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A REVISION OF THE LAMPREY GENUS *ICHTHYOMYZON*

BY

CARL L. HUBBS AND MILTON B. TRAUTMAN

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Director of the Museum of Zoology

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CONTENTS

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INTRODUCTION

The North American fresh-water lamprey genus *Ichthyomyzon* is currently regarded as containing (1) a single parasitic species, *I. concolor,* with which *I. castaneus* has been synonymized by Forbes and Richardson (1909: 9) and Creaser and Hubbs (1922: 8), and (2) a single, degenerate, nonparasitic, "brook" type, *I. fossor,* which has been identified as *I. unicolor* in most recent papers. During the last few years specimens of 2 additional and undescribed species of the nonparasitic type have been collected, *I. gagei* in the lower Mississippi Valley and *I. greeleyi* in the upper Ohio Valley. The discovery of *I. greeleyi* confirmed our suspicions that a generally unrecognized parasitic form exists in the Ohio Valley, which like the new nonparasitic form of the same region is characterized by an increased number of myomeres. This parasitic form of the Ohio River basin seems to be referable to *Petromyzon argenteus* Kirtland (name preoccupied) = *Ichthyomyzon bdellium* (Jordan).

The observation that *gagei, greeleyi,* and *bdellium* all have bicuspid lateral teeth then led us, after the comparative examination of large series, to appreciate the existence of 2 additional, distinct species of the parasitic type. With few exceptions all specimens from eastern tributaries of Lake Michigan, those from most localities in the upper Mississippi Valley, and all from the lower Mississippi Valley, likewise have all or some of the lateral teeth bicuspid, thus corresponding with the descriptions (and with the type) of *Ichthyomyzon castaneus,* which in consequence is resurrected from the synonymy of *Ichthyomyzon "concolor."* On the other hand all available specimens from Lakes Superior, Huron, Erie, and Champlain, and some specimens from the upper Mississippi Valley, including a large series from Lake Pepin, have unicuspid laterals. This evidence has convinced us of the existence of a northeastern species, which prior to 1909 was generally recognized but was designated by the inapplicable names of *argenteus* or *concolor.* Since this species seems never to have received an applicable name, we here describe it as a new species, *Ichthyomyzon unicuspis.* The 6 species of *Ichthyomyzon* as we now recognize them are, therefore:

Parasitic species	Nonparasitic species
I. unicuspis, new species	*I. fossor* Reighard and Cummins
I. castaneus Girard	*I. gagei,* new species
I. bdellium (Jordan)	*I. greeleyi,* new species

Acknowledgments and Materials

We wish especially to thank Dr. Simon Henry Gage, the grand old zoologist of Cornell whose studies of American lampreys have covered an even half century, for submitting to us for description the new brook lamprey of the lower Mississippi Valley, which we are naming *I. gagei* in his honor. We are also indebted to Dr. John R. Greeley, our erstwhile colleague at the University of Michigan, for similarly referring to us the new brook type which he discovered in the upper Ohio basin, and which we are describing as *I. greeleyi.* Later Mr. Edward C. Raney, now of Cornell University, very kindly collected for us about 100 additional specimens of the same form. Messrs. Bernard R. and Louis W. Campbell, of Toledo, spent many cold evenings collecting for us the large type series of *I. unicuspis.*

We appreciate also the courtesy of the officials of the National, Field, American, Ohio State, and Milwaukee Public museums, of the United States Bureau of Fisheries, and of the Wisconsin Geological and Natural History Survey, for permission to study and to report on their lampreys. Virtually all specimens of *Ichthyomyzon* in these institutions, as well as those comprising the large, newly collected series in the Museum of Zoology of the University of Michigan, approximately 600 specimens in all, have been carefully examined, counted, and measured. Laura C. Hubbs has made most of the statistical computations presented in the tables.

As a result of this co-operation we feel that we have been able to gather together for the first time sufficient material on which to base a critical revision of *Ichthyomyzon,* and to arrive at a fairly adequate conception of the systematics of the genus. We have used extensive material of *I. unicuspis,* a fairly adequate representation of *I. castaneus,* relatively few specimens of the third parasitic form, *I. bdellium.* Of the 3 nonparasitic species, we have accumulated adequate series of *I. fossor* and *I. greeleyi,* but have had only scattering examples of *I. gagei.* The reason why these nonparasitic species have only recently been discovered is that the adults are very difficult to secure in ordinary collecting, because they are readily available only during a short spawning season in the spring.

