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A REVISION OF THE HOLARCTIC LAMPREYS By Charles W. Creaser and Carl L. Hubbs

INTRODUCTION

Regan's synopsis of the marsipobranchs of the order Hyperoartii, published in 1911, placed the taxonomy of the lampreys on a fairly sound basis. Although we adopt this classification as a whole, we find it necessary to propose certain refinements, both of taxonomic and nomenclatural character.

In the present revision we deal with all the known Holarctic lampreys, but do not consider the Antarctic types. We have examined the collections of the following museums: United States National Museum, Stanford University collections, American Museum of Natural History, Field Museum of Natural History, and the Museum of Zoology of the University of Michigan. We wish to thank the officials of these institutions for the use of their lamprey material.

¹ Ann. Mag. Nat. Hist., Ser. 8, Vol. 7, pp. 193-204.

This report is only a systematic outline of the northern lampreys. We hope to obtain much additional material, and if possible to find characters by which ammocoete material can be more certainly identified. Until such additional information is at hand, we consider it premature to enter into a discussion of the geographical distribution and evolution of the North American lampreys. The ranges of the various forms, as given in the following key, are completely verified by material examined.

In the classification of the lampreys a comparison of dentition is indispensable. In order to render them clearer, the descriptions of the teeth in the following key should be supplemented by figures, to which we here append references in the following list.

LIST OF THE HOLARCTIC LAMPREYS, WITH REFERENCES TO FIGURES OF DENTITION

Genus Ichthvomvzon Girard.

Subgenus Ichthyomyzon Girard.

Ichthyomyzon concolor Kirtland: Bensley, Contr. Can. Biol., 1911-1914 (1915), pl. 1, fig. 5.

Subgenus Reighardina (new).

Ichthyomyzon unicolor DeKay: Reighard and Cummins, Occ. Pap. Mus. Zool., Univ. Mich., No. 31, 1916, pl. 2, fig. 1.

Genus Petromyzon Linnaeus.

Subgenus Petromyzon Linnaeus.

Petromyzon marinus Linnaeus: Gage, The Wilder Quarter-Century Book, 1893, pl. 6, figs. 19, 20; Smitt, Hist. Scand. Fishes, pt. 2, 1895, p. 1184, fig. 352; Bade, Die mitteleuropäischen Süsswasserfische, 2, 1902, p. 111, fig. 85; Fowler, Proc. Acad. Nat. Sci. Phila., 1907, p. 462, fig. 1.

Subgenus Caspiomyzon Berg.

Petromyzon wagneri Kessler, "Trud. St. Petersb. Obshch. Estestv., 1, 1870, pp. 270, 302, pl. 3, figs. 4, 5."

Subgenus Eudontomyzon Regan.

Petromyzon danfordi Regan: Wajgel, Verh. zool.-bot. Ges. Wien, 33, 1883 (1884), pl. 17, fig. 3 (as Petromyzon planeri; details inaccurate).

Genus Entosphenus Gill.

Subgenus Tetrapleurodon (new).

Entosphenus spadiceus Bean (no figure).

Subgenus Entosphenus Gill.

Entosphenus tridentatus tridentatus Gairdner: Lucas, Rept. Fur-Seal Invest., pt. 3, 1896-1897 (1899), pl. 15. Entosphenus tridentatus ciliatus Ayres (no figure, but dentition as in typical tridentatus).

Subgenus Lethenteron (new).

Entosphenus japonicus Martens: Smitt, Hist. Scand. Fishes, pt. 2, 1895, p. 1191, fig. 353 (as "P. fluviatilis Var."). Entosphenus appendix DeKay: Gage, The Wilder Quarter-Century Book, 1893, pl. 6, fig. 21; Forbes and Richardson, The Fishes of Illinois (Nat. Hist. Surv. Ill., Vol. 3, Ed. 1, 1908, and Ed. 2, 1920, p. 11, fig. 10).

Genus Lampetra Gray.

Subgenus Lampetra Gray.

Lampetra fluviatilis Linnaeus: Günther, An Introduction to the Study of Fishes, 1880, p. 692, fig. 316; Bade, Die mitteleuropäischen Süsswasserfische, 2, 1902, p. 106, figs. 77, 78. Lampetra planeri Bloch: Bade, Die mitteleuropäischen Süsswasserfische, 2, 1902, p. 109, fig. 82.

