nitrophenol, abbreviated as TFM, with or without the synergist 2',5–dichloro–4'–nitrosalicylanilide, abbreviated as Bayer 73) aimed at ammocoetes, beginning in 1957, electromechanical barriers that intercept upstream migrants, beginning before 1957, and later low–head barriers, adjustable–crest barriers, also known as inflatable barriers, traps, and chemosterilization of males. Approximately 258,000 adult Sea Lamprey, were taken between 1953 and 1960 at electrical barriers operated in Lake Superior Basin alone. Between 1958 and 1980, 54.5 million Canadian dollars where spent for Sea Lamprey control and research. Despite some attempts at developing a fishery oriented towards ethnic communities in large cities around the Great Lakes such as Toronto, a fishery for landlocked Sea Lamprey has not become established. Additionally, high levels of mercury in adults preclude their use for human consumption. Historical fisheries for the anadromous form existed in the 1800s on the Merrimack and Connecticut rivers, Massachusetts, when it was abundant, before dams and pollution. Such fisheries have existed for centuries in Europe [England (UK), France, Portugal]. Recipes include Lamproie à la bordelaise, which involves cooking in red wine. There are reports of intoxication through eating this species (Halstead, 1967).

References: Anonymous (2000), Beamish and Potter (1975), Berg (1948), Bonnaterre (1788), Borri (1922), Boutellier (1918), Bryan *et al.* (2005), Cochran and Marks (1995), Dollfus (1955), Fetterolf (1980), Fowler (1908), Gage (1893, 1928),

Gilbertson (1992), Gill (1883b), Haedrich (1977), Halliday, (1991), Halstead (1967), Hardisty (1986a), Heldt (1958), Holčík *et al.* (2004), Hussakof (1912), Jordan and Gilbert (1883), Jordan *et al.* (1930), Joyce *et al.* (2002), Khidir and Renaud (2003), Kott (1971), Kott *et al.* (1988), Lesueur (1818), Linnaeus (1758), Manion (1967, 1972), Manion and Smith (1978), Morkert *et al.* (1998), Morman (1979), Oliva (1953), Renaud (1997), Saemundsson (1927), Seurat and Dieuzeide (1931), Starrett *et al.* (1960), Surface (1899), Vladykov (1949, 1950, 1973b), Vladykov and Kott (1976d, 1980a, 1980b), Volk (1986)

Genus *Tetrapleurodon* Creaser and Hubbs 1922

Synonyms: ***Tetrapleurodon*** Creaser and Hubbs 1922: 3 (proposed as a subgenus of ***Entosphenus***)

This genus comprises two species (1 parasitic and 1 nonparasitic) endemic to México. Two dorsal fins. Supraoral lamina with two unicuspid teeth separated by a wide bridge, which may occasionally bear one or two unicuspid teeth. Labial teeth radially–arranged in a curvilinear fashion and found in all fields of the oral disc but do not fill all of the available space, especially in the lateral and posterior fields. Infraoral lamina cusps internal to the lateralmost ones generally of two sizes. Transverse lingual lamina weakly u–shaped with the median cusp only slightly enlarged. Velar tentacles with tubercles and a median tentacle is present (at least in *T. spadiceus*). The type species is *Lampetra spadicea* Bean 1887. *T. geminis* is believed to be the nonparasitic derivative of *T. spadiceus*. In the upper reaches of the Celio River, Michoacán, México, both species are found in spawning readiness on the same spawning grounds in November.

Tetrapleurodon geminis Álvarez del Villar 1966 **Figs. 128–130**

Synonyms: ***Tetrapleurodon geminis*** Álvarez del Villar 1966: 121 (fig. 5 in the original description is not a photograph of the holotype in side view because the individual in the figure measures only about 120 mm TL; holotype: male, 136 mm TL, whereabouts unknown; type locality: Celio River, at Jacona, Michoacán, México)

FAO Names: En — Jacona Lamprey, Mexican Brook Lamprey; **Fr** — Lamproie de ruisseau mexicaine; **Sp** — Lamprea de Jacona

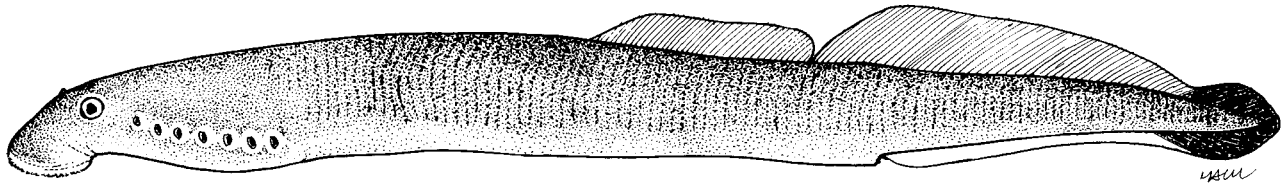

Fig. 128. Side view of *Tetrapleurodon geminis*, adult, about 120 mm TL. After Álvarez del Villar (1966).

Diagnostic Features: Ammocoetes: Álvarez del Villar (1966) could not distinguish larvae of this species from those of *Tetrapleurodon spadiceus* (see species account below) and the following description probably applies to both species. Maximum size attained, 176 mm TL. Body proportions, as percentage of TL (based on 30 specimens measuring 120–173 mm TL): prebranchial length, 6.7–9.3; branchial length, 11.2–13.9; trunk length, 47.0–52.5; tail length, 27.2–31.2. Trunk myomeres, 61–65. Body coloration, dark gray on the dorsal and lateral aspects and cream colored on the ventral aspect. Pigmentation: upper branchial, ++; caudal fin, +++; tongue precursor bulb, –; along elastic ridge of tongue precursor, –. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.
Metamorphosing Ammocoetes: lengths unrecorded.
Adults: 106–148 mm TL. Body wet weight of individuals measuring 108–148 mm TL, 4.3–7.0 g. Body proportions, as percentage of TL [based on 22 specimens for which the range in TL was not given but inferred to be 106–148 mm based on other parts of the text in Álvarez del Villar (1966)]: prebranchial length, 12.0–14.2; branchial length, 9.3–11.6; trunk length, 40.3–50.7; tail length, 26.7–32.9; eye length, 2.0 (holotype); disc length, 5.7 (holotype). The urogenital papilla length, as a percentage of branchial length, in four spawning males measuring 115–126 mm TL, 7.7–12.5. Trunk myomeres, 60–65. Dentition: supraoral lamina, 2 unicuspid teeth; infraoral lamina, 5–9 unicuspid teeth of which 5 are large and 0–4 are small

(87% of specimens possess both large and small cusps); endolaterals on each side 3–4; endolateral formula, typically 2–2-2–2 or 1–1–1, but one to six endolaterals may be missing; 3 rows of anterials; first row of anterials, 2 unicuspid teeth; 1 row of exolaterals; 1 row of posterials; first row of posterials, 8 unicuspid and 1 bicuspid teeth; transverse lingual lamina, 19 unicuspid teeth, the median one slightly enlarged; longitudinal lingual laminae with undetermined number of teeth. Velar tentacle number unrecorded. Body coloration unrecorded. Lateral line neuromast pigmentation unrecorded. Caudal fin pigmentation, +++. Caudal fin shape unrecorded. Oral fimbriae number unrecorded. Oral papillae number unrecorded.

Habitat and Biology: Freshwater, in rivers. Spawning habitat is a fast–flowing, clear–water stream with a stony substrate.

Since Álvarez del Villar (1966) could not distinguish between ammocoetes of the two species of *Tetrapleurodon*, aspects treated here that refer to ammocoetes probably apply to both species. Eggs hatch between the months of November and January and ammocoetes undergo metamorphosis at the end of three years. Ammocoetes live in the mud and feed on plankton (algae of the genera *Rhizosolenia*, *Pleurosigma*, *Pinularia*, *Stauroneis*, *Amphora*, and *Cocconema*, filamentous Chlorophyceae, rotifers, ciliates, and occasionally euglenoid flagellates). The mean total length reached at the end of the first year of larval life is 83 mm; at the end of two years, 135 mm; and at the end of three years, 146 mm. During the rainy season (July) of their first year, ammocoetes exhibit shrinkage in their total length. Metamorphosis occurs in April–August. Adults nonparasitic. After 3–4 months of adult life, spent downstream in the Duero River, they migrate a short distance (3 km) upstream to the spawning grounds in the upper reaches of the Celio River and die after spawning. The duration of the adult life is therefore at most six months. Spawning period between 19 November (when the water temperature reaches about 20°C) and 3 January. Fecundity, 990–3,456 eggs/female. Egg diameter, 0.7–0.8 mm.

Geographic Distribution (Fig. 130): México: Celio River, at Jacona and Duero River (Michoacán State).

Interest to Fisheries: None

References: Álvarez del Villar (1966), Cochran *et al.* (1996), Kott *et al.* (1988), Miller *et al.* (2005), Vladykov and Kott (1979c)

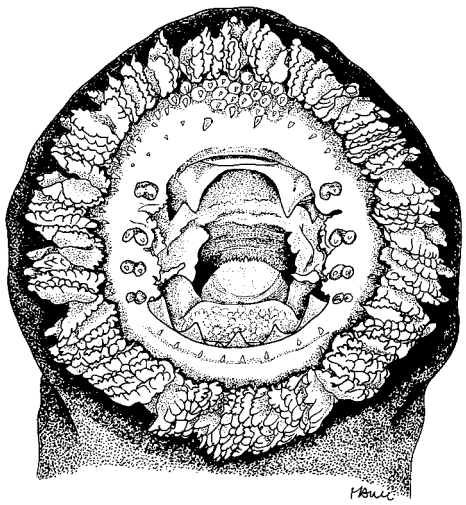

Fig. 129. Oral disc of *Tetrapleurodon geminis*. After a drawing by Susan Laurie–Bourque [128 mm TL, NMC (= CMNFI) 1986–709, Michoacán State, México].

Fig. 130. Geographic distribution of *Tetrapleurodon geminis*.

Tetrapleurodon spadiceus (Bean 1887) Figs. 131–133

Synonyms: ***Lampetra spadicea*** Bean 1887: 374–375, pl. XX, fig. 6 [holotype: adult of undetermined sex, 188 mm TL, USNM 38005; type locality: Guanajuato State, México is given in the original description, but this has been questioned by Álvarez del Villar (1966) because A. Dugès, who sent the holotype to Bean, referred to it as Jacona 'eel', and therefore, the type locality is more probably Jacona, in Michoacán State, México].

FAO Names: En — Chapala Lamprey, Mexican Lamprey; **Fr** — Lamproie mexicaine; **Sp** — Lamprea de Chapala

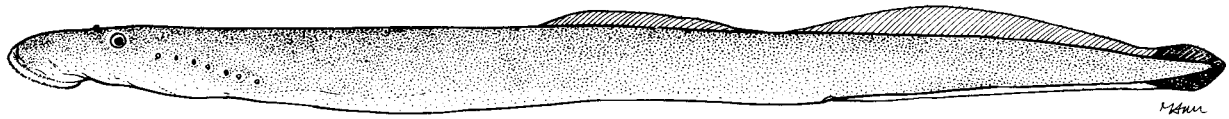

Fig. 131. Side view of *Tetrapleurodon spadiceus*. After a photograph by Brian W. Coad [prespawning adult, 264.5 mm TL, UMMZ 192539, Lake Chapala, Jalisco State, México, 20 June 1969, C.D. Barbour and R.J. Douglass].