It is possible that some of the 6 forms here recognized as full species, particularly *bdellium* and *castaneus,* may prove to be intergrading subspecies on the examination of further series. Ranges of the several forms will probably be extended, certainly will be worked out in greater detail. Differential ecology will be better understood. These ends will not be reached until much additional material is collected.

Some additional literature records might be placed under their proper species, and the doubt now attached to some such references could be removed, by the examination of additional material in the collections of the Academy of Natural Sciences of Philadelphia, the Museum of Comparative

Zoology, the New York State Museum, the Royal Ontario Museum and other Canadian institutions, the Illinois Natural History Survey, and the California Academy of Sciences. It is extremely improbable, however, that the study of this additional material would in any essential way modify our systematic conclusions.

Taxonomic Conclusions

This revisionary study of the lampreys of the genus *Ichthyomyzon* has led to some conclusions which appear significant from the viewpoint of general systematics.

MULTIPLE ORIGIN OF THE NONPARASITIC TYPES

The most interesting of these conclusions is that each of the 3 parasitic forms of *Ichthyomyzon* appears to have given rise to a nonparasitic species. The distinction between these life-history types, and the conclusion that the various nonparasitic or brook lampreys have arisen independently from the more primitive parasitic types, were thus stated by one of us (Hubbs, 1925: 587–588) in a previous paper:

> After metamorphosis the life of the lampreys follows one of two courses. In one type of life-cycle, obviously the more primitive, the transformed lampreys retain a functional alimentary system and develop strong, sharp teeth. They feed in a semi-parasitic fashion on other fishes, and continue to live and grow, usually in the sea, or in lakes and larger streams. Having existed thus for an unknown period of time they re-ascend the smaller streams in spring migrations, spawn, die, and thus complete their life-cycle.
>
> The lampreys of the contrasting life-history type entirely cease their feeding and growth after metamorphosis, which takes place in late summer or early fall (August to October). An entire period or element in the life-cycle is thus eliminated. The alimentary system rapidly degenerates into a non-functional condition. The teeth are reduced in size and particularly in sharpness, and in extreme cases variously decreased in number, or even fragmented. In this degenerate adult condition they continue to live, however, for a period of more than four but less than eleven months, unless prematurely destroyed. Having thus passed through the winter, they spawn in the following spring (March to June); then die, as do the parasitic species.
>
> These degenerate dwarfs comprise several forms, each independently and perhaps even polyphyletically derived from a parasitic species.

Ichthyomyzon fossor is unquestionably the dwarfed derivative of *I. unicuspis*. It agrees distinctively with that species (see Tables I and X, and Figs. 1–6) in the low number of myomeres; in the almost invariably bicuspid supraoral; in the low average number of infraoral cusps and of teeth in the circumoral, anterior, and lateral rows; in the almost invariably unicuspid circumoral teeth; in the strongly bilobed, transverse lingual lamina; on the average in the long tail, and long total distance over the gill opening; in the light and rather even color; and in distribution. It is known to occur only within the range of *I. unicuspis*, to a large degree outside of the range of

I. castaneus, and entirely beyond the limits of any of the other species of the genus (see Map 1, p. 44).

Ichthyomyzon gagei similarly shares diagnostic features with its probable ancestor, *I. castaneus* (see Tables I and X, Figs. 1–6, and Map I). It has, like that form, the myomeres intermediate in number between those of *unicuspis* and *fossor* on the one hand and those of the *bdellium–greeleyi* group on the other hand; in this character *castaneus* and *gagei* are respectively closer to *unicuspis* and *fossor* than to *bdellium* and *greeleyi. I. gagei* is similarly intermediate between *fossor* and *greeleyi* in average number of supraoral cusps, but in this respect differs more from *fossor* than from *greeleyi,* just as *castaneus* differs more from *unicuspis* than from *bdellium. I. gagei* agrees with *castaneus* fairly well in number of infraoral cusps, and in the number of circumoral, anterior, and lateral tooth-rows. The number of biscuspid circumorals gives clear indication of relationship, for this number in *gagei* is very close to that in *castaneus,* and is much higher in both of these forms than in either *unicuspis* or *fossor* (which very seldom have any bicuspid circumorals), but not much fewer than in *greeleyi* or *bdellium. I. gagei* and *castaneus* are the only species of the genus having a linear or weakly bilobed, transverse lingual lamina. In the average relative lengths of tail, snout, disk, and gill region, *gagei* is definitely intermediate between *fossor* and *greeleyi,* just as *castaneus* is intermediate between *unicuspis* and *bdellium. I. gagei* is known to occur only in the southern and southwestern periphery of the range of *I. castaneus,* far southwest of any known record for either *I. unicuspis* or *I. bdellium.*