Subgenus Okkelbergia (new).

Lampetra lamottenii Le Sueur: Creaser and Hubbs, pl. 1 (present work).

A DIAGNOSTIC KEY TO THE HOLARCTIC LAMPREYS

In the construction of this key an attempt is made to express the probable relationships of the Holarctic lampreys, and to make the diagnosis of any subdivision sufficiently complete to serve as its definition.

Family Petromyzonidae

- a¹. Buccal funnel with series of teeth radiating in all directions from the mouth, deflected backward toward the margin of the disc.
 - b1. A single more or less deeply emarginate dorsal fin; dorsal fin not separated from the caudal by a sharp notch; caudal a broadly oval lobe; innermost lateral disc teeth usually unicuspid; base of teeth poorly developed; myotomes between last gill opening and the vent fewer than 60 (49 to 57).

Genus Ichthyomyzon

University of Michigan

c1. Buccal funnel when expanded much greater in diameter than the width of the body; supraoral lamina greatly constricted, with one to four (usually two) approximated cusps; anterior lingual lamina with anterior and posterior transverse elements each provided with sharp denticles; all disc teeth sharp and large; oral fimbriae arranged in a double row; a high marginal membrane inside with weakly ciliate border; intestine well developed and functional in adults; larvae probably transforming at a size of less than 120 mm. Basins of Hudson Bay, Great Lakes, and Mississippi River.

Ichthyomyzon (Ichthyomyzon) concolor.

- c2. Buccal funnel constricted, when fully expanded not greater in diameter than the width of the body; supraoral lamina with two small, blunt, well-separated cusps; anterior lingual lamina with a single transverse element with minute rounded denticles; all disc teeth weak and blunt, mostly obsolescent; oral fimbriae presenting a matted appearance; intestine degenerate and non-functional in adults; larvae transforming at a size of more than 120 mm. Great Lakes basin. Ichthyomyzon (Reighardina)² unicolor.
- b². Two distinct, more or less widely separated dorsal fins; dorsal fin separated from the caudal by a sharp notch; caudal a rather angular lobe; innermost lateral disc teeth enlarged, one or more multicuspid.

Genus Petromyzon

d¹. Anterior lingual lamina so sharply curved as to appear as two sharply denticulated ridges, without a differentiated median cusp; supraoral lamina expanded behind the two heavy divergent anterolateral cusps, which rarely are imperfectly separated; infraoral lamina with 7 to 9 strong cusps; all teeth well developed and pointed; four innermost laterals always bicuspid; buccal funnel wide; oral fimbriae appearing to be arranged in several series, each lateral and posterior fimbria being cleft two or three times nearly to the base, each of the two or three lobes thus formed again cleft and each of the minor lobes minutely cleft; membrane forming edge of oral disc high, with sharply ciliate border and with numerous well-developed papillae along the inner base; myotomes between the last

² Reighardina Creaser and Hubbs, new subgenus; orthotype, Ichthyomyzon fossor Reighard and Cummins (= Ichthyomyzon unicolor).

gill opening and the vent about 70 in number. North Atlantic Ocean and coastwise streams.

Petromyzon (Petromyzon) marinus.

d². Anterior lingual lamina little bent inward medially, its edge crenulate, without a differentiated median cusp; supraoral lamina narrow, with one (usually) or two lobelike cusps; infraoral lamina with five blunt cusps or crenulations; all teeth very blunt and greatly reduced in size, particularly on the posterior field; lateral disc teeth about as in Petromyzon marinus, but much weaker; the innermost (enlarged) teeth grading outward into minute teeth aligned in rows deflected backward much more sharply than in Petromyzon marinus; buccal funnel reduced in size; oral fimbriae smaller than in Petromyzon marinus and less divided; marginal oral membrane scarcely developed. Caspian Sea and tributaries.

Petromyzon (Caspiomyzon) wagneri.4

d³. Anterior lingual lamina little bent inward medially, usually with an enlarged median cusp; supraoral lamina broad and bicuspid; infraoral lamina with 9 to 11 cusps; innermost lateral disc teeth of each side enlarged, the first and third unicuspid or bicuspid, the middle one bicuspid or tricuspid. Transylvania [from Regan].