Diagnostic Features: Ammocoetes: Álvarez del Villar (1966) could not distinguish larvae of this species from those of *Tetrapleurodon geminis* (see preceding species account) and the following description probably applies to both species. Maximum size attained, 176 mm TL. Body proportions, as percentage of TL (based on 30 specimens measuring 120–173 mm TL): prebranchial length, 6.7–9.3; branchial length, 11.2–13.9; trunk length, 47.0–52.5; tail length, 27.2–31.2. Trunk myomeres, 61–65. Body coloration, dark gray on the dorsal and lateral aspects and cream colored on the ventral aspect. Pigmentation: upper branchial, ++; caudal fin, +++; tongue precursor bulb, –; along elastic ridge of tongue precursor, –. Lateral line neuromast pigmentation unrecorded. Caudal fin shape unrecorded.

Metamorphosing Ammocoetes: lengths unrecorded.

Adults: 180–310 mm TL. Body wet weight of individuals measuring 187–225 mm TL, 21.3–26.3 g. Body proportions, as percentage of TL [based on 54 specimens for which the range in TL was not given but inferred to be roughly 180–310 mm TL based on Fig. 6 in Álvarez del Villar (1966)]: prebranchial length, 10.9–15.7; branchial length, 8.2–13.6; trunk length, 41.0–50.3; tail length, 27.2–34.3; eye length unrecorded; disc length unrecorded. The urogenital papilla length, as a percentage of branchial length, in spawning males unrecorded. Trunk myomeres, 60–65. Dentition: supraoral lamina, 2 unicuspid teeth, but 20% of individuals had 1–2 additional unicuspid teeth on the bridge; infraoral lamina, 5–9 unicuspid teeth, of which 4–5 are large and 0–4 are small (84% of specimens possess both large and small cusps); 4 endolaterals on each side, exceptionally 3 or 5; endolateral formula, typically 2–2–2–2, rarely, one of the teeth is tricuspid; 3 rows of anterials; first row of anterials, 6 unicuspid teeth; 1 row of exolaterals; 1 rows of posterials; first row of posterials, 21 unicuspid teeth; transverse lingual lamina weakly u–shaped, 17–22 unicuspid teeth, the median one or two unicuspid teeth slightly enlarged; longitudinal lingual laminae parentheses–shaped, each with 24–25 unicuspid teeth. Velar tentacles, 19–21, with tubercles; the dorsal wings are long, reaching the median tentacle. Body coloration unrecorded. Lateral line neuromasts unpigmented. Caudal fin pigmentation, +++. Caudal fin shape, spade–like. Oral fimbriae, 109–136. Oral papillae, 13–27.

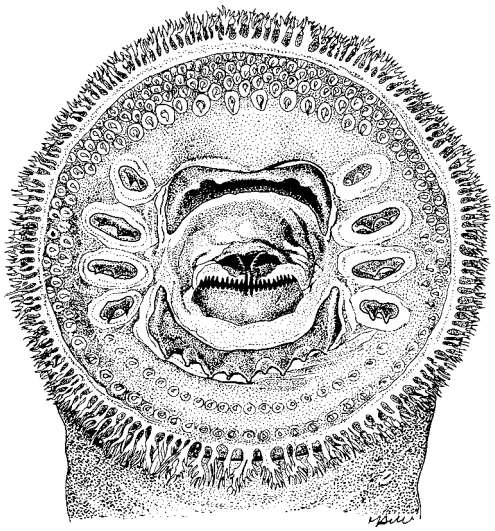

Fig. 132. Oral disc of *Tetrapleurodon spadiceus*. After a drawing by Paul I. Voevodine [female, 247 mm TL, USNM 43766, Tangancícuaro, Michoacán State, México, Aug. 1891].

Habitat and Biology: Freshwater, in lakes and rivers. Spawning habitat is a fast–flowing, clear–water stream with a stony substrate.

Since Álvarez del Villar (1966) could not distinguish between ammocoetes of the two species of *Tetrapleurodon*, aspects treated here that refer to ammocoetes probably apply to both species. Eggs hatch between the months of November and January and ammocoetes undergo metamorphosis at the end of three years. Ammocoetes live in the mud and feed

on plankton (algae of the genera *Rhizosolenia*, *Pleurosigma*, *Pinularia*, *Stauroneis*, *Amphora*, and *Cocconema*, filamentous Chlorophyceae, rotifers, ciliates, and occasionally euglenoid flagellates). The mean total length reached at the end of the first year of larval life is 83 mm; at the end of two years, 135 mm; and at the end of three years, 146 mm. During the rainy season (July) of their first year, ammocoetes exhibit a shrinkage in their total length. Metamorphosis occurs in April–August. Following metamorphosis, adults migrate to Lake Chapala or the Duero River (Lerma River Basin) where they live as ectoparasites of fishes (carp and catfish) for two years. The diet appears to be predominantly blood. A large number of scales of *Moxostoma austrinum* and either of *Algansea popoche*, *Yuriria alta*, or *Y. chapalae*, as well as possibly *Chirostoma* sp. has been found mixed with blood in the intestine of adults. Attacks on the small cyprinids and the atherinopsid almost certainly resulted in their death. Around late June, early July they begin to migrate upstream to the spawning grounds in the upper reaches of the Celio River and die after spawning. Nine individuals in spawning readiness were collected on 19 November (water temperature was about 20°C). Fecundity, 6,617–9,095 eggs/female. Egg diameter, 0.7–0.8 mm.

Geographic Distribution (Fig. 133): México: Celio River, at Jacona and Duero River, at Zamora (Michoacán State), Lerma River and Lake Chapala (Jalisco and Michoacán states). All these drain into the Pacific Ocean through the Santiago River.

Interest to Fisheries: Is presumed to kill a certain number of commercial fish species (*Algansea popoche* and *Chirostoma* sp.) in Lake Chapala.

References: Álvarez del Villar (1966), Bean (1887), Cochran *et al.* (1996), Khidir and Renaud (2003), Miller *et al.* (2005), Vladykov and Kott (1976d, 1979c)

Fig. 133. Geographic distribution of *Tetrapleurodon spadiceus*.

2. LITERATURE CITED

Abbott, C.C. 1860. Descriptions of new species of American fresh–water fishes. *P. Acad. Nat. Sci. Phila.,* 12: 325–328.

Ackerman, J. 1997. Parasites. *Natl. Geogr.,* 192(4): 74–91.

Agassiz, L. 1850. *Lake Superior: Its physical character, vegetation, and animals, compared with those of other regions*. Gould, Kendall, and Lincoln, Boston, Massachusetts. xii + 428 pp. + 8 pls.

Álvarez del Villar, J. 1966. Ictiologia michoacana, IV. Contribución al conocimiento biológico y sistemático de las lampreas de Jacona, Mich., México. *An. Esc. Nac. Cienc. Biol. Mex.,* 13(1–4): 107–144.

Anikin, V.P. 1905. Opisanie novÿkh aziatskikh vidov rÿb. *Izv. Tomsk. Univ.*, 1–18.

Anonymous. 2000. Parasites deal with a nasty shark meal. *Natl. Geogr.,* 198(1): unpaginated, *In Earth Almanac section*.

Anonymous. 2004. Native Fish Strategy for the Murray–Darling Basin 2003–2013. Murray–Darling Basin Commission, Canberra, Australia. viii + 50 pp.

Askerov, F., Y. Zaytsev, R. Kasimov, & Guliyev, Z. 2001. *Biodiversity: Amazing Caspian fishes*. Print Studio Publishing House, Baku, Azerbaijan. 162 pp.

Ayres, W.O. 1855a. Description of *Petromyzon plumbeus*. *The Pacific,* 4(10): 2.

Ayres, W.O. 1855b. Description of new fishes from California. *The Pacific,* 4(20): 2.

Bahr, K. 1933. Das Flussneunauge (*Lampreta fluviatilis*) als Urheber von Fischverletzungen. *Mitt. Deutsch. Seefisch. Ver.,* 49(1): 3–8.

Bailey, R.M. 1980. Comments on the classification and nomenclature of lampreys – an alternative view. *Can. J. Fish. Aquat. Sci.,* 37(11): 1626–1629.

Baldwin, J., K. Mortimer, & Patak, A. 1988. Evolutionary relationships among lamprey families: Amino acid composition analysis of lactate dehydrogenase. *Biochem. Syst. Ecol.,* 16(3): 351–353.

Balon, E.K. & Holčík, J. 1964. Kilka nowych dla Polski form kragłoustych i ryb z dorzecza Dunaju (Czarna Orawa). *Fragm. Faun. (Wars.),* 11: 189–206.

Bănărescu, P. 1969. Cyclostomata şi Chondrichthyes (ciclostomi şi selacieni). *Fauna Republicii Socialista Romania,* 12(1): 5–54.

Bardack, D. & Zangerl, R. 1968. First fossil lamprey: A record from the Pennsylvanian of Illinois. *Science,* 162: 1265–1267.

Barnhart, P.S. 1936. *Marine fishes of southern California*. University of California Press, Berkeley, California, United States. iv + 209 pp.

Beamish, F.W.H. & Potter, I.C. 1975. The biology of the anadromous Sea Lamprey (*Petromyzon marinus*) in New Brunswick. *J. Zool.,* 177: 57–72.

Beamish, F.W.H. & Lowartz, S. 1996. Larval habitat of American Brook Lamprey. *Can. J. Fish. Aquat. Sci.,* 53(4): 693–700.

Beamish, F.W.H., P.K. Ott, & Roe, S.L. 1994. Interpopulational variation in fecundity and egg size in Southern Brook Lamprey, *Ichthyomyzon gagei*. *Copeia,* (3): 718–725.

Beamish, R.J. 1980. Adult biology of the River Lamprey (*Lampetra ayresi*) and the Pacific Lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. *Can. J. Fish. Aquat. Sci.,* 37(11): 1906–1923.

Beamish, R.J. 1982. *Lampetra macrostoma*, a new species of freshwater parasitic lamprey from the west coast of Canada. *Can. J. Fish. Aquat. Sci.,* 39(5): 736–747.

Beamish, R.J. 1985. Freshwater parasitic lamprey on Vancouver Island and a theory of the evolution of the freshwater parasitic and nonparasitic life history types. pp. 123–140. *In* Foreman, R.E., A. Gorbman, J.M. Dodd, & R. Olsson, eds. *Evolutionary Biology of Primitive Fishes: Proceedings of a NATO Advanced Research Workshop*, Plenum Press, New York.

Beamish, R.J. 2001. Updated status of the Vancouver Island Lake Lamprey, *Lampetra macrostoma*, in Canada. *Can. Field Nat.,* 115(1): 127–130.

Beamish, R.J. & Williams, N.E. 1976. A preliminary report on the effects of River Lamprey (*Lampetra ayresii*) predation on salmon and herring stocks. *Tech. Rep. Fish. Mar. Serv.,* No. 611. 26 pp.

Beamish, R.J. & Withler, R.E. 1986. A polymorphic population of lampreys that may produce parasitic and a nonparasitic varieties. pp. 31–49. *In* Uyeno, T., R. Arai, T. Taniuchi, & K. Matsuura, eds. *Indo–Pacific Fish Biology: Proceedings of the Second International Conference on Indo–Pacific Fishes*, Ichthyological Society of Japan, Tokyo, Japan.

Beamish, R.J. & Northcote, T.G. 1989. Extinction of a population of anadromous parasitic lamprey, *Lampetra tridentata*, upstream of an impassable dam. *Can. J. Fish. Aquat. Sci.,* 46: 420–425.

Beamish, R.J. & Neville, C–E.M. 1992. The importance of size as an isolating mechanism in lampreys. *Copeia,* 1992(1): 191–196.

