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Title: SYSTEMATICS, VARIATION, DISTRIBUTION, AND BIOLOGY OF LAMPREYS OF THE GENUS *LAMPETRA* IN OREGON

Abstract approved: Redacted for privacy
Carl E. Bond

Based on the number of velar tentacles and the form of longitudinal lingual laminae found in *Lampetra* (*Entosphenus*) *t. tridentata* and its closely related forms, the taxon *Entosphenus* should not be considered as a genus as commonly adopted, but, along with the taxa *Lethenteron* and *Lampetra*, should be regarded as a subgenus of the genus *Lampetra*. The genus *Lampetra* is distinct for various reasons, including particularly the character that no cusps are present in the area distal to the lateral circumorals.

Six nominal species, belonging to the subgenera *Entosphenus* and *Lampetra*, have been known to occur in four of the seven major drainage systems of Oregon.

The anadromous *L.* (*E.*) *t. tridentata*, is widespread in the Columbia River and Coastal drainage systems, occurring in most

streams with access to the ocean regardless of distance to the ocean, as long as suitable spawning grounds and ammocoete habitats are present. Morphometrics and dentitional features vary little over its geographical range. The number of trunk myomeres and the adult body size vary appreciably so that two categories of regional forms, coastal and inland, may be recognized. The coastal forms are generally smaller and have fewer trunk myomeres compared to those of the larger inland forms. The spawning migration begins from the late spring to late summer for the coastal forms but may occur much earlier for the inland forms. The adult body size appears to be positively correlated with absolute fecundity, but is negatively correlated with relative fecundity. Duration of the larval period is from four to six years. Metamorphosis usually takes place in the fall. Macrophthalmia are known to enter the ocean over a long period, those descending coastal streams enter salt water in the late fall and early winter, whereas the peak of emigration from inland streams is in the early spring. Duration of its marine parasitic phase appears to be from 20 to 40 months. The small landlocked L. (E.) t. kawiaga n. subsp., found only in the Klamath and Goose Lake drainage systems in southern Oregon and northern California, differs from t. tridentata in body size and various meristic and morphometric characters. Its lacustrine parasitic phase is about 12 months long. L. (E.) lethophaga,

the nonparasitic derivative of *tridentata*, occurs in the Klamath and probably also the Goose Lake drainage system. It is characterized by an extension of the larval phase and by a greatly reduced post-larval period. The presumably extinct *L.* (*E.*) *minima*, a parasitic derivative of *tridentata*, found formerly only in Miller Lake, Oregon, possessed a number of characters that were concomitants of dwarfism, the distinctive feature of the species. Relationships and evolution among the subgenus *Entosphenus* were discussed.

Distributional records of *L. ayresii* and *L. richardsoni* of the subgenus *Lampetra* in Oregon were given. Evidence indicates that a complex of clinal races, including *L. pacifica* Vladykov, 1973, may exist in the latter species.

Systematics, Variation, Distribution, and Biology of Lampreys of the Genus *Lampetra* in Oregon

by

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Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

SYSTEMATICS, VARIATION, DISTRIBUTION, AND BIOLOGY OF LAMPREYS OF THE GENUS *LAMPETRA* IN OREGON

INTRODUCTION

General

Lampreys of the family Petromyzonidae[1] (order Petromyzoniformes) are important components of many holarctic ecosystems. Although the larvae are seldom seen, they often form a significant proportion of the vertebrate biomass of freshwaters. Larvae and adults are subject to predation by fish, birds and mammals, and the adults are used regionally as food by man. Depredation by a few parasitic species have brought attention to the group.

The investigations reported here were planned to widen and deepen our knowledge of the several species of the genus *Lampetra* known to occur in Oregon. The aim is to identify and characterize the species, to show their variability and possible divisions into races or subspecies, and to delineate their distributions. In addition the intent is to present information on life histories. Concentration is on the members of the subgenus *Entosphenus*.

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[1] This spelling follows Hubbs and Potter (1971) as opposed to the spelling recommended by the American Fisheries Society (Bailey *et al.*, 1970) which is Petromyzontidae.

Lampetra is known as the most speciose lamprey genus; its species occur in such wide-ranging holarctic regions as western Europe, eastern Asia, and North America. Three subgenera have recently been recognized in the genus (Hubbs and Potter, 1971); species of two of them, *Entosphenus* and *Lampetra*, are widespread in the Pacific Northwest and particularly well-represented in Oregon.

The greatest contribution to the knowledge of speciation among lampreys has been the derivative species concept, first shaped by Hubbs (1925). He indicates that the nonparasitic or brook lampreys, which cease to feed after the onset of metamorphosis, appear to have evolved from species that, as juveniles as well as adults, are parasitic mainly upon teleost fishes. A similar concept was presented later by Zanandrea (1959a), whose term "paired species" is applied to the pairs of closely related and morphologically similar lampreys which overlap in their distribution but differ in their life history. The term has since been designated by biologists as an assemblage, containing no fewer than two members, of closely related species of lampreys. The assemblage is generally composed of both parasitic and nonparasitic species with a primitive parasitic one that has eventually given rise to the others of the assemblage. Hardisty and Potter (1971a) summarized and discussed in detail the current view on "paired species."

"Paired species" have been recognized in all but the genera

Geotria, *Petromyzon*, and *Caspiomyzon* (Okkelberg, 1921; Creaser and Hubbs, 1922; Weissenberg, 1925, 1926 and 1927; Berg, 1931; Hubbs and Trautman, 1937; Berg, 1948; Raney, 1952; Vladykov, 1955; Vladykov and Follett, 1958; Zanandrea, 1959a and 1961; Kux, 1965; Vladykov and Follett, 1965; Alvarez, 1966; Potter, 1968; Potter and Strahan, 1968; Potter, Lanzing and Straham, 1968; Hardisty, Potter and Sturge, 1970; Hubbs, 1971; Hubbs and Potter, 1971; Bond and Kan, 1973; Vladykov, 1973a).

The systematics of lampreys of Oregon, and the Pacific Northwest in general, has been largely ignored since 1836, when J. Richardson, based on information provided by M. Gairdner, described the Pacific lamprey, *Lampetra tridentata*, from the Willamette River, Oregon. Initial merits for an expansion of our knowledge of the subject must be given to Vladykov and Follett who, by detailed analyses (1958 and 1965), concluded that the river *L. ayresii* and brook *L. richardsoni*, lampreys of the western North America are distinct from those of Europe, *L. fluviatilis* and *L. planeri* respectively. However, no comprehensive work has been done, but accounts were briefly included in Schultz and DeLacy (1935), Schultz (1936) and Bond (1961 and 1973). Evidence accumulated in recent years indicated that further study was definitely needed.

Geographical and Geological Considerations

The State of Oregon lies between 42° and 46° 16' North Latitude and 116° 30' and 124° 30' West Longitude, and is bounded on the north by Washington, on the east by Idaho, on the south by Nevada and California, and on the west by the Pacific Ocean. It is composed of 36 counties (Figure 1).

The geography and geology of Oregon was treated respectively by Dickens (1965) and Baldwin (1964) in terms of nine physiographic divisions (Figure 2). In general, the Cascade Mountains divide the State into two provinces climatically and topographically. On the west there are lowlands and low mountains, and an oceanic type of climate prevails. On the east, the land is high, largely flat, and, in some areas, mountainous. The climate is rather continental, with cold winters, hot summers, and less yearly rainfall than the western section.

Essential to the present work is a treatment of the present drainage systems in the area concerned. Past geological and climatic phenomena no doubt greatly influenced the patterns of drainage systems and, in turn, such biological events as dispersal, isolation, extinction, genetic mixture, and secondary contact that in one way or another, are intimately associated with the speciation among fishes. Therefore, behind the existing scene is the interplay of time, space, genetic, and ecological factors.

Continental glaciation extended uninterruptedly along the Cascade Mountains proper to the Columbia River, and affected

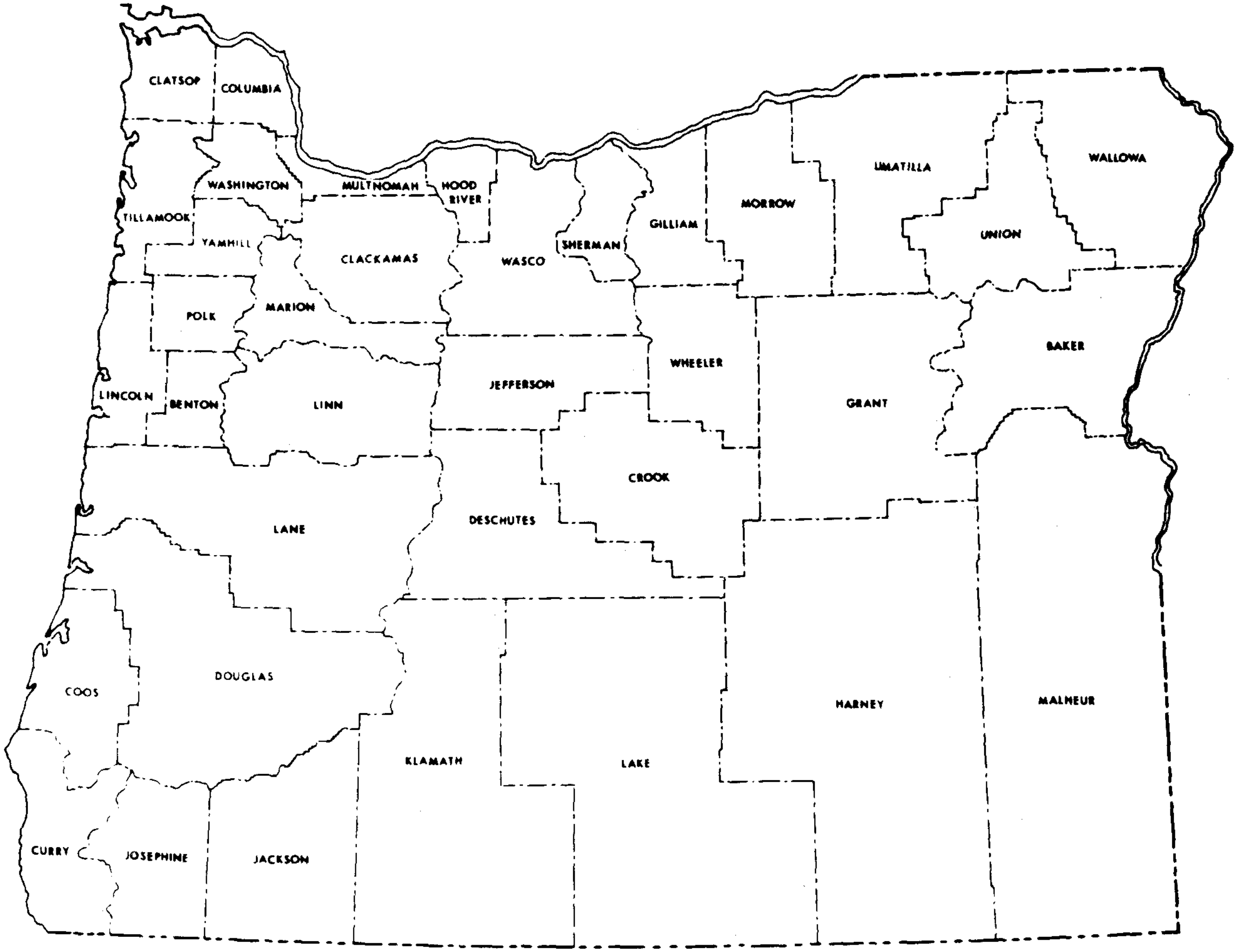

Figure 1. Map of Oregon showing counties.

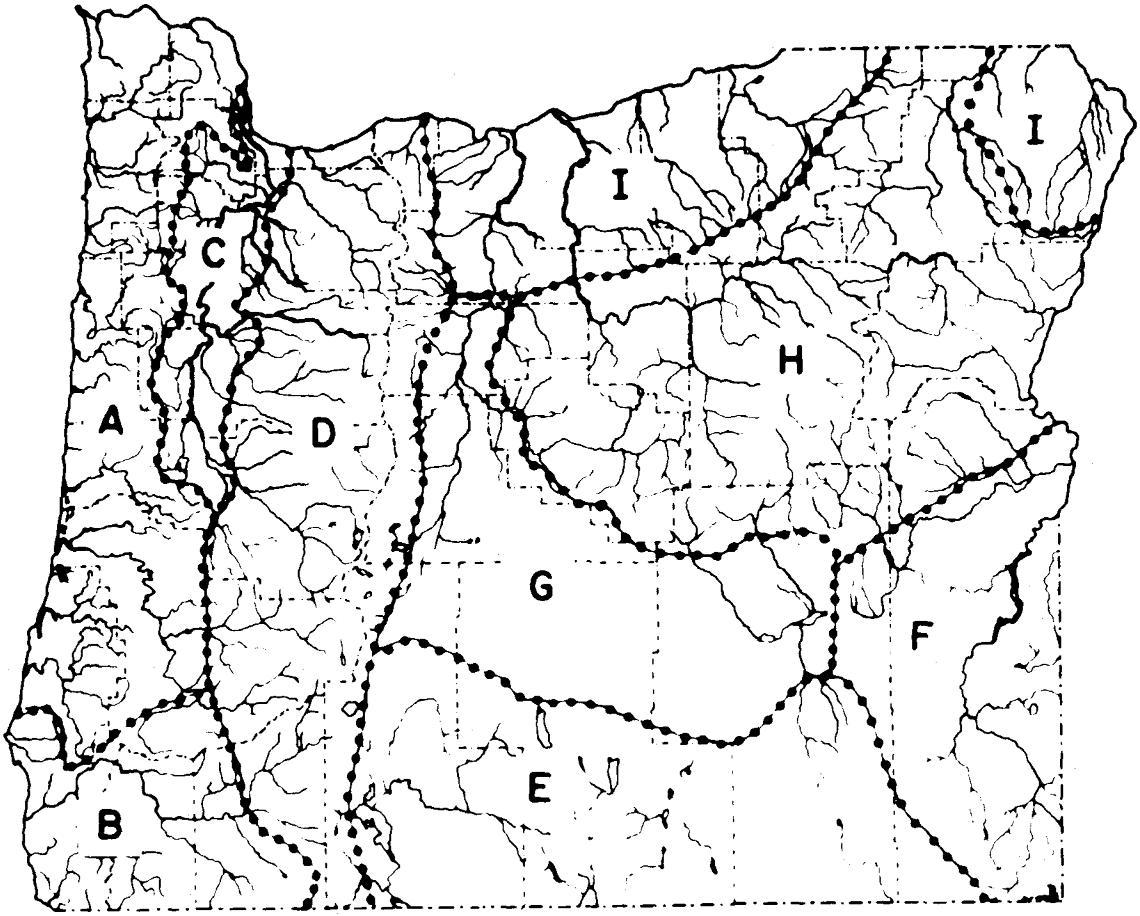

Figure 2. Geological divisions of Oregon.

A - Coast Range
B - Klamath Mountains
C - Willamette Valley
D - Cascade Range
F - Owyhee Upland
G - High Lava Plains
H - Blue Mountains
I - Columbia Basin
E - Basin and Range Province

drainage systems of the Willamette Valley (Flint, 1957). Highland glaciers outside the continuous ice formed in the Mount Hood, Mount Jefferson, and Crater Lake districts, and many separate areas of the Klamath Mountains (Crandell, 1965). Several regions in southern and south central Oregon were influenced indirectly by the ice as they have been geologically connected to the Great Basin where, as a whole, the pluvial stages and glacial periods were approximately coincident (Hubbs and Miller, 1948; Hansen, 1961). McPhail and Lindsey's excellent discussion (1970) on correlations between glacial evidence and present freshwater fish distribution of northwestern Canada and Alaska also concerns Oregon species in many respects.

During the past 11,000 years since the last continental glaciers melted, the weather in the Pacific Northwest has been undergoing cyclic changes. The pollen profiles indicate increasing warmth and dessication to a maximum and then a return to cooler and moister conditions in more recent time (Hansen, 1947, 1961, and 1967). Volcanic activities during the thermal maximum, such as the eruption of Mount Mazama (Crater Lake) some 6,600 years ago (Powers and Wilcox, 1964), would no doubt have impacts on drainage systems and thus fish distributions.

The course of a stream may be altered by small-scaled geological activities. Baldwin and Howell (1949) concluded that the Long Tom River, a tributary to the Willamette River now, joined the

Siuslaw River at one time. Other hydrographical features as temporary interconnection and head water transfer also contribute to the distribution of Oregon freshwater fishes (Bond, 1963; Bisson and Bond, 1971).

In the State seven major drainage systems, Figure 3, are recognized (Bond, 1963). These include the Columbia which drains more than half the area, and, in the south central portion of the State, an extensive system of interior basins which, as previously noted, is related geologically to the Great Basin. East of the Cascade Mountains, along the southern boundary, is located the Klamath drainage, which flows southward to the ocean through California. A former part of the Sacramento System, the Goose Lake drainage, is also found there. Along the coast are numerous shorter drainages, including the Rogue, Coquille, Umpqua, Alsea, and Nehalem, that enter the sea independently.

The following is a description of the major drainage systems with their geographical and ichthyofaunal relationships. Species of the genus Lampetra that occur are listed in Table 1.

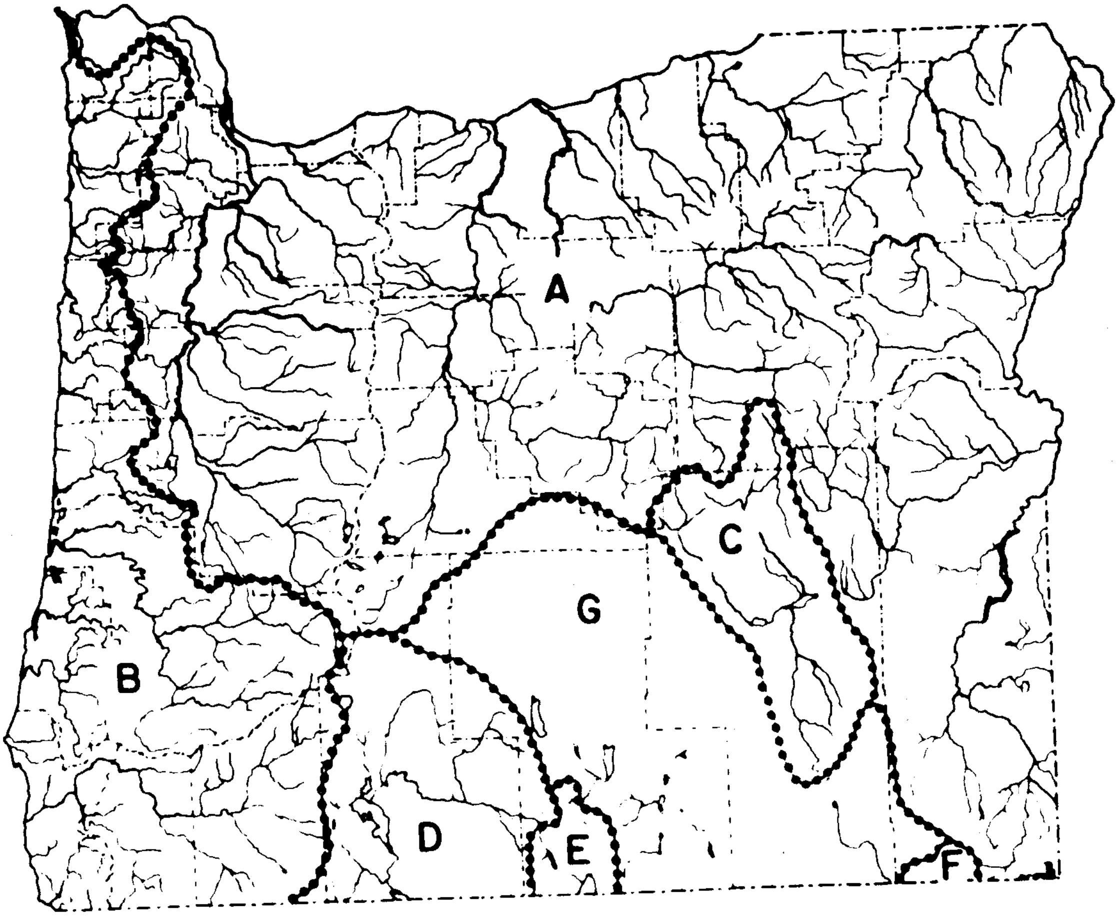

Figure 3. Drainage systems of Oregon.

A - Columbia River System

B - Coastal Drainages

C - Harney Basin

D - Klamath Basin

E - Pit River Drainage (Goose Lake)

F - Lahontan Drainage

G - "Oregon Lakes" System (Interior Basins)

Table 1. Occurrence (XX) of species of the genus *Lampetra* in Oregon drainage systems.

Species	Drainage System			
	Columbia River	Coastal	Klamath	Goose Lake
L. (*Entosphenus*) *t. tridentata*	XX	XX	--	--
L. (*E.*) *t. kawiaga*	--	--	XX	XX
L. (*E.*) *minima*	--	--	XX	--
L. (*E.*) *lethophaga*	--	--	XX	XX(?)
L. (*E.*) sp.	--	--	XX	XX
L. (*Lampetra*) *ayresii*	XX	XX	--	--
L. (*L.*) *richardsoni*	XX	XX	--	--

Columbia River System (Figure 3, A)

This great system is regarded as the principal stream of one of the major ichthyofaunal regions of western North America (Miller, 1958). The fauna of several adjacent drainages are related to and laregely or entirely derived from that of Columbia. These include the Fraser River (Eigenmann, 1895), the Puget Sound lowland and coastal streams of Washington (Snyder, 1908a; Schultz, 1947; Reimers and Bond, 1967), some coastal streams of Oregon (Snyder, 1908a; Bond, 1963), the Harney-Malheur basin (Snyder, 1908b; Hubbs and Miller, 1948; Bisson and Bond, 1971), the Bonneville basin (Hubbs and Miller, 1948), and, to a lesser degree, the Missouri drainage (Jordan, 1928; McPhail and Lindsey, 1970).

Three species of the genus Lampetra occur in the Columbia River System (Table 1); they (tridentata, ayresii, and richardsoni) are also present in the coastal drainages.

Coastal Drainages (Figure 3, B)

As noted above there is a faunal relationship between the Columbia and Coastal drainages. Primary freshwater fishes (see Myers, 1938) of the Willamette River (Dimick and Merryfield, 1945) may get access to at least the larger coastal streams through flooding, stream capture, or alteration of the stream course. One of the

Klamath endemics, a sucker (Catostomus rimiculus), was able to invade the Rogue system (Snyder, 1908b) apparently through some fluvial connection. In general, the fish faunas of Washington (McPhail, 1967) and California coastal streams (Fry, 1973) are similar to those of Oregon coastal streams.

Klamath Basin (Figure 3, D)

This system was regarded as associated with coastal drainages by Snyder (1908a) and by Schultz and DeLacy (1935). However, the geographical isolation of its upstream areas and the high degree of endemism (Evermann and Meek, 1898; Gilbert, 1898; Hubbs and Miller, 1948; Robins and Miller, 1957; Hubbs, 1971; Bond and Kan, 1973) merit its consideration as an independent faunal area formerly connected with the Great Basin (Hubbs and Miller, 1948).

Four species of the genus Lampetra have been found in the Klamath Basin (Table 1).

Pit River Drainage (Goose Lake) (Figure 3, E; Table 1)

The faunal relationship of Upper Pit drainage are with the Klamath Basin and the Great Basin (Hubbs and Miller, 1948). Due to its comparative isolation and aridity, this system has a rather restricted fish fauna. Endemics include a sucker, Catostomus microps, (Rutter, 1908), a sculpin, Cottus pitensis, (Bailey and

Bond, 1963; Bond, 1963), and probably a trout, Salmo sp. (Behnke, 1970; Wilmot, 1974).

Lahontan Drainage (Figure 3, F)

Only a small segment of the Lahontan Basin extends into Oregon. The Lahontan Basin fishes show affinity with the Klamath, Sacramento, Columbia, Bonneville, and Death Valley systems (Hubbs and Miller, 1948; Miller, 1958). No lampreys, however, are found in this drainage system.

"Oregon Lakes" System (Interior Basins) (Figure 3, G)

This system includes a number of isolated basins lying in the desert region west of the Harney Basin between the headwaters of the Deschutes River and the Oregon-Nevada border. The lampreys, a peripheral freshwater fish (see Myers, 1938), appears to be absent from all of these basins.

Harney Basin (Figure 3, C)

This section of the Great Basin is evidently a disrupted part of the Columbia River System (Snyder, 1908b; Hubbs and Miller, 1948; Bond, 1963). Seemingly, none of the Columbia drainage lampreys was able to colonize this basin via the two former invasions traced by Bisson and Bond (1971). If they ever entered the basin, they have since disappeared.

Life History Types

The lamprey is among the few vertebrates that undergoes radical metamorphosis. Prior to this event, the larvae (ammocoetes) live in the silt deposits of rivers and streams for several years, straining from the water the microorganisms on which they feed. However, the mode of life of postlarval forms varies greatly, depending on trophic requirements of the animals. Those which lead a parasitic mode of life are generally migratory, either anadromously or adfluvially. Episodes in their post-metamorphic period may be briefly stated as follows:

1. The transforming and macrophthalmia phases when for periods of a few months the animal is not feeding. During these phases there is some loss in weight, but little or no reduction in length.
2. The downstream migration toward the sea or lake; adaptations for the pelagic life such as body countershading (Denton and Nicol, 1966) develop.
3. The phase of parasitic feeding.
4. The upstream migration, when feeding ceases and gonads are maturing. Marked reductions in weight and length occur.
5. The spawning phase, followed rapidly by the death of the animals.

The majority of known lamprey species are, however, nonparasitic. These forms stop feeding completely at and after metamorphosis and do not perform any extensive migrations. As in the parasitic forms, they soon die after spawning.

The nonparasitic lampreys are now believed to be characterized by an extension of the larval phase and by a greatly reduced postlarval period, in comparison with the corresponding ancestral parasitic species (Hardisty and Potter, 1971a). The considerable demands that the gonadal development makes on body reserves of the spawning nonparasitic lamprey is associated with a marked reduction in the length and weight of the animal, which is nearly always smaller than the metamorphosing ammocoetes (Hardisty and Potter, 1971b). On the other hand, with the exception of a single dwarfed species, Lampetra minima, (Bond and Kan, 1973), no parasitic lamprey is known to have spawners smaller than ammocoetes.

Importance

The view that lampreys are harmful to man because they destroy food and game fishes is largely false. Most species of these animals are nonparasitic and thus harmless. Usually only the larger parasitic forms at feeding stage are capable of inflicting vast damage such as that imposed by Petromyzon marinus on the American Great Lakes fisheries (Applegate, 1950; Smith, 1971). Several species of lampreys of both types, parasitic and nonparasitic, were recently listed as fishes which are "endangered," "rare," or "threatened," and for which conservation measures are needed (Bond, 1966; Miller, 1972; Shay, 1973; and see Bond and Kan, 1973, and Vladykov, 1973b). To protect these animals from extinction is vital not only for ethical reasons concerning natural heritage but also for the significant roles they play in zoology, economics, and in their very own ecosystems as well.

The lampreys are among the most primitive chordates. There are only about 40 living species. Yet, as a group lampreys are highly successful in terms of distribution (Hubbs and Potter, 1971), local abundance (Leach, 1940; Hansen and Haynes, 1962; Smith and McLain, 1962), and survival through long periods of geological time (Bardack and Zangerl, 1968 and 1971). Oregon is especially strategically located for the study of this important group of chordates, as no other regions of comparable size in the world are known to have more species and biological races of lampreys than Oregon does. Unfortunately, except for a note on spawning behavior (McIntyre, 1969) and several taxonomic researches, other aspects of the biology of these species here are virtually unknown. On the other hand, the ammocoetes and the non-feeding transformed brook lampreys are ideal respectively in zoological teaching and as experimental animals.

Lampreys, particularly the parasitic species, have very different economic significance according to the stage of their development. Ammocoetes were reported widely used as fish bait in British Columbia (Pletcher, 1963), Washington (Schultz, 1930), Ontario (Thomas, 1961), Quebec (Vladykov, 1949) and New York (Gage, 1928). Anadromous spawning adults have been always in considerable demand for human consumption and extraction of oil in western Europe (Vladykov, 1949), southern Russia (Berg, 1948), and, to some extent, North America (Pike, 1953; Thomas, 1961). They were esteemed in the Middle Ages as great delicacy by the royalty of the Court of Saint James. According to Jenkins (1958), the city of Gloucester was "under an obligation to forward a dish of lampreys to the Sovereign of England on his accession to the throne, and annually at Christmas. King John fined the men of Gloucester 40 marks because they did not pay him sufficient respect in the matter of his lampreys." Larger upstream spawners, "eels," are known to have been taken in quantity for food by native peoples of the Pacific Northwest. The custom still persists in some places, such as the Siletz River, Lincoln County, Oregon.

The negative impact upon fishery economy exercised by predatory parasitic lampreys is phenomenally demonstrated by P. marinus in the American Great Lakes, resulting in one of the largest and most intensive efforts to control a vertebrate predator ever attempted (Lawrie, 1970; Smith, 1971). In Miller Lake, Oregon, the impact of predation by Lampetra minima upon trout fingerlings led to the apparent destruction of the local population of *minima* through chemical measures (Bond and Kan, 1973).

Judging from its enormous biomass (see below) in streams, the lamprey must be considered to be important in the ecology of river ecosystems. Unfortunately, the significance of its exact role in food chains or energy transfer in such systems has been almost completely ignored. The ammocoetes were estimated to be very high in terms of both number and biomass in most streams studied (Hansen and Haynes, 1962; Smith and McLain, 1962). I fully appreciated the abundance of these animals through sampling many of the Oregon coastal streams. Actually they are the only freshwater vertebrates in the region known to perform microphagous feeding for a prolonged period in their life. Those microorganisms, mainly diatoms, consumed by ammocoetes (Applegate, 1950; Wigley, 1959; Manion, 1967; Hardisty and Potter, 1971c) would otherwise not be utilized directly and significantly by any other vertebrate consumers found in the stream. The ammocoetes themselves are then consumed by many fishes including rainbow trout (*Salmo gairdneri*), smallmouth bass (*Micropterus dolomieui*), northern pike (*Esox lucius*), and as indicated by Perlmutter (1951), eel (*Anguilla rostrata*). Larger upstream spawners, aggregating in staggering numbers during spawning runs, are preyed upon by fishes, water snakes, birds, and mammals (Applegate, 1950). Meanwhile, the decomposition of the bodies of dead postspawners would greatly enrich the nutrient reserve of streams. Finally, as listed by Ronald and Wilson (1968), the lamprey itself hosts a variety of parasites.

MATERIALS AND METHODS

Materials

Nearly 4,000 specimens of Lampetra have been examined in this study. These include individuals of all developmental stages, and represent forms from each major drainage system in Oregon where they are known (Figure 4), and the neighboring areas in Washington and California, Alaska, and the Pacific Ocean. Most of the materials studied were collected by personnel of the Department of Fisheries and Wildlife, Oregon State University. Abbreviations for the listed collections in the text are: CAS, California Academy of Sciences; OS, Fish Collection, Department of Fisheries and Wildlife, Oregon State University; OSUO, Nekton Collection, School of Oceanography, Oregon State University; SIO, Scripps Institution of Oceanography - Fish Collection; SU, Division of Systematic Biology, Stanford University; UBC, Institute of Fisheries, The University of British Columbia; UMMZ, Museum of Zoology, the University of Michigan; USNM, U. S. National Museum.

Methods

In order to obtain lamprey specimens representing all developmental stages, various collecting methods were used.