Petromyzon (Eudontomyzon) danfordi.5

- a². Teeth of the buccal funnel not in distinct radiating series, but in several groups: several enlarged lateral teeth, usually multicuspid, at the edge of the oral opening; a marginal series around edge of disc; few to many teeth on the anterior part of the disc; supraoral broad, the main cusps being separated by a bridge; fins about as in *Petromyzon*.
 - e¹. A posterior series of small teeth developed, parallel to the marginal series and connecting the last pair of enlarged laterals. Genus Entosphenus

³ The posterior disc teeth in *Petromyzon wagneri* are least obsolete in a single series corresponding to that diagnostically retained in *Entosphenus*.

⁴ Petromyzon wagneri Kessler, "Trud. St. Petersb. Obshch. Estestv., I, 1870, pp. 207, 302, pl. 3, figs. 4, 5"; Caspiomyzon wagneri, Regan, Ann. Mag. Nat. Hist., (8), 7, 1911, p. 200. The diagnosis here given by us is based upon a series of specimens from Astrachan, Russia (No. 37293, United States National Museum).

⁵ Eudontomyzon danfordi Regan, Ann. Mag. Nat. Hist., (8), 7, 1911, p. 200.

- f1. Anterior disc teeth very numerous and crowded, in about six rows medially; enlarged laterals four on each side, the first and last bicuspid, the median two either bicuspid or tricuspid; anterior lingual lamina not at all bent inward medially, the edge comb-like with long, pointed serrations; supraoral often with one or two small denticles located laterally on the bridge between the main cusps; infraoral with nine teeth, alternately larger and smaller. Rio Lerma basin, Mexico. Entosphenus (Tetrapleurodon) spadiceus.
- f². Anterior disc teeth not very numerous or crowded; enlarged laterals normally four in number, the first and last bicuspid, the median two tricuspid (one of the median two rarely lacking, a fifth occasionally added by the doubling of the first tooth of the posterior series); anterior lingual lamina slightly bent inward medially, the edge dentate, the median cusp little enlarged; supraoral always tricuspid, the third cusp median; infraoral cusps 4 to 6, uniform in size, the outermost not doubled.

Subgenus Entosphenus

g1. Myotomes between the last gill opening and vent 68 to 74. Pacific Ocean and coastal streams from Unalaska to the Columbia River System.

Entosphenus tridentatus tridentatus.

g². Myotomes between the last gill opening and the vent 57 to 67. Pacific Ocean and coastal streams from southern Oregon to southern California.

Entosphenus tridentatus ciliatus.

f3. Anterior disc teeth not very numerous or crowded; enlarged laterals always three in number, all bicuspid; anterior lingual lamina not at all bent inward medially, the edge dentate or crenulate, with the median teeth notably enlarged; supraoral rarely with a median or submedian denticle, at most weakly developed; infraoral cusps 8 to 11, the outermost two of each side imperfectly separated.

Subgenus Lethenteron7

⁶ Tetrapleurodon Creaser and Hubbs, new subgenus; orthotype, Lampetra spadicea Bean.

⁷ Lethenteron Creaser and Hubbs, new subgenus: orthotype, Lampetra wilderi Gage (= Petromyzon appendix DeKay).

h1. Dorsal fins well separated by an interspace, except in breeding specimens; oral fimbriae relatively slender, with few marginal incisions; all teeth sharp and strong (becoming blunt by wear in breeding individuals); intestine of adults well developed and functional; larvae at transformation much smaller than the larger adults; not breeding at a size of less than 30 cm. Coasts and streams from Bering Sea west to the White Sea and south to the Sea of Japan.

Entosphenus japonicus.

h². Dorsal fins separated only by a notch to base; oral fimbriae palmate; all teeth blunt and weak; intestine of adults degenerate and non-functional; larvae at transformation attaining the adult size (21 cm. or less). Streams of North America and eastern Asia.

Entosphenus appendix.

e². No teeth other than the marginals on the posterior field of the disc; three enlarged laterals.

Genus Lampetra

i. Cusps of supraoral always simple, stronger, well separated by a broad bridge; infraoral lamina with 6 to 9 distinct cusps; a series of teeth extending across the entire anterior part of the buccal disc within the marginal series; cusps of lateral teeth with a common well-marked base; myotomes between the last gill opening and the vent 58 to 70.