Ichthyomyzon greeleyi is similarly indicated as the degenerate derivative of *I. bdellium,* with which it agrees strikingly in having a high number of myomeres, in having all or almost all the circumorals bicuspid, and in the length, slenderness, and strong curvature of the disk teeth. The agreement in number of supraoral and infraoral cusps, and of number of teeth in the circumoral, anterior, and lateral rows is fairly good; in these characters *greeleyi* and *bdellium* together are well distinguished from *fossor* and *unicuspis,* but the distinction from *gagei* and *castaneus* is slight and irregular. In the average number of bicuspid circumorals, *greeleyi* is extreme, but is decidedly most nearly matched by *bdellium. I. greeleyi* and *bdellium* further agree in the moderate to strongly bilobed form of the transverse lingual lamina. In measurements of depth of body, and length of eye, snout, and disk, *greeleyi* and *bdellium* show a very marked approach to one another; but in length of tail and of gill region, they diverge. They are very similar in color (p. 41). The distribution of *I. greeleyi* confirms the morphological evidence of its ancestry. It is known to occur only in the upper tributaries of the Ohio River, which river system is otherwise known to be inhabited only by *I. bdellium,* and, sparingly, by the very dissimilar, large-

TABLE I

RELATIONSHIPS OF THE SPECIES OF *ICHTHYOMYZON*, AS SHOWN BY THE AVERAGE VALUE FOR VARIOUS CHARACTERS

The values for the numerical characters for each species represent actual counts; those for the total length represent measurements in millimeters; those for the other measurements represent the proportionate lengths in thousandths of the total length.

CHARACTER	PARASITIC FORM			NONPARASITIC FORM			DIFFERENCE BETWEEN NONPARASITIC AND PARASITIC FORM
	Mean value	Species	Difference	Difference	Species	Mean value	
Number of myomeres	50.5	*unicuspis*	+ 2.1	+ 1.4	*fossor*	50.9	+ 0.4
	52.6	*castaneus*	+ 4.8	+ 5.6	*gagei*	52.3	− 0.3
	57.4	*bdellium*			*greeleyi*	57.9	+ 0.5
Number of supraoral cusps	2.0	*unicuspis*	+ 0.4	+ 0.6	*fossor*	2.0	0.0
	2.4	*castaneus*	+ 0.2	+ 0.2	*gagei*	2.6	+ 0.2
	2.6	*bdellium*			*greeleyi*	2.8	+ 0.2
Number of infraoral cusps	7.8	*unicuspis*	+ 0.5	0.0	*fossor*	8.7	+ 0.9
	8.3	*castaneus*	+ 0.1	+ 0.7	*gagei*	8.7	+ 0.4
	8.4	*bdellium*			*greeleyi*	9.4	+ 1.0
Number of teeth in circumoral row	19.2	*unicuspis*	+ 1.6	+ 0.6	*fossor*	20.3	+ 1.1
	20.8	*castaneus*	0.0	+ 0.6	*gagei*	20.9	+ 0.1
	20.8	*bdellium*			*greeleyi*	21.5	+ 0.7
Number of teeth in anterior row	3.2	*unicuspis*	+ 1.4	+ 1.6	*fossor*	2.2	− 1.0
	4.6	*castaneus*	− 0.3	+ 0.3	*gagei*	3.8	− 0.8
	4.3	*bdellium*			*greeleyi*	4.1	− 0.2
Number of teeth in lateral row	6.6	*unicuspis*	+ 1.9	+ 2.7	*fossor*	4.7	− 1.9
	8.5	*castaneus*	− 0.2	− 0.2	*gagei*	7.4	− 1.1
	8.3	*bdellium*			*greeleyi*	7.2	− 1.1
Number of bicuspid circumorals	0.0	*unicuspis*	+ 6.5	+ 5.9	*fossor*	0.0	0.0
	6.5	*castaneus*	+ 1.3	+ 2.5	*gagei*	5.9	− 0.6
	7.8	*bdellium*			*greeleyi*	8.4	+ 0.6
Total length, mm.	224	*unicuspis*	− 8	− 12	*fossor*	119	− 105
	216	*castaneus*	− 27	+ 21	*gagei*	107	− 109
	189	*bdellium*			*greeleyi*	128	− 61
Length of tail	302	*unicuspis*	− 20	− 12	*fossor*	304	+ 2
	282	*castaneus*	− 8	+ 5	*gagei*	292	+ 10
	274	*bdellium*			*greeleyi*	297	+ 23
Depth of body	82	*unicuspis*	0	+ 3	*fossor*	74	− 8
	82	*castaneus*	− 9	− 1	*gagei*	77	− 5
	73	*bdellium*			*greeleyi*	76	+ 3
Length of eye	11	*unicuspis*	0	− 1	*fossor*	13	+ 2
	11	*castaneus*	0	+ 1	*gagei*	12	+ 1
	11	*bdellium*			*greeleyi*	13	+ 2
Length of snout	95	*unicuspis*	− 5	+ 11	*fossor*	55	− 40
	90	*castaneus*	− 4	+ 7	*gagei*	66	− 24
	86	*bdellium*			*greeleyi*	73	− 13
Length of disk	86	*unicuspis*	− 9	+ 7	*fossor*	41	− 45
	77	*castaneus*	− 8	+ 5	*gagei*	48	− 29
	69	*bdellium*			*greeleyi*	53	− 16
Length over gill-openings	101	*unicuspis*	− 7	− 2	*fossor*	104	+ 3
	94	*castaneus*	− 5	− 4	*gagei*	102	+ 8
	89	*bdellium*			*greeleyi*	98	+ 9