1 - Necanicum River
2 - Nehalem River
3 - Tillamook Bay system: Miami, Kilchis, Wilson, Trask and Tillamook rivers
4 - Nestucca River
5 - Siletz River
6 - Yaquina River
7 - Alsea River
8 - Siuslaw River
9 - Umpqua River
10 - Coos River
11 - Coquille River
12 - Rogue River
13 - Tualatin River
14 - Clackamas River
15 - Yamhill River
16 - Luckiamute River
17 - Santiam River
18 - Marys River
19 - McKenzie River
20 - Middle Fork Willamette River
21 - Sandy River
22 - Hood River
23 - Deschutes River
24 - Crooked River
25 - Metolius River
26 - Sprague River
27 - Klamath Lake
28 - Lost River
29 - John Day River
30 - Goose Lake
31 - Umatilla River
32 - Grand Ronde River
33 - Wallowa River
34 - Imnaha River
35 - Powder River
36 - Burnt River
37 - Malheur River
38 - Owyhee River
39 - Malheur Lake
40 - Silver Creek
41 - Silvies River
42 - Donner and Blitzen River
43 - Riddle Creek

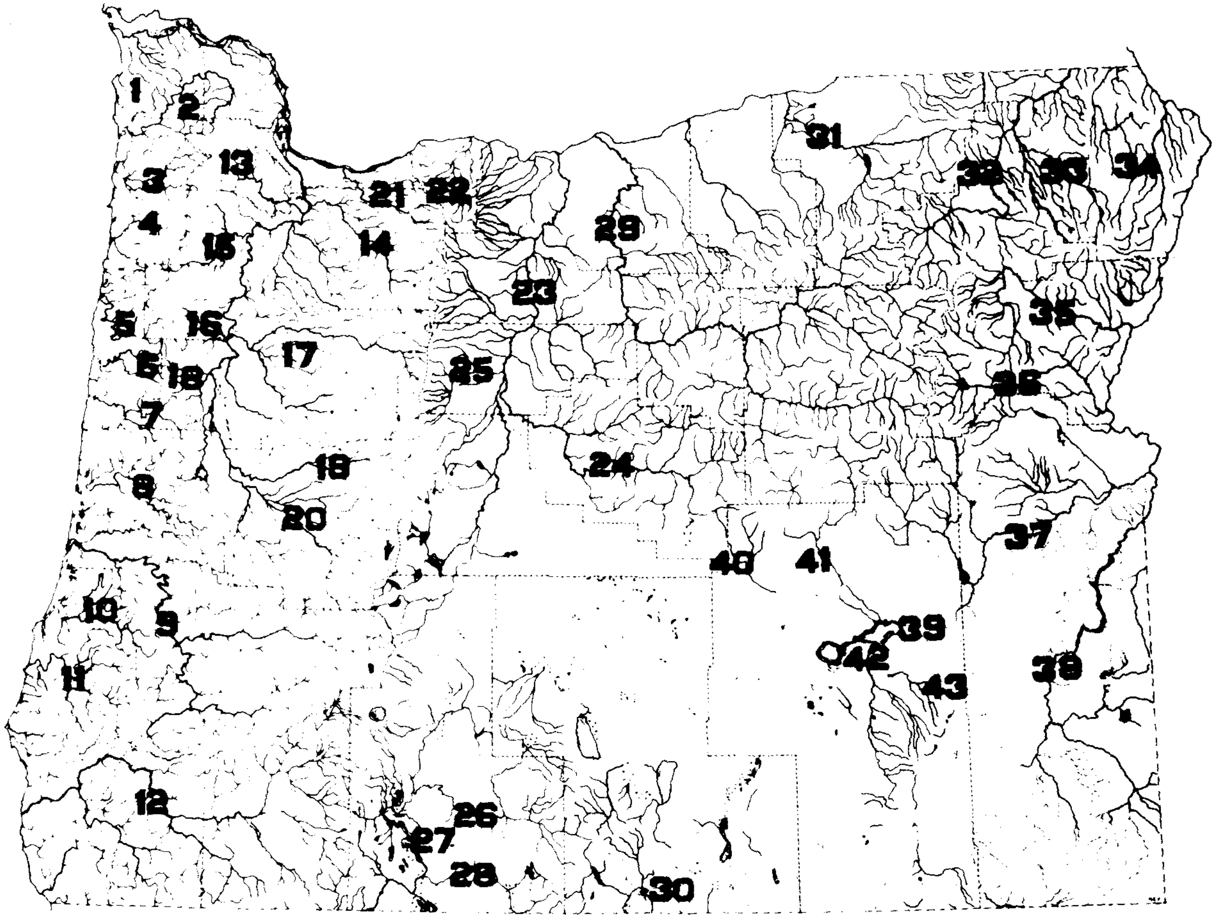

Figure 4. Drainage map of Oregon showing selected systems. (Legend on preceding page)

1. For ammocoetes, the best results were achieved through electrical shocking (see Braem and Ebel, 1961), but laborious mud dredging was indispensable in many occasions.
2. For active parasitic feeders, the application of gill nets was rewarding (see Vincent, 1969). In an attempt to trap the animals, several cages (1'x1'x2'), made of steel wire with meshes sized approximately 3" and containing the sucker, *Catostomus occidentalis*, and the chub, *Gila bicolor*, as live baits, were lowered to various depths in the inlets of Drews Reservoir, Lake County, Oregon. However, the result was considered unsatisfactory as only a few animals were caught in many attempts. From the Pacific Ocean off Oregon, a number of specimens was collected via the midwater trawling cruises conducted mainly by the Oregon Fish Commission.
3. For upstream migrants, the animals were hand-picked at the walls of dams and fishways where they usually aggregated during spawning runs.
4. For spawners of either parasitic or nonparasitic species, the specimens were collected by various means including seining, dip-netting, and electrical shocking.

In addition, collections were obtained from sites where the stream-poisoning operations for pest control had been performed by the Oregon Game Commission.

Ecological observations were recorded for most collections made by the author, usually on a standardized data sheet. Particular attention was given to water temperature and bottom type. Habits and behavior of the animal were observed whenever possible.

Specimens examined were preserved in 36. 5% isopropanol or 4-5% formalin. The latter is better as it helps to retain the original color pattern. The effect of preservation on the shrinkage of the specimen was not determined, although it is believed that, in general, the length of preserved specimens is from 1% to 3% shorter than fresh individuals. The data of meristics and morphometrics were typically taken on the left side of the specimen.

The methods of measuring employed are those of Vladykov (1955) but with one exception (see below). A brief explanation of the measurements, each made with a vernier caliper to the nearest 0. 1 mm, is given below:

Total Length: distance from the most anterior tip of the oral disc to the end of the caudal fin.

Head Length: distance from the most anterior tip of the oral disc to the anterior margin of the first gill opening.

Branchial Length: distance from the anterior margin of the first gill opening to the posterior margin of the last (7th) gill opening.

Trunk Length: distance from the posterior margin of the last (7th) gill opening to the anterior edge of the cloacal slit.

Tail Length: distance from the anterior edge of the cloacal slit to the end of the caudal fin.

Disc Length: distance from the tip of the snout to the posterior edge of the oral disc.

Diameter of Eye: horizontal diameter of the eye.

Height of Second Dorsal Fin: maximum height.

Vladykov (1955) measured the tail length from the posterior edge of the cloacal slit. However, as this edge is not always clearly visible in the spawning female specimens, the better defined anterior edge was taken.

Only those myomeres of the trunk region were counted. The first myomere was the one with its posterior septum setting distinctly and entirely behind the groove, which surrounds the posterior margin of the last gill opening (see Hubbs and Trautman, 1937). To determine the last myomere, a vertical line was extended from the anterior edge of the cloacal slit up to the mid-axis of the body and the myomere of this point was noted. The myomere immediately in front of this one was thus considered as the last myomere of the trunk region.

The taxonomy of lampreys (Class Petromyzones, Berg, 1940) is based primarily on the dentitional patterns despite the fact that the teeth, at least in the parasitic species, undergo periodic structural changes (Vladykov and Mukerji, 1961). The terminology of the different types of teeth of the holarctic species is well-established, but there is considerable discrepancy in its usage (Günther, 1870; Regan, 1911; Creaser and Hubbs, 1922; Berg, 1931; Hubbs and Trautman, 1937; Vladykov, 1949; Clemens and Wilby, 1961; Vladykov and Follett, 1965 and 1967; Hubbs and Potter, 1971). For simplicity and a better expression of the dentition of the species of Lampetra, I followed, in part, respectively, Vladykov and Follett (1967) and Hubbs and Potter (1971). The designation of the terms used in the subsequent text is given below:

Lingual Laminae: the multicuspid tooth plates of the tongue, including a single transverse plate and a pair of longitudinal plates.

Supraoral Lamina: the bicuspid, tricuspid, or quadricuspid tooth plate immediately anterior to the front edge of the esophageal opening.

Infraoral Lamina: the multicuspid tooth plate immediately distal to the posterior edge of the esophageal opening.

Lateral Circumorals: the unicuspid, bicuspid, or tricuspid teeth forming a distinct and more or less continuous series on each lateral side immediately to the esophageal opening.

Anterior Field: the anterior area of the oral disc, lying between the anterior marginals (see below) and the level of supraoral lamina to the anteriormost lateral circumoral tooth; cusps in this field are termed the anterials.

Posterior Field: the posterior area of the oral disc, lying betwen the posterior marginals and the level of infraoral lamina and the posteriormost lateral circumoral tooth; the unicuspid or bicuspid cusps in this field are termed posterials and are arranged in a single curvilinear row.

Marginals: the small teeth forming a single more or less continuous circular row at the outer edge of the oral disc.

Sexes of older ammocoetes, approaching the age of metamorphosis were determined in most cases by examining the gonads under a dissecting microscope. The testis consists of a pair of flattened lobes with some surface indentations, projecting downward to the dorsal surface of the gut (Hardisty, 1965). The ovary is a rather simple structure, being elongated and somewhat coiled with the oocytes visible especially at the anterior end. The stages of maturity of postlarval specimens were determined in this study mainly by either primary, secondary sexual characters, or both. Four stages are designated as follows:

Stage I - Immaturity: including transforming and macrophthalmia specimens; gonads similar to those of older ammocoetes; intestine functional in parasitic species.

Stage II - Early maturity: sexual products rather small but recognizable at higher magnifications; dorsal fins widely separated; teeth sharp and intestine functional in parasitic species.

Stage III - Prespawning period: sexual products well-formed;

dorsal fins adjoining; intestine nonfunctional and greatly reduced.

Stage IV - Spawning period: Body darkened; sexual products occupying entire body cavity; dorsal fins meeting each other; a genital papilla protruding in males and an anal fin fold (not the true anal fin, see Vladykov, 1973c) well-developed in females; teeth loosened in nonparasitic species; intestine at its maximum degeneration; body cavity empty of sexual products in spent specimens.

Vladykov and Follett (1958) considered the spent individuals as of their Stage 6, the postspawning period. However, as the lampreys die soon after spawning and there are little morphological differences between spawning and postspawning forms all the fish at and after spawning were treated together as of the same stage in the present study.

To estimate the absolute fecundity, the animal was first weighed and the ovary removed and weighed. A sample of one gram of the ovary was then taken and the eggs contained were counted. The number thus obtained was multiplied by the weight in grams of the whole ovary. The relative fecundity was then calculated through dividing the number of eggs per gram by the total body weight (in grams).

In the text, all statistical procedures followed those of Snedecor and Cochran (1967). The graphs of comparisons were presented in the style of Hubbs and Hubbs (1953) except that, instead of the standard errors, the confidence limits at 95% level were expressed for the means.

As partially calcified skeletons were recently discovered in the silver lamprey, _Ichthyomyzon unicuspis_, (Bardack and Zangerl, 1971), a number of ammocoete and adult specimens of _Lampetra tridentata_, _L. lethophaga_, and _L. richardsoni_ were cleared and stained (see Hungar, 1969). However, no trace of ossification was found.

THE TAXONOMY OF THE GENUS LAMPETRA

Genus Lampetra Gray, 1851

Lampetra Gray, 1851: 235.[2]

Entosphenus Gill, 1862: 331.

Lethenteron Creaser and Hubbs, 1922: 6.

Diagnosis

Dorsal fins separated, except in spawning and postspawning forms; second dorsal higher than first; caudal fin a rather angular lobe; no true anal fin; oral disc small to moderately large; teeth not numerous, not in curvilinear radiating rows, but in several series; lingual laminae strongly multicuspid in parasitic species; transverse lingual lamina not bilobed, with an enlarged medium cusp on its denticular ridge; supraoral lamina with or without a median cusp; infraoral lamina usually with at least 5 cusps; lateral circumorals 3 or 4, with the first and last ones normally bicuspid; posterials in a single curved row parallel to the marginals and connecting the last pair of lateral circumorals; no teeth in the area outside lateral circumorals; marginals normally in an even file; coloration uniform, dark gray or brown over most of the surface, pale yellowish on lower

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[2] See Vladykov (1973d, p. 3).

surfaces of head, trunk, and anal fin fold; trunk myomeres 50 to 80, mostly 55 to 70; skeletons uncalcified.

Discussion

Earlier authors referred the then known North American species of the genus Lampetra to Petromyzon (LeSueur, 1827; Richardson, 1836; DeKay, 1842); some still did so even after Gray had justifiedly proposed Lampetra as a genus in 1851 (Ayres, 1855; Günther, 1870; Jordan, 1887). Ammocoetes was also adopted as a genus by many, including Günther (1970), Jordan (1878), Jordan and Gilbert (1883), Jordan and Fordice (1885), Jordan (1887) and Eigenmann and Eigenmann (1892). Only about the turn of the century did Lampetra, along with Entosphenus which was erected by Gill in 1862, become widely accepted as a genus by ichthyologists (Bean, 1881 and 1882; Jordan and Starks, 1895; Jordan and Evermann, 1996a and 1896b; Rutter, 1908; Regan, 1911; Starks, 1911).

In 1922, Creaser and Hubbs expanded their Entosphenus to include three subgenera combining all the North American species which are characterized by having posterials arranged in a single curvilinear row. Two of these subgenera, Entosphenus and Lethenteron, were, however, generically recognized later by some, including Jordan, Evermann and Clark (1930), Hubbs (1967), Vladykov and Follett (1967), and Vladykov (1973b). I have examined specimens referrable to *Lethenteron* from Alaska (OS 1132, 1240, 1715 and 2755), and noticed a considerable degree of similarity in the general plan of dentition between them and those of *Entosphenus* and *Lampetra*. In all three types, the gross morphology of transverse lingual lamina, supraoral and infraoral laminae and lateral circumorals is structurally similar, and no teeth of any kind appear in each area outside the two sets of lateral circumorals. I agree with Hubbs and Potter (1971) in regarding the three taxa, *Entosphenus*, *Lethenteron*, and *Lampetra* as subgenera of the genus *Lampetra*, based on dentition as well as other characters (see Diagnosis).

For some years, the designation of several unusual species as members of *Lampetra* has been general. In his revision of the lampreys of the Northern Hemisphere Berg (1931) considered the genus *Lampetra* to be synonymous with not only *Entosphenus* (in part) and *Lethenteron*, but also *Eudontomyzon*, *Okkelbergia*, and even *Tetrapleurodon*. In view of dentitional differences, it seems reasonable at this stage to distinguish the last three from *Lampetra* and to treat them as valid genera (Vladykov and Follett, 1967; Hubbs and Potter, 1971; Vladykov, 1973b; and see Alvarez, 1966).

Subgenus *Entosphenus* Gill, 1862

Entosphenus Gill, 1862: 331.

Description

Transverse lingual lamina comblike, with median cusp slightly enlarged; supraoral lamina tricuspid (occasionally bicuspid or quadricuspid in nonparasitic form); infraoral lamina normally with 5 cusps (occasionally 4 in nonparasitic and 6 or 7 in parasitic forms); lateral circumorals 4, with cusp formula typically 2-3-3-2; posterials 9 to 21, some lateral ones bicuspid, in a single curvilinear row; anterials not more than 24; marginals often in an irregular file; trunk myomeres 60 to 80, mostly 61 to 69; velar tentacles 11 to 18 in adult anadromous forms, fewer in adfluvial, nonparasitic or juvenile form. Western and (chiefly) eastern coastal regions of North Pacific.

Discussion

Entosphenus was originally proposed by Gill in 1862, when he regarded it a genus distinct from *Petromyzon*. Until as late as 1967 (see Hubbs, 1967), it has been considered as an essentially monotypic genus, represented by the parasitic species, *E. tridentatus*. Two derivative species of *tridentatus*, i. e. *tridentata*, were recently described: the first species, *Lampetra* (*Entosphenus*) *lethophaga*, is dwarfed and, as expected, nonparasitic (Hubbs, 1971), while the second one, L. (E.) minima, is extremely dwarfed, yet parasitic (Bond and Kan, 1973). Thus, tridentata is shown to agree with most parasitic species of lampreys in having evolved into a nonparasitic derivative. It is also of great significance to note that tridentata is unique in having given rise to not only a nonparasitic species but also another parasitic one; on the other hand, all of the previously recorded derivatives of parasitic lampreys are nonparasitic while at least two other species, Ichthyomyzon bdellium and Lampetra japonica, as tridentata, may have each given rise to more than one new species (Hubbs and Trautman, 1937; Raney, 1952; Hubbs and Potter, 1971).

Whether to recognize the taxon Entosphenus (represented now by E. tridentata and its two derivative species) as a genus or a subgenus of Lampetra has been a subject of disagreement. While accepting the latter arrangement, Hubbs and Potter (1971, pages 49 and 50) stated:

> The trend for some years has been to treat these three names[3] as synonymous, along with Eudontomyzon, Tetrapleurodon and Okkelbergia, although many others, including Berg (1931) have held Entosphenus distinct. These three taxa, here synonymized as Lampetra, have been generically recognized by some, including Jordan, Evermann and Clark (1930:9), Vladkov and Follett (1967) and Hubbs (1967:308). Since the general plan of dentition is very similar in all three, and there is some overlap in characters (particularly in nonparasitic forms), and since the reference of Lampetra is very general, it is thought best to regard the three types as subgenera.

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[3] Lampetra, Entosphenus, and Lethenteron.

The subgeneric scheme is also adopted in the present study. The lines of reasoning for my adoption are as follows:

1. Gill (1862) erected the genus *Entosphenus* but did not give it a taxonomic diagnosis. Jordan and Evermann (1896b) and Berg (1931) diagnosed the genus as having a tricuspid supraoral lamina and considered it to contain only one species, namely, *E. tridentata*. However, this diagnostic character is by no means consistent in the derivative species of *Entosphenus* described in later time, as reported by Hubbs (1971) that in *L.* (*E.*) *lethophaga* a bicuspid supraoral lamina occurs as frequently as a tricuspid one does and a quadricuspid one also occurs in many occasions. The tricuspid supraoral lamina has apparently been overemphasized as a diagnostic feature of the taxon *Entosphenus*.

2. In his synopsis of world agnaths (order Hyperoartii) (1911), Regan considered the presence of a single row of posterials to be diagnostic for the genus *Entosphenus*. This opinion was also shared later on by Hubbs (1967). According to this view, such species as *Lampetra* (*Lethenteron*) *japonica* and *Lampetra* (*Lethenteron*) *lamottenii* are included in *Entosphenus* (Hubbs and Lagler, 1958). However, as demonstrated by Berg (1948), this character is again inconsistent, since the posterials may be either present, incomplete, or absent even within a single species, namely, *Lampetra* (*Lethenteron*) *reissneri*, a nonparasitic derivative of *japonica*.

Furthermore, the presence of single-rowed posterials is also found in the species of two other holarctic genera *Eudontomyzon* and *Tetrapleurodon*, for example, *E. danfordi* and *T. spadiceus*.

3. In their otherwise fine work, McPhail and Lindsey (1970) held *Entosphenus* to be distinct because of characters, in addition to the tricuspid supraoral lamina and single-rowed posterials, involving numbers of the velar tentacles and cusps on each longitudinal lingual lamina.

a) The finger-like velar tentacles, found only in postlarval forms, are more or less the same in diameter in all adult lampreys presently examined, and, together with a pair of velar valves, form an apparatus which guards the junction between the pharynx and the water (respiratory) tube (Dawson, 1905), preventing water flow from the water tube into the pharynx (Reynolds, 1931). The difference in numbers of the tentacles, 11 to 16 in *E. tridentata* versus 7 or fewer in *Lampetra japonica* and *L. lamottenii*, contributes to McPhail and Lindsey's belief that *Entosphenus* and *Lampetra* are distinct genera. Their counts (11 to 16) are agreeable to those I have made in the anadromous *tridentata* from Oregon and California (10 to 18); however, their claim that a range of 11 to 16 velar tentacles is diagnostic to the taxon *Entosphenus* is now invalid as there are only 7 to 9 such tentacles in the adfluvial *tridentata* from Upper Klamath Lake, 6 to 7 in *L.* (*E.*) *lethophaga*, and as few as 5 to 6 in

L. (E.) minima (Table 2). Thus, at least for the species of Entosphenus, in order to perform an assigned function well, the degree of the development of the velar tentacles must be in direct relation to the size of fully-developed pharynx and, in turn, the animal at maturity. In that scope, the number of velar tentacles seems to diminish in generic significance, though seemingly weighty at the subgeneric or specific level since as indicated by Hardisty and Potter (1971a), the application concerning differences in body size appears to be justified in recognizing members of a paired species complex as distinct species.

b) McPhail and Lindsey (1970) reported a range of 50 to 63 fine points (cusps) on each longitudinal lingual lamina for E. tridentata, in contrast to that of 0 to 26 for L. japonica and L. lamottenii and believed this distinction as one basis for the recognition of Entosphenus as a well-defined genus. However, as seen from Table 3, none of the specimens of anadromous or adfluvial tridentata as well as its derivative species from Oregon has a count exceeding 32 and many of them have counts well within the range (0 to 26) given for Lampetra (as genus) by the two authors. The number of cusps no doubt varies, and the "0" counts supposedly represent laminae that are newly formed or that have been shed, probably postnuptially.

The taxon Entosphenus is therefore considered not to be a sound genus which, in order to be valid, must be based on an overall

Table 2. Number of velar tentacles of species of the genus *Lampetra*.

Species (specimens examined)	Locality	Velar tentacles (mean)	Stage of maturity	Total length (mm) (mean)
L. (*Entosphenus*) *tridentata*	--[1]	11-16	?	up to 760[1]
L. t. tridentata (5)	Thomas River, British Columbia	8-13 (10. 20)	I	114-142 (124. 10)
L. t. tridentata (5)	John Day River tributary, Oregon	14-18 (15. 80)	III	544-585 (565. 60)
L. t. tridentata (2)	Mollala River tributary, Oregon	12 (12)	III-IV	486-570 (528. 00)
L. t. tridentata (2)	Umpqua River tributary, Oregon	10-15 (12. 50)	IV	565-581 (573. 00)
L. t. tridentata (4)	Pacific Ocean off Oregon	12-15 (13. 25)	II	240-266 (252. 00)
L. t. tridentata (5)	California	12-14 (12. 40)	III-IV	485-523 (506. 00)
L. t. kawiaga (3)	Upper Klamath Lake, Oregon	7-8 (7. 33)	II	214-234 (224. 00)
L. t. kawiaga (3)	Thomas Creek, Lake Co., Oregon	7-9 (8. 00)	III	206-219 (214. 67)
L. minima (7)	Miller Lake Oregon	5-6 (5. 43)	IV	85-125 (108. 00)

Table 2. (Continued)

Species (specimens examined)	Locality	Velar tentacles (mean)	Stage of maturity	Total length (mm) (mean)
L. lethophaga (3)	Crooked Creek, Klamath Co., Oregon	6-7 (6.67)	IV	118-152 (136.67)
L. japonica (2)	Lake Iliamna, Alaska	6-7 (6.50)	IV	205-235 (220.00)
L. japonica (1)	Kvichak River, Alaska	8	III	262
L. lamottenii	--[1]	7 or fewer	?	--[1]
L. ayresii (1)	Columbia River, Oregon	3	III-IV	263
L. ayresii (1)	Simpson Creek, Lincoln Co., Oregon	3	III-IV	203
L. richardsoni (4)	Willamette River tributaries, Oregon	3-4 (3.75)	IV	116-139 (126.75)

[1] See pages 53, 54 and 57 in McPhail and Lindsay (1970) for explanations.

Table 3. Number of cusps on lingual laminae of species of the genus *Lampetra*.

Species (specimens examined)	Locality	Cusps on transverse lingual lamina (mean)	Cusps on longitudinal lingual laminae	
			Right (mean)	Left (mean)
L. (Entosphenus) tridentata	--[1]	15-25	50-63[1]	50-63[1]
L. t. tridentata (5)	John Day River tributary, Oregon	17-20 (18.60)	19-24 (21.60)	18-23 (21.40)
L. t. tridentata (2)	Mollala River tributary, Oregon	18-19 (18.50)	22-24 (23.00)	20-25 (22.50)
L. t. tridentata (2)	Umpqua River tributary, Oregon	19-20 (19.50)	24 (24.00)	25-26 (25.50)
L. t. tridentata (4)	Pacific Ocean off Oregon	18-21 (19.25)	22-27 (24.75)	21-28 (24.00)
L. t. kawiaga (3)	Upper Klamath Lake, Oregon	22-23 (22.67)	27-31[2] (28.67)	28-19[2] (29.32)
L. t. kawiaga (3)	Thomas Creek, Lake County, Oregon	21-23 (22.00)	28-29 (28.33)	27 (27.00)
L. minima (5)	Miller Lake, Oregon	19-22 (21.00)	22-25 (23.20)	22-24 (23.00)
L lethophaga (3)	Crooked Creek, Klamath County, Oregon	13-14 (13.33)	10 (10.00)	10-11 (10.67)
L. japonica	--[1]	--[1]	0-26[1]	0-26[1]

Table 3. (Continued)

Species (specimens examined)	Locality	Cusps on transverse lingual lamina (mean)	Cusps on longitudinal lingual laminae	
			Right (mean)	Left (mean)
L. japonica (2)	Lake Iliamna, Alaska	16-17 (16.50)	14-15 (14.50)	12-13 (12.50)
L. japonica (1)	Kvichak River, Alaska	16	13	14
L. lamottenii	--[1]	--	0-26[1]	0-26[1]
L. ayresii (1)	Columbia River, Oregon	?	?	?
L. ayresii (1)	Simpson Creek, Lincoln County, Oregon	11	9	10
L. richardsoni (4)	Willamette River tributary, Oregon	?	?	?

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[1] See pages 53, 54 and 57 in McPhail and Lindsey (1970) for explanations.

[2] Cusps counted by Dr. C. E. Bond.

appreciation and weighing of various considerations including a marked discontinuity characteristically existing between it and other genera (Michener, 1957; Mayr, 1969). As discussed above, the characters adopted by previous workers in defining Entosphenus as genus are found later either unstable, inconsistent, or of narrow specializations, and hence ones with low weight taxonomically (Mayr, 1969). I believe that the taxon Entosphenus, along with taxa Lethenteron and Lampetra, should be regarded as subgenera of the genus Lampetra, which as a whole is distinct for reasons and diagnostic features of the genus Lampetra earlier given (also see Hubbs and Potter, 1971), including particularly the absence of cusps in the area outside the two sets of lateral circumorals. Indeed, this feature alone not only builds the three taxa up into a single higher taxon but also reinforces subsequently the taxon standing apart from others of the same rank.

Species of the subgenus Entosphenus occur along coastal regions of the North Pacific Ocean. Following is a list of the species of Entosphenus treated in this study:

Lampetra (E.) tridentata (Gairdner IN Richardson, 1836)
Lampetra (E.) tridentata kawiaga n. subsp.
Lampetra (E.) minima Bond and Kan, 1973
Lampetra (E.) lethophaga Hubbs, 1971

Subgenus Lethenteron Creaser and Hubbs, 1922

Lethenteron Creaser and Hubbs, 1922:6.

Description

Transverse lingual lamina strongly curved, with median cusp greatly enlarged; supraoral lamina normally bicuspid; infraoral lamina with more than 5 cusps; lateral circumorals 3, with cusp formula typically 2-2-2; posterials not bicuspid, in a single curvilinear row; marginals in an even file; trunk myomeres 60 to 80, being fewer in southern European species; velar tentacles 6 to 8 in adult forms. Circumarctic drainage basins, coastal regions of Bering Sea and western North Pacific, eastern North America, and Po Plain of Italy.

Discussion

The taxon Lethenteron was first proposed as a subgenus of Entosphenus, based entirely on the presence of single-rowed posterials (Creaser and Hubbs, 1922). However, it has since been synonymized as the genus Lampetra by most workers, including Jordan, Evermann and Clark (193) (in part), Berg (1931), Vladykov (1949), Bailey et al. (1960), Bailey et al. (1970), McPhail and Lindsey (1970), and Scott and Crossman (1973), for, apparently, reasons involving such characters as lateral circumorals, supraoral and infraoral laminae. Lethenteron has also been generically recognized (Jordan, Evermann and Clark, 1930, in part; Hubbs, 1967; Vladykov and Follett, 1967; Vladykov, 1973b) for mainly the presence of single-rowed posterials, a character considered here as of little generic significance but useful subgenerically (see Discussion for the subgenus Entosphenus).

None of the five species of subgenus Lethenteron recognized by Hubbs and Potter (1971), occurs in the area covered by the present study. The anadromous species, Lampetra japonica, is widely spread in the circumarctic drainages containing at least one land-locked form which is parasitic (Heard, 1966), The view that L. lamottenii of North America is a dwarfed nonparasitic derivative species of japonica has recently been clouded as the ranges and mean numbers of velar tentacles and of cusps on infraoral lamina are virtually identical in the two forms (McPhail and Lindsey, 1970), and again fogged as no suitable external characters by which the two can be adequately separated by a taxonomic key (Scott and Crossman, 1973). Nevertheless, the two should be considered as separate species for not only in the traditional practice of lamprey systematics that nonparasitic members of the paired species complexes warrant specific ranks but also indeed that reproductive isolations could be rapidly established via disruptive evolution in sympatric species of lampreys with appreciable differences in body sizes (Hardisty and Potter, 1971a). The taxonomic status of the two nonparasitic eastern Asian species, *L. reissneri* and *L. mitsukurii*, has not been well-established although circumstantial evidence shows the former as a derivative species of *japonica* (Hubbs and Potter, 1971). The European species *L. zanandreai*, was thought to be closely related to *L. planeri* (Vladykov, 1955); however, in view of the presence of single-rowed posterials (see Vladykov, 1973a) and the triple sets of lateral circumorals on each side, it seems better to recognize *zanandreai* as a species of the *Lethenteron* series.

Subgenus *Lampetra* Gray, 1851

Lampetra Gray, 1851: 235.

Description

Transverse lingual lamina strongly curved, with median cusp greatly enlarged; supraoral lamina normally bicuspid; infraoral laminal cusps ordinally more than 5; lateral circumorals 3, with cusp formula typically 2-3-2; posterials totally absent; marginals in an even file; trunk myomeres 50 to 70, being fewer in more southern species; velar tentacles 3 to 4 in adult forms. Coastal regions of Europe and western North America.

Discussion

Since Gray proposed *Lampetra* as a genus in 1851 the reference of lamprey species to it has been liberal. It is surprising to note that several previous authors, in referring species of the now recognized genera *Eudontomyzon*, *Tetrapleurodon* and *Okkelbergia* to *Lampetra*, have completely overlooked the feature of naked lateral areas outside the two sets of lateral ciecumorals, a "key character" (see Mayr, 1969) generically. The genus is now regarded to contain taxa *Entosphenus* and *Lethenteron* (see Diagnosis for the genus *Lampetra*), that, together with Gray's *Lampetra* (1851) are considered as three sound subgenera (also see Hubbs and Potter, 1971). In addition to other aspects, *Lethenteron* is similar to *Entosphenus* in having the single-rowed posterials, and, on the other hand, to *Lampetra* in the two triple-set lateral circumorals.