Subgenus Lampetra

- j¹. Dorsal fins usually well separated by an interspace; myotomes between the last gill opening and the vent 63 to 70; all teeth sharp and strong; intestine of adults well developed and functional; larvae at transformation much smaller than the larger adults. Coasts and streams of northern Eurasia and western North America.
 Lampetra fluviatilis.
- j². Dorsal fins separated only by a notch to base; myotomes between the last gill opening and vent 57 to 66; all teeth weak and blunt; intestine of adults degenerate and non-functional; larvae at transformation attaining the adult size. Streams of Eurasia and western North America.
 Lampetra planeri.

i². Cusps of supraoral usually bitubercular, always weak and rounded, separated by a short, narrow isthmus, the base of the cusps poorly developed; infraoral lamina without distinct denticles, the crest crenulated or even nearly entire; all teeth greatly reduced; the anterior field of the disc with but few (about four) denticles, placed laterally and separated by a broad toothless median area; the three laterals of each side obsolescent, with scarcely developed bases, sometimes unicuspid or with the two or three cusps isolated as more or less widely separated denticles; myotomes fewer, 54 to 60 between the last gill opening and vent. Ohio and Potomac River basins.

Lampetra (Okkelbergia)8 lamottenii.

Notes on the North American Species

I. Ichthyomyzon concolor Kirtland

Ammocoetes concolor Kirtland appears to have been based on the larva of the present species. It is certainly a species of *Ichthyomyzon*, and "the irregular series of dark brown dots" mentioned by Kirtland are not developed in the other species of the genus. Furthermore, *I. unicolor* is not known to occur in the Ohio drainage, where the type of concolor was obtained.

Forbes and Richardson⁹ have demonstrated the specific identity of *Ichthyomyzon castaneus* with *I. concolor*. In our own study we have found abundant confirmation of this view.

2. Ichthyomyzon unicolor DeKay

The degenerate relative of *Ichthyomyson concolor*, lately described by Reighard and Cummins,¹⁰ is so distinct that we regard it as the type of a new subgenus, *Reighardina* (defined on p. 4). It has subsequently been referred to as "*Ichthy*-

⁸ Okkelbergia Creaser and Hubbs, new subgenus; orthotype, Ammocoetes aepyptera Abbott (= Lampetra lamottenii).

⁹ The Fishes of Illinois, Nat. Hist. Surv. Ill., Vol. 3, 1908 (Ed. 2, 1920), p. 10.

¹⁰ Occ. Pap. Mus. Zool., Univ. Mich., No. 31, 1916, pp. 1-12, pls. 1, 2.

omyzon sp." by Hankinson,¹¹ and we have found it common throughout Michigan. An ammocoete from the St. Lawrence drainage at Madrid, New York, seems to belong to the same species.

Although not absolutely certain, it is highly probable that the specimens named Ammocoetes unicolor by DeKay,¹² from a tributary to Lake Champlain, and Ammocoetes borealis by Agassiz,¹³ from a stream flowing into Lake Superior, were larvae of this species. It is certain that both names were based on a species of Ichthyomyzon, and the large size and the shape of the types suggest that they belonged to this species rather than to concolor.

3. Petromyzon marinus Linnaeus

We concur in the prevalent view that Petromyzon americanus Le Sueur¹⁴ is identical with P. marinus of Europe. Petromyzon nigricans DeKay¹⁵ merely represents the uniformly colored young, Ammocoetes bicolor DeKay¹⁶ the larva, of the sea lamprey. The dwarfed race (P. marinus dorsatus Wilder),¹⁷ land-locked in the New York lakes, of which we have examined material, does not appear to use worthy of even subspecific recognition.¹⁸ Bathymyzon bairdii Gill¹⁹ and Oceanomyzon wilsoni Fowler²⁰ we hold to be strict synonyms of P. marinus, each having been based on marine specimens

¹¹ Occ. Pap. Mus. Zool., Univ. Mich., No. 89, 1920, p. 5.

¹² New York Fauna, Fishes, 1842, p. 383, pl. 79, fig. 250.

¹³ Lake Superior, 1850, p. 252.

¹⁴ Trans. Am. Phil. Soc., 1, 1818, p. 383.

¹⁵ New York Fauna, Fishes, 1842, p. 381, pl. 79, fig. 247.

¹⁶ Ibid., p. 383, pl. 79, fig. 248.

¹⁷ In Jordan and Gilbert, Bull. U. S. Nat. Mus., 16, 1883, p. 869.