Beamish, R.J., J.H. Youson, & Chapman, L.A. 2001. Status of the Morrison Creek Western Brook Lamprey, *Lampetra richardsoni*, in Canada. *Can. Field Nat.,* 115(4): 573–578.

Bean, T.H. 1881. Descriptions of new fishes from Alaska and Siberia. *Proc. U. S. Nat. Mus.,* 4: 144–159.

Bean, T.H. 1887. Descriptions of five new species of fishes sent by Prof. A Dugès from the province of Guanajuato, Mexico. *Proc. U. S. Nat. Mus.,* 10(637): 370–375 + 1 pl.

Belyĭ, N.D. 1966. Morfologicheskie i nekotorye biologicheskie osobennosti ukrainskoĭ minogi – *Lampetra mariae* (Berg) reki Dnepra. *Zool. Zh.,* 45(4): 585–590.

Berg, L.S. 1906. Ubersicht der Marsipobranchii des Russischen Reiches. *Bull. Acad. Imp. Sci. Saint-Petersbourg,* 24(3): 169–183.

Berg, L.S. 1931. A review of the lampreys of the northern hemisphere. *Ann. Mus. Zool. Acad. Sci. de l'URSS*, 32(1): 87–116 + 8 pls.

Berg, L.S. 1948. Freshwater Fishes of the USSR and Adjacent Countries. *Guide to the Fauna of the USSR* No. 27. Vol. 1, 504 pp. Israel Program for Scientific Translations Ltd., Jerusalem.

Bergstedt, R.A. & Seelye, J.G. 1995. Evidence for lack of homing by sea lampreys. *T. Am. Fish. Soc.,* 124(2): 235–239.

Bloch, M.E. 1784. M. Marcus Elieser Bloch's …, ausübenden Arztes zu Berlin, Oeconomische Naturgeschichte der Fische Deutschlands. Berlin. *Fische Deustchlands* vol. 3: viii + 234 pp. + pls. 73–108.

Bloch, M.E. 1795. *Naturgeschichte der ausländischen Fische*. Vol. 9. Berlin, Germany.

Bonaparte, C.L. 1832. *Iconografia delle fauna italica per le quattro classi degli animali vertebrati.* Tomo III. *Pesci*. Roma. 556 pp. + 78 pls.

Bond, C.E. & Kan, T.T. 1973. *Lampetra (Entosphenus) minima* n. sp., a dwarfed parasitic lamprey from Oregon. *Copeia,* 1973(3): 568–574.

Bonnaterre, J.P. 1788. Tableau encyclopédique et méthodique des trois règnes de la nature. *Ichthyologie*. Paris, France. lvi (there is no p. iii), + 215 pp. + pls. A and B + 100 pls.

Borri, C. 1922. L'apparecchio labiale dei Petromyzonti. *Atti Soc. Tosc. Sci. Nat.,* 34 : 249–316 + 2 pls.

Boutellier, P. 1918. *La pêche maritime au Maroc*. G. Mercié & Co., Casablanca. 94 pp.

Burr, B.M. & Warren, M.L. Jr. 1986. A distributional atlas of Kentucky fishes. *Ky. Nat. Pres. Comm. Sci. Tech.,* no. 4.

Bryan, M.B., D. Zalinski, K.B. Filcek, S. Libants, W. Li, & Scribner, K.T. 2005. Patterns of invasion and colonization of the Sea Lamprey (*Petromyzon marinus*) in North America as revealed by microsatellite genotypes. *Mol. Ecol.,* 14: 3757–3773.

Burmeister, H.C.C. 1868. [*Petromyzon macrostomus*, descriptión de una nueva especie de pez.] *An. Mus. Nac. B. Aires (Actas de la Sociedad Paleontológica de Buenos Aires),* 1: xxxv–xxxvii.

Carl, G.C. 1953. Limnobiology of Cowichan Lake, British Columbia. *J. Fish. Res. Board Can.,* 9(9): 417–449.

Case, B. 1970. Spawning behaviour of the Chestnut Lamprey (*Ichthyomyzon castaneus*). *J. Fish. Res. Board Can.,* 27(10): 1872–1874.

Chang, M.–m., J. Zhang, & Miao, D. 2006. A lamprey from the Cretaceous Jehol biota of China. *Nature,* 441: 972–974.

Chappuis, P.A. 1939. Über die Lebensweise von *Eudontomyzon danfordi* Regan. *Arch. Hydrobiol.,* 34: 645–658 + 1 pl.

Chase, S.D. 2001. Contributions to the life history of adult Pacific Lamprey (*Lampetra tridentata*) in the Santa Clara River of southern California. *Bull. South. Calif. Acad. Sci.,* 100(2): 74–85.

Cheng, Y., S. Hou & Hou, C. 1993. *The freshwater fishes of China in coloured illustrations*. Vol. 3, K. Zhu, ed., Institute of Hydrobiology, Chinese Academy of Sciences.

Choudhury, A. & Dick, T.A. 1993. Parasites of Lake Sturgeon, *Acipenser fulvescens* (Chondrostei: Acipenseridae), from central Canada. *J. Fish Biol.,* 42: 571–584.

Chute, W.H., R.M. Bailey, W.A. Clemens, J.R. Dymond, S.F. Hildebrand, G.S. Myers, & Schultz, L.P. 1948. A list of common and scientific names of the better known fishes of the United States and Canada. *Spec. Publ. Am. Fish. Soc.,* no. 1: 1–45. Ann Arbor, Michigan.

Close, D.A., M.S. Fitzpatrick, & Li, H.W. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific Lamprey. *Fisheries,* 27(7): 19–25.

Cochran, P.A. 1997. Giants & satellites: Alternative life histories and reproductive behaviors in the American Brook Lamprey (*Lampetra appendix*). Abstract, p. 99. 77th Annual Meeting of the American Society of Ichthyologists and Herpetologists, 26 June – 2 July 1997, University of Washington, Seattle, Washington.

Cochran, P.A. & Marks, J.E. 1995. Biology of the Silver Lamprey, *Ichthyomyzon unicuspis*, in Green Bay and the lower Fox River, with a comparison to the Sea Lamprey, *Petromyzon marinus*. *Copeia,* 1995(2): 409–421.

Cochran, P.A., J. Lyons, & Merino–Nambo, E. 1996. Notes on the biology of the Mexican lampreys *Lampetra spadicea* and *L. geminis* (Agnatha: Petromyzontidae). *Ichthyol. Explor. Freshwat.*, 7(2): 173–180.

Cochran, P.A., J. Lyons, & Gehl, M.R. 2003. Parasitic attachments by overwintering silver lampreys, *Ichthyomyzon unicuspis*, and chestnut lampreys, *Ichthyomyzon castaneus*. *Environ. Biol. Fish.,* 68(1): 65–71.

Comtois, A., F. Chapleau, C.B. Renaud, H. Fournier, B. Campbell, & Pariseau, R. 2004. Inventaire printanier d'une frayère multispécifique: l'ichtyofaune des rapides de la rivière Gatineau, Québec. *Can. Field Nat.,*118(4): 521–529.

Cook, F.A. 1952. Occurrence of the lamprey *Lampetra aepyptera* in the Tombigbee and Pascagoula drainages, Mississippi. *Copeia,* 1952(4): 268.

Cook, R.D., I.C. Potter, & Hilliard, R.W. 1990. Morphology and innervation of the buccal glands of the Southern Hemisphere lamprey, *Geotria australis*. *J. Morphol.,* 206(1): 133–145.

Couch, S.L.L. & Lance, M.M. 2004. Diet composition and breeding success of Brandt's cormorants in the Columbia River estuary. *Northwestern Nat.,* 85(2): 62–66.

Creaser, C.W. & Hubbs, C.L. 1922. A revision of the Holarctic lampreys. *Occas. Pap. Mus. Zool.*, University of Michigan No. 120: 1–14 + 1 pl.

Daniels, R.A., D.M. Carlson, R.S. Morse, & Weatherwax, B.R. 2006. Fish, *Ichthyomyzon bdellium, Ichthyomyzon greeleyi, Noturus flavus, Moxostoma breviceps, Lythrurus umbratilis, Notropis buccatus, Misgurnus anguillicaudatus, Morone americana, Lepomis cyanellus, Ammocrypta pellucida*: Distribution extensions. *Check List,* 2(1): 10–13.

de Buen, F. 1961. Las lampreas (Marsipobranchii o Ciclostomi) en aguas de Chile. *Invest. Zool. Chil.,* 7: 101–124.

de Castelnau, F. 1872. Contribution to the ichthyology of Australia. No. 1. The Melbourne fish market. *Proc. Zool. & Accl. Soc. Vic.,* 1: 29–242.

DeKay, J.E. 1842. Zoology of New–York, or the New–York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New–York, with brief notices of those occasionally found near its borders, and accompanied by appropriate illustrations. Part IV. *Fishes*. W. A. White & J. Visscher, Albany, New York. xv + 415 pp. + 79 pls.

Delarbre, C., C. Gallut, V. Barriel, P. Janvier, & Gachelin, G. 2002. Complete mitochondrial DNA of the hagfish, *Eptatretus burgeri*: The comparative analysis of mitochondrial DNA sequences strongly supports the cyclostome monophyly. *Mol. Phylogenet. Evol.,* 22(2): 184–192.

Dill, W.A. 1990. *Inland fisheries in Europe*. EIFAC Technical Paper No. 52, FAO, Rome. 471 pp.

Docker, M.F., J.H. Youson, R.J. Beamish, & Devlin, R.H. 1999. Phylogeny of the lamprey genus *Lampetra* inferred from mitochondrial cytochrome *b* and ND3 gene sequences. *Can. J. Fish. Aquat. Sci.,* 56(12): 2340–2349.

Dollfus, R.P. 1955. Première contribution à l'établissement d'un fichier ichthyologique du Maroc atlantique de Tanger à l'embouchure de l'oued Dra. Travaux de l'institut scientifique chérifien, *Sér. Zool.,* no. 6: 1–226 + 1 map.

Donoghue, P.C.J., P.L. Forey, & Aldridge, R.J. 2000. Conodont affinity and chordate phylogeny. *Biol. Rev.*, 75: 191–251.

Dybowski, B.N. 1869. Vorläufige Mittheilungen über die Fischfauna des Ononflusses und des Ingoda in Transbaikalien. *Verhandl. d. k. k. zool. bot. Ges.*, 19: 945–958 + 1 table + pls. 14–18.

Eigenmann, C.H. 1927. The fresh–water fishes of Chile. *Mem. Natl. Acad. Sci.*, 22: 1–63 + 7 figs. + 16 pls.

Enequist, P. 1937. Das Bachneunauge als Ökologische Modifikation des Flussneunauges – Über die Fluss – und Bachneunaugen Schwedens Vorläufige Mitteilung. *Ark. Zool.,* 29A(20): 1–22.

Espanhol, R., P.R. Almeida, & Alves, M.J. 2007. Evolutionary history of lamprey paired species *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch) as inferred from mitochondrial DNA variation. *Mol. Ecol.*, 16(9): 1–16.

Etnier, D.A. & Starnes, W.C. 1993. *The fishes of Tennessee*. The University of Tennessee Press, Knoxville, Tennessee. xiv + 681 pp.

Farlinger, S.P. & Beamish, R.J. 1984. Recent colonization of a major salmon–producing lake in British Columbia by Pacific Lamprey (*Lampetra tridentata*). *Can. J. Fish. Aquat. Sci.,* 41(2): 278–285.

Fetterolf, C.M. Jr. 1980. Why a Great Lakes Fishery Commission and why a Sea Lamprey International Symposium. *Can. J. Fish. Aquat. Sci.,* 37(11): 1588–1593.

