

## FAO Species Catalogue of Lampreys of the World

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### 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.

#### 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

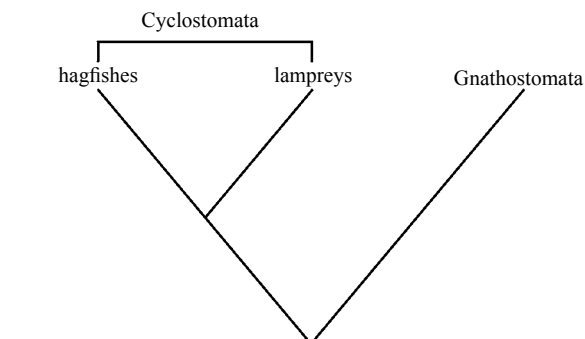


Fig. 1. Relationships among living agnathans and gnathostomes according to the cyclostome hypothesis.

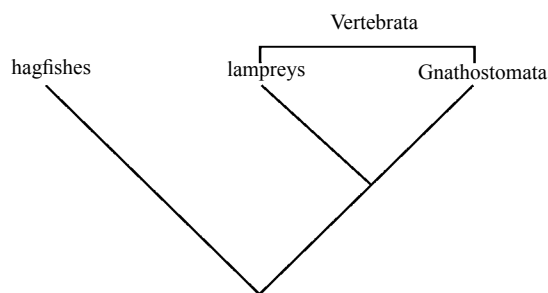


Fig. 2. Relationships among living agnathans and gnathostomes according to the vertebrate hypothesis.

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 20° 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, *Priscosmyzon 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 referred to as transformed or metamorphosed individuals. So radical is this metamorphosis that 19<sup>th</sup> 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 cirri. 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. Additionally, 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 1<sup>st</sup> and 2<sup>nd</sup> 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 12<sup>th</sup> 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 châtilions. 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.

**Ageing.** 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 zanandreaei*). 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 macrophthalmia 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 macrophthalmia individuals, which he described as 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.g.s. *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.

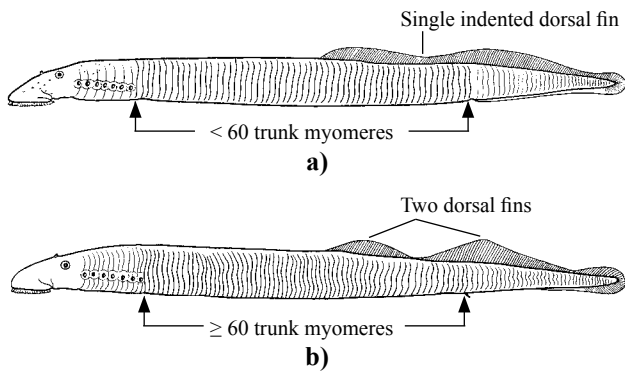
**Cases of Repeat Spawning.** Lampreys are semelparous (i.e. they die after spawning). Two reports (Michael, 1980, 1984) however, have claimed that one species, *Entosphenus tridentatus*, may exhibit repeat spawning, based on the capture of marked upstream migrants during two successive spawning migrations.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

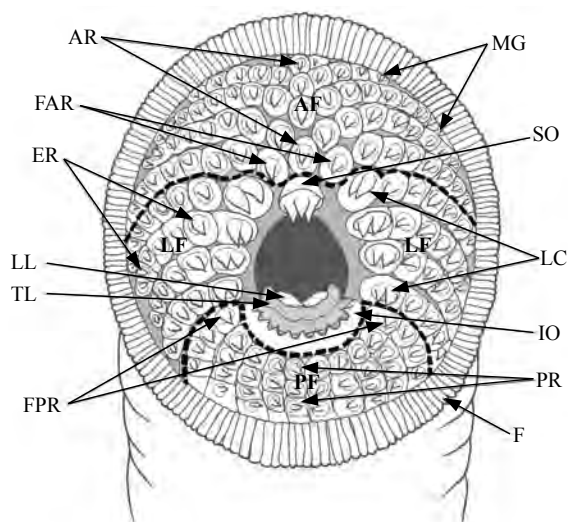
**Counts.** Number of trunk myomeres: The first myomere is the one whose anterior myoseptum lies on or is posterior to the posterior edge of the 7<sup>th</sup> branchial opening and the last myomere is the one in which the lower angle of its posterior myoseptum lies at or is anterior to the anterior 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,