The subgenus *Lampetra* is restricted to the *L. fluviatilis*/*planeri* complex and to the *L. ayresii*/*richardsoni* complex. The former occurs in Europe; its species are most broadly studied among all lampreys, as about one third of the references cited in the two volumes of *The Biology of Lampreys* (Hardisty and Potter, 1971d and 1972)dealt directly or indirectly with these species. The latter occurs in western North America; both species are found in Oregon and will be treated in this study.

THE LAMPREYS OF OREGON

Lampetra (*Entosphenus*) *tridentata tridentata*
(Gairdner IN Richardson, 1836)
Pacific Lamprey

Petromyzon tridentatus Gairdner (MS), in Richardson, 1836: 293; (type locality: Falls of Walamet, now Willamette, Oregon).

Petromyzon ciliatus, Ayres, 1855:43.

Petromyzon lividus and *astori*, Girard, 1858:379-380.

Ammocoetes cibarius, Girard, 1858:383.

Entosphenus epihexodon, *ciliatus* and *tridentatus*, Gill, 1862:331.

Ichthyomyzon tridentatus and *astori*, Günther, 1870:506.

Lampetra tridentatus, *astori* and *epihexodon*, Jordan and Gilbert, 1883:7-8.

Ammocoetes tridentatus, Jordan and Fordice, 1885:291.

Lampetra tridentata, Green, 1891:32.

Entosphenus tridentatus (Gairdner), Jordan and Evermann, 1896a:12.

Entosphenus tridentatus tridentatus Richardson and *tridentatus ciliatus* Ayres, Creaser and Hubbs, 1922:10-11.

Entosphenus tridentatus (Richardson), Vladykov and Follett, 1958:47.

Lampetra tridentata (Gairdner), Bond, 1961:14.

Lampetra (*Entosphenus*) *tridentata* (Richardson), Hubbs and Potter, 1971:50.

Lampetra (*Entosphenus*) *tridentata* (Gairdner), Bond, 1973:9.

Differential Diagnosis

The postlarval form of Lampetra (Entosphenus) t. tridentata can be distinguished from that of all its congeners by the following combination of characters: transverse lingual lamina rectilinear and comblike, having 17 to 21 cusps with the median one somewhat enlarged; longitudinal lingual laminae paired, each with 18 to 27 cusps; supraoral lamina invariably tricuspid; lateral circumorals always arranged in a formula 2-3-3-2; infraoral lamina typically with 5 cusps; anterials irregularly placed, 6 to 11 in number, usually fewer in post-spawning individuals; posterials 15 to 21, arranged in a single curvilinear row with the first to fourth outermost pairs occasionally bicuspid; trunk myomeres 59 to 72, mostly 67 to 69; total lengths of upstream spawners ranging up to 620 mm, rarely shorter than 350 mm.

The near-term ammocoete of L. t. tridentata can be distinguished from that of species of the subgenus Lampetra by a heavily pigmented caudal fin and a higher number of trunk myomeres (rarely fewer than 64). It differs from that of L. (E.) lethophaga in having an evenly pale lower surface of the trunk region while in the latter melanophores are irregularly scattered here. It differs from that of L. (E.) minima mainly by the higher number of trunk myomeres (64 and usually more).

L. t. tridentata is anadromous and in Oregon is known to occur only in the coastal and Columbia drainages.

Description and Comparisons

Size

Total lengths of 98 L. t. tridentata macrophthalmia from Oregon and British Columbia were from 96 to 155 mm (sample mean 119.86 mm), a range comparable to those of other North Hemisphere anadromous species (Bigelow and Schroeder, 1948; Vladykov, 1949; Vladykov and Follett, 1958; Heard, 1966) and also of those from the South Hemisphere (Strahan, 1960; Potter, Lanzing and Strahan, 1968). The length of 32 active feeders, caught at sea off Oregon, has a range so wide (105 to 754 mm) that it apparently includes the length of individuals belonging to two or more age classes. Hubbs (1967) recorded a juvenile (170 mm long, SIO 67-22-4) from the Pacific off Baja California. Evermann and Latimer (1910) had specimens from San Pablo Bay, California, with lengths ranging from 127 to about 185 mm. By comparison, several specimens of the anadromous sea lamprey, Petromyzon marinus, varying from 152 to 178 mm long, were taken from Chesapeake Bay (Mansueti, 1960). Lelek (1973) recorded a marinus from the open sea in the North Atlantic with total length measured at 407 mm, apparently the longest for the sea lamprey of feeding stage ever reported. Lengths of 132 prespawners from Oregon and northern California range from 393 to 620 mm (sample mean 515.83 mm); 88 Oregon spawning and postspawning fishes were shorter, varying from 332 to 542 mm (sample mean 420.93 mm). The maximum length of Oregon forms of t. tridentata is thus intermediate between that from southern California[4] (575 mm, UMMZ 133774; see Hubbs, 1967) and those from British Columbia and Alaska (690 and 760 mm; see Hart, 1973; Scott and Crossman, 1973; and McPhail and Lindsey, 1970). L. t. tridentata grows to a maximum length of only 590 mm in watershed of northern seas of the western Pacific (Lindberg and Legeza, 1959) where another anadromous species, L. japonica, ranging from about 250 mm (Berg, 1948) to 630 mm (Okada, 1955) long, sympatrically occurs. The longest lamprey species (up to 900 mm; Bigelow and Schroeder, 1948) is P. marinus which, according to Hubbs and Potter (1971) generally moves farther away from coastline than any other anadromous species do and is distributed over the greatest area, namely, the eastern North American, northern European and Mediterranean watersheds.

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[4] Miller and Lea in the presentation of L. t. tridentata in their publication Guide to the Coastal Marine Fishes of California (1972; p. 32) stated "Length to 27 in." (=685.50 mm), a figure nearly identical to that of British Columbia forms (690 mm) (see text) and presumably representing the longer length of the species rather than the maximum length of California forms.

Of some 1,100 *L. t. tridentata* ammocoetes from Oregon and neighboring areas of Washington and California examined, total lengths range from 16 to 158 mm. Larger ammocoetes in 53 samples varied from 55 to 158 mm long, with a sample mean of 107.25 mm. As the shortest macrophthalmia of the species from this region was measured at 101 mm, it is probable that ammocoetes here will not metamorphose until reaching about 100 mm long. Scott and Crossman (1973) gave a range of 122 to 303 mm for British Columbia *t. tridentata* ammocoetes at the time of metamorphosis. The latter figure is unusually high when comparing with those of other anadromous species of lampreys, as the longest ammocoete of these species mentioned by various authors were 140 mm for *L. japonica* (Berg, 1948), 172 mm for *L. ayresii* (Vladykov and Follett, 1958), 198 mm for *L. fluviatilis* (McDonald, 1959), 130 mm for *Caspiomyzon wagneri* (Berg, 1948), 260 mm for *P. marinus* (McDonald, 1959), 162 mm for *Mordacia mordax* (Strahan, 1960), and 89 mm for *Geotria australis* (strahan, 1960).

Body Proportions (expressed as percentages of total length)
(Table 4)

Allometric growth is rather common in fishes (Martin, 1949) and in other animal groups (Huxley, 1932). In *L. t. tridentata* it has been found to be especially great during larger ammocoete and

Table 4. Range of proportional measurements (percentages of total length) of *Lampetra t. tridentata* from Oregon and neighboring areas. Values of sample mean in parentheses.

Development period	Number of samples	Total length (mm)	Tail length	Trunk length	Branchial length	Head length	Eye diameter	Disc length	Second dorsal fin height
Ammocoete	53	55.00-158.00 (107.25)	25.14-32.91 (28.50)	48.73-55.28 (51.21)	10.00-14.81 (12.27)	6.01-10.53 (8.02)	--	--	--
Macrophthalmia									
Male	19	101.00-155.00 (119.37)	28.07-32.28 (29.53)	43.39-51.28 (47.40)	8.66-10.43 (9.55)	8.92-16.03 (13.50)	2.11-4.34 (2.91)	2.56-6.61 (5.42)	2.27-4.06 (2.92)
Female	6	115.00-139.50 (126.33)	26.77-29.46 (28.20)	49.22-52.17 (50.50)	9.32-10.43 (9.71)	10.43-12.20 (11.52)	2.02-2.60 (2.23)	3.22-4.80 (4.12)	2.17-2.83 (2.47)
Feeding									
Male	6	137.00-292.00 (221.50)	27.02-29.58 (28.46)	43.37-48.39 (47.23)	9.42-10.99 (10.27)	12.69-15.96 (14.03)	2.07-3.73 (2.57)	5.52-6.77 (6.18)	2.48-3.52 (3.27)
Female	6	107.00-266.00 (197.29)	24.58-28.89 (27.21)	48.12-51.61 (49.00)	9.39-11.25 (10.30)	12.04-15.43 (3.55)	1.88-2.95 (2.38)	5.04-6.51 (5.91)	2.93-5.76 (3.39)
Prespawning									
Male	7	393.00-620.00 (503.05)	26.01-31.70 (29.63)	45.47-50.74 (47.59)	10.09-11.60 (10.95)	10.60-12.50 (11.81)	1.29-1.96 (1.65)	4.50-6.11 (5.47)	3.47-4.64 (4.28)
Female	5	444.00-614.00 (533.71)	25.54-31.90 (28.64)	46.08-52.07 (48.89)	10.18-11.17 (10.89)	10.74-12.50 (11.57)	1.29-1.88 (1.55)	4.90-6.28 (5.42)	3.50-5.39 (4.11)
Spawning									
Male	13	371.00-523.00 (441.04)	28.96-31.99 (30.19)	41.78-46.51 (44.52)	11.08-13.25 (11.84)	12.88-14.82 (13.46)	1.63-2.70 (2.08)	5.55-7.45 (6.37)	4.85-7.04 (5.66)
Female	12	332.00-542.00 (399.16)	23.56-29.42 (25.62)	45.99-56.36 (50.05)	10.35-12.23 (11.23)	11.62-13.58 (13.09)	1.61-2.50 (2.13)	5.53-6.92 (6.25)	4.48-8.12 (5.98)

macrophthalmia states. Allometry and geographical variation in body proportions of this species will be discussed later (see Variation). In comparison with southern California prespawning forms (see Hubbs, 1967), the Oregon form at the corresponding stage is slightly shorter in diameter of eye and lengths of the disc and branchial region. Differences in body proportions due to sex are appreciable and will be treated in a later section.

Since body proportions vary considerably during the various life history stages in *L. t. tridentata*, it is taxonomically meaningful to compare only individuals from different localities belonging to similar length groups, or more ideally, year classes. A 124 mm long ammocoete of *t. tridentata* from southern California has body proportions (Hubbs, 1967) similar to those of Oregon forms of comparable lengths.

Trunk Myomeres (Table 5)

The number of myomeres in ammocoete *L. t. tridentata* ranges from 61 to 71 with a mean of 66.48. In adult fishes it has a range from 64 to 72 (mean 67.96). The wide range occurring in forms in this region confirms that variation of the number of myomeres in *t. tridentata* is local rather than geographical, a conclusion drawn by Professor Hubbs (1967), who earlier had co-reported (Creaser and Hubbs, 1922) that two geographical subspecies, a northern

Table 5. Number of trunk myomeres of *Lampetra t. tridentata* from Oregon and neighboring areas.

Development period	Number of specimens	Total length (mm)	Number of myomeres														
			59	60	61	62	63	64	65	66	67	68	69	70	71	72	Mean
Ammocoete	729	16-158	-	-	1	11	23	42	130	172	204	105	29	8	4	-	66.48
Macrophthalmia	98	101-155	1	-	1	5	8	13	20	16	17	14	3	-	-	-	64.83
Feeding	32	102-292	-	-	-	-	-	1	4	6	6	9	5	1	-	-	67.12
Prespawning	132	393-620	-	-	-	-	-	1	5	25	28	29	24	12	7	1	67.82
Spawning	88	332-542	-	-	-	-	-	2	5	10	18	14	17	12	6	4	68.16
TOTAL	1079	16-620	1	-	2	16	31	59	164	229	273	171	78	33	17	5	66.59

L. t. tridentatus and a southern *L. t. ciliatus*, can be differentiated based solely on difference in myomere counts (68 to 74 versus 57 to 67).

In nearly every lamprey species so studied, the adult always has a higher average myomere count than that of ammocoete (Vladykov, 1949, 1950 and 1955, Vladykov and Follett, 1958 and 1965; McPhail and Lindsey, 1970; Bond and Kan, 1973; Scott and Crossman, 1973; Vladykov, 1973a). Reasons for this disparity are thought to be mainly ecological. Most of the time, ammocoetes burrow and then rest in mud or silt deposits to lead a relatively inactive life (see Hardisty and Potter, 1971c). On the contrary, the mobility is necessary for transformed fishes to perform such activities as migration, active feeding, or both. As summarized in Gosline (1971) and Marshall (1971), more segments in body musculature give more body flexibility and movement in fishes. Indeed, the body flexibility is essential for feeding or adult lampreys as shown by their feeding or spawning behavior, in that body arching and bending are considerably involved (Lennon, 1954; Hagelin, 1959; McIntyre, 1969). Thus, those transformed fishes with more myomeres are considered to be more successful in feeding and, in turn, a better chance to survive to and throughout adulthood than those with fewer myomeres.

Dentition

In *L. t. tridentata*, teeth do not form in metamorphosing individuals and only begin to develop in macropthalmia ones. The transverse lingual lamina appears first and the paired longitudinal laminae follow. Other teeth at this time are still developing at their respective sites in oral disc in the form of pads, covered by white thin tissues. Cusps are soon evident and then become sharpened in downstream migrating juveniles. They are very sharp in active feeders but become progressively blunt in upstream migrants. During these stages, the periodic replacement of tooth corneous sheath, as described by Vladykov and Mukerji (1961) for *P. marinus*, seems to occur. Hubbs (1971) stated that disc teeth degenerate and are fused into a cornified mass in spent individuals of *t. tridentata*. Apparently, this process first sets in some of the prespawning fishes (OS 4096, 4097 and 4101).

Lingual Laminae (Table 6)

The transverse lamina of *L. t. tridentata* is nearly rectilinear, having 17 to 21 cusps with the median one slightly enlarged. Sample means of specimens from three localities are 19. 20, 18. 63 and 19. 19, and are close to the mean of four southern California specimens (18.00) (Hubbs, 1967). McPhail and Lindsey (1970) gave a range of 15 to 25

Table 6. Number of cusps on lingual laminae of Lampetra t. tridentata from Oregon. Mean value in parentheses.

Locality	Number of specimens	Cusps on transverse lamina	Cusps on longitudinal laminae	
			Right	Left
Pacific Ocean off Oregon	6	18-21 (19. 20)	21-24 (22. 47)	21-24 (22. 33)
Clear Creek, John Day River	40	17-21 (18. 63)	19-24 (20. 60)	18-24 (20. 95)
Cow Creek, Umpqua River	31	17-21 (19. 19)	23-27 (23. 87)	23-26 (24. 39)
TOTAL	77	17-21 (18. 90)	19-27 (22.06)	18-26 (22. 44)

cusps for the northwestern Canada and Alaskan *t. tridentata*.

On each paired longitudinal lamina of *L. t. tridentata*, there are 18 to 27 cusps, a range significantly different from that (50 to 63) given by McPhail and Lindsey (1970). The two authors adopted the number of cusps on each longitudinal lamina as a basis in recognizing *Entosphenus* as a genus, a claim which seems to be invalid.

Supraoral and Infraoral Laminae

The *L. t. tridentata* supraoral lamina bears two large sharp cusps on either end and a third smaller one in the center. Jordan and Evermann (1896b) and Berg (1931) diagnosed *Entosphenus* as a monotypic genus by having a tricuspid supraoral lamina. Indeed, this character is stable in *t. tridentata*; of 341 countable laminae of specimens from various localities examined, all are tricuspid. Elsewhere within the species' range, a tricuspid supraoral lamina is always found (McPhail and Lindsey, 1970; Hubbs, 1967; Scott and Crossman, 1973).

In *L. t. tridentata*, the semicircular infraoral lamina typically has five sharp cusps with the lateral ones somewhat larger. Among 349 specimens examined, however, four, one female from Trout Creek of the Molalla River system (in OS 4102), and one female and two males from Clear Creek of the John Day River system (in OS 4094), have counts: 6, 6, 6, and 9 respectively. Higher counts have also been encountered in Canadian and Alaskan forms (McPhail and Lindsey, 1970; Scott and Crossman, 1973), and also in Japanese forms (Okada, 1960). Counts higher than 5 may be due to abnormal branching from any of the five regular cusps.

Lateral Circumorals

There are four pairs of sharp teeth on either side of the oral disc immediately distal to the mouth opening. The first and last pairs are bicuspid and middle pairs tricuspid. This pattern (2-3-3-2) is apparently constant in L. t. tridentata.[5]

Anterials

These teeth in L. t. tridentata are invariably unicuspid and are irregularly scattered in the anterior field of the disc. In general, they decrease in size and sharpness outwardly. As seen from Table 7A, anterials (mean value 9.37) are most developed in fishes engaging in active feeding at sea. In later stages (Development Periods III and IV), they (mean values 7.70 and 7.32) degenerate and become

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[5] I consider Scott and Crossman's account (1973) that three or four pairs (p. 37) or three pairs (p. 42) of inner lateral teeth (i. e. lateral circumorals) are found in L. t. tridentata to be inaccurate. Besides, their figures for the dentition of t. tridentata (same pages) are misleading, as in those posterials are totally missing and the orientation of oral papillae in the disc margin are too schematic. Better figure for dentition of the species is in Hubbs, 1963 (p. 942).

Table 7. Numbers of anterials and posterials of *Lampetra t. tridentata* from Oregon, British Columbia, and the Pacific Ocean off Oregon.

A. Anterials

Development period	Number of specimens	Number of Cusps 5	6	7	8	9	10	11	12	Mean
Macrophthalmia	41	-	4	7	16	10	4	-	-	8.07
Feeding	30	-	-	2	3	11	10	4	-	9.37
Prespawning	47	-	1	21	16	9	-	-	-	7.70
Spawning	78	6	15	20	24	11	2	-	-	7.32
TOTAL	196	6	20	50	59	41	16	4	-	7.88

B. Posterials

Development period	Number of specimens	Number of Cusps 14	15	16	17	18	19	20	21	Mean
Macrophthalmia	41	-	-	1	6	20	7	4	3	18.39
Feeding	30	-	-	-	5	10	13	2	-	18.40
Prespawning	40	-	1	1	14	20	4	-	-	17.63
Spawning	74	-	2	4	25	33	10	-	-	17.61
TOTAL	185	-	3	6	50	93	34	6	3	17.91

less recognizable.

Posterials (Table 7B)

These teeth, arranged in a single curvilinear row immediately posterior to the infraoral lamina in *L. t. tridentata*, have numbers ranging from 14 to 21 (mean 17.91). As many as four lateral pairs of posterials may be bicuspid while the middle ones are unicuspid. As anterials, posterials are sharp and well-developed in active feeders and degenerate in upstream spawners. Numbers of posterials and anterials from southern California *t. tridentata* (Hubbs, 1967) are close to those from this region.

Coloration

Younger ammocoetes of *L. t. tridentata* are slate above and paler below. The head region is heavily pigmented except in the small area around pineal eye which is conspicuously colorless. The branchial region is in general much lighter than the head. In larger ammocoetes the contrast between above and below becomes more apparent, with however a small area above the first gill slit which remains clear. The dorsal fins and caudal fin are at first largely clear, except for, in the latter, a narrow dark streak bordering the muscle mass. With increasing size the caudal fin grows darker, progressively outward, but the dorsal fins remain relatively clear.

The general coloration of *L. t. tridentata* macrophthalmia is similar to that of its large ammocoetes. However, the caudal fin is now completely darkened and the posterior portion of second dorsal fin darkens. Countershading in body coloration, as observed by Denton and Nicol (1966) in *P. marinus*, is only moderately developed in *t. tridentata* at sea. The color of the latter grades from pale yellow on the belly to bluish gray above; the caudal fin is slate-gray and the dorsal fins are slightly lighter.

Prespawning individuals of *L. t. tridentata* are uniformly slate-gray over most of the body surface, being somewhat paler on the ventral side of the body. Irregular white bars resembling parr marks were found scattered extensively on the lower surface of the body, especially in the branchial region, in some specimens (OS 4101, 4102), a condition only barely reminiscent of albinism which is known to occur occasionally in three species of lampreys, *P. marinus*, *Okkelbergia aepyptera*, and *L. lamottenii* (Braem and King, 1971). In spawning season, the body, including all fins, is dark gray. Apparently, body darkness in lampreys is associated with the nuptial condition (Hubbs and Trautman, 1937; Vladykov, 1949; McPhail and Lindsey, 1970; Hubbs, 1971).

Sexual Dimorphism

Sexual differences in body proportions of *L. t. tridentata* are given in Table 4. The males have a greater disc length, eye diameter, and height of second dorsal fin; the females have a greater trunk length.

The external appearance of spawning males and females of *L. t. tridentata* is similar to that of other species of *Lampetra* as described by Vladykov and Follett (1958 and 1965), McPhail and Lindsey (1970), Bond and Kan (1973), and Vladykov (1973a). The spawning males have a well-developed genital papilla and a straight or occasionally downturned tail. The spawning females on the other hand, have a swelled anal region with the genital papilla barely visible, and an upturned tail.

A small gular bulge just behind the oral disc was found in a number of sexually mature *L. t. tridentata* males (OS 4098, and several in OS 4099). This structure, also occasionally seen in *P. marinus* (Hubbs and Potter, 1971) is comparable to the gular pounch--a peculiar feature known only in the mature males of two Southern Hemisphere anadromous species, *Geotria australis* and *Mordacia mordacia* (Eigenmann, 1928; Potter, Lanzing and Strahan, 1968). The function of the gular pouch is unknown, although Ivanova-Berg (1968) has suggested that it might be used to move stones during courtship.

Minute brush-like outgrowths appear along the rear edges of both dorsal fins in *L. t. tridentata* spawners. They seem to be more pronounced in females than in males.

Teratology

Of the 350 postlarval specimens of L. t. tridentata examined, one male and one female (in OS 4095; 453 and 485 mm long, respectively) have a deformed caudal fin in that the terminal lobe is totally missing. The deformity seems not to hinder such events as migration, feeding, and growth, since both specimens are normal in size, gross morphology, and in the condition of gonadal development. The deformed tail could be due to injury followed by abnormal regeneration when the lamprey was still young. Niazi (1963 and 1964) has indicated that all tissues in the caudal area of P. marinus ammocoetes are capable of regeneration.

Distribution

Both ecological and geographical distribution are important in the taxonomy of lampreys. Within the genus Ichthyomyzon, Hubbs and Trautman (1937) referred to ecological preferences of certain species for particular regions of the river system. Vladykov and Follett (1958 and 1965) distinguished the river and brook lampreys of North America, L. ayresii and L. richardsoni, from those of Europe, L. fluviatilis and L. planeri, partially on the basis of a marked geographical discontinuity.

Habitats

Local distribution of L. t. tridentata meets the divergent ecological requirements of ammocoete, and young as well as spawning adults. Thus, within a river system, the lamprey could be found at locations that are ideal for both the establishment of stable ammocoete beds and the existence of conditions that are suitable for spawning. While in an area at sea, a supply of fishes or marine mammals susceptible to the parasitic predation by t. tridentata is necessary for the occurrence of this form there.

Ammocoete Habitats

Collection records indicate that the ammocoete L. t. tridentata occurs only in a particular type of habitat which provides favorable conditions for the burrowing behavior. The most heavily colonized regions are the shallow backwater and eddy areas along the edge of the stream, where the substrate is composed of mud, silt, or silt and sand. Accumulated materials high in organic content, such as decayed leaves and other vegetable debris, are often present. The flow of surface water is slow (considered to be less than 0. 1 m per second) or moderate (0. 1 to 0. 5 m per second). Cover or shade over the ammocoete beds is limited even at locations in smaller creeks with dense vegetation on shore. Stream width does not appear to limit the occurrence of *t. tridentata* ammocoetes since similar sized specimens were taken from streams with a great range in width; for example, smaller ammocoetes were collected from sites in a tributary to the Kilchis River (OS 4896), Cow Creek of the Umpqua River system (OS 4020), and the Nehalem River (OS 4900) which have widths of less than 2 m, about 20 m, and more than 75 m respectively.

Smaller ammocoetes of *L. t. tridentata* (under 50 mm in total length) were found to show a marked preference for bottoms with fine silt, an observation also made for *L. planeri* (Hardisty, 1944), landlocked *P. marinus* (Applegate, 1950), and *M. mordacia* and *M. praecox* (Potter, 1970). Larger ammocoetes, on the other hand, appear to seek out an favorable areas in terms of substrate, water movement, and food supply. Active swimming by large ammocoetes for brief periods was observed on many occasions and was recorded in *P. marinus* by Thomas (1962). Earliest macrophthalmia of *t. tridentata* were also collected from the typical ammocoete beds (OS 4886 and 4897); they were apparently sedentary under normal conditions but were very active when disturbed. Recolonization to certain areas previously "fished out" was evident, for example, specimens under 50 mm in total length were taken in two separate collections (OS 4919 and 4900) made at the same site but on different occasions. This process could be completed either by active seeking for suitable habitats by larger ammocoetes or by passive transport of small ones through such events as flooding and current movement.

Occurrences at Sea

Thirty-two specimens of L. t. tridentata were collected from the open ocean and the coastal regions of Oregon and Washington (Table 8). Six of them, all less than 140 mm in their total lengths, were taken from nearshore sites and were considered to be forms in their early feeding stage. Others were larger and were caught in waters over the continental shelf and slope with distances from about 10 to more than 100 km offshore. Depths of water range from several to 800 m. One specimen, OS 4860, measured alive at 754 mm, is the longest lamprey ever recorded from the sea.

Based on conditions of gut size and tooth sharpness, and collection notes as well, all L. t. tridentata specimens here examined were apparently lampreys undergoing parasitic feeding. The ocean off Oregon is influenced by coastal upwelling (Smith, 1964); such a region, as summarized by Cushing (1971), is in general rich in nutrients and production of fishes is usually large. Species of fishes occurring in this region were recorded by Pearcy (1964) and Beardsley and Bond (1970).

Other distributional records of L. t. tridentata at sea were

Table 8. Occurrences of *Lampetra t. tridentata* at sea off Oregon and Washington.

Catalogued number	Number of specimens	Approximate locality	Depth of water (m)	Date	Total length (mm) (mean)
OSUO 1693-1694	3	Yaquina Bay	3-5	X:12:56	107-138 (121.33)
OS 4152	1	off Columbia R.	?	V:29:1961	131
OS 13	1	off Newport	?	VIII:10:48	135
OS 4126	1	off Washington coast	?	summer, 61	137
OS 4144	3	26 km W of Netarts Bay	172	IV:24:67	155-191 (174.33)
OS 4093	2	W of Cape Meares	174	IV:25:67	172-200 (186.00)
OS 4145	5	19 km W of Seaside	?	IV:30:67	182-218 (198.60)
OS 4143	6	14.5 km W of Arch Cape	106	VII:31:66	149-254 (202.67)
OS 4870	2	off Cannon Beach	106	IX:1:72	221-248 (234.50)
OS 4869	1	SW of Cannon Beach	143	IX:3:72	240
OS 4864	1	off Coos Bay?	161	IX:4:72	246
OS 4867	1	off Coos Bay?	183	IX:2:72	247
OS 4868	1	off Coos Bay?	132	IX:2:72	248
OSUO?	1	117 km W of Newport	0-180	IX:19:66	256
OS 4866	1	off Coos Bay	134	I :2:72	266
OSUO 1729	1	115 km W of Lincoln City	800	VI:4:65	292
OS 4860	1	off Garibaldi	146	VI:3:74	754

summarized in Hubbs (1967). They are mostly in the Pacific coastal regions north of Monterey Bay. A few occurrences were from the pelagic zone off Baja California (Hubbs, 1967), the epipelagic and neritic zone off Oregon (Pearcy, 1964), and the high seas of the Aleutian area (Larkin, 1964).

Spawning Sites

Spawning activities of _L. t. tridentata_ were observed mostly in stream segments of rather low gradient. The substrate was composed of gravel and sand with pebbles superimposed. The water over the spawning sites was clear and moderately swift with stream surface velocity of about 0. 5 to 1 m per second, so that it was presumably well-oxygenated. Depths from the water surface here ranged from approximately 0. 4 to 1 m. Accordingly, the spawning site of _L. t. tridentata_ is often found just above riffles where the calmer water begins to break up. In the vicinity of the spawning area, usually adjacent to the river bank, a slow and soft-bottomed stretch was often present, providing an ideal habitat for the newly-hatched ammocoetes.

Geographical Distribution (Figure 5)

L. t. tridentata occurs in the watersheds flowing into North Pacific Ocean. In Oregon, it is found only in the coastal and

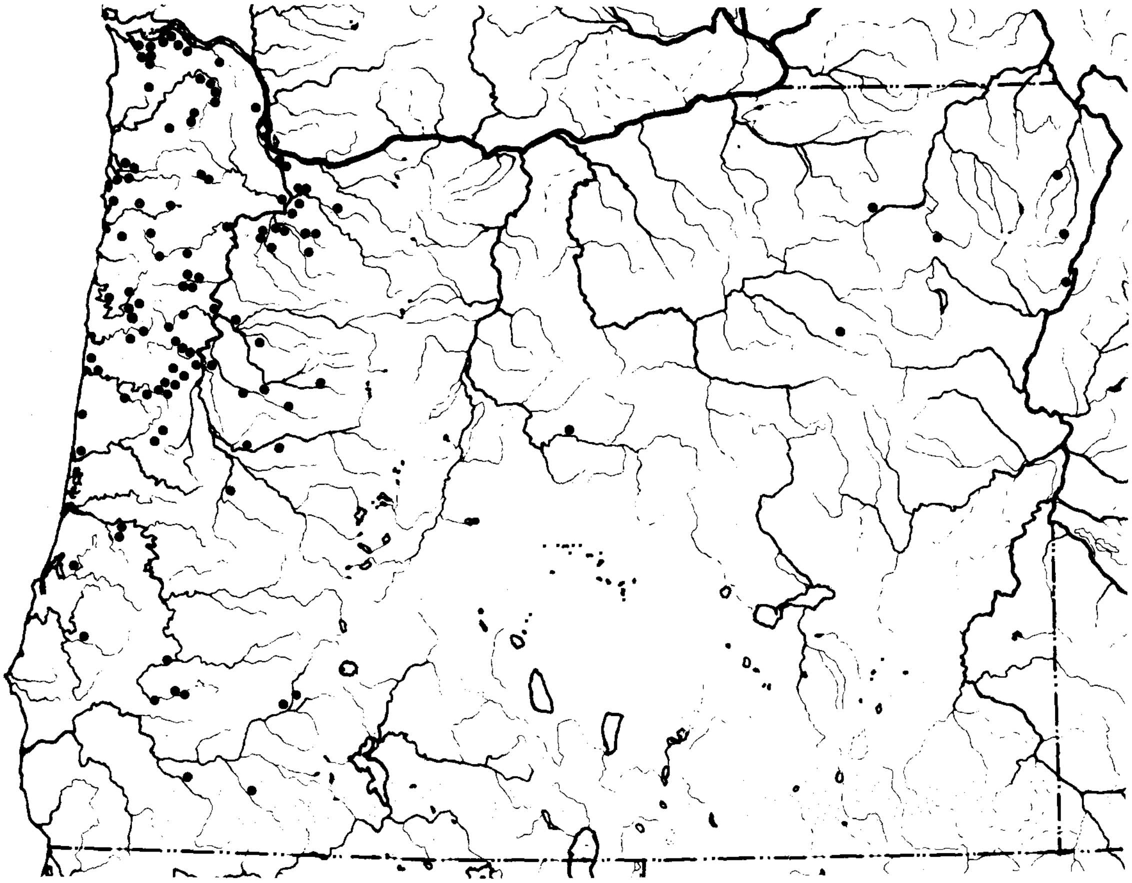

Figure 5. Distributional records of Lampetra t. tridentata in Oregon.