¹⁸ See also Meek, Ann. N. Y. Acad. Sci., 3, 1886, pp. 285-289.

¹⁹ Proc. U. S. Nat. Mus., 5, 1883, p. 254.

²⁰ Proc. Acad. Nat. Sci. Phila., 59, 1907 (1908), p. 462.

with aberrant dentition; we have examined numerous typical specimens from rather deep water in the North Atlantic.

Regan's record²¹ of this species from Muscatine, Iowa, is probably erroneous, although based on specimens of *P. marinus* so labelled by Meek (some of which we have re-examined). It seems more likely that labels were transposed than that *marinus* should have been taken in the Mississippi basin.

4. Entosphenus spadiceus Bean

This species is sharply differentiated by its dentition, which seems to be more generalized than that of other members of the *Entosphenus-Lampetra* series. We make it the type of a new subgenus, *Tetrapleurodon* (defined on p. 6). In addition to the types, we have examined specimens taken by Dugés at Tanganzicuaro, Mexico, and by Nelson in Lago de Chapala.

5. Entosphenus tridentatus tridentatus Richardson

We find it necessary to divide this West American species into a northern and a southern subspecies, as in the specimens examined from the Columbia River system and northward the myotomes between gill slits and anus vary from 68 to 74, whereas in those from the Klamath basin and southward the myotomes number 57 to 67.

Petromyzon lividus Girard²² and P. astori Girard²³ fall into the synonymy of the typical subspecies of Entosphenus tridentatus as thus restricted.

²¹ Ann. Mag. Nat. Hist., Ser. 8, Vol. 7, 1911, p. 198.

²² Pac. R. R. Exp., Fish., 1858, p. 379.

²³ Pac. R. R. Exp., Fish., 1858, p. 380.

6. Entosphenus tridentatus ciliatus Ayres

Two names, Petromyzon ciliatus Ayres²⁴ and Petromyzon epihexodon Gill²⁵ have been based on this southern form of Entosphenus tridentatus, which is characterized by the reduced number of segments.

7. Entosphenus japonicus Martens

The large lamprey of Japan is an *Entosphenus*, as Regan²⁶ has shown. The species is of wide distribution, occurring also in the White Sea, as Regan suggested. We are now able to state that the lamprey of the Yukon, described as *Ammocoetes aureus* by Bean,²⁷ is also conspecific with *japonicus*.

In our opinion, Lampetra mitsukurii major Hatta,²⁸ of which we have examined topotypic material,²⁹ is based on breeding individuals of Entosphenus japonicus. The distinctive features of this nominal form, as pointed out by the describer, are just those which, as Gage³⁰ has shown, distinguish breeding from non-breeding adults of Petromyson marinus; the bluntness of the teeth is due to wear. We find that like changes take place in Entosphenus tridentatus and in Lampetra fluviatilis (q. v.).

8. Entosphenus appendix DeKay

Petromyson appendix DeKay³¹ we regard as assuredly based on the species currently known as Lampetra or Entosphenus

²⁴ Proc. Cal. Acad. Nat. Sci., 1855, p. 44.

²⁵ Proc. Acad. Nat. Sci. Phila., 1862, p. 331.

²⁶ Ann. Mag. Nat. Hist., Ser. 8, Vol. 7, 1911, p. 202.

²⁷ Proc. U. S. Nat. Mus., 4, 1881, p. 159.

²⁸ Annot. Zool. Jap., 7, 1911, p. 268, pl. 9.

²⁹ Recorded by Jordan and Snyder (Proc. U. S. Nat. Mus., 23, 1901, p. 734), as Lampetra mitsukurii.

³⁰ Wilder Quarter-Century Book, 1893, p. 439, pl. 3.

³¹ New York Fauna, Fishes, 1842, p. 381, pl. 64, fig. 211.

wilderi. We find the range of this form to extend from southern New England and northern New York south to Maryland (specimens in National Museum), and west to Wisconsin and Iowa, in North America.

Furthermore, we are wholly unable to distinguish from this form, a nominal species, Lampetra mitsukurii, described by Hatta³² from Japan, and also recorded by him from eastern Siberia (the species will probably be found to occur also in intervening localities). Regan³³ has erroneously referred mitsukurii to the synonymy of Lampetra planeri, despite the fact that Hatta described its generic characters. It is possible, however, that Hatta did include specimens of L. planeri, which also occurs in Japan, in his material, particularly that of Lampetra mitsukurii minor. Under this name he redescribed the same form in 1911,³⁴ without, however, indicating a definite type-locality; this we here designate as Sapparo, Hokkaido.