Fine, J.M., L.A. Vrieze, & Sorensen, P.W. 2004. Evidence that petromyzontid lampreys employ a common migratory pheromone that is partially comprised of bile acids. *J. Chem. Ecol.,* 30(11): 2091–2110.

Forey, P.L. 1995. Agnathans recent and fossil, and the origin of jawed vertebrates. *Rev. Fish Biol. Fish.,* 5(3): 267–303.

Fowler, H.W. 1908. Notes on lancelets and lampreys. *P. Acad. Nat. Sci. Phila.*, 59: 461–466.

Fowler, H.W. 1940. Fishes obtained in Chile by Mr. B.S. Bullock. *P. Acad. Nat. Sci. Phila.*, 92: 171–190.

Fukutomi, N., T. Nakamura, T. Doi, K. Takeda, & Oda, N. 2002. Records of *Entosphenus tridentatus* from the Naka River system, central Japan; physical characteristics of possible spawning redds and spawning behavior in the aquarium. *Jpn. J. Ichthyol.,* 49(1): 53–58.

Gage, S.H. 1893. *The lake and brook lampreys of New York, especially those of Cayuga and Seneca lakes*. Wilder Quarter Century Book, Ithaca, New York. pp. 421–493 + 8 pls.

Gage, S.H. 1928. The lampreys of New York State – Life history and economics. pp. 158–191. *In* A Biological Survey of the Oswego River System. Supplement to Seventeeth Annual Report, 1927, State of New York Conservation Department, Albany, New York.

Gaudron, S.M. & Lucas, M.C. 2006. First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *J. Fish Biol.,* 68: 640–644.

Gess, R.W., M.I. Coates, & Rubidge, B.S. 2006. A lamprey from the Devonian period of South Africa. *Nature,* 443: 981–984.

Gilbertson, M. 1992. PCB and dioxin research and implications for fisheries research and resource management. *Can. J. Fish. Aquat. Sci.,* 49(5): 1078–1079.

Gill, H.S., C.B. Renaud, F. Chapleau, R.L. Mayden, & Potter, I.C. 2003. Phylogeny of living parasitic lampreys (Petromyzontiformes) based on morphological data. *Copeia,* 2003(4): 687–703.

Gill, T.N. 1862. Notes on some genera of fishes of western North America. *P. Acad. Nat. Sci. Phila.*, 14: 329–332.

Gill, T.N. 1883a. Note of the petromyzontids. *Proc. U. S. Nat. Mus.*, 5(310): 521–525.

Gill, T.N. 1883b. Diagnosis of new genera and species of deep–sea fish–like vertebrates. *Proc. U. S. Nat. Mus.,* 6(380): 253–260.

Gill, T.N. 1893. Families and subfamilies of fishes. *Mem. Nat. Acad. Sci.,* 6: 127–138.

Girard, C.F. 1858. Fishes. pp. 1–400 + 21 pls. *In* General Report on the Zoology of the Several Pacific Railroad Routes. United States Pacific Railroad Route Explorations and Surveys volume 10, pt. 4, War Department, Washington, D.C.

Goodwin, C.E., D. Griffiths, J.T.A. Dick, & Elwood, R.W. 2006. A freshwater–feeding *Lampetra fluviatilis* L. population in Lough Neagh, Northern Ireland. *J. Fish Biol.,* 68: 628–633.

Gratzianow, V. 1907. Minogi Rossiĭskoĭ Imperii. *Dnevnik Zool. otd. Imp. Obshch. lyub. estetstvozn. antropol. i etnografii.,* 3: 18.

Gray, J.E. 1851. List of the specimens of fish in the collection of the British Museum. Part I. *Chondropterygii*. British Museum (Natural History), London. xi + 160 pp. + 2 pls.

Greene, C.W. 1935. *The distribution of Wisconsin fishes*. State of Wisconsin Conservation Commission, Madison, Wisconsin. 235 pp.

Günther, A. 1870. Catalogue of the fishes in the British Museum. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii in the British Museum. Taylor & Francis, London. 8: i–xxv + 1–549.

Günther, A. 1872. Report on several collections of fishes recently obtained for the British Museum. *Proc. Zool. Soc. Lond.,* 1871, pt. 3: 652–675 + pls. 53–70.

Haedrich, R.L. 1977. A Sea Lamprey from the deep ocean. *Copeia,* 1977(4): 767–768.

Hagelin, L–O. & Steffner, N. 1958. Notes on the spawning habits of the River Lamprey (*Petromyzon fluviatilis*). *Oikos,* 9: 221–238.

Hall, J.D. 1963. *An ecological study of the Chestnut Lamprey, Ichthyomyzon castaneus Girard, in the Manistee River, Michigan*. University of Michigan, Ann Arbor, Michigan. vi + 101 pp. (unpublished Ph.D. thesis)

Halliday, R.G. 1991. Marine distribution of the Sea Lamprey (*Petromyzon marinus*) in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.*, 48(5): 832–842.

Halstead, B.W. 1967. *Poisonous and venomous marine animals of the world*. Vol. 2. *Vertebrates*. United States Government Printing Office, Washington, D.C. xxxi + 1070 pp.

Hankó, B. 1922. Ernö Csiki állattani kutatasai Albániában. I. Halak. Magyar Tudom. Åkad. Balk. – *Kutat. Tudom. Ered.*, 1–6 + 1 pl.

Hardisty, M.W. 1961. Studies on an isolated spawning population of the brook lamprey (*Lampetra planeri*). *J. Anim. Ecol.*, 30(2): 339–355.

Hardisty, M.W. 1964. The fecundity of lampreys. *Arch. Hydrobiol.*, 60(3): 340–357.

Hardisty, M.W. 1986a. *Petromyzon marinus* Linnaeus, 1758. pp. 94–116. *In* Holčík, J., ed. *The Freshwater Fishes of Europe*, Vol. 1, Part I, Petromyzontiformes, AULA–Verlag, Wiesbaden.

Hardisty, M.W. 1986b. *Lampetra fluviatilis* (Linnaeus, 1758). pp. 249–278. *In* Holčík, J., ed. *The Freshwater Fishes of Europe*, Vol. 1, Part I, Petromyzontiformes, AULA–Verlag, Wiesbaden.

Hardisty, M.W. & Potter, I.C. 1971. Paired species. pp. 249–277. *In* Hardisty, M.W. & I.C. Potter, eds. *The Biology of Lampreys*, Vol. 1, Academic Press, London.

Heard, W.R. 1966. Observations on lampreys in the Naknek River system of southwest Alaska. *Copeia,* 1966(2): 332–339.

Hedges, S.B. 2001. Molecular evidence for the early history of living vertebrates. pp. 119–134. *In* Ahlberg, P.E., ed. *Major Events in Early Vertebrate Evolution – Palaeontology, Phylogeny, Genetics, and Development*, Taylor & Francis Inc., New York.

Heldt, H. 1958. Sur la présence de la lamproie (*Petromyzon marinus* L.) dans les eaux tunisiennes. *Rapp. p-v. reun. Comm. int. explor. sci. Mer Mediterr.,* 14: 369–370.

Hensel, K. 1963. A note on lampreys of the Mutantiang River, tributary of the Sungari River, in China. *Ichthyologica*, 11(1–2): 85–86.

Holčík, J. 1963. Notes on the Czechoslovakian lampreys with redescription of *Lampetra* (*Eudontomyzon*) *vladykovi* (Oliva & Zanandrea), 1959. *Vest. Cs. Spol. Zool.,* 27(1): 51–61 + figs. 3, 6–8.

Holčík, J. 1986. *Caspiomyzon wagneri* (Kessler, 1870). pp. 119–142. *In* J. Holčík, ed. *The Freshwater Fishes of Europe*. vol. 1, part I, Petromyzontiformes, AULA–Verlag GmbH, Wiesbaden.

Holčík, J. 2003. The occurrence of the Ukrainian Brook Lamprey [*Eudontomyzon mariae* (Berg, 1931)] in the middle Danube. *Biologia,* 58(2): 241–244.

Holčík, J. & Mrakovčić, M. 1997. First record of *Lethenteron zanandreai* (Cyclostomata, Petromyzontidae) in the Adriatic Basin of the Balkan Peninsula and its zoogeographic consequences. *Folia Zool.*, 46(3): 263–271.

Holčík, J. & Delić, A. 2000. New discovery of the Ukrainian Brook Lamprey in Croatia. *J. Fish Biol.,* 56: 73–86.

Holčík, J. & Šorić, V. 2004. Redescription of *Eudontomyzon stankokaramani* (Petromyzontes, Petromyzontidae) – a little known lamprey from the Drin River drainage, Adriatic Sea Basin. *Folia Zool.*, 53(4): 399–410.

Holčík, J., A. Delić, M. Kučinić, V. Bukvić, & Vater, M. 2004. Distribution and morphology of the Sea Lamprey from the Balkan coast of the Adriatic Sea. *J. Fish Biol.,* 64: 514–527.

Honma, Y. 1960. Sado Awashima Kinkai ni okeru Kuromekura Unagi to Kawayatsume. *Saishu to Shiiku,* 22(2): 34–36.

Hubbs, C.L. 1924. The life–cycle and growth of lampreys. *Pap. Mich. Acad. Sci., Arts Lett.*, 4: 587–603.

Hubbs, C.L. 1967. Occurrence of the Pacific Lamprey, *Entosphenus tridentatus*, off Baja California and in streams of southern California; with remarks on its nomenclature. *Trans. San Diego Soc. Nat. Hist.,* 14(21): 301–312.

Hubbs, C.L. 1971. *Lampetra* (*Entosphenus*) *lethophaga*, new species, the nonparasitic derivative of the Pacific Lamprey. *Trans. San Diego Soc. Nat. Hist.,* 16(6): 125–164.

Hubbs, C.L. & Trautman, M.B. 1937. A revision of the lamprey genus *Ichthyomyzon*. Miscellaneous Publications of the Museum of Zoology, University of Michigan no. 35: 7–109 + 2 pls.

Hubbs, C.L. & Potter, I.C. 1971. Distribution, phylogeny and taxonomy. pp. 1–65. *In* Hardisty, M.W. & I.C. Potter, eds. *The Biology of Lampreys*, vol. 1, Academic Press, London.

Huggins, R.J. & Thompson, A. 1970. Communal spawning of brook and river lampreys, *Lampetra planeri* Bloch and *Lampetra fluviatilis* L. *J. Fish. Biol.,* 2: 53–54.

Hughes, R.L. & Potter, I.C. 1969. Studies on gametogenesis and fecundity in the lampreys *Mordacia praecox* and *M. mordax* (Petromyzonidae). *Aust. J. Zool.*, 17(3): 447–464.

Hussakof, L. 1912. The spawning habits of the Sea Lamprey, *Petromyzon marinus*. *Am. Nat.*, 46: 729-740.

Ivanova–Berg, M.M. 1968. Discovery of the southern lamprey (*Geotria australis* Gray) in the Scotia Sea near Georgia Island. *Probl. Ichthyol.*, 8: 138–141.

Iwata, A, A. Goto, & Hamada, K. 1985. A review of the Siberian Lamprey, *Lethenteron kessleri*, in Hokkaido, Japan. *Bull. Fac. Fish. Hokkaido Univ.*, 36(4): 182–190.

Jamieson, B.G.M. 1991. *Fish evolution and systematics: Evidence from spermatozoa*. Cambridge University Press, Cambridge, England. xiv + 319 pp.

Janvier, P. 1981. The phylogeny of the Craniata, with particular reference to the significance of fossil “agnathans”. *J. Vertebr. Paleontol.,* 1(2): 121–159.