**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 = anterior rows; ER = exolateral rows; F = oral fimbria; FAR = first anterior row; FPR = first posterior row; IO = infraoral lamina; LC = lateral circumorals or endolaterals; LF = lateral field; LL = longitudinal lingual lamina; MG = marginals; PF = posterior field; PR = posterior rows; SO = supraoral lamina; TL = transverse lingual lamina)

anterials, and supraoral lamina; lateral – marginals, exolaterals, and endolaterals; posterior – marginals, posterials, and infraoral 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 anterior, exolateral, and posterial teeth.

Hubbs and Trautman (1937) include a marginal tooth in their count of the number of anterior 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 circummorals, 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 circummorals 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 circummorals 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 anterior and posterior teeth (referred 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, Lantaigne (1981) used the number of bicuspid 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 Circummorals.

**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 Circummorals 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 circummoral. 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;

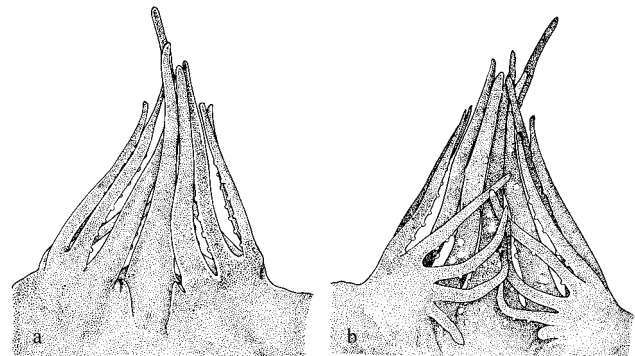
3 = tricuspid. Thus, an endolateral formula of 2–3–3–2 means that there are four endolaterals on one side of the disc, the first one being bicuspid, the second tricuspid, ...

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

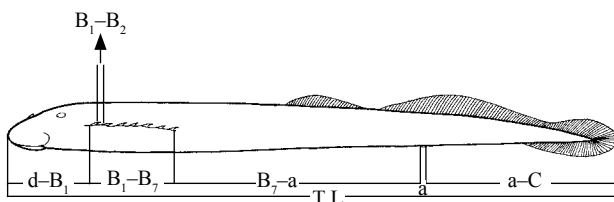


**Fig. 5. Velar apparatus in an adult lamprey. a. Ventral view. b. Dorsal view. In the dorsal view can be seen lateral tentacles folded over to form “wings”; one on either side of the velar apparatus.**

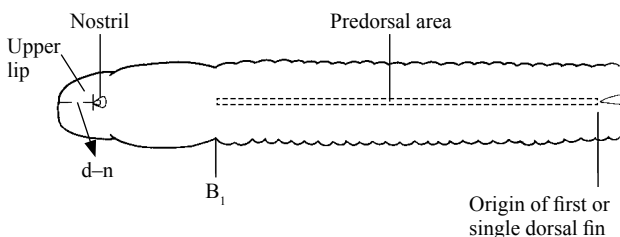
of the shrinkage due to preservation will happen in the oral disc, trunk, and tail areas. Shrinkage due to preservation has been estimated at 1–3% of the total length by Hubbs and Trautman (1937) and Vladykov (1949). Additionally, natural shrinkage occurs in lampreys when they go through metamorphosis 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 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.

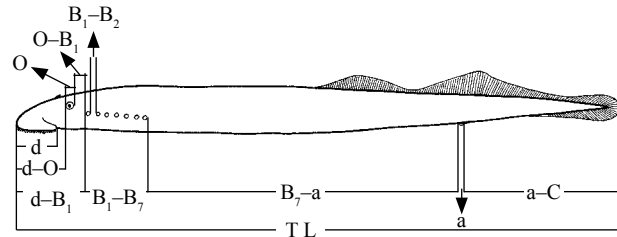
**Eye Length (O):** from the anterior to the posterior edge. Also called eye diameter by some.