9. Lampetra fluviatilis Linnaeus

A race of lampreys inhabiting San Francisco Bay and Puget Sound, and doubtless ascending West Coast streams to spawn, we identify after careful examination with this species. On examples of this race the names *Petromyzon plumbeus* Ayres³⁵ and *Petromyzon ayresii* Gunther³⁶ have been based.

Lőnnberg³⁷ and Smitt³⁸ have both claimed that *Lampetra fluviatilis* and *L. planeri* intergrade and are inseparable specifically. While we expect to return to this problem at a later time, and do consider the intergradation as not improbable,

³² Annot. Zool. Jap., 4, 1901, p. 24.

³³ Ann. Mag. Nat. Hist., Ser. 8, Vol. 7, 1911, p. 203.

³⁴ Annot. Zool. Jap., 7, 1911, p. 268, pl. 9.

³⁵ Proc. Calif. Acad. Sci., 1854, p. 28.

³⁶ Cat. Fishes Brit. Mus., 8, 1870, p. 505.

³⁷ Bih. Sv. Vet-Akad. Handl., 1893, 18, Afd. 4, No. 2, pp. 1-13.

³⁸ Hist. Scand. Fishes, pt. 2, 1895, p. 1188.

we may state here that the authors quoted apparently arrived at their conclusion from erroneous data. They seem to have compared only non-breeding with breeding specimens of fluviatilis, believing the latter to represent L. planeri. Wajgel³⁹ also concluded that fluviatilis and planeri intergrade, but he confused Eudontomyzon danfordi with Lampetra planeri. Other authors have expressed like views, but so far as we know, no one has presented any conclusively supporting evidence.

10. Lampetra planeri Bloch

We refer to this form many specimens examined from Europe, Japan, and from Western North America (from Alaska to central California). The material represents numerous races, without geographical significance, and apparently not recognizable nomenclaturally. Indeed, as suggested above, planeri may even intergrade with fluviatilis.

The brook lampreys of California have passed under the name Lampetra cibaria, but Ammocoetes cibarius Girard⁴⁰ was described as having the dorsal fins separated, and hence was probably based on either Entosphenus t. tridentatus or Lampetra fluviatilis.

³⁹ Verh. zool.-bot. Ges. Wien, 33, 1883 (1884), pp. 311-320, pl. 17.

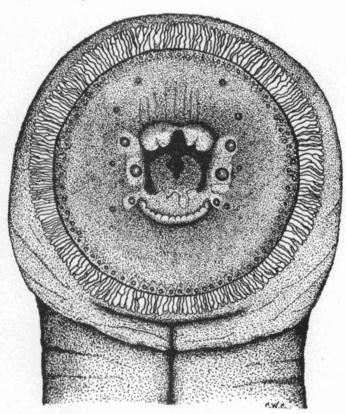
⁴⁰ Pac. R. R. Exp. Fish., 1858, p. 383.

11. Lampetra lamottenii Le Sueur (Plate I)

The name lamottenii Le Sueur⁴¹ is revived for this aberrant brook lamprey, as the obsolescent dentition, partial union of the dorsal fins, and the coloration as shown in the type figure indicate that Le Sueur had the present species. It is the only representative of the genus Lampetra, as now restricted, which occurs in eastern North America. Ammocoetes aepyptera Abbott⁴² is its only synonym. It is the most degenerate of all the known lampreys.

We base on this species a new subgenus, Okkelbergia, named in honor of Dr. Peter Okkelberg, of the University of Michigan, in recognition of his careful studies on the history of the germ cells in lampreys. The subgeneric and specific characters are both indicated in the diagnostic key (see p. 8).

⁴¹ In DeKay, New York Fauna, Fishes, 1842, p. 382, pl. 79, fig. 249. ⁴² Proc. Acad. Nat. Sci. Phila., 1860 (1861), p. 327; type redescribed by Fowler, *ibid.*, 1901, p. 328; and *ibid.*, 1907, p. 466.



Dentition of Lampetra (Okkelbergia) lamottenii