Janvier, P. 1999. Catching the first fish. *Nature*, 402: 21–22.

Janvier, P. & Lund, R. 1983. *Hardistiella montanensis* n. gen. et sp. (Petromyzontida) from the lower Carboniferous of Montana, with remarks on the affinities of the lampreys. *J. Vertebr. Paleontol.,* 2(4): 407–413.

Jenkins, J.T. 1925. *The fishes of the British Isles both fresh water and salt*. Frederick Warne and Co. Ltd., London. vii + 376 pp.

Jordan, D.S. 1882. Report on the fishes of Ohio. Report of the Geological Survey of Ohio 4(Pt.1, sect. 4): 735–1002.

Jordan, D.S. 1885. A catalogue of the fishes known to inhabit the waters of North America, north of the tropic of Cancer, with notes on the species discovered in 1883 and 1884. Report of the Commissioner for 1885, United States Commission of Fish and Fisheries Part 13(24): 789–973.

Jordan, D.S. 1923. A classification of fishes including families and genera as far as known. Stanford University Publications, University Series, Biological Sciences 3(2): 77–243 + i–x.

Jordan, D.S. & Gilbert, C.H. 1883. Synopsis of the fishes of North America. *Bull. U. S. Natl. Mus.*, No. 16: i–lvi + 1–1018.

Jordan, D.S. & Evermann, B.W. 1896. The fishes of North and Middle America: A descriptive catalogue of the species of fish–like vertebrates found in the waters of North America, north of the isthmus of Panama. *Bull. U. S. Natl. Mus.*, no. 47, Part I, vol.1: lx + 954 pp.

Jordan, D.S., B.W. Evermann, & Clark, H.W. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Report of the United States Commissioner of Fisheries for the fiscal year 1928, Washington, District of Columbia, United States. Appendix X, 670 pp.

Joyce, W.N., S.E. Campana, L.J. Natanson, N.E. Kohler, H.L. Pratt, Jr., & Jensen, C.F. 2002. Analysis of stomach contents of the porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. *ICES J. Mar. Sci.*, 59: 1263–1269.

Jyrkkanen, J. & Wright, D.G. 1979. First record of the Northern Brook Lamprey, *Ichthyomyzon fossor*, in the Nelson River drainage, Manitoba. *Can. Field-Nat.*, 93(2): 199–200.

Kan, T.T. 1975. *Systematics, variation, distribution, and biology of lampreys of the genus Lampetra in Oregon*. Oregon State University, Corvallis, Oregon. 194 pp. (unpublished Ph.D. thesis)

Kan, T.T. & Bond, C.E. 1981. Notes on the biology of the Miller Lake Lamprey *Lampetra* (*Entosphenus*) *minima*. *Northwest Sci.*, 55(1): 70–74.

Karaman, M.S. 1974. *Eudontomyzon vladykovi stankokaramani* n. ssp., a new subspecies of lamprey from tributaries of the Ohrid–Drim–Skadar System in west Balkan Peninsula. *Folia Balc.*, 3(5): 1–10, 2 figs., 6 tables.

Kentucky State Nature Preserves Commission. 2004. *Endangered, threatened, special concern, and historical biota of Kentucky*. Frankfort, Kentucky. 18 pp.

Kessler, K. 1870. Volzhskaya minoga (*Petromyzon wagneri* n. sp.). *Trudy Sankt–Peterburgskogo obshchestva estetvoznaniya* 1: 207–214.

Khidir, K.T. & Renaud, C.B. 2003. Oral fimbriae and papillae in parasitic lampreys (Petromyzontiformes). *Environ. Biol. Fish.*, 66(3): 271–278.

Kille, R.A. 1960. Fertilization of the lamprey egg. *Exp. Cell Res.*, 20:12–27.

Kirtland, J.P. 1838. Report on the zoology of Ohio. First Annual Report of the Geological Survey of the State of Ohio. *Rept. Zool. Ohio*: 157–197.

Kirtland, J.P. 1840. Descriptions of the fishes of the Ohio River and its tributaries. *Boston J. Nat. Hist.,* 3(3–4): 338–352, 469–482, pls. 4–6, 27–29.

Kott, E. 1971. Characteristics of pre–spawning American brook lampreys from Big Creek, Ontario. *Can. Field-Nat.*, 85(3): 235–240.

Kott, E. 1974. A morphometric and meristic study of a population of the American Brook Lamprey, *Lethenteron lamottei* (LeSueur), from Ontario. *Can. J. Zool.*, 52(8): 1047–1055.

Kott, E., C.B. Renaud, & Vladykov, V.D. 1988. The urogenital papilla in the Holarctic lamprey (Petromyzontidae). *Environ. Biol. Fish.*, 23(1–2): 37–43.

Kottelat, M. 1997. European freshwater fishes. An heuristic checklist of the freshwater fishes of Europe (exclusive of former USSR), with an introduction for non–systematists and comments on nomenclature and conservation. *Biologia,* 52(Suppl. 5): 1–271.

Kucheryavyi, A.V., K.A. Savvaitova, D.S. Pavlov, M.A. Gruzdeva, K.V. Kuzishchin, & Stanford, J.A. 2007. Variations of life history strategy of the Arctic Lamprey *Lethenteron camtschaticum* from the Utkholok River (western Kamchatka). *J. Ichthyol.*, 47(1): 37–52.

Kux, Z. 1965. *Lampetra gracilis*, nový neparasitický druh mihule z východního slovenska. *Acta Mus. Morav.*, 50: 293–302.

Kux, Z. & Steiner, H.M. 1972. *Lampetra lanceolata*, eine neue Neunaugenart aus dem Einzugsgebiet des Schwarzen Meeres in der nordöstlichen Türkei. *Acta Mus. Morav.*, 56–57: 375–384 + 10 figs.

Lacepède, B.G.E. 1802. *Histoire naturelle des poissons*. Vol. 4. Paris.

Lahille, F. 1915. Apuntes sobre las lampreas argentinas y los acraniotas. *An. Mus. Nac. Hist. Nat. Buenos Aires*, 26: 361–382 + pls. 12–13.

Lanteigne, J. 1981. The taxonomy and distribution of the North American lamprey genus *Ichthyomyzon*. University of Ottawa, Ottawa. xi + 150 pp. (unpublished M. Sc. thesis)

Lanteigne, J. 1988. Identification of lamprey larvae of the genus *Ichthyomyzon* (Petromyzontidae). *Environ. Biol. Fish.*, 23(1–2): 55–63.

Leach, W.J. 1939. The endostyle and thyroid gland of the brook lamprey, *Ichthyomyzon fossor*. *J. Morphol.*, 65(3): 549–593 + 6 pls.

Leach, W.J. 1940. Occurrence and life history of the Northern Brook Lamprey, *Ichthyomyzon fossor*, in Indiana. *Copeia,* 1940(1): 21–34.

Legendre, V. 1962. Author and type of *Lampetra*. *Copeia,* 1962(1): 221–222.

Lesueur, C.A. 1818. Descriptions of several species of chondropterigious fishes, of North America, with their varieties. *T. Am. Philos. Soc.*, 1(33): 383–387.

Lesueur, C.A. 1827. *American ichthyology, or, natural history of the fishes of North America: with coloured figures from drawings executed from nature*. New–Harmony, Indiana. 1–8 + 4 figs.

Lethbridge, R.C. & Potter, I.C. 1979. The oral fimbriae of the lamprey *Geotria australis*. *J. Zool.*, London 188: 267–277.

Levin, B.A. 2001. Finding of the Ukrainian lamprey *Eudontomyzon mariae* (Petromyzontidae) in the Volga Basin. *J. Ichthyol.*, 41(9): 810–811.

Levin, B.A. & Holčík, J. 2006. New data on the geographic distribution and ecology of the Ukrainian Brook Lamprey, *Eudontomyzon mariae* (Berg, 1931). *Folia Zool.*, 55(3): 282–286.

Linnaeus, C. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1, Laurentii Salvii, Holmiae (= Stockholm), Sweden.

Lohniský, K. 1966. The spawning behaviour of the brook lamprey, *Lampetra planeri* (Bloch, 1784). *Věst. Čs. Spol. Zool.*, 30(4) : 289–307.

Lorion, C.M., D.F. Markle, S.B. Reid, & Docker, M.F. 2000. Redescription of the presumed–extinct Miller Lake Lamprey, *Lampetra minima*. *Copeia,* 2000(4): 1019–1028.

Ma, C.F. & Yu, C.L. 1959. Preliminary observations on *L. morii*. *Chin. J. Zool.*, 3(3): 115–117 (in Chinese).

Maisey, J.G. 1986. Heads and tails: A chordate phylogeny. *Cladistics,* 2(3): 201–256.

Mallatt, J., J.Sullivan, & Winchell, C.J. 2001. The relationship of lampreys to hagfishes: A spectral analysis of ribosomal DNA sequences. pp. 106–118. *In* Ahlberg, P.E., ed. *Major Events in Early Vertebrate Evolution – Palaeontology, Phylogeny, Genetics, and Development.* Taylor and Francis Inc., New York.

Manion, P.J. 1967. Morphological abnormalities among lampreys. *Copeia,* 1967(3): 680–681.

Manion, P.J. 1972. Fecundity of the Sea Lamprey (*Petromyzon marinus*) in Lake Superior. *T. Am. Fish. Soc.*, 101(4): 718–720.

Manion, P.J. & Purvis, H.A. 1971. Giant American brook lampreys, *Lampetra lamottei*, in the upper *Great Lakes. J. Fish. Res. Board Can.*, 28: 616–620.

Manion, P.J. & Smith, B.R. 1978. Biology of larval and metamorphosing sea lampreys, *Petromyzon marinus*, of the 1960 year class in the Big Garlic River, Michigan, Part II, 1966–72. *Great Lakes Fish. Comm. Tech. Rep.*, No. 30. 35 pp.

Manion, P.J. & Hanson, L.H. 1980. Spawning behavior and fecundity of lampreys from the upper three Great Lakes. *Can. J. Fish. Aquat. Sci.*, 37(11): 1635–1640.

Maskell, F.G. 1929. On the New Zealand lamprey, *Geotria australis* Gray. Part 1. Biology and life history. *Trans. & Proc. New Zealand Inst.*, 60: 167–201.

Mayden, R.L., B.M. Burr, L.M. Page, & Miller, R.R. 1992. The native freshwater fishes of North America. Chap. 29: 827-863. *In* Mayden, R.L., ed. *Systematics, Historical Ecology, and North American Freshwater Fishes*, Stanford University Press, Stanford, California.

Mayden, R.L., R.H. Matson, B.R. Kuhajda, J.M. Pierson, M.F. Mettee, & Frazer, K.S. 1989. The Chestnut Lamprey, *Ichthyomyzon castaneus* Girard, in the Mobile Basin. *Proc. S.E. Fishes Council,* (20): 10–13.

McDowall, R.M. 1990. *New Zealand Freshwater Fishes – A Natural History and Guide*. Heinemann Reed, Auckland and MAF Publishing Group, Wellington, New Zealand. 553 pp. + 79 pls.

McPhail, J.D. & Lindsey, C.C. 1970. Freshwater Fishes of Northwestern Canada and Alaska. *Bull. Fish. Res. Board Can.*, 173, Ottawa. 381 pp.

Mecklenburg, C.W., T.A. Mecklenburg, & Thorsteinson, L.K. 2002. *Fishes of Alaska*. American Fisheries Society, Bethesda, Maryland. xxxvii + 1037 pp.