Columbia River drainages.

L. t. tridentata has a great coastal distribution. Girard (1858) recorded this species from Astoria, Clatsop Co. Snyder (1908a) remarked on its appearance in Nestucca R., Umpqua R., Coquille R., and Rogue R. Bond (1961 and 1973) stated that it is found in "most streams with access to the ocean," including, of course, the Columbia River. Some additional coastal records are (A=ammocoete, M= macrophthalmia, P=prespawner, and S=spawner): Humbug Cr. of the Nehalem R. system (A), Clatsop Co.; Nehalem R. (A, S) and its tributary, Wolf Cr. (A, S), Columbia Co.; Kilchis R. at Bay City (A), Trask R. (A), Sand Cr. near Sand Lake (A), Niagara Cr. of the Nestucca R. system (A), and Wood R., a tributary to Alder Cr. of the Nestucca R. system (A), Tillamook Co.; Fogarty Cr. near Siletz Bay (A), Siletz R. (S), Cedar Cr. (A) and Rock Cr. (A, P) of the Siletz R. system, a small stream that discharges into Yaquina Bay (M), Yaquina R. (A, S), Simpson Cr. of the Yaquina R. system (A), Beaver Cr. (south of Newport), Eckman Cr., a tributary to Alsea Bay (A), Alsea R. (A), Lobster Cr. of the Alsea R. system (A), and Yachats R. (S), Lincoln Co.; Alsea R. North Fork (M), Alsea R. North and South Forks (A), and Crooked Cr. of the Alsea R. system (S), Benton Co.; Tenmile Cr. (north of Florence) (A), Munsel Cr., near Florence (A), Triangle L. tributary (M) and Fish Cr. below Triangle L. (S), Lane Co.; Loon L. tributary (A), and Camp Cr. (M) and Cow Cr. (A, P) of the Umpqua R. system, Douglas Co.; Coos R. (A), and Holmes Cr. of the Coquille R. system (A), Coos Co.; Sixes R., Curry Co.; Applegate R. of the Rogue R. system (A, M), Josephine Co.; and Rogue R. (M, P) and its tributary, Bear Cr. (A, M), Jackson Co.

L. t. tridentata was first described from specimens from Willamette Falls, Clackamas Co. (Richardson, 1836). Other distributional records of this species in the Willamette River system were given by Dimick and Merryfield (1945), including, Peoria, Buena Vista, Oregon City below falls, and Portland at Sellwood Bridge along the main river; Clackamas R., Pudding R., Santiam R. at Jefferson, S. Santiam R. below and above Lebanon, Santiam R. Middle Fork, and McKenzie R. at Coburg Bridge on the east of the main river; and Tualatin R. near the mouth, Scoggin Cr., Yamhill R., near the mouth, Yamhill R. above Willamina, Rickreall Cr. below Dallas, Luckiamute R. at Pedee and above Hoskins, Marys R. at Corvallis, Muddy Cr. at Bruce, Rock Cr., Marys R. at Wren Bridge, and Coast Fork above Cottage Grove on the west of the main river. Additional records in this system follow: Willamette R. near West Linn (P), Tickle Cr. of the Clackamas R. system (A), and Trout Cr. (A) and Milk Cr. (A) of the Molalla R. system, Clackamas Co.; Agency Cr. of the S. Yamhill R. system (A), Yamhill Co.; Rogue R. of the S. Yamhill R. system (A), Polk Co.; S. Santiam R.

near Crabtree (M), Moose Cr. of the S. Santiam R. system (A), Calapooya R. (A), and Courtney Cr. of the Calapooya R. system (A), Linn Co.; Marys R. at Bellfountain (A, M), and Oliver Cr. of the Marys R. system (A); and McKenzie R. at Leaburg (A), Holden Cr. of the McKenzie R. system (A), and Willamette R. Middle Fork above Oakridge, Lane Co.

L. t. tridentata was recently reported from tributaries of the lower Columbia River (Reimers, 1964; McPhail, 1967; and Reimers and Bond, 1967). On the Oregon side, it was found in Youngs R. and its tributaries, and Big Cr., Clatsop Co., and Clatskanie R. and a stream near Westport, Columbia Co. Additional records from this region are: a Walluski R. tributary (A), Clatsop Co. and Scappoose Cr. (A), Columbia Co. Apparently no record of *L. t. tridentata* was given for specific localities in the middle Columbia River drainages in Oregon although it was known from Walla Walla R., Garrison Cr. and Rock Island Dam in Washington (see Schultz and DeLacy, 1935). Following are the distributional records of this species in the middle Columbia River and Snake River drainages in Oregon: Columbia R. at Celilo, Wasco Co. (A); Clear Cr. (S) and Canyon Cr. (A) of the John Day River system, Grant Co.; Catherine Cr. (A) of the Grande Ronde River system and an unknown stream (A), Union Co.; Little Sheep Cr. (A) and Grouse Cr. (A) of the Imnaha River system, Wallowa Co.; and Snake R. below Ox Bow Dam, Baker Co.

Field observations, especially from the coastal watersheds and the lower Columbia River drainages, indicated that the specimens of *L. t. tridentata* were often taken together with those of salmonines and the species of *Cottus*, an association also observed by Bond (1963). These three types of fishes are considered not to be primary freshwater fishes, and, according to Darlington (1957), their dispersal is associated with geography of the sea.

Judging from the geographical and local distributions of *L. t. tridentata* in Oregon, it seems that the primary consideration for the occurrence of this species is the access rather than distance to the ocean, as long as suitable spawning grounds and ammocoete beds are present. Accordingly, it was collected from its suitable habitats at localities ranging from only a few hundred meters (OS 4896) to more than 1,000 km (OS 4125) away from the sea.

Biology

Fecundity

Number of eggs and estimates of relative fecundity of *L. t. tridentata* from three different drainage localities in Oregon are given in Table 9. Diameter of eggs ranges from 0.6 to 1.0 mm with a mean of 0.8 mm. The number of eggs (absolute fecundity) produced by this species is thus comparable to that of *P. marinus*

Table 9. Egg numbers and estimates of relative fecundity of *Lampetra t. tridentata* from three localities in Oregon. Mean values are in parentheses. Confidence limits for means are at 95% level.

Locality	Number of specimens	Egg diameter (mm)	Body weight (g)	Egg numbers	Relative fecundity No. egg/g body wt.
Clear Cr. John Day R. system	7	0.7-1.0 (0.84)	264.00-366.60 (328.84)	98,300-193,900 (137,435.39)	339.21-537.64 (417.94±48.67)
Trout Cr. Molalla R. system	9	0.7-1.0 (0.82)	194.50-392.80 (267.86)	105,450-180,200 (134,851.44)	412.40-590.28 (503.44±38.87)
Cow Cr. Umpqua R. system	9	0.6-0.9 (0.74)	222.00-422.40 (290.60)	107,160-238,400 (151,736.80)	403.58-726.26 (522.15±72.34)
TOTAL	25	0.6-1.0 (0.80)	194.50-422.40 (292.71±25.34)	98,300-238,400 (140,312±12,924.80)	339.21-726.26 (486.23±37.45)

(Table 10); both species grow to a larger size and migrate for a longer distance than other anadromous lamprey species do. However, the relative fecundity of *t. tridentata* is larger than that of *marinus*. The reason is that *t. tridentata* in general grows to a smaller size than *marinus* does.

The numbers of eggs produced by fishes at one time would eventually approach the limit imposed by the body size of the adults (Svärdson, 1949). Levels of fecundity in lampreys appear to be determined by the environment, the habit of life, and the intrinsic, genetically controlled component which represents the adaptive outcome of natural selection. For anadromous species the number of eggs produced is in general positively correlated with the adult body size (see Figure 6) and also the migration distance (Hardisty, 1971). Relative fecundity however is often negatively correlated with the adult body size in these species (Hardisty, 1964 and 1971). This negative correlation may exist because in lampreys with long migrations only a certain portion of the lipid reserves accumulated during the parasitic phase would be incorporated into the form of gonadal products and the remainder would have to be consumed during the long journey from feeding grounds at sea to spawning areas in streams. Some evidence of the operation of this phenomenon is provided by a comparison of the relative fecundities of the three Oregon populations of *L. t. tridentata* (Table 9). Mean relative

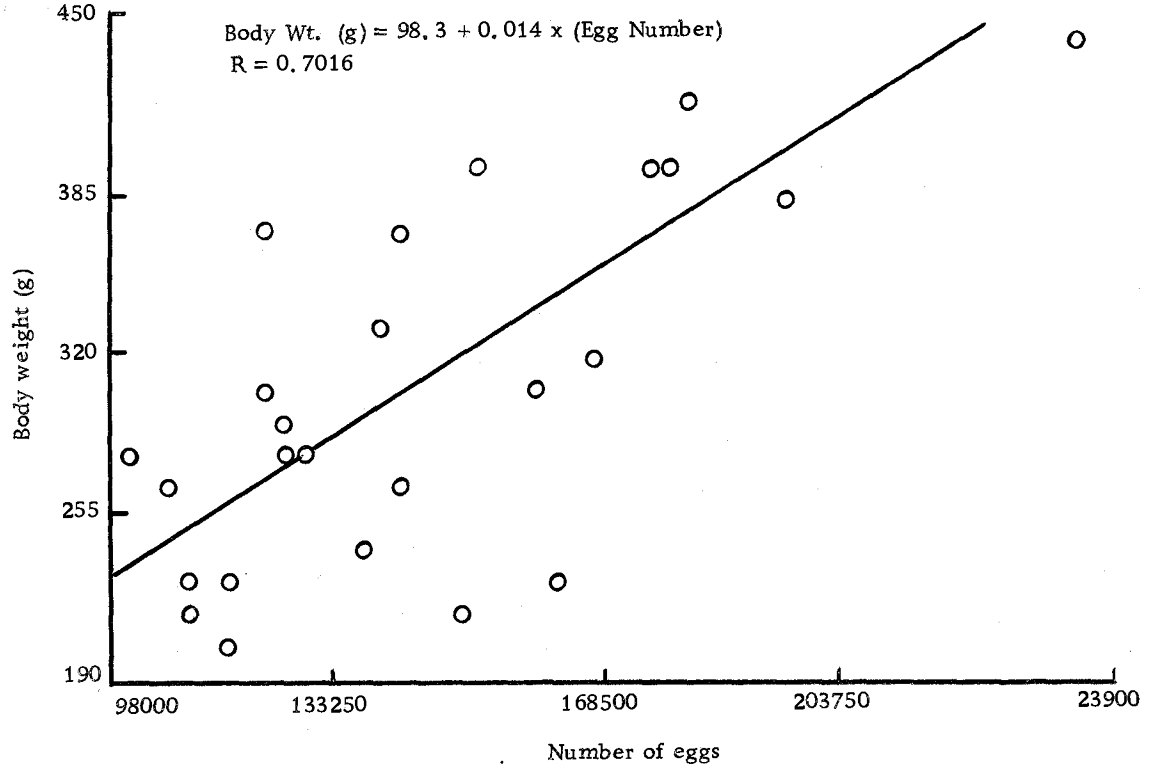

Figure 6. Relation of body weight to the number of eggs produced by Lampetra t. tridentata from Oregon.

Table 10. Egg numbers and estimates of relative fecundity of five species of anadromous parasitic lampreys. Ranges are in parentheses.

Species	Source	Egg number	Relative fecundity (no. of eggs/g body wt.)
Petromyzon marinus	Vladykov, 1951	172, 000 (124, 000-260, 000)	204
Lampetra t. tridentata	Table 9	140, 312±12, 924.80[1] (98, 300-238, 400)	486.23±37.45
Lampetra japonica japonica	Berg, 1948	(80, 000-107, 000)	---
Lampetra japonica septrentionalis	Berg, 1948	25, 000	---
Lampetra fluviatilis	Hardisty, 1964	16, 000	375 - R. Trent 405 - R. Severn

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[1] Confidence limits for means are at 95% level.

fecundity was calculated at 522.15 for the sample from the Umpqua River system, 503.44 for the Molalla sample, and only 417.94 for the John Day specimens. No significant difference was found ($t=1.15$, $P<0.30$) between the first two means but a significant difference was detected ($t=2.56$, $P<0.02$) in the last two means. The large-bodied fishes of the John Day River system must travel over 700 km in streams in order to reach their spawning area while those from the Molalla and the Umpqua river systems need only to migrate up about 250 to 300 km inland to reach their respective spawning grounds.

Duration of the Larval Period

Because of the absence of bony structure in lampreys,[6] attempts to age these animals by examining some of the head and body cartilages were proved unsuccessful (Abakumov, 1960). Investigations on ammocoete growth have been conducted through field experiments with known-age, isolated populations (Applegate and Thomas, 1965; Manion and McLain, 1971) and, mostly, based on the analysis of length-frequency data (McDonald, 1959; Hardisty, 1961 and 1969; Potter, 1970; and others).

The duration of larval period of L. t. tridentata was estimated at three or more years by Hubbs (1925). Based on Pletcher (1963),

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[6] Some partially calcified skeletons were however traced in Ichthyomyzon unicuspis, (Bardack and Zangerl, 1971).

Scott and Crossman (1973) gave it as five or six years for British Columbia populations. The length-frequency distribution of 317 specimens collected at the same time from Cow Creek of the Umpqua River system in Oregon (Figure 7) shows four modes at 23, 43, 63 and 83 mm, which can almost certainly be assigned to age classes 0 to III. Older age classes may represent some of the specimens in the length range over about 105 mm. These longer specimens could be in their fifth or sixth year. The annual increments represented by the intervals between successive modes indicate that the maximum growth in length occurs during the first year of larval life and the growth rate becomes smaller in subsequent years. The possibility of a sixth larval year shown in Figure 8 is a situation similar to that of certain landlocked populations of _P. marinus_ in which a prolongation in time beyond the normal length of larval period was observed (Manion and McLain, 1971). A five-peaked length-frequency distribution was also noticed in _t. tridentata_ ammocoetes, collected mostly during the spring and summer months, from the coastal watersheds (Figure 8), as well as from the Willamette River tributaries (Figure 9), suggesting that the growth rates did not vary much in populations from these streams. The duration of _t. tridentata_ larval period now estimated is thus nearly identical to that of _marinus_ studied by McDonald (1959) and Hardisty (1969).

Some of the _L. t. tridentata_ macrophthalmia specimens

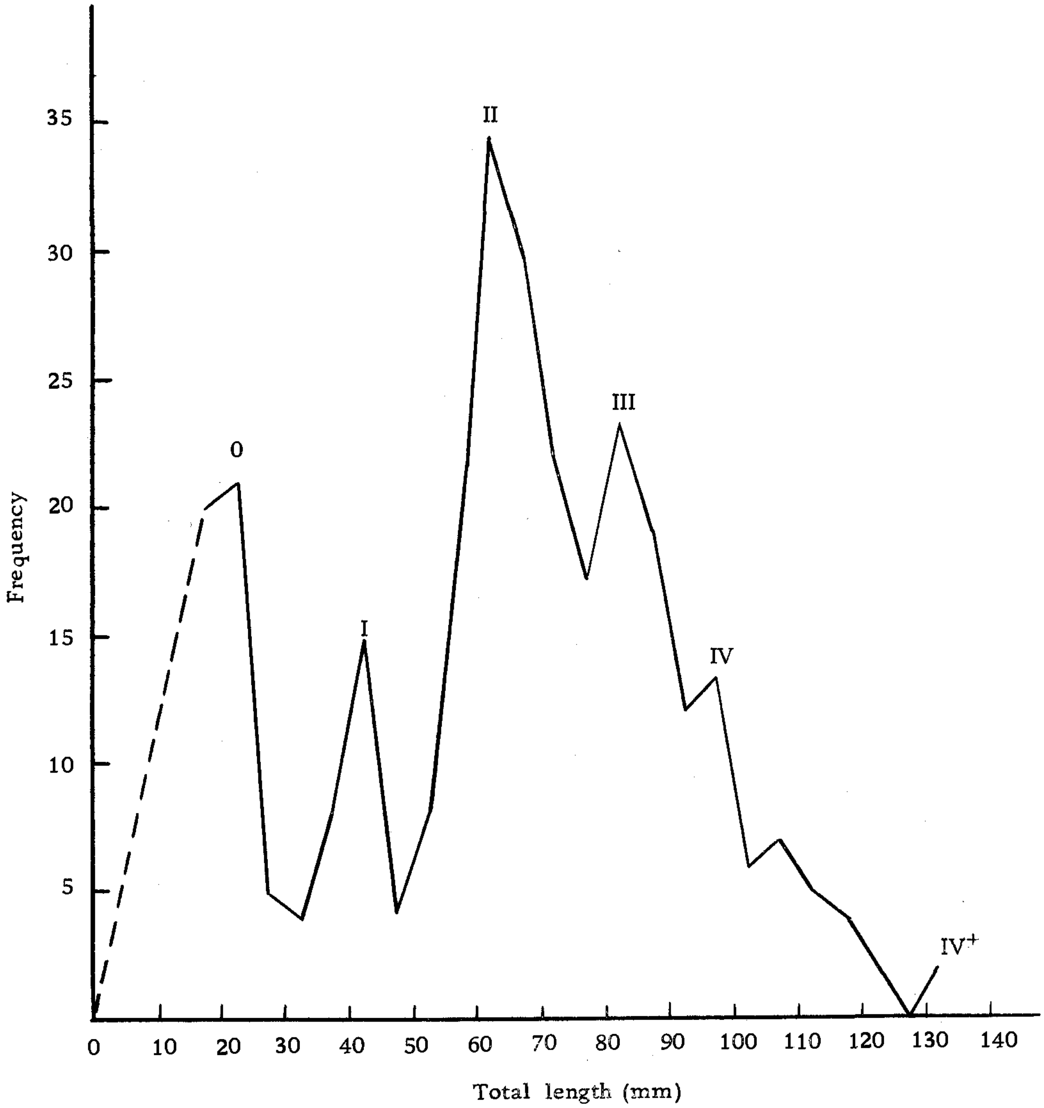

Figure 7. Length-frequency distributions for 317 Lampetra t. tridentata ammocoetes taken from Cow Creek, Douglas County, Oregon on July 30, 1970.

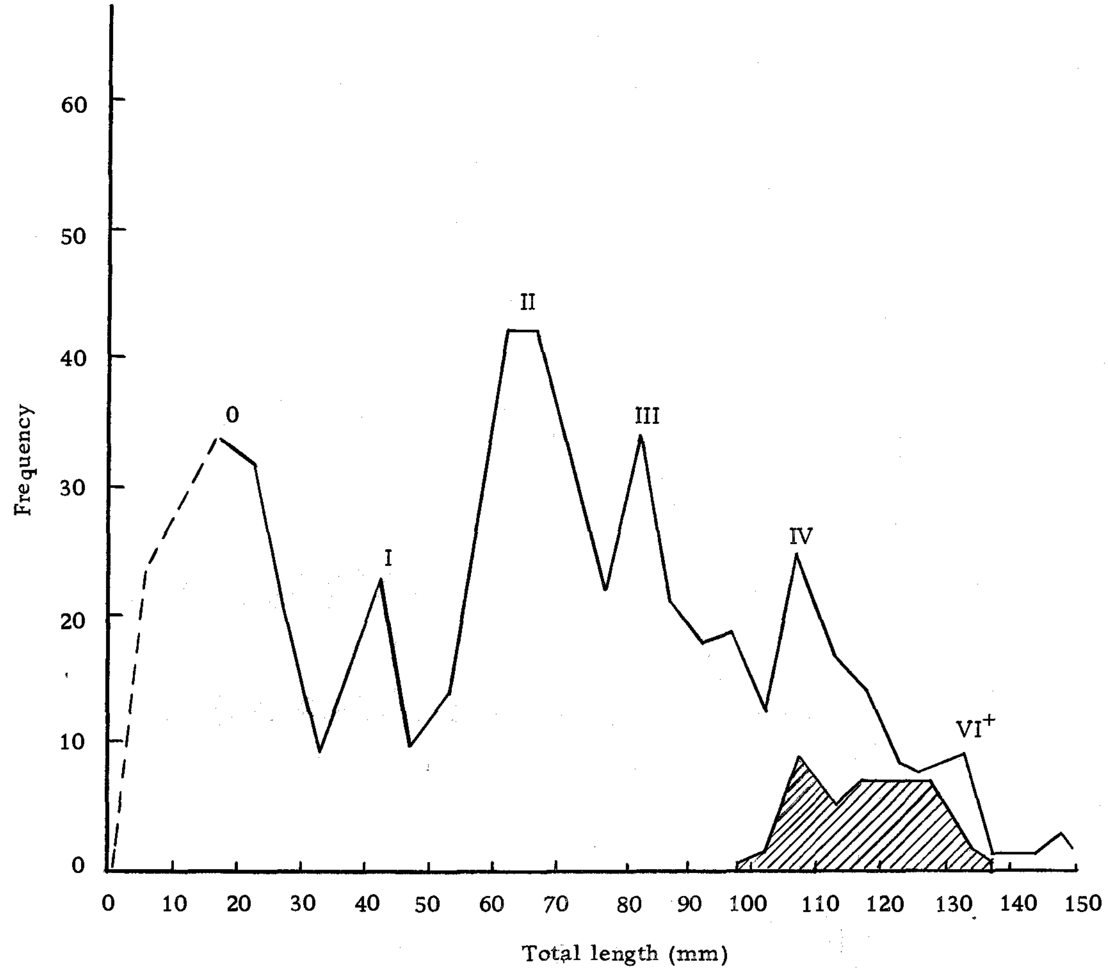

Figure 8. Length-frequency distributions for 507 ammocoetes and 42 macrophthalmia (striped area) of Lampetra t. tridentata from Oregon coastal streams.

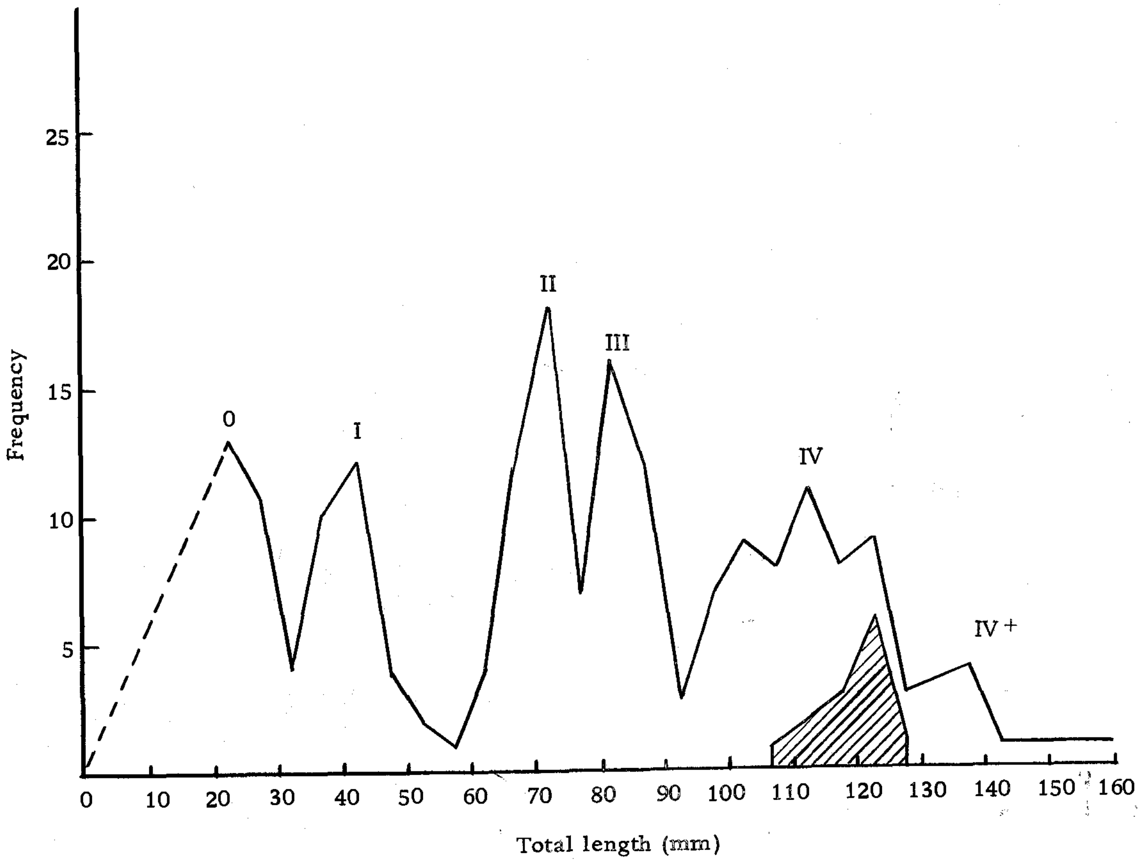

Figure 9. Length-frequency distributions for 192 ammocoetes and 13 macrophthalmia (striped area) of Lampetra t. tridentata from the Willamette River system, Oregon.

examined were shorter than 105 mm in total length (Figures 8 and 9). Hence, these were fishes that did not grow or only grew slightly during the year preceding metamorphosis. This phase of retarded growth was also observed in *P. marinus* (Gage, 1928), *Ichthyomyzon fossor* (Leach, 1940 and 1951), and *M. mordax* (Potter, 1970). Several *t. tridentata* specimens, representing fishes apparently at the onset of metamorphosis, were found to be longer than 125 mm and probably belonged to the sixth age class. Therefore, it seems that neither total length nor age is a critical factor that triggers metamorphosis in *t. tridentata*. Sterba (1969) suggested that metamorphosis in lampreys is controlled directly by the pituitary gland. Leach (1951) indicated that even in the smaller, pre-metamorphic ammocoetes of *I. fossor*, the pituitary and the nasohypophysial stalk exhibit cytological changes which may be considered as a prelude to the external morphological changes of metamorphosis.

The Parasitic Phase: Duration and Growth

Little information has been published on duration of the parasitic phase of the larger anadromous species of lampreys. According to their characteristic adult body size, Hardisty and Potter (1971b) suggested that *P. marinus*, *L. t. tridentata*, and *Geotria australis* spend over 18 months but no more than 30 months in the sea before they commence their spawning migrations.

The duration of the parasitic phase of _L. t. tridentata_ is difficult to estimate because of the very few ocean-caught specimens available. In addition, macrophthalmia are known to enter the ocean over a long period, those descending coastal streams enter salt water in the late fall and early winter, whereas the peak of emigration from inland streams seems to be in early spring (Melvin Collins, Fish Comm. of Oregon, personal communication). This means that specimens significantly longer than macrophthalmia, caught in late spring or summer, could represent coastal stocks after six months, or inland stocks after a year, in the ocean. Firm data that form the point of departure for interpretation are these: downstream migrants have a mean length of about 120 mm and upstream migrants are 510 mm long on the average.

A possible interpretation (Table 11) is that, ignoring the exceptional 754 mm specimen, all the specimens shown, ranging from 107 to 292 mm long, could all be within their first year of ocean life. Those under 150 mm long, being close to the size of downstream migrants, can be considered as having spent less than six months in the ocean, and those greater than 150 mm, more than six months up to about a year. The potential for growth that this interpretation represents allows for the fastest growing individuals, such as the 292 mm specimen, to reach migratory size within two years. The 754 mm specimen (OS 4860) collected in mid-May, 1974, was found to

Table 11. Length ranges and mean lengths of Lampetra t. tridentata from the Pacific Ocean off Oregon, showing month of capture and estimated duration of ocean life. (Lengths in mm, number of specimens in parentheses following range, means in parentheses below range)

	Estimated years in ocean				
	< 1/2	1/2 to 1	1 to 2	2 to 3	> 3
April		155-205(10) (188.9)			
May	131(1)				754(1)
June		292(1)			
July	149(2) (149.0)	207-254(4) (229.5)			
August	135-137(2) (136)				
September		221-266(7) (245.1)			
October					
November	107-138(3) (121.3)	256(1)			
TOTAL	107-149(8) 133.1	155-292(23) 220.5			754(1)

have an ovary in a condition still belonging to a rather early developing stage with the oocyte visible only through higher magnifications. This specimen can be considered as a fish which was in its late third year as a parasitic feeder when caught and probably would have had to remain in the sea for up to one additional year before maturation.

Like the landlocked *P. marinus* (see Applegate, 1950), *L. t. tridentata* grows rapidly in open waters. According to the present limited data, the annual increment in length is about 300 mm for a 220 mm fish in its second year in the ocean and about 250 mm for a 500 mm fish if it still remains at sea during the third year (Table 11).

Sex Ratio

As seen from Table 12, sex ratio changes markedly in different life history stages of *L. t. tridentata*. A preponderance of females was observed in larger-ammocoete samples from all localities studied while the reverse was shown in all macrophthalmia samples. This phenomenon seems to be attributed to a sex difference in the time of metamorphosis. Hardisty and Potter (1971b) suggested that in reasonably large ammocoete populations, the males may tend to metamorphose at an earlier age than the female, and that, for the females, metamorphosis may still not take place for years after their male cohorts metamorphose. Moreover, some female ammocoetes may never metamorphose, as indicated in observations

Table 12. Sex ratios of Lampetra t. tridentata from Oregon, British Columbia and the Pacific off Oregon.

Locality	Number of specimens	Sex ratio (%)		
		Male		Female
Ammocoetes (> 90 mm in total length)				
Coastal drainages, Oregon	101	37.6		62.4
Willamette R. drainages, Oregon	63	28.6		71.4
Mid-Columbia R. and Snake R. drainages, Oregon	24	41.7		58.3
TOTAL	188	35.1		64.9
			(1:1.85)	
Macrophthalmia				
Coastal drainages, Oregon	46	58.7		41.3
Willamette R. drainage	12	58.3		41.7
Snake R., Oregon	2 (♂s)	-		-
Thompson R., B. C.	33	57.6		42.4
TOTAL	93	59.1		40.9
			(1:0.69)	
Active parasitic feeders				
Pacific Ocean off Oregon	23	43.5		56.5
			(1:1.30)	
Prespawners				
Oregon streams	108	57.4		42.6
Spawners				
Oregon streams	113	54.9		45.1
TOTAL (pre- and spawners)	221	56.1		43.9
			(1:0.78)	

made from known-age, artificially isolated populations of P. marinus (Manion and McLain, 1971). Direct evidence for a sex difference in age at metamorphosis was also provided by these observations. Indirect evidence largely based on the tendency to have a significant excess of females in the older age classes was seen in Hardisty (1965) and Smith and King (1968).

An excess of males was seen in the samples of L. t. tridentata spawning populations (Table 12). Similar situations were reported for P. marinus (Applegate, 1950) and for other species (see Hardisty and Potter, 1971b). Apparently, this is a consequence of the sex difference in the time of metamorphosis. However, the sex ratio for 23 active parasitic feeders of t. tridentata found here is 1 ♂ : 1. 3 ♀, a ratio probably incorrect due to the insufficient data.

Life History

The Spawning Migration

In Oregon, the spawning migration in L. t. tridentata generally begins from the spring to late summer for coastal populations, but it may occur much earlier for inland populations. A specimen (OS 4877), still with features reflecting an oceanic feeding life as heavy eyelids and sharp teeth, was taken alive in January from a Willamette River tributary at West Linn, Multnomah Co. On the other hand, many specimens (in OS 4096), collected from a John Day River tributary and classified as of the prespawning stage, apparently were upstream migrants that had already been in fresh water for several months before their capture in July, 1970. Pletcher (1963) reported for some British Columbia *t. tridentata* populations that as long as seven months lapsed between the onset of upstream run and beginning of actual spawning. A population of March-spawning *t. tridentata* in the Alsea River apparently overwinter in fresh water and are subject to heavy mortality during severe floods (C. E. Bond, personal communication). Longer periods of time spent on upstream migration were also observed in such anadromous species as *P. marinus* (Bigelow and Schroeder, 1948), *M. mordax* (Potter, Lanzing and Strahan, 1968), and *G. australis* (Potter and Strahan, 1968), whose populations often ascend for a distance of up to several hundred kilometers to spawn.