water form, *I. unicuspis*. *I. greeleyi* is known to occur farther upstream even than *I. bdellium,* but their ranges probably overlap, or have overlapped within historical time.

We conclude that the common tendency of lampreys to undergo independent, parallel evolution, in their degeneration from parasitic to nonparasitic types, has been repeated 3 times within the genus *Ichthyomyzon.* There is, furthermore, no convincing proof that any of the 3 brook types has been derived monophyletically from its parasitic ancestor, although the seemingly compact distribution and relatively constant characters of each nonparasitic species argues for its phyletic unity. This is least true of *I. gagei,* which has a rather wide range and shows some rather marked local differentiation, and may very well have had a polyphyletic origin (p. 85). It is quite possible that additional nonparasitic forms remain to be discovered: there is no logical reason to assume that each parasitic form has given rise to only one nonparasitic species.

OTHER PHYLOGENETIC CONSIDERATIONS

The tendency of the lampreys as a whole to lead toward the degenerate, nonparasitic condition in their phylogeny (Hubbs, 1925: 590) is repeated within the genus *Ichthyomyzon. I. unicuspis,* which we consider to be the most primitive species, is probably the largest form and certainly has the largest disk and snout, and the strongest teeth; *I. castaneus* is intermediate in the characters related to the parasitic habit; *I. bdellium* is probably the smallest of the parasitic species, and has by far the smallest disk. This parallelism extends even to the color, for the series *unicuspis* → *castaneus* → *bdellium* is one of increasing darkness and of increasing tendency toward a bicolored pattern, and each nonparasitic form is darker and more bicolored than its apparent parasitic ancestor.

The tendency of *castaneus* and especially of *bdellium* to approach the nonparasitic lampreys is not parelleled by a similarly increasing degeneration in their nonparasitic derivatives. On the contrary, *I. fossor,* the derivative of *unicuspis,* is by far the most degenerate of the 3 nonparasitic types, and *I. greeleyi* is the least degenerate. *I. greeleyi* averages larger in total length and in size of disk (and snout) than *I. fossor,* and has much more numerous and very much longer and sharper teeth. In fact *greeleyi* diverges relatively little from its parasitic ancestor *bdellium* in dentition, and differs much less from *bdellium* in size of mouth than *fossor* does from *unicuspis.* The divergence of *gagei* from *castaneus* is consistently intermediate. The tendency of *fossor* to diverge most widely from *unicuspis,* and of *greeleyi* to diverge least from *bdellium,* in the various characters related to feeding, is clearly shown by the data in Table I and by the histograms in Figures 1–2 and 4–5. That is, the apparently true phyletic line *unicuspis* → *cas-*