Medland, T.E. & Beamish, F.W.H. 1987. Age validation for the Mountain Brook Lamprey, *Ichthyomyzon greeleyi*. *Can. J. Fish. Aquat. Sci.*, 44(4): 901–904.

Michael, J.H. Jr. 1980. Repeat spawning of Pacific Lamprey. *Calif. Fish Game*, 66(3): 186–187.

Michael, J.H. Jr. 1984. Additional notes on the repeat spawning by Pacific Lamprey. *Calif. Fish Game,* 70(3): 186-188, 192.

Miller, D.J. & Lea, R.N. 1972. Guide to the coastal marine fishes of California. *Calif. Dept. Fish and Game Fish Bull.,* 157: 1–235.

Miller, R.R., W.L. Minkley, & Norris, S.M. 2005. *Freshwater Fishes of México*. The University of Chicago Press, Chicago, Illinois. xxv + 490 pp. + 99 pls.

Monette, S.N. & Renaud, C.B. 2005. The gular pouch in Northern Hemisphere parasitic lampreys (Petromyzontidae). *Can. J. Zool.*, 83(4): 527–535.

Moore, G.A. & Kernodle, M. 1965. A new size record for the Chestnut Lamprey, *Ichthyomyzon castaneus*, Girard in Oklahoma. *Proc. Okla. Acad. Sci.*, 45: 68–69.

Morkert, S.B., W.D. Swink, & Seelye, J.G. 1998. Evidence for early metamorphosis of sea lampreys in the Chippewa River, Michigan. *N. Am. J. Fish. Manage.*, 18: 966–971.

Morman, R.H. 1979. Distribution and ecology of lampreys in the lower peninsula of Michigan, 1957–75. *Great Lakes Fish. Comm. Tech. Rep.*, No. 33, 59 pp.

Morris, S. 1975. The lamprey at Kettle Falls. *The Beaver,* 55(2): 18–19.

Moyle, P.B. 1976. *Inland fishes of California*. University of California Press, Berkeley, California. viii + 405 pp.

Müller, A. 1856. On the development of the lampreys. *Ann. Mag. Nat. Hist.,* 18: 298–301.

Müller, J. 1841. Vergleichende Anatomie der Myxinoiden. Dritte Fortsetzung. Über das Gefässystem. Abh. Dtsch. Akad. Wiss. Berlin. 1839: 175–304 + 5 pls.

Mundahl, N.D. & Sagan, R.A. 2005. Spawning ecology of the American Brook Lamprey, *Lampetra appendix*. *Environ. Biol. Fish.,* 73(3): 283–292.

Mundahl, N.D., C. Erickson, M.R. Johnston, G.A. Sayeed, & Taubel, S. 2005. Diet, feeding rate, and assimilation efficiency of American Brook Lamprey larvae. *Environ. Biol. Fish.*, 72(1): 67–72.

Naseka, A.M., S.B. Tuniyev, & Renaud, C.B. 2009. *Lethenteron ninae*, a new nonparasitic lamprey species from the north–eastern Black Sea basin (Petromyzontiformes: Petromyzontidae). *Zootaxa,* 2198: 16–26.

Neave, F.B. 2004. *The utility of meristic, morphometric, pigmentation and gonad analysis in the identification of Ichthyomyzon lamprey larvae*. University of Guelph, Guelph, Ontario, Canada. iii + 119 pp. (unpublished M. Sc. thesis)

Neira, F.J. 1984. Biomorfologia de las lampreas parasitas chilenas *Geotria australis* Gray, 1851 y *Mordacia lapicida* (Gray, 1851) (Petromyzoniformes). *Gayana*, *Zool.*, 48(1–2): 3–40.

Neira, F.J., J.S. Bradley, I.C. Potter, & Hilliard, R.W. 1988. Morphological variation among widely dispersed larval populations of anadromous southern hemisphere lampreys (Geotriidae and Mordaciidae). *Zool. J. Linn. Soc.*, 92: 383–408.

Nelson, E.W. 1887. Part III. Field notes on Alaskan fishes. The Miscellaneous Documents of the Senate of the United States for the first session of the 49th Congress, Washington. Vol. 8, Misc. Doc. No. 156: 299–322 + pls. XIII – XXI.

Nelson, J.S., E.J. Crossman, H. Espinosa–Pérez, L.T. Findley, C.R. Gilbert, R.N. Lea, & Williams, J.D. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. *Spec. Publ. Am. Fish. Soc.*, 29, Bethesda, Maryland. ix + 386 pp.

Nursall, J.R. & Buchwald, D. 1972. Life history and distribution of the Arctic Lamprey (*Lethenteron japonicum* (Martens)) of Great Slave Lake, N.W.T. *Fish. Res. Board Can. Tech. Rep.*, 304: iv + 28 pp.

Ogilby, J.D. 1896. A monograph of the Australian Marsipobranchii. *Proc. Linn. Soc. N.S.W.,* 21(part 3): 388–426.

Okada, Y. 1955. *Fishes of Japan*. Maruzen Co. Ltd., Tokyo, Japan. 462 pp.

Oliva, O. 1953. Příspěvek k přehledu našich mihulí (Petromyzones Berg 1940). *Věstník Královské české společnosti nauk* no. 9: 1–19 + 2 pls.

Oliva, O. & Zanandrea, G. 1959. Posizione sistematica di una lampreda di Cilistovo (Cecoslovacchia). *Doriana,* 2(98): 1–5.

Oliva, O. & Hensel, K. 1962. On the occurrence of the south Russian lamprey, *Lampetra* **(***Eudontomyzon***)** *mariae* Berg 1931, in the Vistula basin. *Acta Univ. Carol. Biol.*, 1962(1): 99–104.

Page, L.M. & Burr, B.M. 1991. *A field guide to freshwater fishes of North America north of Mexico*. The Peterson Field Guide Series, 42, Houghton Mifflin Co., Boston, Massachusetts. xii + 432 pp.

Pallas, P.S. 1814. *Zoographia Rosso–Asiatica, sistens omnium animalium in extenso Imperio Rossico et adjacentibus maribus observatorum recensionem, domicilia, mores et descriptiones, anatomen atque icones plurimorum*. St. Petersburg, Russia. vol. 3, 427 pp.

Philippi, R.A. 1857. Ueber einige Chilenische Vögel und Fische. *Arch. Naturgesch.*, 23(1): 262–272.

Philippi, R.A. 1858. Beschreibung neuer Wirbelthiere aus Chile. *Arch. Naturgesch.*, 24(1): 303–311.

Philippi, R.A. 1863. Kurze Nachricht über ein paar Chilenische Fische. *Arch. Naturgesch.*, 29(1): 207–212 + pl. 10.

Philippi, R.A. 1865. Ueber die chilenische Anguilla. *Arch. Naturgesch.*, 31(1): 107–109.

Piavis, G.W. 1971. Embryology. pp. 361–400. In Hardisty, M.W. and I.C. Potter, eds. *The Biology of Lampreys*, vol. 1, Academic Press, London.

Piavis, G.W., J.H. Howell, & Smith, A.L. 1970. Experimental hybridization among five species of lampreys from the Great Lakes. *Copeia,* 1970(1): 29–37.

Plate, L. 1897. Ein neuer Cyclostom mit grossen normal entwickelten Augen, *Macrophthalmia chilensis*, n.g. n. sp. *SitzBer. Gesell. Naturf. Freunde Berlin*, 137–141.

Plate, L. 1902. Studien über Cyclostomen. I. Systematische Revision der Petromyzonten der südlichen Halbkugel. *Zool. Jahrb.*, Suppl. 5: 651–674 + pl. 19.

Platina, B. (pseudonym of B. Sacchi) 1505. *Platine en francoys*. Translation by D. Christol in French of De honesta voltuptate. F. Fradin, Lyon, France. 209 pp.

Pletcher, F.T. 1963. *The life history and distribution of lampreys in the Salmon and certain others rivers in British Columbia, Canada*. University of British Columbia, Vancouver, British Columbia. xii + 195 pp. (unpublished M. Sc. thesis)

Poltorykhina, A.N. 1971. Metamorphosis of the Arctic Brook Lamprey (*Lampetra japonica kessleri* (Anikin)) in the upper Irtysh. *J. Ichthyol.*, 11(2): 281–285.

Poltorykhina, A.N. 1974. Morphological characteristics and variability of the Siberian Lamprey (*Lampetra japonica kessleri*) in the upper Irtysh Basin. *J. Ichthyol.*, 14(2): 192–202.

Potter, I.C. 1968. *Mordacia praecox*, n. sp., a nonparasitic lamprey (Petromyzonidae), from New South Wales, Australia. *Proc. Linn. Soc. N. S. W.,* 92(Pt. 3): 254–261 + pl. XIV.

Potter, I.C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *J. Zool.*, London 161: 487–511 + 1 pl.

Potter, I.C. & Strahan, R. 1968. The taxonomy of the lamprey *Geotria* and *Mordacia* and their distribution in Australia. *Proc. Linn. Soc. Lond.*, 179(2): 229–240.

Potter, I.C. & Osborne, T.S. 1975. The systematics of larval lampreys. *J. Zool.*, London 176: 311–329.

Potter, I.C. & Hilliard, R.W. 1986. Growth and average duration of larval life in the southern hemisphere lamprey, *Geotria australis* Gray. *Experientia,* 42: 1170–1173.

Potter, I.C. & Hilliard, R.W. 1987. A proposal for the functional and phylogenetic significance of differences in the dentition of lampreys (Agnatha: Petromyzontiformes). *J. Zool.*, Lond. 212: 713–737.

Potter, I.C. & Welsch, U. 1997. The structure of the gular pouch of mature males of the lamprey *Geotria australis*. *Acta Zool.* (Stockholm), 78: 97–106.

Potter, I.C., W.J.R. Lanzing, & Strahan, R. 1968. Morphometric and meristic studies on populations of Australian lampreys of the genus *Mordacia*. *Zool. J. Linn. Soc.*, 47(313): 533–546.

Potter, I.C., P.A. Prince, & Croxall, J.P. 1979. Data on the adult marine and migratory phases in the life cycle of the Southern Hemisphere lamprey, *Geotria australis* Gray. *Environ. Biol. Fish.*, 4: 65–69.

Potter, I.C., R.W. Hilliard, & Bird, D.J. 1980. Metamorphosis in the Southern Hemisphere lamprey, *Geotria australis*. *J. Zool.*, London 190: 405–430.

Potter, I.C., R.W. Hilliard, D.J. Bird, & Macey, D.J. 1983. Quantitative data on morphology and organ weights during the protracted spawning–run period of the Southern Hemisphere lamprey *Geotria australis*. *J. Zool.,* London 200: 1–20.

Potter, I.C., G.J. Thomson, R.D. Cook, J.M. Cox, & Macey, D.J. 1995. Buccal glands of adults of the lamprey *Mordacia mordax*, including comparisons with other species. *J. Morphol.*, 226(3): 339–349.

Raney, E.C. 1941. Records of the brook lamprey, *Lampetra aepyptera* (Abbott), from the Atlantic drainage of North Carolina and Virginia. *J. Elisha Mitchell Sci. Soc.*, 57(2): 318–320.

Raney, E.C. 1952. A new lamprey, *Ichthyomyzon hubbsi*, from the upper Tennessee river system. *Copeia,* 1952(2): 93-99 + 1 pl.

Regan, C.T. 1911. A synopsis of the marsipobranchs of the order Hyperoartii. *Ann. Mag. Nat. Hist.*, 7, Series 8: 193–204.

Reighard, J. & Cummins, H. 1916. Description of a new species of lamprey of the genus *Ichthyomyzon*. *Occ. Pap. Mus. Zool. U. Michigan,* No. 31: 1–12 + 2 pls.