Water temperatures during the time of spawning migration are given as 5° to 20°C for coastal *L. t. tridentata*. Judging from their much earlier entry into freshwater, a still colder water temperature may not hinder the upstream movement of interior migrants. Applegate (1950) gave a range of 4.5° to 18.5°C during spawning runs of the landlocked *P. marinus*.

A photophobic response has been observed in upstream migrants of several species (see Hardisty and Potter, 1971b). Whether this response is also true for L. t. tridentata is unknown; although, in may occasions during day time, prespawning fishes were seen attaching by means of the sucking disc to the shaded side of fishway walls.

Based on possible time of entering into fresh water, time of capture and approximate stream distance, the swimming speed of L. t. tridentata from Clear Creek of the John Day River system is estimated at 4. 5 km per day. This rate probably would be much reduced when the fish is in fast flowing waters, but would be greatly increased on occasions when the fish could engage in repeated short surges of rapid swimming in slow waters. According to Wigley (1959), the average rate of upstream movement of landlocked P. marinus is 3. 2 km per day, a rate that is reduced to about 0. 5 km farther upstream in fast flowing areas. For anadromous marinus, a faster rate (some 12 km per day) is possible (Bigelow and Schroeder, 1948). Nevertheless, the lamprey is considered not to be a good swimmer in comparison with anadromous teleost fish (Beamish, 1974). Apparently, the absence of paired fins and the development of small unpaired fins in these animals may render them poor in swimming performance, especially against strong currents (see Marshall, 1966). The lamprey is aided in ascending fast flowing stretches by attaching to rocks and other objects with its sucking disc, thus maintaining position between swimming bursts.

Spawning

Collection records indicate that *L. t. tridentata* usually begins to spawn in Oregon coastal streams in April when the water temperature reaches about 8.5° C. Most spawning fishes from these watersheds were collected in May with water temperatures ranging from 10° to 12.5° C. Seemingly, the spawning would occur any time between spring and early fall when the water temperature is within the order of 10° to 15° C. Inland *t. tridentata* populations appear to begin spawning much later; both spawning and prespawning fishes were collected at the same time (OS 4096) in July from Clear Creek of the John Day River system.

Spawning acts in *L. t. tridentata* were observed in redds which are generally built in the middle of a shallow stream with little or no cover or shade. Redds, estimated as 30 cm wide and 3 cm deep, were constructed by both sexes of similar size through moving stones by sucking disc to form an oval depression. Polyandrous associations were occasionally seen. In the pairing act, the male normally approached the female from behind and moved forward attaching itself parallel to the body of its mate. The tail of the male was then maneuvered to coil around the female until the cloacal regions of both fishes were adjacent. A close pairing of the bodies of both sexes with similar size seems to be necessary in maintaining the efficiency of fertilization, as the swimming life of the lamprey sperm, according to Kille (1960), is very short. Therefore, a mechanical barrier in copulation may be formed in lampreys with quite different sizes (see Hagelin, 1959). Hardisty and Potter (1971a) emphasized the size difference as a basis in the speciation among paired species of lampreys.

As other anadromous species, L. t. tridentata undergoes marked reduction in body length from prespawning to spawning and postspawning stages (Table 4). Shrinkages in total length of fishes through these stages was about 18.5% (12% in males and 25% in females). The reduction in size is apparently related to the release of gonadal products and to the expenditure of body reserves for spawning activities. L. t. tridentata appears to die soon after reproduction, as spawning fish, recently dead fish, and older dead bodies were often seen at one site at the same time. Pletcher (1963) reported that a period of one to 14 days elapsed between spawning and subsequent death of t. tridentata in British Columbia.

Larval Life

The incubation time for L. t. tridentata in Oregon streams is unknown. Carl (1953) estimated a period of two to three weeks (19 days at 15° C) for certain British Columbia landlocked populations. Piavis (1971) reared P. marinus fertilized eggs to hatch in ten to 13 days at a constant 18.4° C.

The burrowing habit of lamprey larvae first occurs about 13 to 17 days after fertilization (Smith, Howell and Piavis, 1968). Smallest (16 mm long) burrowing ammocoetes of *L. t. tridentata* (OS 4020), were collected in late July from Cow Creek, an Umpqua River tributary, suggesting that they probably had hatched out in the preceding May. The fact that smaller larvae prefer a soft substrate composed of fine silt while larger ones are found in coarser material clearly indicates a positive correlation between the burrowing ability and the size of ammocoetes. The construction of burrows may be facilitated by the mucoid secretion produced by the endostyle (Sterba, 1962).

As other species of lampreys (Manion and McLain, 1971; Moore and Beamish, 1973; and see Hardisty and Potter, 1971c), the ammocoete *L. t. tridentata* feed mostly on diatoms. The endostyle also contributes to the formation of the mucus strands involving feeding (Sterba, 1962). Judging from its well-concealed habitats, the mortality of ammocoetes due to predation by fishes is considered as low. Though a number of authors wrote of such predation (see Hardisty and Potter, 1971c) and ammocoetes were seen being chased by small salmonids (Field Note K 735-3-3), the actual occurrence of predation on ammocoetes by fishes is uncertain. Moreover, experiments suggested that both adult and larval *t. tridentata* may be avoided by fish in feeding because of a noxious secretion of skin glands (Pfeiffer and Pletcher, 1964).

In the four to six years in streams, L. t. tridentata ammocoetes appear to lead a sedentary life. However, they periodically relocate due to habitat selection corresponding to the growth in body size or, as stated in Sterba (1962), from selective feeding resulting from the decrease in "fineness" of the oral filter with age.

Metamorphosis and Downstream Migration

Date of collections indicates that L. t. tridentata, about 100 mm long, begins to metamorphose, somewhat synchronically (see Beamish and Potter, 1972) from late September to October in Oregon coastal watersheds and in the Willamette River drainages as well. However, macrophthalmia were taken as early as in March and April from Snake River, Oregon (OS 4124). Thus, for interior t. tridentata populations, metamorphosis may take place in spring months as water temperatures are rising to a suitable level, or, more likely, still in the fall but the metamorphosed fish remain in the general area until next spring, as evidenced by an October collection (OS 4151) of early macrophthalmia from Crooked River, a Deschutes River tributary. Water temperatures recorded were 15° C for the metamorphosing fish at Bear Creek, Umpqua River system, and 8.4° C for the Crooked River fish.

Newly-transformed L. t. tridentata are relatively inactive in the pre-migratory stage; both macrophthalmia and larger ammocoetes were collected simultaneously from ammocoete beds in several occasions (OS 4052, 4060, 4886, 4887, 4897, 4907 and 4125). Duration of this inactive period is uncertain. Based on information provided by body length data and by collection dates, two months is considered as the shortest possible interval from the onset of transformation to the completion of downstream migration for coastal t. tridentata. As long as seven months is estimated for interior t. tridentata. Due to its smallness and poor swimming ability (see Beamish, 1974), downstream migration of the t. tridentata macrophthalmia appears to be mainly passive, involving high waters and spring floods as reported for P. marinus by Applegate and Brynildson (1952).

L. t. tridentata of the earliest macrophthalmia stage have a nonfunctional gut and feeble teeth, and appear not to be engaging in feeding. At their later stage, however, a well-developed digestive system enables them to feed (OS 4083). For anadromous species migrating downstream a great distance, such as t. tridentata, P. marinus (Davis, 1967), and possibly L. ayresii (Withler, 1955), an early initiation of feeding habit is obviously essential.

Little information is available on the estuarine life of macrophthalmia. Three specimens of this stage (OSUO 1693, 1694) were taken from brackish waters of Yaquina Bay, and another was attached to a coho salmon, Oncorhynchus kisutch, when collected off the Columbia River (OS 4152). Considering the great effort expended in trawling in Yaquina Bay and other Oregon estuaries by various agencies during the past decade, it seems likely that juvenile lampreys have not been captured more often because they move rapidly through the estuaries to the ocean. Other anadromous species have been noted as spending some time in brackish environments as juveniles (Mansueti, 1962; Potter, Lanzing and Strahan, 1968). Hardisty and Potter (1971b) have suggested that the osmotic load of lampreys is reduced from that of the teleost because of the parasitic habit that allows lampreys to swallow blood and body fluids at about 170 to 230 mM/l NaCl instead of sea water at about 540 mM/l NaCl.

Marine Parasitic Phase

L. t. tridentata at active parasitic feeding stage were taken from mid-water over shelf region off Oregon (Pearcy, 1964). Duration of this stage is estimated to be from 20 to 40 months (see Biology).

Attachment of the lamprey to the host-prey is facilitated by the sucking disc. The secretion of the buccal glands in L. t. tridentata (Baxter, 1956), similar chemically to "lamphredin" of P. marinus (Lennon, 1954), plays an important role in feeding, both by its anticoagulant properties and its effects on tissues of living fish (Lennon, 1954; Baxter, 1956). Rendering a potential attack probable, the host-prey of *t. tridentata* may behave similarly to that of *marinus* in that no attempt is made to avoid the approach and attack of the attacker (Lennon, 1954; Farmer and Beamish, 1973).

Salmonids preyed upon by *L. t. tridentata* at sea include *Oncorhynchus kisutch* (OS 13 and 4152; Birman, 1950), *O. nerka* (Williams and Gilhousen, 1968), and *O. gorbuscha* (Birman, 1950; Williams and Gilhousen, 1968). Most *t. tridentata* at feeding stage presently studied were collected by midwater trawls for groundfish investigations (M. J. Hosie, personal communication); thus, the citation of such fishes as pleuronectiforms, anoplopomatids, and gadiforms as hosts of *t. tridentata* (Novikov, 1963) is possibly correct. The open ocean, midwater fish, *Lampris regius* also serves as a host of *t. tridentata* (Bell and Kask, 1936). Williams and Gilhousen (1968) suggested that a greater mortality may be inflicted by *t. tridentata* to the Pacific salmons in Georgia Strait, British Columbia.

In relation to *L. t. tridentata*, marine mammals are both predators (Pike, 1951; Fisher, 1952) and the prey (Pike, 1951; Nemoto, 1955).

Variation

Although the biological species concept is generally accepted by modern taxonomists, in actual practice, especially when non-morphological characters are difficult to define, morphological discontinuity is the main basis for species separation or racial analysis. Because the morphological character is regarded as an indicator for genotypic discontinuity, its designation must be given carefully, and, in systematics, the study of its variation is important (Mayr, 1942 and 1969).

External morphological characters used in specific or intraspecific recognition of the members of genus Lampetra involve differences in dentition, number of trunk myomeres, and body proportions. As environmental changes often operate on the processes determining meristic or morphometric characters in fishes, information on the variability of such characters is thus of crucial concern.

Meristic Variation

Meristic characters are body parts which, in a strict sense, are related to body segmentation. In common exercise, however, they refer to whatever are countable. Both ontogenetic and geographical variation are recognized in meristic characters.

Ontogenetic Variation

In *L. t. tridentata*, as in certain other lamprey species, the number of trunk myomeres is usually higher for adult than for ammocoete specimens (Table 13). Teeth in general are reduced

Table 13. Number of trunk myomeres of various life history stages of *Lampetra t. tridentata* from the Pacific Ocean and southern Oregon coastal drainages. Total length range is in parentheses.

Locality	Number of specimens	Life history stage	Total length (mm)	Number of myomeres
Cow Creek, Umpqua River	79	Pro-ammocoete	29.09 ± 2.40[1] (16-50)	64.96±0.38[1] (61-68)
Cow Creek, Umpqua River	156	Ammocoete	68.32±1.41 (51-85)	66.53±0.28 (62-71)
Cow Creek, Umpqua River	66	Ammocoete	97.70±2.34 (86-120)	66.39±0.28 (64-70)
Cow Creek, Umpqua River	3	Ammocoete	128.01±0.71 (121-133)	66.33±1.30 (65-67)
Bear Creek, Rogue River	11	Macrophthalmia	126.36±3.72 (117-139)	67.00±0.64 (65-68)
Pacific Ocean off southern Oregon	4	Feeding	251.75±8.14 (246-266)	66.75±0.82 (66-68)
Cow Creek, Umpqua River	31	Prespawning	506.32±13.24 (448-581)	67.09±0.39 (66-69)
Sixes River	15	Spawning	424.07±13.02 (390-475)	68.00±0.92 (66-72)

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[1] Confidence intervals are at 95% significance level.

in sharpness or in number, or both, from feeding to spawning stages (Table 7).

Geographical Variation

In fish species, meristic differences are often considered to be effects of the environment, such as through a gradient of temperature or salinity (Hubbs, 1925; Tåning, 1952; Lindsey, 1954; Barlow, 1961; and many others), rather than a product of genetic dissimilarities. Thus, only those characters showing no or little clinal variation should be regarded as important in separation of the taxa at or above the species level.

Myomeres. As shown by Figures 10, 11, and 12, the number of trunk myomeres is extremely variable in L. t. tridentata. No latitudinal gradient among the means is evident. However, means of the inland forms are higher than those of the coastal ones. This is especially readily seen in the larger ammocoete and macrophthalmia stages.

Teeth. No meristic variation of any kind was found in cusp numbers of the supraoral lamina and the lateral circumorals in Oregon L. t. tridentata (see Description and Comparisons - Dentition). Four, all inland specimens, out of 349 countable infraoral laminae had a cusp count higher than the typical one of five; the extent of occurrences was less than 1.15%.

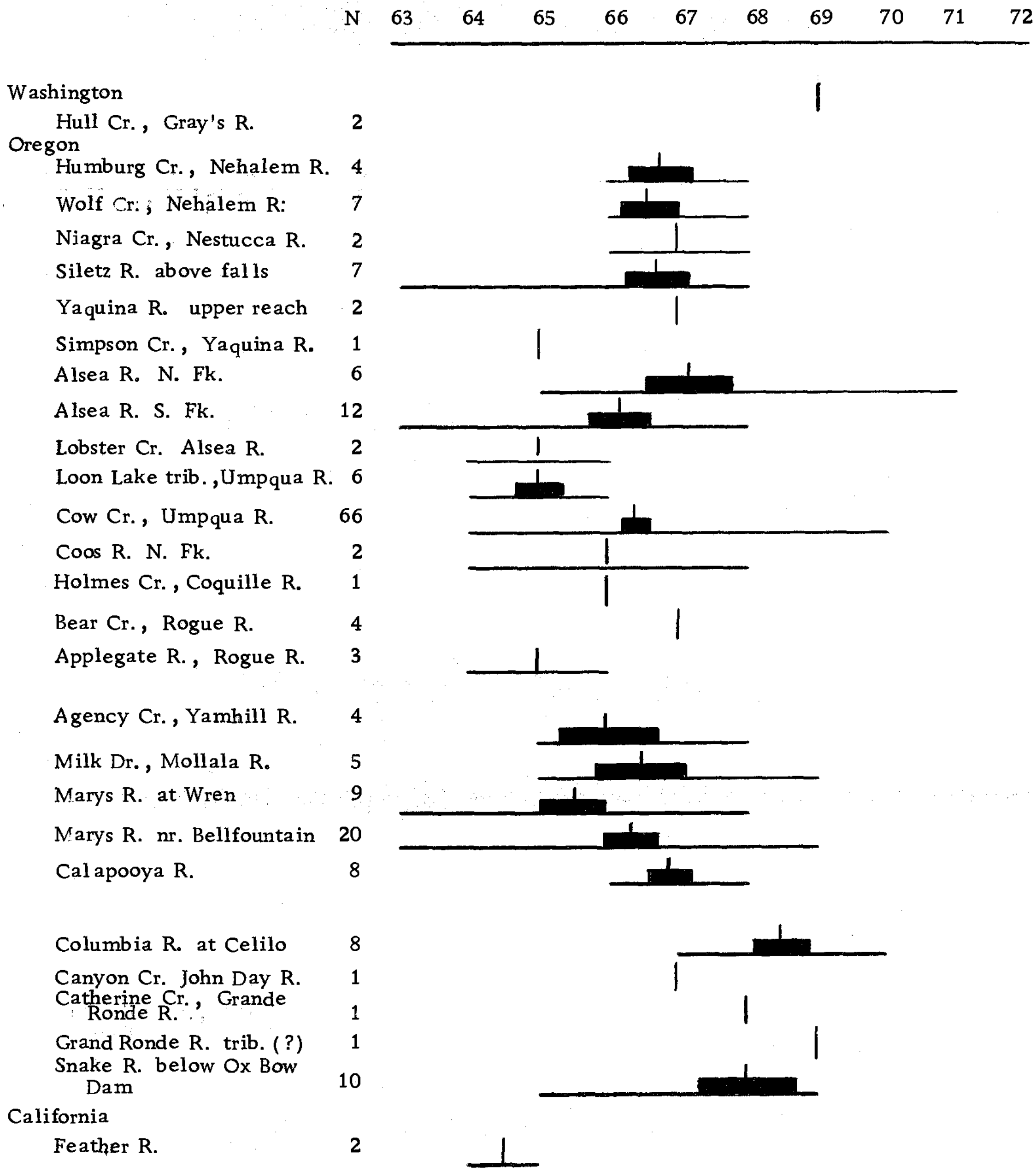

Figure 10. Variation in the number of trunk myomeres in larger ammocoete Lampetra t. tridentata. The diagram indicate the mean (vertical line) , 95% confidence intervals of the mean (black rectangle), and sample range (basal line) "N" represents sample size.

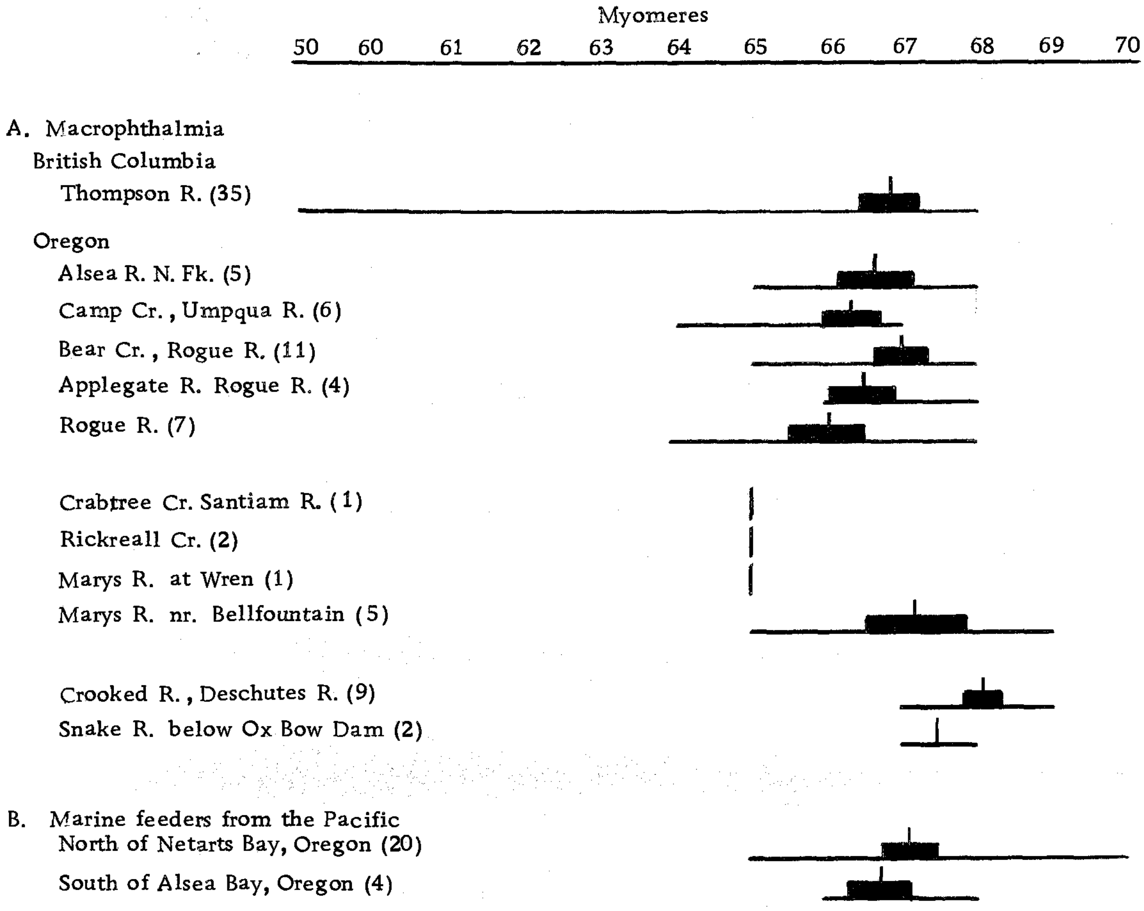

Figure 11. Variation in the number of trunk myomeres in macrophthalmia and marine feeding stages of Lampetra t. tridentata. See legend for Figure 10 for explanation of the diagram. The sample size is given in parentheses.

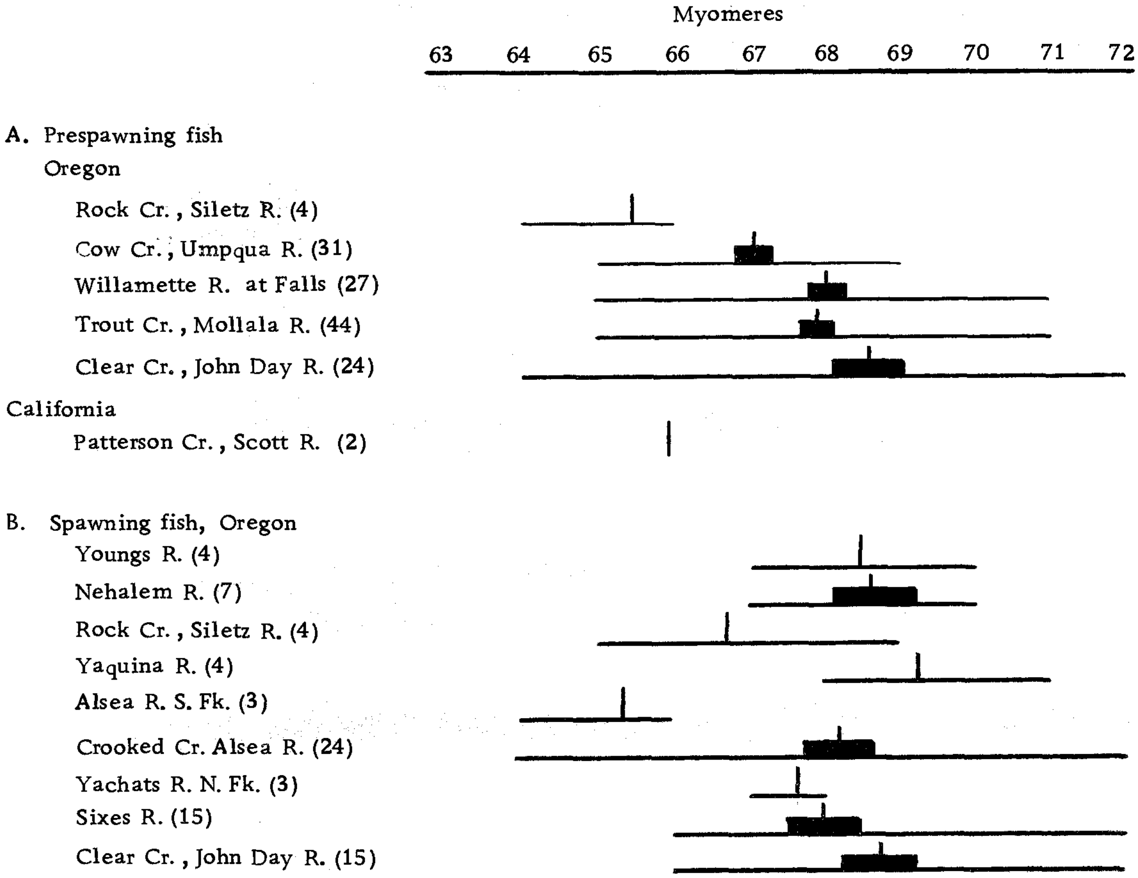

Figure 12. Variation in the number of trunk myomeres in prespawning and spawning stages of <u>Lampetra t. tridentata</u>. See legend for Figure 10 for explanation of the diagram. The sample size is given in parentheses.

Numbers of cusps on the transverse lingual lamina varies little in L. t. tridentata geographically (Table 6 and see Hubbs, 1967). However, some variation in cusp counts of the paired longitudinal lingual laminae was noticeable in John Day River (means 20.60 and 20.95, for right and left lamina, respectively) and Umpqua River (23.87 and 24.39) samples (Table 6). Factors causing this difference were apparently ontogenetic rather than geographical, as the former was a prespawner-spawner mixed sample while the latter a homogeneous sample comprised entirely of prespawners whose teeth in general undergo a lesser degree of degeneration than spawners do.

Discussion

Readily recognizable differences in counts of teeth would exist among the forms of L. t. tridentata if these differences were determined directly by the environment. Since such differences were not found, it seems that the numbers of teeth have a genetic basis and are important in the defining of this subspecies.

On the other hand, the number of trunk myomeres in L. t. tridentata varies markedly. The variation is probably due to differences in temperature during the time of incubation and early larval development. Indication for a genetic basis for variation of this sort is difficult to identify (Dobzhansky, 1970). Therefore the number of trunk myomeres seems to be of limited use in species separation among the subgenus Entosphenus. Nevertheless this character is useful to distinguish regional forms of Oregon t. tridentata; two groups of such forms, coastal and inland, may be recognized. These forms are apparently isolated from one another in fresh water but possibly not at sea. Their mingling in the sea however will not alter their genotypes.

Morphometric Variation

Values of morphometric characters are presented in ratios, each expressed as a percentage of total length.

Allometry - Ontogenetic Morphometric Changes

Table 14 gives the mean of various body proportions of L. t. tridentata ammocoetes in different size groups. Negative allometry is consistent in head, branchial and trunk lengths while the reverse is true in tail length. Development of a longer, probably more versatile, tail corresponds with the shift in niches from a largely sedentary life for small ammocoetes to a relatively active one for larger ammocoetes (see Distribution - Habitats).

L. t. tridentata shows a considerable allometry during post-larval stages (Table 4). An increase in length of the head region occurs after metamorphosis, attributed to the elongation of the snout and the development of the oral disc. Relatively larger eye

Table 14. Mean and its 95% confidence intervals of body proportions (percentages of total length) of *Lampetra t. tridentata* ammocoete samples from Cow Creek, Umpqua River, Oregon. Range of means is given in parentheses.

Size group	Number of specimens in group	Head length	Branchial length	Trunk length	Tail length	Total length (mm)
<51 mm	79	11.70±0.54 (8.00-16.66)	16.85±0.39 (12.23-25.00)	54.69±0.50 (51.11-58.82)	16.95±0.98 (10.00-24.44)	29.09±2.40 (16-50)
51-85 mm	156	8.21±0.10 (6.34-10.34)	14.35±0.10 (12.90-15.78)	51.75±0.16 (48.61-57.19)	25.70±0.19 (22.41-28.57)	68.32±1.41 (51-85)
86-120 mm	66	7.38±0.12 (5.68-8.98)	13.18±0.18 (11.20-14.60)	51.33±0.19 (48.90-53.40)	28.08±0.23 (26.13-30.17)	97.70±2.34 (86-120)
> 120 mm	3	7.02±0.38 (6.76-7.40)	11.98±0.40 (11.60-12.30)	50.79±0.46 (50.37-51.20)	30.21±0.61 (29.80-30.82)	128.01±0.71 (121-133)

diameters are characteristic for the newly transformed fish; however, this juvenile character disappears with increasing of body size. Disc lengths are longer in feeding and spawning stages. Except for the length of the trunk region, all body parts show a positive allometry in spawning and postspawning stages, apparently a consequence of the spawning body shrinkage.

Sexual Variation (Table 4)

The females of L. t. tridentata have a longer trunk region than males in all postlarval stages. This is especially true at the spawning stage (mean 50.05 versus 44.52).

Geographical Variation

Size. In Oregon, the inland macrophthalmia L. t. tridentata are longer in total length than those of coastal streams and the Willamette River drainage (Figure 13). The variation is probably caused by a difference in life history, in that an additional year as ammocoetes is probably spent by inland forms. Fish from the inland localities are also larger in either prespawning or spawning stage (Figure 14). A difference in body size at maturity is useful in identifying biological races within a lamprey species (Berg, 1931).

Body Proportions. Tables 15, 16 and 17 summarize data on proportional measurements in various life history stages of Oregon

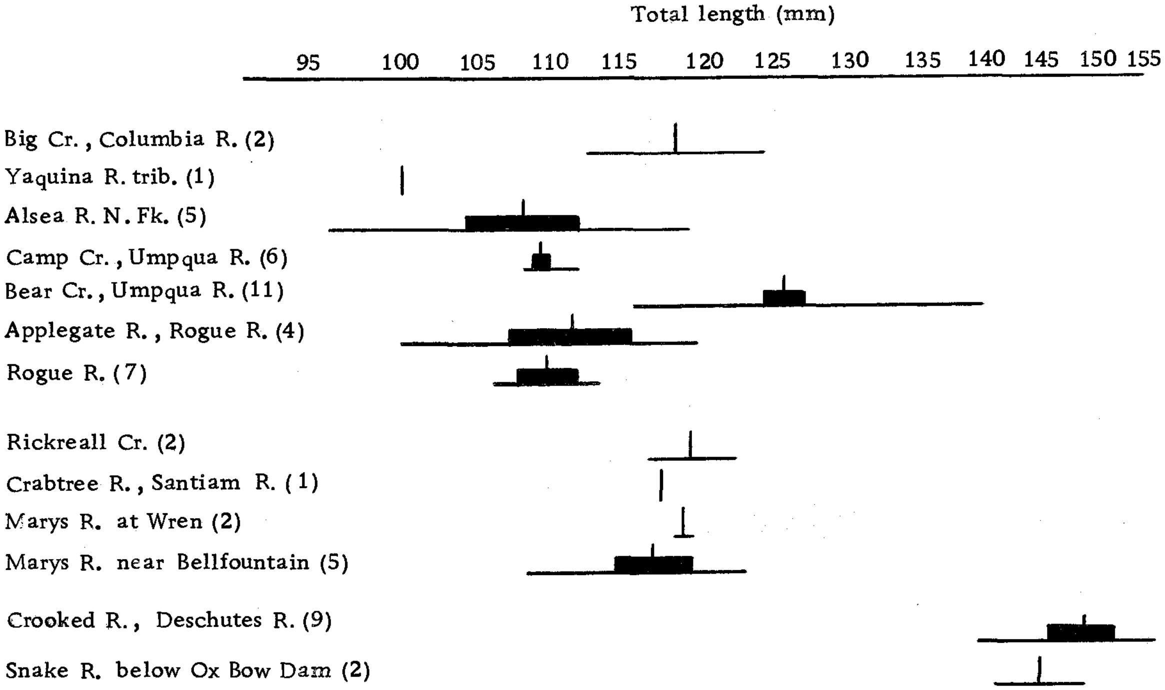

Figure 13. Variations in the total length in macrophthalmia stage of Lampetra t. tridentata from Oregon. See legend for Figure 10 for explanation of the diagram. The sample size is given in parentheses.