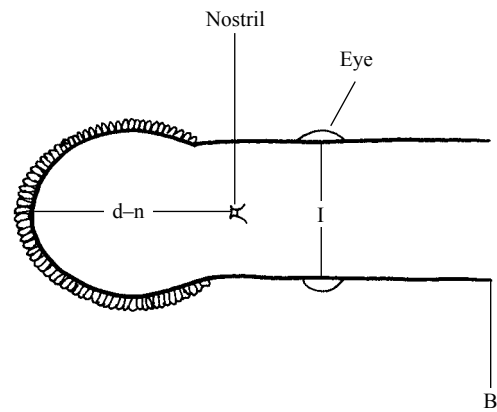
**Fig. 6. Side view of larval lamprey showing various body measurements. a = cloacal slit length; a-C = tail length;  $B_1-B_2$  = interbranchial opening distance;  $B_1-B_7$  = branchial length;  $B_7-a$  = trunk length;  $d-B_1$  = prebranchial length; TL = total length. After Renaud (1982a).**



**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.

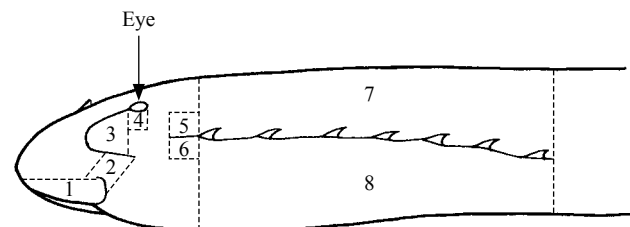
The intestinal diameter is measured at the level of the origin of the first dorsal fin or the anterior lobe of the single dorsal fin, accordingly.

**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

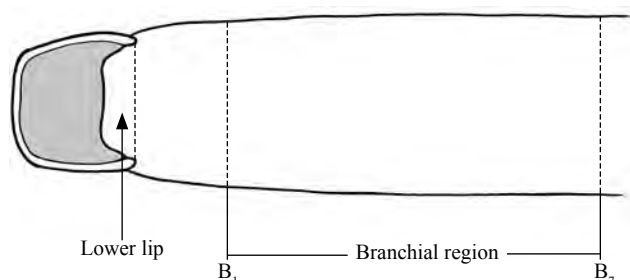
prebranchial, lower prebranchial, upper branchial, lower branchial, ventral branchial, lower lip (called transverse lip by Neira *et al.* 1988), predorsal area, and caudal fin. The caudal fin area evaluated for pigmentation is from the deepest part of the caudal fin membrane to its posterior tip. The 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

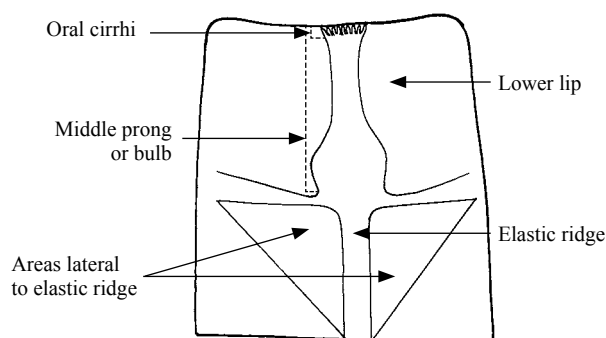


**Fig. 10. Side view of the head and branchial regions of a larval lamprey showing various pigmentary areas: 1– upper lip, 2– between upper lip and cheek, 3– cheek, 4– subocular, 5– upper prebranchial, 6– lower prebranchial, 7– upper branchial, 8– lower branchial. After Renaud (1982a).**



**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<sup>1</sup> counts in the general text of this document incorporate the new species.

<sup>1</sup> 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 1 or 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. Posteriors present as a single complete row ..... → 13
- 12b. Posteriors 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 anterior 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 arterials. . . . . *Eudontomyzon morii*  
**20b.** 5–13 teeth in first row of arterials. . . . . → 21
- 21a.** 2–4 rows of arterials . . . . . *Eudontomyzon mariae*  
**21b.** 4–7 rows of arterials . . . . . *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 arterials . . . . . *Lethenteron reissneri*  
**29b.** Second dorsal fin usually with a dark blotch; trunk myomeres, 65–77; 15–38 arterials . . . . . → 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 arterials; 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*<sup>1</sup>
- 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 zanandreae*

### 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. zanandreae* (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*<sup>1</sup> (Greece),  
*E. mariaae* (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)

<sup>1</sup> *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.