Rembiszewski, J.M. 1968. Observations on hybrids of *Lampetra* (*Lampetra*) *planeri* (Bloch, 1784) X *Lampetra* (*Eudontomyzon*) *mariae* Berg, 1931. *Vest. Cs. Spol. Zool.,* 32(4): 390–393.

Renaud, C.B. 1982a. *Revision of the lamprey genus Eudontomyzon Regan, 1911.* University of Ottawa, Ottawa. xvi + 146 pp. (unpublished M.Sc. thesis)

Renaud, C.B. 1982b. Food and feeding habits of the Caspian Lamprey after metamorphosis. Abstract no. 252. Abstracts of the Fourth Congress of European Ichthyologists, Hamburg, Germany, 20–24 Sept. 1982.

Renaud, C.B. 1986. *Eudontomyzon hellenicus* Vladykov, Renaud, Kott, & Economidis, 1982. pp. 186–195. *In* Holčík, J., ed. *The Freshwater Fishes of Europe*, Vol. 1, Part I, Petromyzontiformes, AULA–Verlag, Wiesbaden.

Renaud, C.B. 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). *J. Appl. Ichthyol.,* 13(3): 143–148.

Renaud, C.B. 2002. The Muskellunge, *Esox masquinongy*, as a host for the Silver Lamprey, *Ichthyomyzon unicuspis*, in the Ottawa River, Ontario/Québec. *Can. Field-Nat.*, 116(3): 433–440.

Renaud, C.B. 2008. Petromyzontidae, *Entosphenus tridentatus*: Southern distribution record, Isla Clarión, Revillagigedo Archipelago, Mexico. *Check List,* 4(1): 82–85.

Renaud, C.B. & Holčík, J. 1986. *Eudontomyzon danfordi* Regan, 1911. pp. 146–164. *In* Holčík, J., ed. *The Freshwater Fishes of Europe*, Vol. 1, Part I, Petromyzontiformes, AULA–Verlag, Wiesbaden.

Renaud, C.B. & Holčík, J. 1988. *Lampetra* (*Eudontomyzon*) *gracilis*, a synonym of *Eudontomyzon danfordi*. *Environ. Biol. Fish.*, 23(1–2): 127–130.

Renaud, C.B. & de Ville, N. 2000. Three records of the Chestnut Lamprey, *Ichthyomyzon castaneus*, new to Québec. *Can. Field-Nat.*, 114(2): 333–335.

Renaud, C.B., S.C. Ribey, & Chapleau, F. 1996. Four records of the Chestnut Lamprey, *Ichthyomyzon castaneus*, new to Ontario. *Can. Field-Nat.*,110(3): 450–453.

Richards, J.E., R.J. Beamish, & Beamish, F.W.H. 1982. Descriptions and keys for ammocoetes of lampreys from British Columbia, Canada. *Can. J. Fish. Aquat. Sci.*, 39: 1484–1495.

Richardson, J. 1823. *Notices of the fishes*. No. 6: 705–728 + pls. 25–26. *In* Franklin, J. *Narrative of a journey to the shores of the Polar Sea in 1819–1822 with an appendix on various subjects relating to science and natural history*. London.

Richardson, J. 1836. Fauna Boreali–Americana; or the zoology of the northern parts of British America: Containing descriptions of the objects of natural history collected on the late northern land expeditions under command of Captain Sir John Franklin, R.N. Part 3. *The fish*. J. Murray, London. xv + 327 pp. + pls 74–97.

Richardson, J. 1846. Ichthyology of the voyage of H.M.S. Erebus & Terror. pp. 53–74 + pls. 31–44. *In* Richardson, J. and J.E. Gray eds. *The zoology of the voyage of the H.M.S. Erebus & Terror, under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843*. vol. 2(2), London.

Risso, A. 1827. *Histoire naturelle des principales productions de l'Europe méridionale, et particulièrement de celles des environs de Nice et des Alpes maritimes.* F.G. Levrault, Paris & Strasbourg. Vol. 3: xvi + 480 pp. + 16 pls.

Roffe, T.J. & Mate, B.R. 1984. Abundances and feeding habits of pinnipeds in the Rogue River, Oregon. *J. Wildl. Manage.,* 48(4): 1262–1274.

Rohde, F.C. 1980. *Lampetra appendix* (DeKay), American Brook Lamprey. pp. 23. *In* Fishes, Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister, and J.R. Stauffer, Jr., eds. *Atlas of North American Freshwater*, North Carolina State Museum of Natural History, Raleigh, North Carolina. x + 867 p.

Rohde, F.C., R.G. Arndt, & Wang, J.C.S. 1976. Life history of the freshwater fishes lampreys, *Okkelbergia aepyptera* and *Lampetra lamottenii* (Pisces: Petromyzonidae), on the Delmarva Peninsula (East Coast, United States). *Bull. South. Calif. Acad. Sci.*, 75(2): 99–111.

Rondelet, G. 1558. *L'histoire entière des poissons*. Part 1, 418 pp.; Part 2, 181 pp. M. Bonhome, Lyon, France.

Roos, J.F., P. Gilhousen, S.R. Killick, & Zyblut, E.R. 1973. Parasitism on juvenile Pacific salmon (*Oncorhynchus*) and Pacific Herring (*Clupea harengus pallasi*) in the Strait of Georgia by the River Lamprey (*Lampetra ayresi*). *J. Fish. Res. Board Can.*, 30(4): 565–568.

Roy, J.–M. 1973. Croissance, comportement et alimentation de la lamproie du nord (*Ichthyomyzon unicuspis*, Hubbs & Trautman) en captivité. *Trav. pech. Que.*, (41): 3–144.

Ruiz–Campos G., & González–Guzmán, S. 1996. First freshwater record of Pacific Lamprey, *Lampetra tridentata*, from Baja California, Mexico. *Calif. Fish Game,* 82: 144–146.

Ruiz–Campos, G., S. Contreras–Balderas, M. de L. Lozano–Vilano, S. González–Guzmán, & Alaníz–García, J. 2000. Ecological and distributional status of the continental fishes of northwestern Baja California, Mexico. *Bull. South. Calif. Acad. Sci.*, 99(2): 59–90.

Saemundsson, B. 1927. *Synopsis of the fishes of Iceland*. Rit Vísindafélags Íslendinga II. Prentsmiðjan Gutenberg, Reykjavik, Iceland. 68 pp. + 1 fig.

Salewski, V., B. Kappus, & Renaud, C.B. 1995. Velar tentacles as a taxonomic character in central European lampreys. *Acta Univ. Carol. Biol.*, 39(3–4): 215–229.

Schuldt, R.J. & Goold, R. 1980. Changes in the distribution of native lampreys in Lake Superior tributaries in response to Sea Lamprey (*Petromyzon marinus*) control, 1953–77. *Can. J. Fish. Aquat. Sci.*, 37(11): 1872–1885.

Schultz, L.P. 1930. The life history of *Lampetra planeri* Bloch, with a statistical analysis of the rate of growth of the larvae from western Washington. *Occ. Pap. Mus. Zool. U. Michigan,* no. 221: 1–35 + 2 pls.

Seagle, H.H., Jr. & Nagel, J.W. 1982. Life cycle and fecundity of the American Brook Lamprey, *Lampetra appendix*, in Tennessee. *Copeia,* 1982(2): 362–366.

Seurat, L.G. & Dieuzeide, R. 1931. Sur la capture d'une lamproie marine (*Petromyzon marinus* L.) sur les côtes algériennes. *Bull.Stn Aquic.Peche Castiglione*, Fasc. 2: 85–92.

Seversmith, H.F. 1953. Distribution, morphology and life history of *Lampetra aepyptera*, a brook lamprey, in Maryland. *Copeia,* 1953(4): 225–232.

Shaw, G. 1804. General zoology or systematic natural history. Pisces. 5(part 2): i–vi + 251–463 + pls. 132–182. G. Kearsley, London.

Sidorov, L.K. & Pichugin, M.Yu. 2005. Lampreys of the genus *Lethenteron* of Lake Sopochnoe (Iturup Island, the southern Kuril Islands). *J. Ichthyol.*, 45(5): 402–406.

Silver, M.R., H. Kawauchi, M. Nozaki, & Sower, S.A. 2004. Cloning and analysis of the lamprey GnRH–III cDNA from eight species of lamprey representing the three families of Petromyzoniformes. *Gen. Comp. Endocrinol.,* 139: 85–94.

Sorensen, P.W. & Vrieze, L.A. 2003. The chemical ecology and potential application of the Sea Lamprey migratory pheromone. *J. Great Lakes Res.*, 29(Suppl. 1): 66–84.

Starrett, W.C., W.J. Harth, & Smith, P.W. 1960. Parasitic lampreys of the genus *Ichthyomyzon* in the rivers of Illinois. *Copeia,* 1960(4): 337–346.

Stock, D.W. & Whitt, G.S. 1992. Evidence from 18S ribosomal RNA sequences that lampreys and hagfishes form a natural group. *Science,* 257: 787–789.

Strahan, R. 1959. The status of *Yarra singularis* and *Geotria australis* (Petromyzontidae). *J. R. Soc. West. Aust.*, 42: 49–52.

Strahan, R. 1960. A comparison of the ammocoete and macrophthalmia stages of *Mordacia mordax* and *Geotria australis* (Petromyzonidae). *Pac. Sci.*,14(4): 416–420.

Surface, H.A. 1899. Removal of lampreys from the interior waters of New York. 4th Annual Report of the New York Commissioners of Fisheries, Game and Forests for 1898. Albany, New York. pp. 191–245.

Takezaki, N., F. Figueroa, Z. Zaleska–Rutczynska, & Klein, J. 2003. Molecular phylogeny of early vertebrates: Monophyly of the agnathans revealed by sequences of 35 genes. *Mol. Biol. Evol.*, 20(2): 287–292.

Thomazi, A. 1947. *Histoire de la pêche des âges de la Pierre à nos jours*. Payot, Paris. 645 pp.

Tilesius von Tilenau, W.G. 1811. Piscium camtschaticorum descriptiones et icones. *Acad. sci. St. Pétersb. Mém.*, 3: 225–285 + pls. 8–13.

Turner, L.M. 1886. Contributions to the natural history of Alaska. Part IV. Fishes. The Miscellaneous Documents of the Senate of the United States for the first session of the 49th Congress, Washington. Vol. 8, Misc. Doc. No. 155: 87–113 + pls. 1–15.

Van Beneden, P.–J. 1857. Un nouveau poisson du littoral de Belgique (*Petromyzon Omalii*). Bulletins de l'Académie Royale des Sciences, des Lettres et des Beaux–Arts de Belgique, 2e série, 2(7): 549–554 + 1 pl.

Vladykov, V.D. 1925. Űber einige neue Fische aus der Tschechoslowakei (Karpathorußland). *Zool. Anz.,* 64(11/12): 250–252.

Vladykov, V.D. 1927. Zur Frage über das Absterben unserer Lampreten (Petromyzonidae) nach der Laichzeit. *Zool. Anz.,* 74(10): 237–239.

Vladykov, V.D. 1931. Poissons de la Russie sous–carpathique (Tchécoslovaquie). *Mem. Soc. Zool. France*, 29(4): 217–374.

Vladykov, V.D. 1949. Quebec lampreys (Petromyzonidae). I. List of species and their economical importance. Department of Fisheries, Province of Quebec, Contribution No. 26: 7–67.

Vladykov, V.D. 1950. Larvae of eastern American lampreys (Petromyzonidae). I. Species with two dorsal fins. *Nat. Can.*, 77(3–4): 73–95.