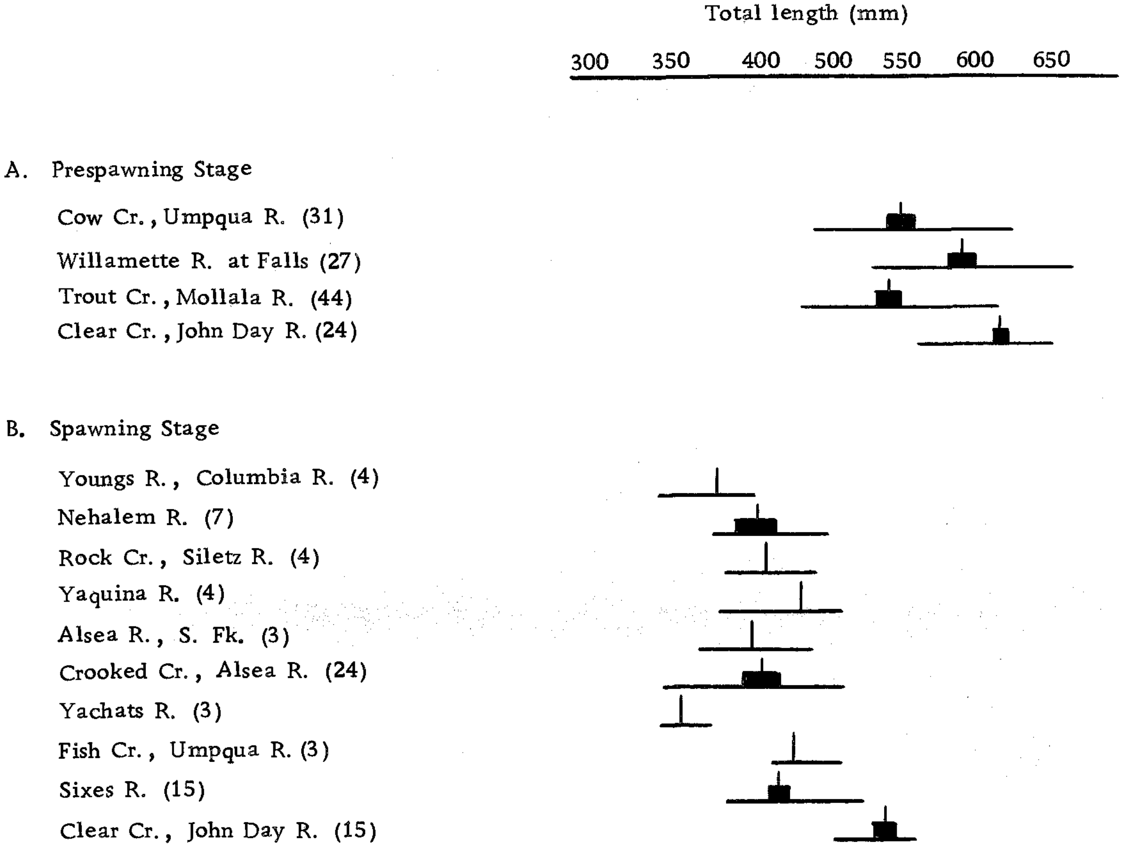

Figure 14. Variation in total length in prespawning and spawning stages of Lampetra t. tridentata from Oregon. See legend for Figure 10 for explanation of the diagram. The sample size is given in parentheses.

Table 15. Mean and its 95% confidence intervals of proportional measurements (percentages of total length) of larger ammocoetes of *Lampetra t. tridentata* from Oregon. Value in parentheses following localities is the number of subsamples. Other values in parentheses are subsample ranges.

Drainage	Total length (mm)	Head length	Branchial length	Trunk length	Tail length
Coastal watersheds (12)	105±3.46 (96.50-115.25)	8.30±0.98 (7.38-9.31)	12.60±0.03 (11.53-13.76)	50.65±0.36 (49.43-51.81)	28.40±0.42 (27.27-29.44)
Willamette River drainages (11)	103.44±3.10 (86.20-115.00)	8.21±0.28 (7.38-8.98)	12.67±0.03 (12.19-13.10)	51.11±0.33 (50.06-52.22)	27.99±0.32 (27.11-28.54)
Interior (Mid-Columbia and Snake Rivers) drainages (5)	102.33±5.81 (90.88-109.00)	7.82±0.33 (7.29-8.25)	12.07±0.35 (11.54-12.68)	51.14±0.95 (49.48-52.81)	28.99±0.77 (27.64-19.98)

Table 16. Mean and its 95% confidence intervals of proportional measurements (percentages of total length) of the macrophthalmia of Lampetra t. tridentata from Oregon. Value in parentheses following localities is the number of subsamples. Other values in parentheses are subsample ranges.

Drainage	Total length (mm)	Head length	Branchial length	Trunk length	Tail length	Eye diameter	Disc length	Second dorsal fin height
Coastal watersheds (4)	112.57±2.81 (101.00-126.36)	13.64±1.42 (12.30-15.84)	9.70±0.21 (9.38-9.90)	47.26±1.24 (45.54-48.98)	29.40±0.51 (28.71-30.01)	3.05±0.25 (2.78-3.46)	5.66±0.91 (4.65-6.93)	2.84±0.82 (2.32-3.34)
Willamette River drainages (10)	117.68±2.68 (109.00-123.00)	13.71±0.52 (12.50-15.17)	9.57±0.20 (9.17-10.16)	47.88±0.72 (46.20-49.91)	29.30±1.81 (28.07-31.10)	2.90±0.62 (2.50-3.41)	5.68±0.25 (5.00-6.14)	2.94±0.16 (2.61-3.40)
Interior (Mid-Columbia and Snake Rivers) drainages (2)	144.67 (143.00-146.33)	12.93 (12.22-13.63)	9.17 (9.09-9.25)	47.79 (47.54-48.04)	30.09 (29.73-30.45)	2.73 (2.67-2.79)	5.01 (4.78-5.24)	2.79 (2.60-2.97)

Table 17. Mean and range of proportional measurements (percentages of total length) of the prespawning and spawning *Lampetra t. tridentata* from Oregon. Value in parentheses following localities is the number of subsamples.

Drainage	Total length (mm)	Head length	Branchial length	Trunk length	Tail length	Eye diameter	Disc length	Second dorsal fin height
A. Prespawning stage								
Coastal watersheds (3)	514.44 (506.32-526.00)	11.90 (11.50-12.13)	10.90 (10.76-11.01)	48.37 (46.77-49.19)	28.83 (27.80-30.33)	1.68 (1.54-1.84)	4.99 (4.50-5.32)	4.10 (3.81-4.46)
Willamette River drainages (4)	447.10 (347.50-548.25)	12.25 (11.37-13.67)	10.95 (10.75-11.22)	47.94 (46.56-49.63)	28.85 (27.91-30.03)	1.85 (1.45-2.37)	6.00 (5.49-6.85)	4.45 (3.98-5.70)
Mid-Columbia River drainage (1)	573.42	11.44	10.83	47.55	30.15	1.47	5.65	4.17
B. Spawning stage								
Coastal watersheds (10)	403.88±5.70[1] (351.00-439.50)	13.38±0.43 (13.14-13.95)	11.52±0.06 (10.83-12.07)	47.54±4.00 (45.46-50.71)	27.62±0.74 (25.07-29.20)	2.12±0.11 (1.94-2.55)	6.18±0.17 (5.76-6.81)	5.99±0.55 (4.96-8.12)
Willamette River drainages (2)	465.00 (458.00-472.00)	13.43 (12.88-13.98)	11.62 (11.44-11.79)	44.76 (43.01-46.51)	30.16 (28.82-31.57)	2.16 (2.14-2.18)	6.46 (6.25-6.66)	5.17 (4.85-5.49)
Mid-Columbia River drainage (1)	496.00	13.08	11.78	45.76	29.36	1.78	6.55	6.07

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[1] Confidence intervals are at 95% level.

L. t. tridentata. Variation in these characters in each stage due to geographical difference is very slight. This is especially true of the length of the branchial region.

Discussion

Because of their relative constancy over the geographical range, the body proportions are useful in distinguishing *L. t. tridentata* from its congeners. The application of these characters however must be made carefully since sexual and ontogenetic changes in body proportions are considerable. Only samples composed of fish of similar life history stage are useful in morphometric comparisons.

Material Examined

A total of 1, 203 specimens from 16 to 754 mm in total length (A=ammocoetes, M=macrophthalmia, F=feeders, S=prespawners and/or spawners):

British Columbia

UBC: 53-269, 1 (280), S; 58-346, 35 (102-144), M.

Washington

OS: 4076, 1 (115), M; 4872, 1 (375), S; 4998, 5 (20-65) A; 5014, 2 (67-92), A; 5027, 3 (115-124), A; 5030, 1 (84), A.

Oregon

Coastal Drainages

OS: 4, 1 (456), S; 328, 1 (108), A; 777, 1 (130); A; 4016, 91 (70-130), A; 4017, 86 (47-70), A; 4018, 20 (65-133), A; 4019, 28 (54-90), A; 4020, 79 (16-55), A; 4021, 11 (38-45), A; 4023, 16 (44-115), A; 4026, 20 (30-148), A; 4028, 2 (88-105), A; 4032, 19 (40-106), A; 4034, 1 (103), A; 4039, 4 (97-115), A; 4040, 13 (52-108), A; 4041, 17 (80-139), A; 4046, 2 (63-71), A; 4050, 8 (57-112), A; 4051, 2 (83-105), A; 4052, 2 (98-109), A; 4053, 10 (53-127), A; 4054, 50 (23-137, A; 4060, 5 (96-120), M; 4062, 7 (107-121), M; 4083, 1 (101), M; 4087, 1 (126), M; 4095, 33 (448-581), S; 4097, 8 (392-528), S; 4099, 15 (390-475), S; 4100, 24 (359-469), S; 4160, 1 (88), A; 4862, 6 (109-112), M; 4863, 2 (39-60), A; 4871, 3 (372-448), S; 4873, 4 (418-461), S; 4874, 1 (511), S; 4876, 2 (495-557), S; 4878, 1 (351), S; 4880, 3 (332-365), S; 4883, 4 (387-464), S; 4885, 7 (376-457), S; 4886, 11 (117-139), M; 4887, 5 (103-124), A; 4888, 8 (30-143), A; 4892, 7 (92-132), A; 4893, 9 (90-134), A; 4896, 4 (up to 20), A; 4897, 4 (101-121), M; 4898, 50 (25-84), A; 4900, 3 (up to 20), A; 4907, 6 (67-107), A; 4910, 6 (109-121), A; 4916, 3 (94-100), A; SIO 72-46, 2 (404-409), S.

Willamette River Drainages

OS: 286, 1 (458), S; 4062, 22 (52-139), A; 4061, 1 (119), M; 4080, 1 (114), M; 4081, 1 (117), M; 4082, 1 (123), M; 4086, 5 (91-116), A; 4101, 24 (440-570), S; 4102, 20 (444-552), S; 4103, 14 (505-620), S; 4104, 14 (483-600), S; 4861, 1 (118), M; 4877, 1 (475), S; 4881, 1 (393), S; 4882, 1 (472), S; 4884, 1 (458), S; 4889, 4 (87-116), A; 4895, 1 (78), A; 4899, 21 (45-121), A; 4901, 18 (25-109), A; 4905, 35 (35-82), A; 4906, 1 (81), A; 4909, 3 (39-41), A; 4911, 3 (81-85), A; 4914, 56 (20-120), A; 4917, 4 (86-142), A.

The Columbia and Snake River Drainages

OS: 1996, 1 (96), A; 2289, 3 (53-69), A; 4038, 2 (109-131), A; 4085, 7 (79-123), A; 4094, 17 (484-614), S; 4096, 23 (459-593), S; 4124, 2 (140-146), M; 4125, 13 (55-140), A; 4151, 8 (139-155), M; 4155, 2 (113-125), M; 4159, 12 (73-133), A; 4164, 4 (43-108), A; 4879, 4 (346-418), S; 4915, 1 (103), A.

The Pacific and Coastal Waters (F)

OS: 13, 1 (143); 4093, 2 (172-200); 4125, 1 (131); 4143, 6 (149-254); 4144, 3 (151-191); 4145, 5 (182-218); 4860, 1 (754); 4864, 1 (246); 4865, 1 (255); 4866, 1 (266); 4867, 1 (247); 4868, 1 (248); 4869, 1 (240); 4870, 2 (221-248); OSUO: ?, 1 (256) (44° 43g'N, 125° 29.7' W, x 1-19-1966); 1693-4, 3 (107-138); 1729, 1 (286).

California

OS: 61, 1 (137), A; A; 4875, 2 (497-511), S; 4908, 4 (110-141), A; 4912, 1 (126), A; 4913, 1 (107), A; SIO: 72-47, 2 (414-438), S; CAS: ?, 1 (428) S (S. Fk Trinity R., V-5-1968).

Lampetra (Entosphenus) tridentata kawiaga n. subsp.
Klamath Parasitic Lamprey

Entosphenus tridentatus (Gairdner), Gilbert, 1898:2.

Entosphenus tridentatus ciliatus Ayres, (in part), Creaser and Hubbs, 1922:11.

Entosphenus tridentatus ciliatus - "Goose Lake race," Hubbs, 1925: 588-589.

Entosphenus tridentatus Hubbs and Miller, 1948:70.

Lampetra tridentata (Gairdner), (in part), Bond, 1961:4.

Lampetra tridentata - "precocious stock . . . . from the Klamath River system," Hubbs, 1971:139.

Lampetra (Entosphenus) tridentata (Gairdner), (in part), Bond, 1973:9.

Lampetra tridentata - "adfluvial. . . ," Bond and Kan, 1973:571.

Differential Diagnosis

Lampetra (Entosphenus) tridentata kawiaga is distinguished from the anadromous L. (E.) t. tridentata by having (1) a shorter maximum total length, rarely longer than 290 mm; (2) a lower number of trunk myomeres, ranging from 59 to 66, mostly 62 to 64; (3) different body proportions; (4) fewer velar tentacles in adult forms; and (5) different geographical distribution.

This subspecies is largely landlocked in Oregon and is known to occur only in the Klamath Basin and Goose Lake drainages. It is parasitic.

Holotype

OS 4925, a male at prespawning stage, 262 mm long, from Sprague River, Oregon, June 7, 1974. Collected by James K. Andreasen.

Paratypes

OS 2880, 21 specimens with total lengths ranging from 214 to 299 mm, Williamson River, Oregon, May 16, 1970. Collected by Carl E. Bond, William Johnson and Ting T. Kan.

Description and Comparisons

Size

Total lengths of 97 L. t. kawiaga prespawners were from 205 to 299 mm (sample mean 240. 50 mm). They were shorter than prespawning anadromous L. t. tridentata from either Umpqua River system (range 448 to 581 mm; mean 506.32 mm) or John Day River system (538 to 614 mm; 573.32 mm). Two macrophthalmia t. kawiaga (104.50 and 112 mm, respectively) are however similar in size to early t. tridentata transformers. This subspecies appears to begin its parasitic life while still in small streams before entering Klamath River or a lake, as five males, 115 to 125 mm long (OS 4088), with sharp teeth and distended gut, were collected from Spencer Creek, Klamath County, in early spring. Forty-five t. kawiaga with lengths ranging from 161 to 294 mm were taken from the lake.

Of the 54 larger L. t. kawiaga ammocoetes examined, total lengths vary from 52 to 165 mm with a mean of 86.56 mm. Since the shortest macrophthalmia is 104.50 mm, this subspecies appears not to undergo metamorphosis until reaching about 100 mm long, a situation which is similar to that of L. t. tridentata from Oregon and adjacent regions.

Body Proportions (Tables 18 and 19)

Difference in proportional measurements were found in nearly all categories at all life history stages (also see Bond and Kan, 1973) between L. t. kawiaga and L. t. tridentata. Upstream-migrating t. kawiaga has a larger eye and oral disc but a lower second dorsal fin. Special attention here is directed to the length of the branchial

Table 18. Mean of proportional measurements (percentages of total length) of *Lampetra t. tridentata* and *L. t. kawiaga*. Range is given in parentheses.

	Macrophthalmia Stage[1]		Feeding Stage (sexes combined)		
	L. t. tridentata	*L. t. kawiaga*	*L. t. tridentata*	*L. t. kawiaga*	
	Oregon and adjacent areas[2]	Spencer Cr., Klamath Co. (N=5)	Pacific Ocean[3]	U. Klamath L. (N=39)	Drews Res., Lake Co. (N=5)
Total length (mm)	119.31 (96-155)	121.00 (115-125)	209.65 (185-292)	224.15±11.24[4] (161-294)	202.80 (185-218)
Head length	13.50 (8.92-16.03)	14.55 (13.60-15.65)	13.79 (12.04-15.96)	13.44±0.18 (12.00-14.60)	13.04 (11.92-13.59)
Branchial length	9.55 (8.66-10.43)	9.42 (9.16-9.60)	10.29 (9.39-11.25)	9.67±0.13 (8.60-10.30)	9.56 (8.95-9.80)
Trunk length	47.40 (43.39-51.28)	44.13 (43.33-44.80)	48.12 (43.37-51.61)	46.29±0.34 (44.20-48.40)	47.53 (46.56-48.75)
Tail length	29.53 (28.07-32.28)	31.89 (30.43-33.33)	27.84 (24.58-29.58)	30.60±0.21 (29.20-31.90)	29.45 (28.15-30.88)
Eye diameter	2.91 (2.11-4.34)	2.09 (1.96-2.17)	2.48 (1.88-3.73)	1.66±0.06 (1.30-2.00)	1.91 (1.61-2.61)
Disc length	5.42 (2.56-6.61)	7.60 (7.20-8.00)	6.05 (5.04-6.77)	6.73±0.10 (6.10-7.40)	6.43 (5.50-7.02)
Second dorsal fin height	2.92 (2.27-4.07)	3.31 (3.20-3.47)	3.33 (2.48-5.76)	2.80±0.09 (2.20-3.20)	2.61 (2.42-2.75)

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[1] For male specimens only; [2] Data obtained from 19 samples; [3] Data obtained from 12 samples; [4] Confidence intervals at 95% level.

Table 19. Mean and its 95% confidence intervals of proportional measurements (percentage of total length) of prespawning *Lampreta t. tridentata* and *L. t. kawiaga.* Range is given in parentheses.

	Lampetra t. tridentata		*Lampetra t. kawiaga*		
	Clear Cr., John Day R. (N=24)	Cow Cr., Umpqua R. (N=31)	Williamson R., Oregon (N=40)	Thomas Cr., (Goose L.) (N=37)	Klamath R., California (N=10)
Total length (mm)	573.42±8.84 (512-614)	506.32±13.24 (458-581)	249.85±7.64 (205-299)	216.32±3.95 (195-253)	238.00±9.55 (223-271)
Head length	11.44±0.14 (10.74-12.28)	11.50±0.16 (10.60-12.50)	11.73±0.15 (10.70-13.20)	12.52±0.18 (10.74-13.28)	13.86±0.35 (12.97-14.35)
Branchial length	10.83±0.09 (10.34-11.22)	11.01±0.13 (10.20-11.60)	9.88±0.13 (9.30-10.50)	10.10±0.27 (9.40-10.77)	9.23±0.20 (8.71-9.87)
Trunk length	47.55±0.36 (46.03-49.01)	49.14±0.28 (47.70-51.40)	46.62±0.34 (44.30-48.80)	47.36±0.56 (44.83-50.43)	48.68±0.57 (47.47-50.41)
Tail length	30.15±0.43 (28.71-31.90)	28.35±0.24 (26.20-29.30)	31.80±0.29 (29.60-33.80)	30.07±0.45 (27.51-32.88)	28.24±0.40 (27.05-29.15)
Eye diameter	1.47±0.04 (1.32-1.80)	1.54±0.04 (1.30-1.80)	1.60±0.05 (1.30-1.90)	1.79±0.06 (1.44-2.13)	1.78±0.47 (1.64-2.02)
Disc length	5.65±0.08 (5.21-6.13)	5.32±0.08 (4.90-5.90)	6.20±0.10 (5.50-6.90)	6.31±0.18 (5.01-7.10)	7.70±0.47 (7.07-8.39)
Second dorsal fin height	4.17±0.15 (3.58-4.60)	4.46±0.07 (4.10-5.00)	3.28±0.05 (3.10-3.60)	3.84±0.11 (3.33-4.53)	3.04±0.06 (2.91-3.26)

region which, as noted previously, varies little geographically in *t. tridentata*, and is consistently longer in this subspecies as compared with that of *t. kawiaga*.

Trunk Myomeres (Table 20)

The number of trunk myomeres in *L. t. kawiaga* ranges from 59 to 66 (mean 63. 09), whereas in *L. t. tridentata* from Oregon and British Columbia, it ranges from 59 to 72 (mean 66. 59).

Velar Tentacles

The number of velar tentacles varies from six to eight (mean 6. 7) in adult *L. t. kawiaga* from Sprague River, Oregon, and from six to seven in those from Klamath River, California. For spawning *L. t. tridentata* from coastal rivers and the Columbia drainage, Oregon, it ranges from 10 to 18 with a mean of 14. 22. McPhail and Lindsey (1970) gave a range of 11 to 16 in *t. tridentata* from Canada and Alaska.

Dentition

General pattern of the dentition of *L. t. kawiaga* is similar to that of its ancestral form. The transverse lingual lamina has 18 to 21 cusps with the median one slightly enlarged. There are 24 to 28 cusps on each of the paired longitudinal lingual laminae. The form

Table 20. Number of trunk myomeres of *Lampetra tridentata kawiaga* from Oregon and northern California. Number in parenthesis is count for *L. t. tridentata* (see Table 4).

Development period	Number of specimens	Total length (mm)	Number of myomeres								Mean
			59	60	61	62	63	64	65	66	
Ammocoete	82	36-163	2	3	14	19	24	13	7	-	62.67 (66.48)
Macrophthalmia	7	105-125	2	1	-	2	2	-	-	-	61.14 (64.83)
Feeding	45	161-294	-	-	2	10	13	11	5	4	63.42 (67.12)
Prespawning	98	193-299	-	2	5	17	23	29	19	3	63.44 (67.82)
TOTAL	232	36-299	4	6	21	48	62	53	51	7	63.09 (66.59)[1]

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[1] Number is myomere count for specimens in all development periods, including spawning stage.

and number of anterials or posterials are of the t. tridentata type.

The pattern of lateral circumorals, supraoral and infraoral laminae is almost invariable in all L. t. tridentata examined. Differentiation from this pattern however is characteristically present in L. t. kawiaga (Table 22). The supraoral lamina is still typically tricuspid, but its median cusp is reduced in size with respect to the other two. Furthermore, two (out of 149) laminae (in OS 3935 and SU 35555, respectively) exhibit the true bicuspid condition. Occurrences of a hexacuspid or heptacuspid infraoral lamina frequent much more often in t. kawiaga (seven in 149) than in t. tridentata (four in 349). Deviation from the typical t. tridentata 2-3-3-2 lateral circumoral formula are also common in those teeth of t. kawiaga.

Coloration

Young ammocoetes of L. t. kawiaga are practically indistinguishable from those of L. t. tridentata. In larger ones, however, t. kawiaga lacks the small clear area above the first gill slit and occasionally has melanophores sparsely scattering on the ventral surface of the trunk region. These two forms are again difficult to separate in the macrophthalmia stages as both begin to develop the countershading coloration. The development of this coloration in the feeding stage appears to be less in t. kawiaga than in t. tridentata. As in t. tridentata, t. kawiaga becomes bluish gray when its upstream migration commences.

Teratology

An otherwise normal female (OS 2902-437) had its second dorsal fin branching onto the right body in the anal region. Apparently the tail now observed was a regenerate one (see Niazi, 1963 and 1964). Another female, a prespawner (OS 3935-684), was found to have only six left gill slits.

Geographical Distribution (Figure 15)

Gilbert (1898) first recorded *L. t. kawiaga* (his *Entosphenus tridentatus*) from Upper Klamath Lake. Snyder (1908b) reported its occurrences in Goose Lake and Sacramento River Basins. Later authors who mentioned this form from these two general regions include Hubbs (1925), Schultz and DeLacy (1935), and Bond (1961 and 1973). Other California records were given by Hubbs (1971) as Shasta River, Klamathon, and Copco Lake (see also Coots, 1955).

Following are additional distributional records of *L. t. kawiaga*:

Oregon: Williamson R., Sprague R., Sycan R. S. Fork, Spencer Cr., Agency L., and (?) Jack Cr., Klamath Co.; New Pine Creek, Cottonwood Cr., Drews Reservoir, and Thomas Cr., Lake Co.

California: Klamath R. at Klamathon, Beaver Cr., Tulelake, and Pit R., Siskiyou Co.

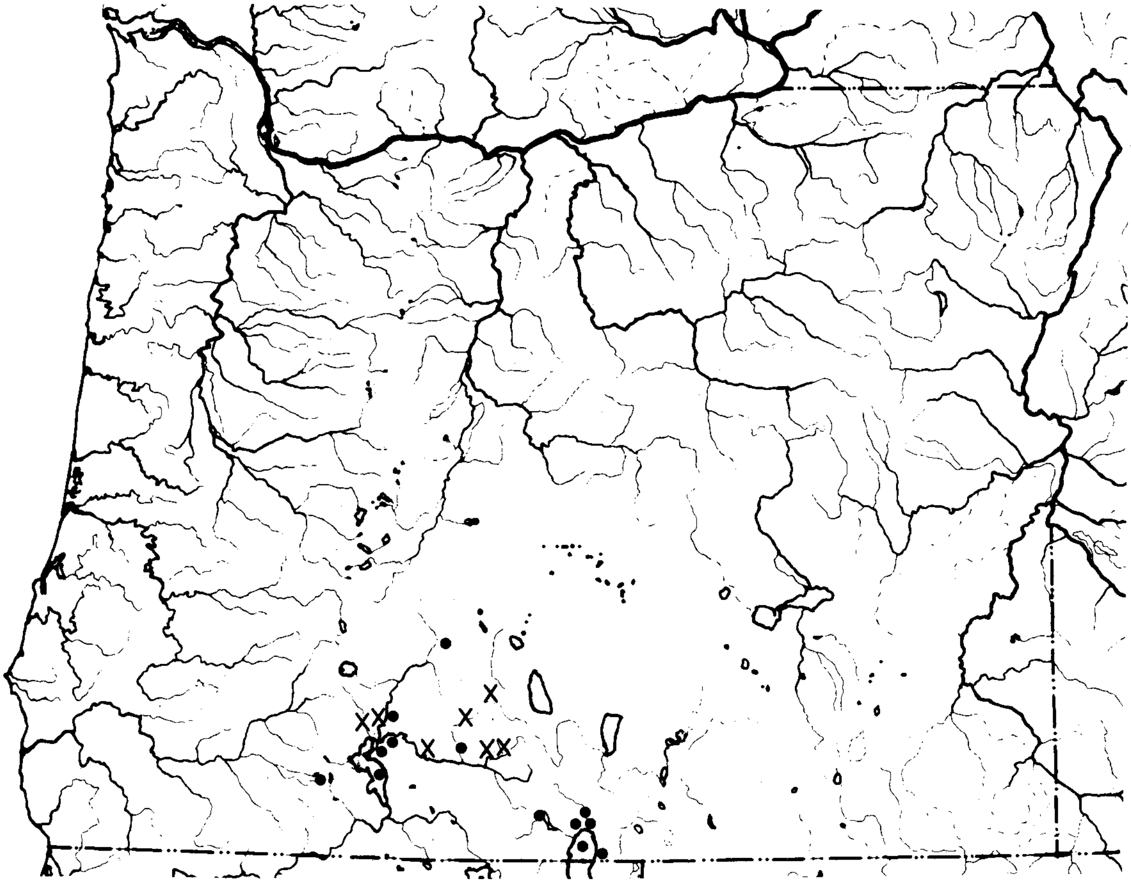

Figure 15. Distributional records of Lampetra tridentata kawiaga (solid circles) and of Lampetra lethophaga (crosses) in Oregon.

Upstream-migrating L. t. kawiaga were collected from Klamath Lake basin on May 16, 1970 and July 11, 1974, and from Thomas Creek of the Goose Lake system on May 7 to 11, 1971. Water temperature then ranged from 10° to 15° C.

Table 21 compares absolute and relative fecundities between L. t. tridentata and L. t. kawiaga. Corresponding to its smaller body size, the actual number of eggs produced by t. kawiaga is much fewer than that produced by t. tridentata. On the contrary, the relative fecundity of t. kawiaga is higher, correlating with a shorter migration distance for this largely landlocked form.

No modes were found to be conspicuous in the length- frequency distribution of 83 L. t. kawiaga ammocoetes from Oregon. This may be caused by small sample size, variability of growth rates in different river systems, and a decrease in growth with age. Since the shortest macrophthalmia t. kawiaga is comparable in size to the early t. tridentata transformers (about 100 mm long), the larval period of this subspecies is probably at least four years, a duration which is similar to that of its ancestral form. According to collection dates, t. kawiaga metamorphoses in the fall, and begins to feed and migrate downstream in the following spring.

Vincent (1969) regularly sampled Upper Klamath Lake in

Table 21. Egg numbers and estimates of relative fecundity of *Lampetra t. tridentata* and *L. t. kawiaga* from Oregon. Mean values are in parentheses. Confidence limits for means are at 95% level.

Species	Number of specimens	Body wt. (g)	Egg numbers	Relative fecundity no. egg/g body wt.
L. t. tridentata[1]	25	194.50-422.40 (292.71 ± 25.34)	98,300-238,000 (140,312 ± 12924.80)	339.21-726.26 (486.23 ± 37.45)
L. t. kawiaga				
Williamson R.	10	17.50-28.00 (21.35)	9,568-18,154 (13,718.90)	503.58-895.26 (644.84 ± 64.20)
Thomas Cr.	10	13.00-25.00 (16.50)	8,372-15,925 (11,972.11)	510.49-749.88 (659.45 ± 44.83)

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[1] Data obtained from Table 9.

certain months between 1964 and 1966. Only 39 *L. t. tawiaga* were caught during this period; however, they were informative in estimating the duration of this form's parasitic phase. Figure 16 shows well a monthly increase in mean total length. Fish belonging to at least two year classes appear to be included in the July samples. Smaller fish (shorter than 210 mm) were those that had entered the lake only recently, while the one (294 mm long) apparently had already spent more than one full year in the lake. As no upstream migrants were found to be longer than 299 mm, the latter fish would be conceived as ready to start its spawning run. This readiness was indicated by its gonadal condition which was in a far more advanced state than those of other smaller July-caught fish. Based on dates of collection and the information yielded by the total length data, it appears that the Klamath Basin *t. kawiaga*, 130 to 150 mm in length, enters the lake from the spring to mid-summer and spends 12 to 15 months there, growing to an average of 255 mm and then commencing its spawning migration in a time from late spring to later summer.

L. t. kawiaga is parasitic. Coots (1955) reported its predation upon *Catostomus rimiculus* in Copco Lake, California. *C. occidentalis* and *Gila bicolor* were apparently attacked by *t. kawiaga* when they were used as live bait in this study in an attempt to trap lampreys in Drews Reservoir, Lake County, Oregon. Lamprey scars were observed (C. E. Bond, personal communication) on such Upper

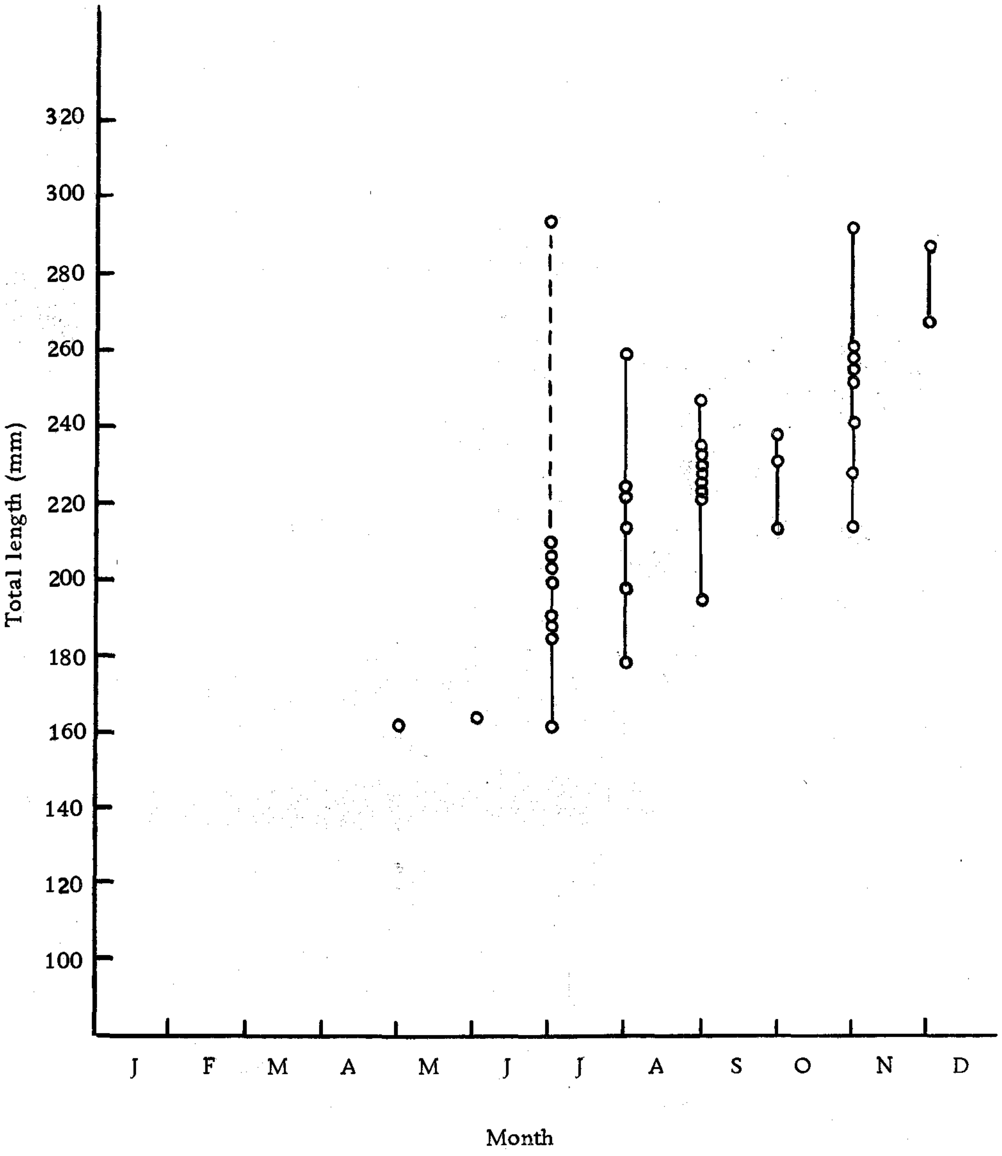

Figure 16. Months of capture and total lengths for 39 Lampetra tridentata kawiaga from Upper Klamath Lake.

Klamath Lake fish as Ictalurus nebulosus (OS 4918), G. bicolor, Catostomus sp., Salmo gairdneri, and Cottus klamathensis.

Variation

Deviation from the typical subgenus Entosphenus dentition was found in all L. t. kawiaga samples (Table 22). Seemingly, the dentition of Goose Lake populations is more variable than that of those from Klamath Basin. The lateral circumorals are more prone to regional variation than either supraoral or infraoral laminae, a situation which is similar to that of L. lethophaga, the nonparasitic derivative of L. tridentata (Hubbs, 1971).

As in other species of lampreys, L. t. kawiaga ammocoetes have on the average fewer trunk myomeres than the adults (Table 20). Geographically, the number of myomeres in this form varies in a mosaic manner since the overlap is rather broad. For the three streams the counts for prespawners follow: Williamson River (40 specimens), 62 to 66, mean and its 95% confidence intervals 63.58 ± 0.33; Klamath River (10), 60 to 64, 61.70 ± 0.74; Thomas Creek, Goose Lake (37), 62 to 66, 64.18 ± 0.29.

Body proportions, particularly length of the branchial region, vary little geographically in L. t. tridentata (Tables 15, 16 and 17). The same situation obtained in L. t. kawiaga from three river systems (Tables 18 and 19). On the other hand, the total length of Klamath

Table 22. Occurrences of non-typical *Entosphenus* dentitional features in *Lampetra tridentata kawiaga*. The sample size is in parentheses following the sample locality.

Locality	Occurrences			
	Supraoral lamina	Lateral circumorals	Infraoral lamina	Total
Klamath Basin, Oregon (95)	0	5	3	8
Klamath River, California (10)	1	0	2	3
Goose Lake Basin, Oregon (44)	1	6	2	9
TOTAL 149	2	11	7	20

Basin specimens is consistently longer than those from the Goose Lake drainage (mean 224.15 versus 202.80 mm for feeders; 249.85 versus 216.32 mm for May upstream migrants). Causes for this difference could be genetic, or could be possibly due to a better food supply in the extremely enriched Upper Klamath Lake (Phinney and Peek, 1961).

Derivation of Name

The subspecific name, kawiaga, means "small lamprey" in the Klamath Indian language (see Gatschet, 1890).

Material Examined

A total of 244 specimens from 35 to 299 mm in total length (A=ammocoetes, M=macrophthalmia, F=feeders, S=upstream migrants):

Oregon

OS 1922, 1 (63), A; 2872, 19 (205-293), S; 2877, 3 (185-206), F; 2880, 21 (214-299), S (Paratypes); 2883, 4 (64-101), A; 2884, 1 (164), F; 2885, 1 (178), F; 2886, 1(259), F; 2887, 1 (223), F; 2888, 1 (259), F; 2889, 3 (217-254), F; 2890, 1 (223), F; 2891, 2 (228-260), F; 2892, 2 (269-289), F; 2893, 1 (268), F; 2894, 1 (230), F; 2895, 1 (205), F; 2896, 1 (197), F; 2897, 1 (204), F; 2898, 1 (187), F; 2899, 1 (162), F; 2900, 1 (254), F; 2901, 2(231-238), F; 2902, 3 (234-247), F; 1903, 1 (186), F; 2904, 2 (161-189), F; 2905, 2 (195-231), F; 2906, 2 (175-294), F; 2907, 1 (293), F; 2908, 1 (210), F; 2909, 1 (189), F; 2910, 8 (55-98), A; 2911, 1 (213), F; 3935, 13 (197-253), S; 3936, 24 (195-234), S; 4027, 2 (160-163), A; 4030, 1 (156), A; 4036, 12 (81-120), A; 4047, 8 (74-150), A; 4088, 5 (115-125), M; 4089, 1 (218), F; 4109, 1 (205), F; 4158, 3 (121-125), A; 4920, 2 (42-44), A; 4921, 2 (56-75), A; 4922, 27 (35-103), A; 4923, 1 (132), A; 4924, 1 (108), A; 4925, 1 (262), S (Holotype); 4926, 18 (223-281), S; 4927, 1 (293), F; 4928, 2 (105-112), M.

California

CAS?, 1 (148), M (Klamath R., Siskiyou Co., X-15-1952); ?, 1 (193), S (Beaver Cr., Siskiyou Co., VI-6-1954); 25952, 14 (36-134), A; SU 35555, 10 (211-271), S.

Lampetra (Entosphenus) lethophaga Hubbs, 1971
Pit-Klamath Brook Lamprey

Entosphenus tridentatus, Rutter, 1908:120.

Lampetra planeri, Hubbs, 1925:594.

Lampetra sp., Bond, 1961:14.

Differential Diagnosis

The postlarval form of Lampetra (Entosphenus) lethophaga can be distinguished from that of L. (E.) tridentata by the following combination of characters: supraoral limina bicuspid, or tricuspid with the median cusp greatly reduced in size; infraoral limina with four to seven cusps; lateral circumorals in general arranged in a formula 1-2-2-1; posterials nine to 15; a smaller oral disc; smaller eyes; its nonparasitic habit and its much smaller size at maturity. The near-term lethophaga ammocoete is conspicuous in having the melanophores scattering on the ventral surface of the body and having body proportions differing from those of the other form.

Description and Comparisons

Size

In the 211 L. lethophaga near-term ammocoetes examined, total lengths vary from 56 to 205 mm with a mean of 121.65 mm. They are longer than L. t. tridentata (107.28 mm - sample mean) and than L. t. kawiaga (mean 86.56 mm).

Nine L. lethophaga transforming fish are from 128 to 173 mm long (mean 157.55 mm). Ten prespawners range from 143 to 195 mm in total length (mean 160.80 mm). These values indicate that prior to metamorphosis lethophaga grow to a longer size than its closely-related parasitic forms do. The spawning fish are shorter; 18 specimens from Crooked Creek, Klamath County, Oregon, range from 110 to 170 mm (mean 140.78 mm).

Body Proportions

L. lethophaga has a smaller head and a shorter branchial region than *L. t. tridentata* or *L. t. kawiaga* do (Table 23; and see Bond and Kan, 1973). This nonparasitic species is also smaller in regard to such characters as the eye diameter, the second dorsal fin height, and, as to be expected, the size of the oral disc.

Trunk Myomeres

The number of trunk myomeres is highly variable in *L. lethophaga* (Hubbs, 1971). For specimens from Klamath Basin, Oregon, the counts follow: ammocoetes (95 specimens), 62 to 69, mean and its 95% confidence intervals, 65.71 ± 0.16; transforming fishes (9), 61 to 65, 62.56 ± 1.04; prespawners (10), 63 to 66, 64.50 ± 0.60; spawners (18), 64 to 70, 66.33 ± 0.78. Value of these means appears to be higher than that of *L. t. kawiaga* at corresponding stages (62.67; 61.14; 63.42; and 63.44; respectively); however, the difference among them is considered as insignificant ($t=2.15$, $P < 0.2$).

Table 23. Mean and its 95% confidence intervals of proportional measurements (percentages of total length) of three forms of subgenus *Entosphenus*. Range is given in parentheses.

	Prespawners			Spawners	
	t. tridentata Cow Cr., Umpqua R. (N=31)	*t. kawiaga* Williamson R., Oregon (N=40)	*lethophaga* Klamath Basin, Oregon (N=10)	*t. tridentata* Sixes R. Oregon (N=15)	*lethophaga* Crooked Cr., Klamath Co, Ore (N=18)
Total length (mm)	506.32±13.24 (458-581)	249.85±7.64 (205-299)	160.80±9.57 (143-195)	424.07±13.02 (390-475)	140.78±5.64 (110-170)
Head length	11.50±0.16 (10.60-12.50)	11.73±0.15 (10.70-13.20)	9.38±1.25 (8.65-10.49)	13.44±0.19 (12.58-13.84)	12.17±0.49 (10.44-13.51)
Branchial length	11.01±0.13 (10.20-11.60)	9.88±0.13 (9.30-10.50)	9.27±0.97 (8.65-10.51)	11.98±0.19 (11.41-12.64)	10.27±0.30 (8.89-11.46)
Trunk length	49.14±0.28 (47.70-51.40)	46.62±0.34 (44.30-48.80)	49.54±1.48 (47.22-51.01)	45.46±0.94 (43.30-49.19)	46.50±1.27 (43.53-52.54)
Tail length	28.35±0.24 (26.20-29.30)	31.80±0.29 (29.60-33.80)	32.64±0.71 (29.37-33.52)	29.10±0.83 (25.64-31.14)	30.92±0.89 (27.07-33.53)
Eye diameter	1.54±0.04 (1.30-1.80)	1.60±0.05 (1.30-1.90)	1.23±0.06 (1.07-1.39)	2.00±0.07 (1.68-2.17)	1.55±0.13 (1.11-2.11)
Disc length	5.32±0.08 (4.90-5.90)	6.20±0.10 (5.50-6.90)	3.81±0.66 (3.47-4.38)	6.36±0.15 (6.08-6.92)	5.03±0.32 (3.62-6.18)
Second dorsal fin height	4.46±0.07 (4.10-5.00)	3.28±0.05 (3.10-3.60)	2.52±0.74 (2.01-3.47)	6.41±0.22 (5.70-7.02)	3.42±0.14 (2.90-3.79)

Velar Tentacles

Adult *L. lethophaga* have a range of six to seven velar tentacles which is nearly identical to that of *L. t. kawiaga* (six to eight) but is considerably less than that of *L. t. tridentata* (10 to 18).

Dentition

In correlation with the nonparasitic mode of life, degeneration in the dentition of *L. lethophaga* is apparent. The general pattern is of the *Entosphenus* type but the teeth are usually weak and occasionally reduced in number.

The tricuspid supraoral is invariable for *L. t. tridentata* and is typical for *L. t. kawiaga*. For *L. lethophaga* however the bicuspid condition is representative (Table 24). Reduction in the number of cusps on each of the four lateral circumorals from the typical *t. tridentata* 2-3-3-2 pattern occurs frequently in *lethophaga* (Table 25). The number of posterials is also reduced in *lethophaga* (nine to 15) in comparison with that of *t. kawiaga* or *t. tridentata* (15 to 21).

Coloration

Transforming and prespawning *L. lethophaga* specimens are dusky purplish over most of the body surface and pale yellowish on lower surfaces of head and trunk. Countershading is barely observed.

Table 24. Number of cusps on supraoral and infraoral laminae of Lampetra lethophaga from Klamath Basin drainages in Oregon.

Locality	Number of cusps per lamina								Mean
	1	2	3	4	5	6	7	8	
Supraoral lamina									
Williamson R. (5)[1]	-	3	2	-	-	-	-	-	2.40
Sprague R. (3)	-	2	1	-	-	-	-	-	2.33
Crooked Cr. (33)	-	28	4	1	-	-	-	-	2.18
Infraoral lamina									
Williamson R. (5)[1]	-	-	-	-	3	-	2	-	5.80
Sprague R. (3)	-	-	-	-	2	-	1	-	5.67
Crooked Cr. (33)	-	-	-	5	23	5	-	-	5.00

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[1] Number of specimens examined.

Table 25. Numbers of cusps on each lateral circumoral tooth, on each side, of *Lampetra lethophaga* from Klamath Basin drainages, Oregon.

Tooth number[1]	Locality	Cusps per tooth				Mean
		1	2	3	4	
I	Williamson R. (10)[2]	6	4	-	-	1.40
	Sprague R. (4)	4	-	-	-	1.00
	Crooked Cr. (56)	5	51	-	-	1.91
	TOTAL (70)	15	55	-	-	1.79
II	Williamson R. (10)	-	10	-	-	2.00
	Sprague R. (4)	-	3	1	-	2.25
	Crooked Cr. (56)	-	42	14	-	2.25
	TOTAL (70)	-	55	15	-	2.21
III	Williamson R. (10)	-	9	1	-	2.10
	Sprague R. (4)	-	2	2	-	2.50
	Crooked Cr. (56)	-	49	7	-	2.13
	TOTAL (70)	-	60	10	-	2.14
IV	Williamson R. (10)	5	5	-	-	1.50
	Sprague R. (4)	4	-	-	-	1.00
	Crooked Cr. (56)	36	20	-	-	1.36
	TOTAL (70)	45	25	-	-	1.36

[1] The teeth are numbered from the anteriormost on each side.

[2] Number of teeth examined.

Spawning and postspawning specimens are blackish purple on darker areas and on the basal parts of both dorsal fins; the region about the cloaca is paler. The caudal fin is darkened in the larger ammocoete stage and all stages thereafter. Dorsal fins are however waxy-pale in those stages.

Young L. lethophaga ammocoetes are almost uniformly darkened, barely lighter below. Near-term ammocoetes are similar in coloration to the transforming fish. Melanophores are extensively scattered along the mid-ventral line in the region between the seventh gill slit and the cloaca of larger ammocoetes.

Geographical Distribution (Figure 15)

Hubbs (1971) reported the occurrences of L. lethophaga in northern California (Pit River system) at North Fork of Pit R. at mouth of Joseph Cr., Modoc Co.; head of Fall R., lower Hat Cr., and three localities along Pit R., Shasta Co.; and in southern Oregon (Klamath River System) at Sprague R. North Fork, Sprague R. (T 36S, R13E), Sycan R. and Crooked Cr., Klamath Co. Additional Oregon localities are Williamson R. and Meryl Cr., Klamath Co.

Biology - Life History

In addition to morphology, L. lethophaga differs from L. t. tridentata in life history.

Hubbs (1971) indicated that *L. lethophaga*, as *L. t. tridentata*, metamorphoses in the fall. Two transforming *lethophaga*, one along with larger ammocoetes (OS 4935) and the other with prespawners (OS 4934), were however collected respectively in the spring and summer. Since sexually maturing ammocoetes were also taken from early May to late October (Hubbs, 1971) it is probable that *lethophaga* metamorphoses anytime during this long period.

One of the essential criteria adopted to delineate a brook lamprey form in a paired species complex as valid species has been the rapid maturation of its gonads, beginning shortly before or after the onset of metamorphosis (see Hardisty and Potter, 1971a). Neotenic ammocoetes, all females with eggs appearing to be fully developed and readily visible through the body wall, were observed in the North Italian brook lamprey, *L. zanandreai* (see Zanaadrea, 1957). In *L. lethophaga*, several prespawners (OS 4084, 4937; Hubbs, 1971), taken in August and October, apparently exhibited a neotenic condition as they possessed fully developed eggs but no normal prenuptial morphological characters (see Sexual Dimorphism for *L. t. tridentata*). Associated with neoteny and the rapid maturation at the time of metamorphosis, the post-metamorphic period of brook lampreys is greatly shortened. Length of this period for *lethophaga* is estimated to be five to ten months, as spawners have only been collected from March to May. In this short period, the animal undergoes a series of morphological changes similar to those occurring during the entire period of adult life in parasitic species including development of tooth sharpness and secondary sexual characters.

None of the transformed *L. lethophaga* specimens was found to contain food in the gut which was itself greatly atrophied. The weak teeth suggested that feeding was improbable. Indirect evidence for the abstention of adults from feeding also comes from a comparison of total lengths between larger ammocoetes and the transformed fish, in that many of the former were significantly longer than the latter. With the exception of *L. minima* (Bond and Kan, 1973), no parasitic species of lampreys has been known to have its spawners shorter than its ammocoetes.

Absolute fecundities (egg counts) for three *L. lethophaga* from Klamath Basin, Oregon, are 895, 900 and 1, 140. Relative fecundities are 308. 62, 333. 33 and 356. 25, with a mean of 332. 72. By comparison, these values are smaller, especially for egg counts, than those of *L. t. tridentata* or *L. t. kawiaga* (see Table 20). Differences in fecundities between parasitic and nonparasitic forms have also been observed in members of other paired species complexes (Vladykov, 1951; Hardisty, 1964; Hughes and Potter, 1969). Although these differences may be related to the disparity in adult body size usually occurring between the two forms, they nevertheless have a genetic basis since characteristic differences in oocyte numbers are already established in early stages among *L. fluviatilis*, *L. planeri*, and *P. marinus*, at a time marked species differences in body size do not exist (Hardisty, 1971). The fecundity therefore should be considered as an important criterion to recognize the brook and parasitic forms in a paired species complex as valid species.

Length-frequency distribution of 192 ammocoetes, mostly collected in late fall from Crooked Creek in Klamath Basin, suggests that the larval period of L. lethophaga is from five to six years. (Figure 17). Since transforming lethophaga are characteristically longer than the macrophthalmia L. t. tridentata (Table 26), this nonparasitic species appears to delay the metamorphosis for an additional year in comparison with its related parasitic species (see Figures 11 to 13), a phenomenon which is also seen in other paired species complexes (see Hardisty and Potter, 1971c). A delayed metamorphosis apparently enables the animal to engage in microphagous feeding longer and to develop to a certain degree of sexual maturity while still being ammocoetes. This phenomenon is associated with such events as adult nonfeeding, neoteny, the rapid maturation of gonads at the time of metamorphosis, and, to a certain extent, the reduction in fecundity.

Variation

Regional diversity of various meristic and morphometric characters occurs in L. lethophaga (Hubbs, 1971), leading to the hypothesis that the origin of this nonparasitic species may have been

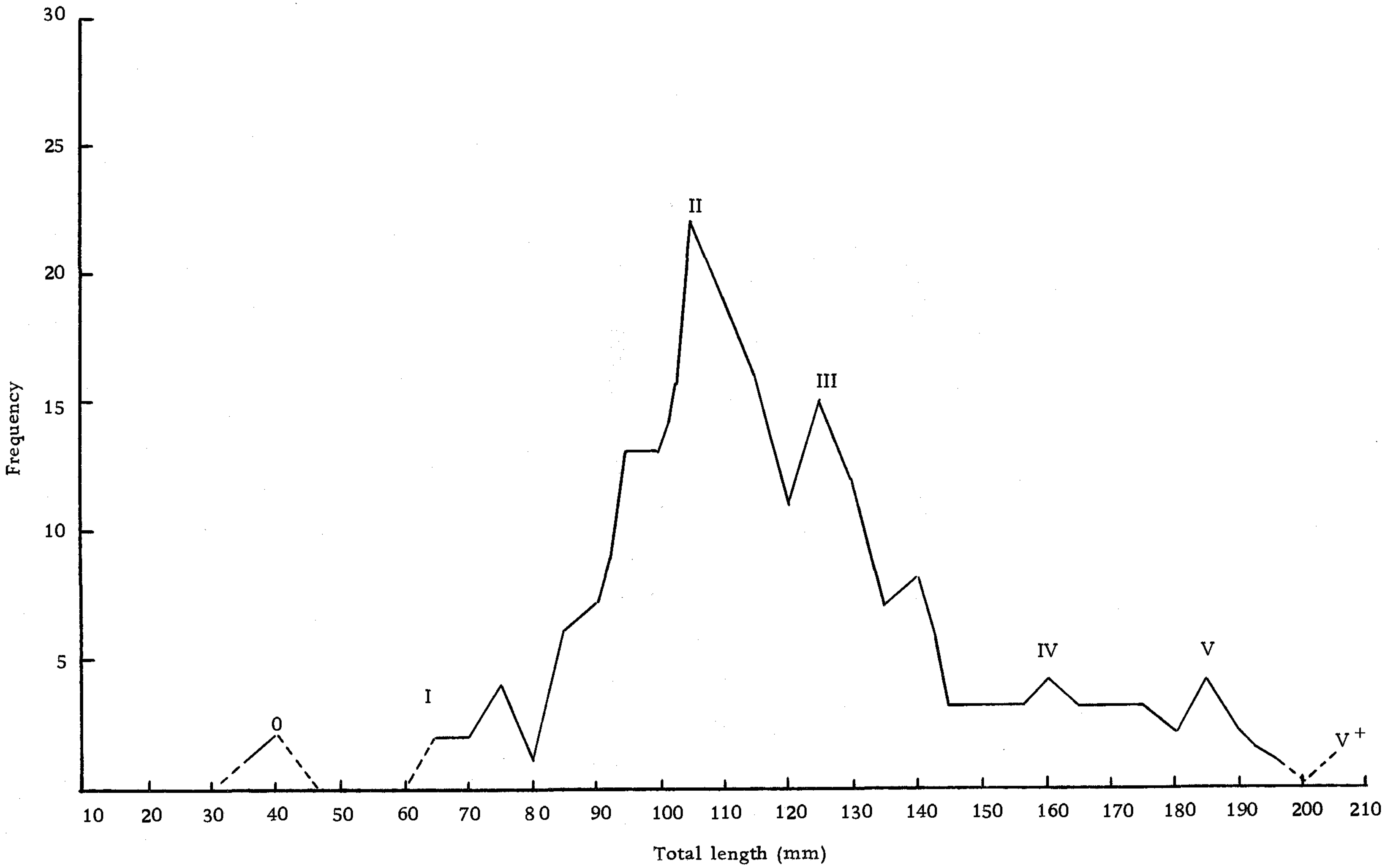

Figure 17. Length-frequency distribution for 192 *Lampetra lethophaga* ammocoetes from Crooked Creek, Oregon.

Table 26. Length-frequency distribution for the transforming _Lampetra lethophaga_ from Klamath Basin, Oregon, and Hat Creek, California, and for the macrophthalmial _L. tridentata tridentata_ from coastal Willamette River drainages, Oregon.

Total length (mm)	_L. t. tridentata_	_L. lethophaga_
A. Frequency		
91-100	1	-
101-110	12	-
111-120	22	-
121-130	16	1
131-140	1	-
141-150	-	2
151-160	-	2
161-170	-	-
171-180	-	4
B. Range	96-133	128-176
C. Mean	116.13	158.44

polyphyletic (see below Discussion of the subgenus Entosphenus; Hubbs and Trautman, 1937; Hubbs, 1971).

Material Examined

A total of 268 specimens from 37 to 205 mm (A=ammocoetes, T =transforming fish, P=prespawners, S=spawners):

Oregon

OS 20, 11 (118-141), S; 2855, 9 (110-157), S; 2856, 6 (134-150), S; 2857, 2 (144-170), S; 2858, 3 (136-160), S; 2859, 6 (89-188), A; 2860, 91 (37-205), A; 2861, 4 (97-151), A; 4022, 45 (79-191), A; 4024, 45 (159-187), P; 4029, 4 (97-151, A; 4084, 2 (143-144), P; 4091, 3 (159=176), P; 4932, 1 (147), S; 4933, 1 (139), S; 4934 3(128-169), T, P; 4935, 8 (121-189), T, P; 4936, 1 (195), P; 4937, 3 (60-149), A; 4938, 5 (90-121), A; 4940, 4 (93-113), A, T;

California

CAS 13391, 7 (144-173), T; 13392, 7 (48-126), A; 25968, 1 (63), A.

Lampetra (Entosphenus) sp.

A number of specimens represent the Entosphenus forms whose taxonomic position are at present difficult to identify. Significance of these forms in the evolution in the subgenus is considered to be great and will be discussed later.

Sevenmile Creek Form

A postspawning female (OS 4090), collected on July 30, 1970 from Sevenmile Creek, a tributary to Agency Lake, Klamath County, Oregon, has counts and proportional measurements as follows: supraoral lamina tricuspid with the median cusp greatly reduced in size; infraoral lamina pentacuspid; lateral circumorals 2-3-3-2; posterials 15 to 17 with two bicuspid on the left and one on the right; trunk myomeres 63; total length 164 mm; head length 14.45; branchial length 10.84; trunk length 44.51; tail length 30.49; eye diameter 2.38; disc length 7.40; and second dorsal fin height 5.00. For a postspawning lamprey, its teeth are regarded as sharp. Its body coloration is of the postnuptial _L. t. kawiaga_ type but with dorsal fins much less pigmented.

Goose Lake Drainage Forms

a. Three prespawning fish, taken in May and June, 1971 from two localities in Lake County, Oregon (OS 3934, Dog Cr., 1 male and 1 female; OS 3933, Bauer Cr., 1 female), were first regarded as referrable to _L. lethophaga._ They are similar to this species in the coloration, trunk myomere number, and conditions of gut and gonadal development for lamprey in the prespawning stage. Except for the exceptionally large eye, their body proportions are closer to those of lethophaga than to those of L. t. kawiaga (Table 27). Their dentition is however of the t. tridentata type. Egg counts for the two females (1,023 and 1,240, respectively) are higher than lethophaga's (895 to 1140, mean 978.33). Whether these specimens represent an undescribed form or merely a regional form of lethophaga (see Hubbs, 1971) awaits future study based on additional information.

b. Two collections made from Lake County, Oregon (OS 4048, Thomas Cr., 1 adult male and 3 ammocoetes; OS 4941, Cottonwood Cr., all adults - 2 males and 4 females), contain specimens representing a form similar to L. minima in total length but different from it in body proportions (Table 28). This form may again be a local L. lethophaga form or, as seen from the same table, an extremely dwarfed L. t. kawiaga type. Tables 17 and 18 show that t. kawiaga is markedly smaller in the Goose Lake region than in the Klamath Basin.

Lampetra (Entosphenus) minima Bond and Kan, 1973
Miller Lake Lamprey

Lampetra (Entosphenus) minima was a dwarfed parasitic derivative of L. t. tridentata found only in Miller Lake, Oregon. Fish control operations during the 1950's caused the apparent extinction of this species (John Rayner, personal communication).

Table 27. Mean of proportional measurements (percentage of total length) of the macrophthalmial *L. t. kawiaga*, and the prespawning *L. lethophaga* and *L.* sp. (OS 3933, 3934). Range is given in parentheses.

	L. t. kawiaga Klamath Basin (N=5)	*L. lethophaga* Klamath Basin (N=10)	*L.* sp. Goose Lake drainage (N=3)
Total length (mm)	121.00 (115-125)	160.80 (143-195)	128.33 (129-132)
Head length	14.55 (13.60-15.65)	9.38 (8.65-10.49)	10.90 (10.48-11.62)
Branchial length	9.42 (9.16-9.60)	9.27 (8.65-10.51)	10.12 (9.67-10.85)
Trunk length	44.13 (43.33-44.80)	49.54 (47.22-51.01)	48.32 (47.28-49.19)
Tail length	31.89 (30.43-33.33)	32.64 (29.37-33.52)	30.64 (30.23-31.06)
Eye diameter	2.09 (1.96-2.17)	1.23 (1.17-1.39)	1.83 (1.71-1.89)
Disc length	7.60 (7.20-8.00)	3.81 (3.47-4.38)	4.15 (3.87-4.04)
Second dorsal fin height	3.31 (3.20-3.47)	2.52 (2.01-3.47)	3.12 3.03-3.22)

Table 28. Mean of proportional measurements (percentage of total length) of the spawning L. sp. (OS 4048), L. lethophaga and L. minima, and the prespawning L. t. kawiaga. Range is given in parentheses.

	Lampetra sp. Goose Lake drainage (N=6)	L. lethophaga Klamath Basin (N=18)	L. minima Miller Lake (N=45)	L. t. kawiaga Goose Lake drainage (N=37)
Total length (mm)	103.41 (91-120)	140.78±5.64[2] (110-170)	84.62±2.61 (72-129)	216.32±3.95 (195-253)
Head length	12.55 (12.24-13.16)	12.17±0.49 (10.44-13.51)	14.78±0.18 (13.40-16.40)	12.52±0.18 (10.74-13.28)
Branchial length	10.33 (9.47-11.67)	10.27±0.30 (8.89-11.46)	9.21±0.16 (7.90-10.80)	10.10±0.27 (9.40-10.77)
Trunk length	47.87 (44.74-50.28)	46.50±1.27 (43.53-52.59)	45.22±0.65 (42.60-51.30)	47.36±0.56 (44.83-50.43)
Tail length	29.23 (27.62-31.58)	30.92±0.89 (27.07-33.53)	30.71±0.47 (25.90-32.90)	30.07±0.45 (27.51-32.88)
Eye diameter	2.18 (1.94-2.42)	1.55±0.13 (1.11-2.11)	2.44±0.06 (2.10-3.10)	1.79±0.06 (1.44-2.13)
Disc length	5.39 (5.10-5.70)	5.03±0.32 (3.62-6.08)	6.17±0.16 (5.00-7.40)	6.31±0.18 (5.61-7.10)
Second dorsal fin height	4.48 (4.17-4.95)	3.42±0.14 (2.90-3.79)	5.00±0.11 (4.40-6.10)	3.84±0.11 (3.33-4.53)

[1] Data from Bond and Kan (1973).

[2] Confidence intervals at 95% level.

Bond and Kan (1973) described *L. minima* in detail. The biology of this species can be studied only in retrospect, based on preserved specimens and notes and observations made at the time of collection.

Unlike all other parasitic species, *L. minima* was considerably smaller in total length in the spawning stage than in both feeding and late larval stages (Figure 18). This uniqueness suggested that the postlarval period of *minima* was shortened. Collection notes show that this species metamorphosed in the fall and spawned in the spring and summer. The feeding period was therefore less than a year. During this short period, *L. minima* fed fiercely when prey were available. Lamprey marks were observed on *Gila bicolor*, and the planted fingerlings *Salmo trutta* and *Salvelinus fontinalis*. Cannibalism (see Davis, 1967) also played a part in the nutrition of *minima* as scars and mined-out holes were found on specimens in collections composed entirely of *minima* at feeding stage (OS 2879 and 2881). Scavenging was seen on several occasions (C. E. Bond, personal communication).