Vladykov, V.D. 1951. Fecundity of Quebec lampreys. *Can. Fish Cul.*, no. 10: 1–14.

Vladykov, V.D. 1955. *Lampetra zanandreai*, a new species of lamprey from northern Italy. *Copeia,* (3): 215–223 + 4 pls.

Vladykov, V.D. 1972. Sous–division en trois sous–familles des lamproies de l'hémisphère–nord de la famille Petromyzonidae. *Ass. Can.–Franc. Avance. Sci.*, 39: 148 (Abstract).

Vladykov, V.D. 1973a. *Lampetra pacifica*, a new nonparasitic species of lamprey (Petromyzontidae) from Oregon and California. *J. Fish. Res. Board Can.*, 30(2): 205–213 + 9 figs.

Vladykov, V.D. 1973b. A female sea lamprey (*Petromyzon marinus*) with a true anal fin, and the question of the presence of an anal fin in Petromyzonidae. *Can. J. Zool.*, 51(2): 221–224.

Vladykov, V.D. 1985a. Does neoteny occur in Holarctic lampreys (Petromyzontidae)? *Syllogeus,* 57: 1–13.

Vladykov, V.D. 1985b. Record of 61 parasitic lampreys (*Ichthyomyzon unicuspis*) on a single sturgeon (*Acipenser fulvescens*) netted in the St. Lawrence River (Québec). *Nat. Can.*, 112(3): 435–436.

Vladykov, V.D. & Roy, J.–M. 1948. Biologie de la lamproie d'eau douce (*Ichthyomyzon unicuspis*) après la métamorphose. *Rev. Canad. Biol.*, 7(3) : 483–485.

Vladykov, V.D. & Follett, W.I. 1958. Redescription of *Lampetra ayresii* (Günther) of western North America, a species of lamprey (Petromyzontidae) distinct from *Lampetra fluviatilis* (Linnaeus) of Europe. *J. Fish. Res. Board Can.*, 15(1): 47–77 + 15 figs.

Vladykov, V.D. & Follett, W.I. 1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. *J. Fish. Res. Board Can.*, 22(1): 139–158 + 9 figs.

Vladykov, V.D. & Follett, W.I. 1967. The teeth of lampreys (Petromyzonidae): their terminology and use in a key to Holarctic genera. *J. Fish. Res. Board Can.*, 24(5): 1067–1075.

Vladykov, V.D. & Kott, E. 1976a. Is *Okkelbergia* Creaser and Hubbs, 1922 (Petromyzonidae) a distinct taxon? *Can. J. Zool.,* 54(3): 421–425.

Vladykov, V.D. & Kott, E. 1976b. A new nonparasitic species of lamprey of the genus *Entosphenus* Gill, 1862, (Petromyzonidae) from south central California. *Bull. South. Calif. Acad. Sci.*, 75(2): 60–67.

Vladykov, V.D. & Kott, E. 1976c. A second nonparasitic species of *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River system, California. *Can. J. Zool.*, 54(6): 974–989.

Vladykov, V.D. & Kott, E. 1976d. The taxonomic significance of velar tentacles in Holarctic lampreys (Petromyzonidae). *Rev. Trav. Off. Pech. Marit.*, 40(3–4): 787–789.

Vladykov, V.D. & Kott, E. 1978a. 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. *Biol. Pap. Univ. Alaska*, no. 19: 1–74.

Vladykov, V.D. & Kott, E. 1978b. A new nonparasitic species of *Lethenteron* Creaser and Hubbs 1922 (Petromyzonidae) from Hokkaido, Japan. *Can. J. Zool.*, 56(8): 1792–1800.

Vladykov, V.D. & Kott, E. 1979a. A new parasitic species of the Holarctic lamprey genus *Entosphenus* Gill, 1862 (Petromyzonidae) from Klamath River, in California and Oregon. *Can. J. Zool.*, 57(4): 808–823.

Vladykov, V.D. & Kott, E. 1979b. Satellite species among the Holarctic lampreys (Petromyzonidae). *Can. J. Zool.*, 57(4): 860–867.

Vladykov, V.D. & Kott, E. 1979c. List of Northern Hemisphere lampreys (Petromyzonidae) and their distribution. Department of Fisheries and Oceans Miscellaneous Special Publication 42: 30 pp.

Vladykov, V.D. & Kott, E. 1980a. Description and key to metamorphosed specimens and ammocoetes of Petromyzonidae found in the Great Lakes region. *Can. J. Fish. Aquat. Sci.*, 37(11): 1616–1625.

Vladykov, V.D. & Kott, E. 1980b. First record of the Sea Lamprey, *Petromyzon marinus* L., in the Gulf of Mexico. *Northeast Gulf Sci.*, 4(1): 49–50.

Vladykov, V.D. & Kott, E. 1982a. Correct scientific names for the Least Brook Lamprey and the American Brook Lamprey (Petromyzonidae). *Can. J. Zool.*, 60(5): 856–864.

Vladykov, V.D. & Kott, E. 1982b. Comment on Reeve M. Bailey's view of lamprey systematics. *Can. J. Fish. Aquat. Sci.*, 39(8): 1215–1217.

Vladykov, V.D. & Kott, E. 1984. A second record for California and additional morphological information on *Entosphenus hubbsi* Vladykov and Kott 1976 (Petromyzontidae). *Calif. Fish Game,* 70(2): 121–127.

Vladykov, V.D., E. Kott, & Pharand–Coad, S. 1975. A new nonparasitic species of lamprey, genus *Lethenteron* (Petromyzonidae), from eastern tributaries of the Gulf of Mexico, U.S.A. *Publs. Zool. Natn. Mus. Nat. Sci. Can.*, 12: 1–36.

Vladykov, V.D., E. Kott, & McAllister, D.E. 1980. *Lampetra alaskanse* (Vladykov and Kott), Darktail Lamprey. p. 22. *In* Lee, D.S., C.R. Gilbert, C.H. Hocutt, R.E. Jenkins, D.E. McAllister, and J.R. Stauffer, Jr., eds. *Atlas of North American Freshwater Fishes*. North Carolina State Museum of Natural History, Raleigh, North Carolina.

Vladykov, V.D., C.B. Renaud, E. Kott, & Economidis, P.S. 1982. A new nonparasitic species of Holarctic lamprey, genus *Eudontomyzon* Regan 1911 (Petromyzontidae), from Greece. *Can. J. Zool.*, 60(11): 2897–2915.

Vogt, K.D. 1988. The occurrence of *Lampetra tridentatus* in the northern Bering Sea. Japanese *J. Ichthyol.*, 35(3): 403–404.

Volk, E.C. 1986. Use of calcareous otic elements (statoliths) to determine age of Sea Lamprey ammocoetes (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.*, 43: 718–722.

von Martens, E. 1868. Ueber einige ostasiatische Süsswasserthiere. *Arch. Naturgesch.,* 34: 1–64 + 1 pl.

Wajgel, L. 1884. Die Zusammenziehung der Zwei Arten von *Petromyzon* (*P. Planeri* und *P. fluviatilis*) in *Eine. Verh. der k.k. zool.-bot. Ges. in Wien,* 33: 311–319 + pl. 17.

Walsh, S.J. & Burr, B.M. 1981. Distribution, morphology and life history of the Least Brook Lamprey, *Lampetra aepyptera* (Pisces: Petromyzontidae), in Kentucky. *Brimleyana,* No. 6: 83–100.

Wills, J.H., Jr. 1966. *Seafood toxins*. National Academy of Sciences, National Research Council, Washington, D.C., Publication no. 1354: 147–163.

Wolf, B.O. & Jones, S.L. 1989. Great Blue Heron deaths caused by predation on Pacific Lamprey. *The Condor, 91(2): 482–484.*

Yalden, D.W. 1985. Feeding mechanisms as evidence for cyclostome monophyly. *Zool. J. Linn. Soc.*, 84: 291–300.

Yamazaki, Y. & Goto, A. 1997. Morphometric and meristic characteristics of two groups of *Lethenteron reissneri*. *Ichthyol. Res.*, 44: 15–25.

Yamazaki, Y. & Goto, A. 1998. Genetic structure and differentiation of four *Lethenteron* taxa from the Far East, deduced from allozyme analysis. *Environ. Biol. Fish.*, 52: 149–161.

Yamazaki, Y., S. Konno, & Goto, A. 2001. Interspecific differences in egg size and fecundity among Japanese lampreys. *Fish. Sci.*, 67(2): 375–377.

Yamazaki, Y., A. Goto, & Nishida, M. 2003. Mitochondrial DNA sequence divergence between two cryptic species of *Lethenteron*, with reference to an improved identification technique. *J. Fish Biol.*, 62: 591–609.

Yamazaki, Y., A. Goto, H–K. Byeon, & Jeon, S.–R. 1999. Geographical distribution patterns of the two genetically divergent forms of *Lethenteron reissneri* (Pisces: Petromyzontidae). *Biogeography,* 1: 49–56.

Yamazaki, Y., R. Yokoyama, M. Nishida, & Goto, A. 2006. Taxonomy and molecular phylogeny of *Lethenteron* lampreys in eastern Eurasia. *J. Fish Biol.,* 68(Suppl. B): 251–269.

Zanandrea, G. 1959a. Lamprede parassite e non parassite nel bacino del Danubio e la nuova entità sistematica *Eudontomyzon danfordi vladykovi*. *Arch. Zool. Ital.*, 44: 215–250 + 2 pls.

Zanandrea, G. 1959b. *Lampetra fluviatilis* catturata in mare nel Golfo di Gaeta. *Pubbl. Stn. Zool. Napoli*, 31(2): 265–307 + 2 pls.

Zanandrea, G. 1959c. Recenti ricerche sulle forme “appaiate” di lamprede dell’Italia e del Danubio. *Boll. Zool.*, 26: 545–554.

Zanandrea, G. 1961. Studies on European lampreys. *Evolution,* 15(4): 523–534.

Zhukov, P.I. 1969. New data on the biology of freshwater lampreys in White Russia. *J. Ichthyol.*, 9(2): 181–186.

3. INDEX OF SCIENTIFIC AND VERNACULAR NAMES

EXPLANATION OF THE SYSTEM

Italics : Valid scientific names (double entry by genera and species)
Italics : Synonyms and misidentifications (double entry by genera and species)
ROMAN : Family names
ROMAN : Names of orders, class, subclass, superfamilies
Roman : FAO names
Roman : Local names

A

B

C

D

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H

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Lampreys are aquatic, jawless vertebrates belonging to the Order Petromyzontiformes. The order comprises 39 species widely distributed in the Northern and Southern hemispheres, but virtually absent in the intervening tropical zone. There is one family in the Northern Hemisphere (Petromyzontidae) comprising 35 species and two families in the Southern Hemisphere (Geotriidae and Mordaciidae) comprising, respectively, one and three species. Lampreys undergo a radical metamorphosis from the larval to the adult form. While lamprey larvae (ammocoetes) of all species are very similar in their habits (filter-feeding on microorganisms in a freshwater habitat), the adults vary considerably in their mode of life. Some are parasitic and anadromous, others parasitic but restricted to fresh water, while still others are nonparasitic (non-feeding) and restricted to fresh water. The taxonomic characters used to describe ammocoetes and adults are fully explained and illustrated. A key to adults and a partial key to larvae are presented. This catalogue provides an account for each of the 39 species. Each species account gives information on the taxonomy including synonyms, common names, diagnostic features of ammocoetes and adults (with drawings of the adult body and oral disc), habitat and biology, geographic distribution (with map), interest to fisheries and references.

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