Egg counts for 10 *L. minima* range from 503 to 727 with a mean of 604.40. Relative fecundities varied from 432.50 to 596.00 (mean 525.43±29.93). Compared with that of other lampreys as listed by Hardisty (1971), the absolute fecundity of *minima* is the lowest, apparently a consequence of its extreme smallness as adult. On the other hand, the relative fecundity of *minima* is among the highest, indicating that a larger portion of the lipid reserves accumulated during the parasitic period would be incorporated into gonadal products and that upstream migration would be greatly curtailed. Evidence shows that *minima* had eliminated completely or reduced considerably the migration; all ammocoetes and spawners were collected along the lakeshore although some spawners were observed from cold tributary streams (C. E. Bond, personal communication).

Length-frequency distribution of 102 ammocoetes collected mostly in the fall indicates the larval period of *L. minima* to be three years (Figure 18). By comparison, this duration is at least one year shorter than the larval period of *L. t. tridentata*.

Discussion of the Subgenus *Entosphenus*

Relationships

Entosphenus is one of the compact paired species complexes within the genus *Lampetra*. Relationships among members of this complex are inferred from characters including the dentition and the adult body size, as well as from life history types.

L. t. tridentata appears to be the most primitive *Entosphenus* species because it possesses such features, regarded as typical for the most primitive species within any paired species complex of

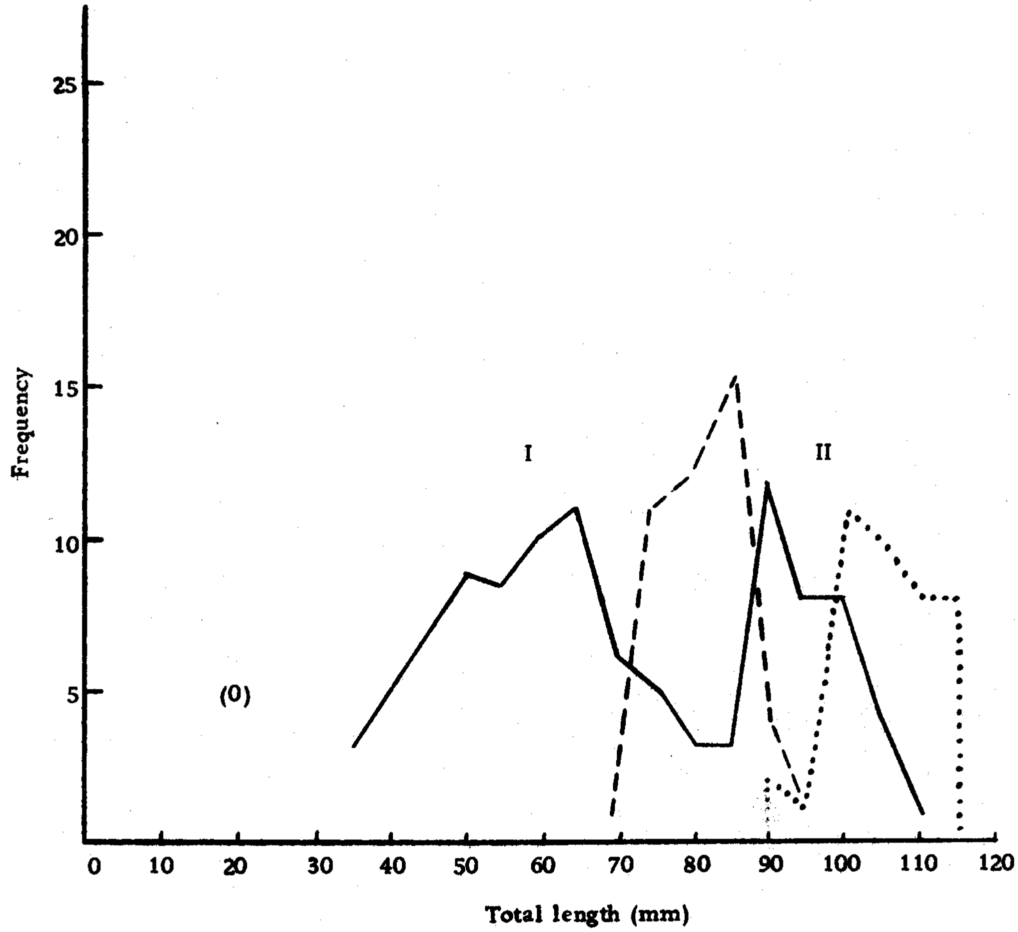

Figure 18. Length-frequency distributions for Lampetra minima ammocoetes (102 specimens, indicated by solid line), feeders (44, dotted line), and spawners (40, broken line) from Miller Lake, Oregon.

lampreys (Hubbs and Potter, 1971; Hardisty and Potter, 1971a), viz, wide geographical distribution, an enormous adult body size, a parasitic life history type, and relative constancy in morphology. From t. tridentata, two phylogenetic lineages seem to have developed.

L. minima itself represented an independent lineage. Its dentition was constant and differed very little from the ancestral L. t. tridentata type. However its adult body size was extremely reduced. All of the non-t. tridentata features exhibited by minima appeared to be concomitants of the dwarfism, including a large eye and the general reduction in meristic counts such as numbers of the trunk myomeres, the posterials, and the cusps on longitudinal lingual laminae (Bond and Kan, 1973). Fecundity was greatly lowered. Durations of both larval and feeding periods were shortened. Elimination or reduction of a migration habit should also be considered as a form of reduction.

L. t. kawiaga, L. lethophaga, and L. sp. form another subgroup in Entosphenus. All are sympatric in the Klamath Basin, and probably also in Goose Lake drainages. Although there is no doubt that they are derivatives of a L. t. tridentata type, their interrelationships are ambiguous. Based on the intermediacy exhibited by t. kawiaga between t. tridentata and lethophaga in certain dentitional features, the adult body size and the length of postlarval life, a direct t. tridentata to t. kawiaga to lethophaga relationship may be plausible (see Hubbs, 1971). However no intermediacy exists in the trunk myomere count and in some body proportions (Table 23).

The Sevenmile Creek specimen, L. sp. (OS 4090), may be a form that bears on the problem of possible hybridization between parasitic and nonparasitic members of a paired species complex. This specimen was first considered as referrable to L. lethophaga, then was thought to merely represent a dwarfed example of L. t. kawiaga. Neither alignment however appears to be proper. By comparison, this specimen is unique in several respects, as follows:

Size

This specimen (a postspawning female, 164 mm in total length) is definitely smaller than any prespawning female L. t. kawiaga from the Upper Klamath Lake region (214 to 299 mm); yet is considerably larger than the spawning L. lethophaga females (110 to 145 mm). Since parasitic lampreys shrink greatly in total length during and after spawning, for example, up to 25% in some L. t. tridentata females, it is still possible that this specimen is an exceptionally small t. kawiaga.

Dentition

The regular pattern for supraoral and infraoral laminae (cusps 3 and 5, respectively) and for the lateral circumorals on either side

(2-3-3-2) tends to align the Sevenmile Creek specimen to t. kawiaga. Moreover the teeth are sharper than those of L. lethophaga spawners. However, the number of posterials (15 to 17) is characteristically intermediate between that of lethophaga (9 to 15) and of t. kawiaga (15 to 21).

Body Proportions

The Sevenmile Creek specimen differs markedly in body proportions from those of either L. lethophaga or L. t. kawiaga (Table 29). Yet, interestingly, it resembles in these respects to a specimen (SIO 65-144), presumably representing a local Entosphenus form, Hubbs (1971) described from Willow Creek of the Klamath River system in California.

Coloration

The Sevenmile Creek specimen exhibits the typical L. lethophaga nuptial coloration. Its dorsal fins are however intermediate in the degree of pigmentation between that of L. t. kawiaga and lethophaga. Its general appearance, including a strongly turgid face, approximates that of the spawning lethophaga females.

Life History Type

Judging from tooth sharpness and size of the oral disc, this

Table 29. Proportional measurements of *Lampetra t. kawiaga*, *L. lethophaga* and *L.* sp. Range is given in parentheses.

	L. t. kawiaga Williamson R. 12 prespawning ♀s	*L. lethophaga* Crooked Cr., Or. 7 spawning ♀s	*L.* sp. (OS 4090) Sevenmile Cr., Or. 1 postspawning ♀	*L.* sp. (SIO 65-144)[1] Willow Cr., Calif. 1 postspawning ♂
Total length (mm)	257.50±15.19[2] (214-299)	132.43±8.00 (110-145)	164	176
Head length	11.73±0.22 (11.10-12.40)	11.03±0.38 (10.35-11.82)	14.45	--
Branchial length	10.00±0.22 (9.60-10.20)	9.71±0.49 (8.89-10.50)	10.84	10.80
Trunk length	47.06±0.59 (45.30-48.50)	49.50±1.22 (47.59-52.59)	44.51	--
Tail length	31.33±0,60 (29.60-32.70)	29.30±1.38 (27.07-32.08)	30.49	34.10
Eye diameter	1.51±0.84 (1.30-1.70)	1.46±0.15 (1.11-1.82)	2.38	2.40
Disc length	5.98±0.17 (5.70-6.80)	4.33±0.40 (3.62-5.19)	7.40	6.40
Second dorsal fin height	3.30±0.13 (3.10-3.60)	3.38±0.31 (2.73-3.76)	5.00	--

[1] Data taken from Hubbs (1971).

[2] Mean and its 95% level confidence intervals.

unique specimen would be a form with the parasitic type of life history.

Therefore, it does not seem to be justified to align the Sevenmile Creek specimen with either *L. lethophaga* or with *L. t. kawiaga*. Based on such extreme features as several body proportion characters, this specimen seems to be a representative of a distinct local *Entosphenus* form. Or, as demonstrated by its general intermediacy in such features as the dorsal fin pigmentation, the number of posterials, and, possibly, the adult body size or duration of the postlarval life, it should be regarded as an interspecific hybrid (see among others Hubbs, 1955; Simon and Noble, 1968; and Smith, 1973 on hybridization in terms of character intermediacy in fishes). The latter would be disagreeable to the opinion held by Hardisty and Potter (1971a) and others that genes do not effectively interflow between members of parasitic/nonparasitic pairs, mainly because the size difference, always seen in members of a pair, acts as a barrier to hybridization. Nevertheless, in spite of the apparent difference in the chromosome numbers among them (see Potter and Robinson, 1971), hybridization between members of a pair has been artificially accomplished (Weissenberg, 1925; Cotronei, 1942; Piavis, Howell and Smith, 1970; Piavis, 1971), and a few hybrid ammocoetes have survived to at least the second year (Haridsty and Potter, 1971a).

Evolution

Distribution and speciation of the *Entosphenus* forms appear to have been strongly influenced by the Pleistocene glaciation and by massive geological activities.

Around the periphery of the North Pacific, *L. t. tridentata* ranges southward from Bering Island on the west and from Bering Sea and Unalaska on the east (McPhail and Lindsey, 1970; Hubbs, 1971). The sporadic Asian records, from as far south as southern Japan (approximately 35° North Latitude), apparently represent the species' recent geographical extension. On the American side, *L. t. tridentata* has been recorded from southern California in fresh water and from Baja California at sea (approximately 30° N). Its occurrences in regions north of the Columbia River may again be fairly recent. McPhail and Lindsey (1970) included *t. tridentata* as one of the many northwestern North America freshwater fishes that evidently retreated southward to a "Pacific refuge," in the Pacific watersheds south of the Cordilleran ice sheet, during the Pleistocene glaciation. The northward postglacial redistribution of the species appears to have been accomplished mainly through rapid dispersal along the coast.

In Oregon, *L. t. tridentata* is widely spread in coastal streams and in the Willamette River tributaries. However it is not as generally distributed in streams west of the Cascade Range. Some local forms that formerly occurred in the area of the Cascade Range or in areas immediately to the west of this may have become extinct through the disturbance of habitats and the blockage of migration routes by orogenisis of the High Cascades during the Pliocene and the Pleistocene (Baldwin, 1964). Quaternary uplifts of the Coast Range could have affected local forms similarly. Although continental glaciation did not appear to extend south of the Columbia River, montane glaciation probably did affect the east-side drainage systems of the Willamette Valley (see Flint, 1957). Former Willamette drainage forms adapted to certain upstream spawning areas also would likely have become extinct. On the other hand, the Oregon interior forms were much less affected by the Pleistocene glaciation because the Columbia River basin was not then glaciated and the River itself was still capable of serving as a migration route. Therefore the variation in body size and in the number of trunk myomeres between coastal and interior forms of Oregon t. tridentata may be fundamentally caused by their different evolutionary histories.

In spite of the adversities brought on by massive geological activities in the Pleistocene in northern California and southern Oregon (see Reed, 1933; Wahrhaftig and Birman, 1965), a number of inland L. t. tridentata populations apparently survived there. They then gave rise to L. t. kawiaga, and later L. lethophaga and

L. minima. Reasons for their survival must have been due to the presence of several large lakes in the region that were used alternatively as feeding grounds since their anadromous migrations became impossible with the blockages formed by the Cascade and the Klamath mountain-buildings. Some of these lakes are now recognized as Upper and Lower Klamath Lakes, Tule (Rhett) Lake of the Klamath System, and Goose Lake of the Sacramento System. These adfluvial populations have been isolated from their anadromous relatives, and have evolved allopatrically into a new form, namely *t. kawiaga,* with different characters including size, body proportions, fecundity, and a faster maturation rate. Natural barriers to adfluvial migration may have been involved in the speciation of the nonparasitic *lethophaga,* which has eliminated long migrations and does not feed in the adult stage.

As indicated by the geographical variation evident in several characters in both *L. t. kawiaga* and *L. lethophaga,* it appears that parallel evolution has been operating within these forms. Populations of both species are probably geographically isolated from one another in different drainage systems. However the observed variation in these populations does not seem to reach the degree to warrant them specific or subspecific distinction. Furthermore, based on similarity in such as life history, breeding season, and especially, adult body size, these populations should be considered as capable of interbreeding once in contact. For *t. kawiaga,* each lake is seemingly colonized by only one breeding population, as evidenced by the body size data of the Upper Klamath fish. For *lethophaga,* as well as for other nonparasitic lampreys, a polyphyletic origin has been indicated (Hubbs and Trautman, 1937; Hubbs, 1971).

The evolution of _L. minima_ apparently took place in the Miller Lake drainage following disruption of its connection with the remainder of the Klamath Lake drainage. The great Mount Mazama exploded about 6,600 years ago (Powers and Wilcox, 1964) with thick ashfall covering the surrounding area including the present Miller Lake district (Williams, 1942). The forerunner of _minima_ survived the ashfall, either in Miller Lake itself or in the outlet stream, but it seems probable that there were severe and lasting effects upon spawning sites and on food supply, so that the numbers surviving must have been small. Acquisition of the shoreline spawning habit may have been due to limited suitable space in the small tributaries and to their cold temperatures. The only other fish species thought to have survived in the system was the tui chub, _Gila bicolor_, which has heavy scales and, except in very young stages, is not easy prey for a dwarf lamprey with adults less than 130 mm long. In response to the supposed food paucity, _L. minima_ had evidently become adaptive through two seemingly contrasting processes: to feed fiercely on whatever was available and to mature and spawn even on a starvation diet. According to its characteristic adult body size and its observed feeding habits such as predation, cannibalism, and scavenging, these two processes were apparently operating. As a result, _L. minima_ remained extremely dwarfed even though they were later allowed to feed heavily following introduction of other species. The impact of predation upon planted trout fingerlings led to the destruction of the species through chemical control measurements during the 1950's (John Rayner, personal communication).

Speciation Rate

Zeuner (1958) has suggested that the maximum rate of speciation in animals in nature is about 500,000 years. Yet, for fishes under special conditions, the speciation rate is much faster. Hubbs (1940) stated in regard to the western United States freshwater fishes that "in several isolated waters, evolution has proceeded far enough to produce new subspecies within what appears to be a few hundred years, at most a few thousand." Greenwood (1965) indicated a time-span of 4,000 years to be sufficient for the speciation of cichlid species in the African lake Nobugabo.

The speciation rate of _L. minima_ is estimated to be less than 6,600 years. Factors that played an important role in bringing about this rapid rate include: (1) geographical isolation, (2) ecological conditions, and (3) genetic processes.

Roles of geographical isolation in the process of gradual speciation have long been a subject of discussion. Mayr (1963) has accumulated a great deal of evidence indicating that the process of speciation invariably requires geographical isolation, the allopatric model of speciation. The hypothesis of sympatric speciation has now been largely discredited (see Mayr, 1969 and 1970). Recently, a stasipatric model of speciation was proposed (White, 1968). However it seems that there is no fundamental distinction between the stasipatric and sympatric models. L. minima appeared to become geographically isolated from probably a L. t. kawiaga type ancestry following the impact inflicted by the Mazama volcanism. Duration of the isolation, some 6,600 years, would be sufficient to allow for the differentiation of a form to a full species level (see Hubbs, 1949 and Miller, 1961). During this period L. minima has accumulated enough distinctive characters of its own including dwarfism, feeding habits, and partial elimination of adfluvial migration.

No doubt the physicochemical makeup of the water in Miller Lake was greatly altered through addition of a large amount of hot volcanic ash generated by the Mazama eruption. Most native fishes, including the lamprey, probably died out because of the sudden drastic environmental change. Adaptations to the altered ecological conditions that the relatively few surviving fishes had to make are thought to play an important part in speciation.

After a sudden drastic environmental change has taken a heavy toll from a species, the species as a whole is reduced to a very small population. As the genotype of a majority had already been proven unsuccessful to meet the changed environment, the remnant of the now decimated species is faced with only two alternatives: to either perish or emerge as a new species by becoming essentially homozygous with a new set of adaptive traits. The latter can be reached through intense inbreeding (Mayr, 1963). Population size of the incipient *L. minima* in Miller Lake was apparently very small, judging from the impact caused by the Mazama ashfall. By comparison with those of *L. t. kawiaga*, the dentition, number of trunk myomeres, and adult body size of *minima* were remarkably constant, suggesting that inbreeding in a small population had occurred. On the other hand, the generation time, the length of time needed by individuals of a species to attain reproductive capability, of *minima* was also shorter. A short generation time appears to favor a rapid speciation rate in isolated freshwater fishes (Miller, 1961).

Lampetra (*Lampetra*) *ayresii* (Günther, 1870)
Western River Lamprey

Petromyzon plumbeus, Ayres, 1855:28.

Lampetra plumbea, Gill, 1862:331

Ammocoetes cibarius, Günther, 1870:505.

Petromyzon ayresii, Günther, 1870:505.

Ammocoetes plumbeus, Jordan, 1878:413.

Lampetra cibaria, Jordan and Evermann, 1896a:13.

Lampetra fluviatilis, Regan, 1911:202-203.

Lampetra ayresii, Jordan, Evermann and Clark, 1930:10.

Lampetra reissneri, Berg, 1931:103-104.

Petromyzon ayresi, Berg, 1931:112.

Lampetra ayresi, Evermann and Clark, 1931:19.

This species was for a long time confused with the morphologically similar European river lamprey, *Lampetra fluviatilis* (Linnaeus). The distinction of *L. ayresii* by Vladykov and Follett (1958) has been one of the important contributions in lamprey systematics. They give a full description and synonymy.

Very little is known of the life history of *L. ayresii*. According to collection dates, this species spawns in the spring. Egg number in one specimen from Simpson Cr., Lincoln Co. (OS 537) is about 174, 000, a number being within the range estimated for those of the Sacramento River specimens (11, 398 to 37, 288; see Vladykov and Follett, 1958). Duration of the larval period is unknown. Metamorphosis apparently takes place over a long period as newly transformed specimens have been taken from the Sacramento River in December (117 to 155 mm) and from the Necanicum River in April (104 to 110 mm). *L. ayresii* is parasitic. Hosts include the smelt, *Hypomesus* sp. (?) (OS 4146), the herring, *Clupea harengus pallasi* (?) (OS 4092), the kokanee, *Oncorhynchus nerka* (Vladykov and Follett, 1958), and the coho salmon, *O. kisutch*, (Withler, 1955). *L. ayresii* is preyed upon by a number of fishes including the lingcod, *Ophiodon elongatus* (Vladykov and Follett, 1958) and the striped bass, *Morone saxatilis* (Thomas, 1967), and possibly by birds (Scott and Crossman, 1973).

It seems probable that *L. ayresii* is ecologically segregated from *L. t. tridentata* in the sea. Countershading is strongly developed in *ayresii*, suggesting that this species is adapted to surface layers. Moreover, all specimens of feeding stage examined in this study were taken from either the nearshore (OS 4092, 4146) or from estuarine localities (OS 17, 537, 4630).

Occurrences of *L. ayresii* are rare and are restricted to the Pacific coast from the Sacramento River, California, to Tee Harbor near Juneau, Alaska (Scott and Crossman, 1973). In Oregon, this species has been reported from Yaquina Bay and the Columbia River near Bonneville Dam (Vladykov and Follett, 1958). Additional records (see Figure 19) follow (A=ammocoetes, M=macrophthalmia, F=feeders, S=spawners): Big Cr., Clatsop Co., A, OS 4992; Simpson Cr., Lincoln Co., A, OS 4994; Necanicum R., Clatsop Co., M, OS 4953; Columbia R., Clatsop Co., F, OS 343; Pacific O., off Tillamook, Tillamook Co., F, OS 4092; 1446; Yaquina Bay, Lincoln Co., F, OS 4630; Yaquina R., Lincoln Co., S, OS 537; Simpson Cr., Lincoln Co., S, OS 4071.

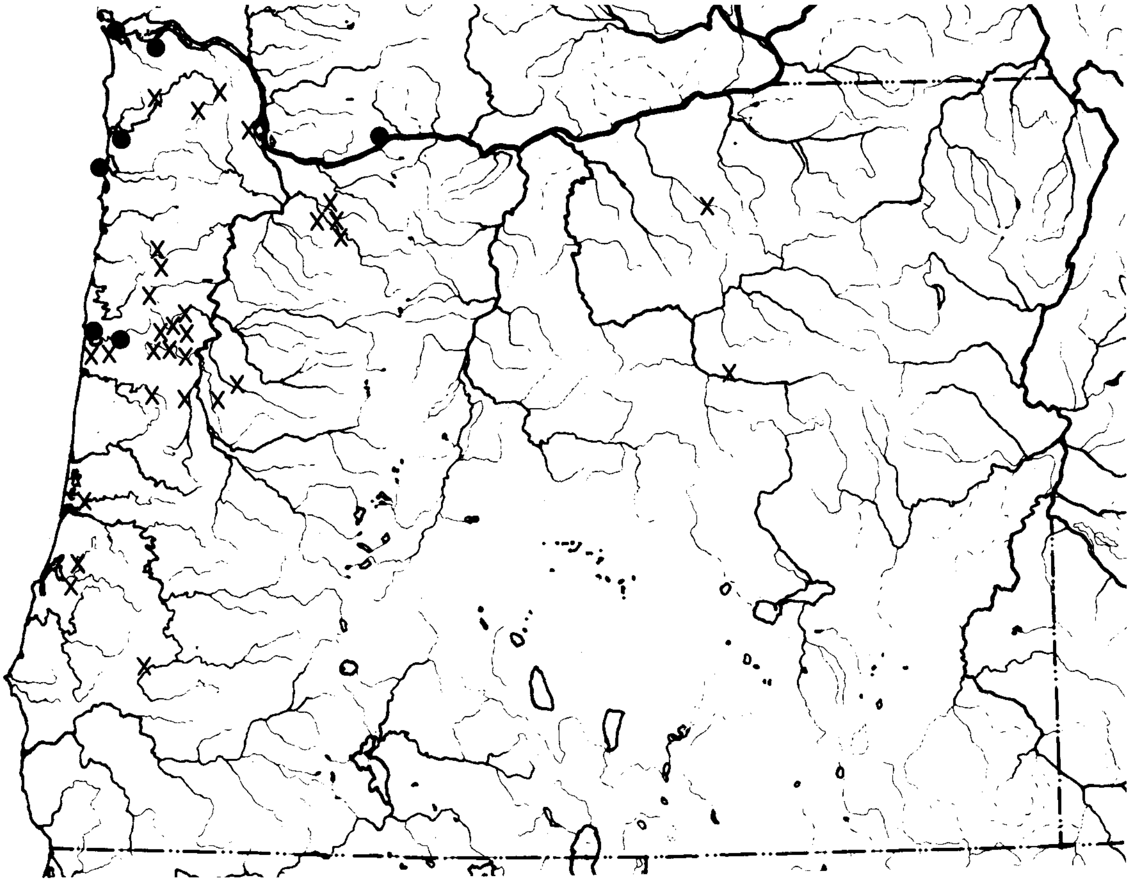

Figure 19. Distributional records of Lampetra ayresii (solid circles) and of Lampetra richardsoni (crosses) in Oregon.

Lampetra (*Lampetra*) *richardsoni* Vladykov & Follett, 1965
Western Brook Lamprey

Petromyzon branchialis, Günther, 1870:505.

Lampetra planeri Bloch, Creaser and Hubbs, 1922:13.

Lampetra pacifica, Vladykov, 1973:205.

Lampetra (*Lampetra*) *richardsoni* was described in detail by Vladykov and Follett (1965) and by Vladykov (1973).

According to collection notes, *L. richardsoni* spawns in the spring and early summer in Oregon. Nests are built in coarse gravel and sand at the head of a riffle in quiet water in a shaded stretch of small creeks. Usually only a single individual, either male or female, performs the nest building at one time. Nests are dug mainly by vibrating the body or tail; stones are carried in the oral disc away from the nest. At spawning, the male engages in a brief overturing "sliding-feeling" courtship (Pletcher, 1963) during which it slides with oral disc up to the body and gradually to the head of the female. The male then coils around the female so that their anal regions approximate and eventually the spawning occurs (see McIntyre, 1969). Egg numbers for nine specimens from the Willamette River system range from 2,500 to 5,500 with a mean of about 3,360. The incubation time is probably ten days in water with a temperature of about 12° C (McIntyre, 1969). Length of the larval period has been estimated to span three to five years for Washington forms (Schultz, 1930) and at least six years for British Columbia forms (Pletcher, 1963). Metamorphosis apparently takes place in the fall; newly metamorphosed specimens have been taken in September from Salmon River, Washington (OS 4075) and in October from Marys River (OS 4965), and Pass Creek in Douglas County (OS 4959), Oregon. The transformed overwinter without feeding, start to mature in the spring, spawn, and die.

L. richardsoni is limited to western North America; in streams of the Pacific coast from southern California to British Columbia and possibly Alaska (Vladykov and Follett, 1965; Hubbs and Potter, 1971; Vladykov, 1973). Within the range, a complex of races probably exists (see Discussion of the subgenus Lampetra).

In Oregon, L. richardsoni has been reported from Crystal Springs Creek, Multnomah County, Clackamas River near Estacada, Clackamas County, and Willamette River near Bellfountain, Benton County (Vladykov, 1973), and from a tributary to Umpqua River near Reedsport, Lane County (Vladykov and Follett, 1965). Additional records (see Figure 19) are: Necanicum R., Clatsop Co.; Nehalem R., Clatskanie R., Lost Cr., Columbia Co.; Scoggin Cr., Washington Co.; Clackamas R., Tickle Cr., Deep Cr., Clackamas Co.; Mill Cr., S. Yamhill R. trib., Agency Cr., Yamhill Co.; Rhea Cr., Morrow Co.; Rogue R., Polk Co.; Rock Cr., Yaquina Bay trib., Big Elk Cr., Flynn Cr., Simpson Cr., Lincoln Co.;

Soap Cr., Rock Cr., Greasey Cr., Oak Cr., Berry Cr., Alsea R. S. Fk., Marys R., Oliver Cr., Squaw Cr., Benton Co.; Strawberry Cr., Grant Co.; Long Tom R., Swamp Cr., Haynes Cr., Noti Cr., Taylor Cr., Wolf Cr., Munsel Cr., Maple Cr., Bear Cr., Lane Co.; Pass Cr., Douglas Co.; Coos Bay trib., Tenmile Cr., Coos Co.

Discussion of the Subgenus *Lampetra* in North America

The recognition of *L. ayresii* and *L. richardsoni* as paired species is based mainly on the similarity in their dentitional pattern and their geographical distribution. *L. ayresii* is regarded as the ancestral type because of its larger adult body size, wider distributional range, and, in particular, parasitic type of life history. The evolution toward a nonparasitic type no doubt involves the formation of unsurmountable barriers that makes migration impossible. These barriers may be natural, or even man-made. In suggesting a very recent origin of certain European brook lamprey types, Zanandrea (1961) and Young (1962) included such artificial events as dam and stream pollution as possible barriers to migration. *L. richardsoni* appears to be capable of living in rather polluted waters as it has been collected in streams that were apparently contaminated to some degree by the introduction of the effluent from timber plants (Field Notes K734-4-2, K734-3-1) and by the presence of such objects as automobile wreckages (K735-2-5) or beverage cans (Kottcamp and Moyle, 1972).

Vladykov (1973) considered certain Oregon and California brook lampreys of the subgenus Lampetra to be a species, L. pacifica, distinct from L. richardsoni which he previously co-described from mostly Washington and British Columbia specimens (Vladykov and Follett, 1965). The main basis adopted for the distinction of pacifica is that it has fewer trunk myomeres (53 to 58) than richardsoni does (60 to 67). Yet information yielded from additional Oregon materials indicates the difference in myomere numbers to be a largely clinal phenomenon (Tables 30 and 31). Other characters used to designate pacifica are body proportions involving the size of oral disc and the height of second dorsal fin, and pigmentation pattern involving the tail and the tongue precursor. Difference in each of these characters between richardsoni and pacifica as given by Vladykov (1973) seems to be small.

It is probable that L. richardsoni, as certain other brook lamprey species (Hubbs and Trautman, 1937; Hubbs, 1971), has a polyphyletic origin. In spite of local variations evident in characters including the number of trunk myomeres, L. richardsoni is well defined by its tooth pattern, general geographical distribution, and nonparasitic type of life history.

Table 30. Number of trunk myomeres of transformed Lampetra richardsoni from Oregon. Figure in parentheses is the number of specimens examined.

Locality	Number of myomeres												Mean
	53	54	55	56	57	58	59	60	61	62	63	64	
Columbia Co.													
Clatskanie R. (1)							1						59.0
Lost Cr. (1)							1						59.0
Nehalem R. (9)					1	3	5						58.4
Clatsop Co.													
Necanicum R. (4)					1		1	1	1				59.3
Washington Co.													
Scoggin Cr. (2)						2							58.0
Morrow Co.													
Rhea Cr. (4)											2	2	63.5
Polk Co.													
Rogue R. (5)					1		2	2					59.0
Clackamas Co.													
Clackamas R. N. Fk. (3)	1		1	1									54.7
Lincoln Co.													
Yaquina Bay trib. (5)					3	1	1						57.6
Flynn Cr. (4)			2		2								56.0
Benton Co.													
Berry Cr. (11)		1	1	3	3	1	2						56.7
Soap Cr. (15)					1	9	4	1					58.3
Oak Cr. (15)		1	1	4	5	2	2						56.8
Rock Cr. (7)				1	2	3	1						57.6
Grant Co.													
Strawberry Cr. (1)					1								57.0
Lane Co.													
Taylor Cr. (1)					1								57.0
Noti Cr. (1)			1										55.0
Douglas Co.													
Swamp Cr. (8)		1	4	2	1								55.4
Pass Cr. (2)					2								57.0
Coos Co.													
Tenmile L. (1)			1										55.0
TOTAL (100)	1	3	11	11	24	21	20	4	1		2	2	57.6

Table 31. Number of trunk myomeres of transformed Lampetra richardsoni from British Columbia, Washington, Oregon, and California. Figure in parentheses is the number of specimens examined.

Region[1]	Number of myomeres																
	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	Mean
British Columbia (46)									2	3	7	10	9	9	4	2	63.6
Washington (12)									2	1	2	6			1		62.4
Oregon (100)		1	3	11	11	24	21		20	4	1		2	2			57.6
California (2)		1	1														53.5

[1] Data for British Columbia and Washington were from Vladykov and Follett (1965), for California were from Vladykov (1973).

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