taneus → *bdellium* and the false line of independently derived forms, *fossor* → *gagei* → *greeleyi*, tend to converge. The convergence of these lines in respect to length of disk and of snout receives clear numerical expression in the decrease in the differences between the members of the three successive pairs of parasitic and nonparasitic species in the average lengths of these parts (see last column of Table I); the divergence of the lines in respect to length of tail and length over the gill openings is in part at least due to the greater differences between the parasitic and the nonparasitic forms in these characters. The great divergence of *fossor* may well have resulted from a relatively ancient separation from *unicuspis*, while the comparatively slight separation of *greeleyi* may be due to a much more recent origin.

The tendency toward degeneration in the phylogeny of *Ichthyomyzon* is correlated with a change in habitat. The species best fitted for parasitism, *I. unicuspis*, inhabits the largest waters, where the greatest number of large host fishes, particularly the scaleless fishes of the catfish and sturgeon groups, occurs or did occur before their depletion by the white man. *I. castaneus*, with a somewhat smaller mouth and weaker teeth, is more of a river and large creek species, and has perhaps been less generously supplied with suitable hosts. *I. bdellium*, which most closely approaches the nonparasitic form in small size and reduced disk, inhabits the smallest waters, where large, suitable host fish are, or were, least abundant.

The relatively small mouth of *bdellium* may be quite sufficient to enable this species to hold to its generally rather small prey. Its numerous and very sharp, curved, awl-like disk teeth may, in fact, be adaptations to feeding on scaly fishes, and may compensate for the smaller size of the teeth and mouth.

We can not, in fact, assert with full confidence that the *unicuspis* → *castaneus* → *bdellium* series is a phyletic series which has evolved exactly in that order and direction, although that conclusion is the most plausible one to explain the character gradients (shown by Table I and Figs. 1–5). In this series there is a marked increase in the number of myomeres, of supraoral cusps, and of bicuspid circumorals; a weakening but lengthening of the teeth; a probable decrease in size; a marked decrease in the proportionate lengths of tail, snout, disk, and gill region; an increase in the darkness of the body and in the tendency toward a bicolored pattern. In compensation there must be an increase in the length of the mid-region of the body, that is, in the distance from the last gill-slit to the anus—an increase correlated with and approximately proportionate to the increase in the number of myomeres in this region. No such gradient is evident in depth of body (the low value for the depth of *bdellium* merely reflects the paucity of breeding specimens), nor in length of eye, nor in the intensity of black pigmentation on the sense organs of the lateral line system. The gradient is slight in respect to number of infraoral cusps and is irregular in respect to the number of teeth in the circumoral, anterior, and lateral rows, which average a little higher in *castaneus* and *bdellium* than in *unicuspis,* but average quite as high if not very slightly higher in *castaneus* than in *bdellium.* The shape of the anterior lingual lamina is similar in *unicuspis* and *bdellium,* but distinctive in *castaneus;* the denticulation of the lamina, however, is intermediate in *castaneus.*

The extreme degeneration of the nonparasitic types has seemingly been correlated with their habitation of small rivers, creeks, and brooks, where suitable host fishes are not plentiful, but where the food and shelter conditions for ammocoete life are superior. Viewed in this light the degeneration of the lampreys has been a definite specialization to environmental conditions. Since the brook conditions are repeated endlessly it is small wonder that the nonparasitic types of lampreys have frequently been evolved along independent lines.

POSSIBLE INTERGRADATIONS AND HYBRIDIZATION

The evidence of our present study on *Ichthyomyzon* does not confirm the rather well-grounded suspicion entertained by several workers[1] on the lampreys that some or all of the parasitic types and their respective nonparasitic derivatives may intergrade. The relatively slight differentiation of *greeleyi* from *bdellium,* however, indicates that these two forms may be found to intergrade. Intermediate forms between *gagei* and *castaneus* may eventually also be found, but present intergradation between the widely divergent forms *fossor* and *unicuspis* is hardly conceivable.

Intergradation between the 3 nonparasitic species of *Ichthyomyzon* can hardly be expected to occur, for these forms are quite distinct in characters and apparently also in origin. Intergradation between the parasitic species, on the other hand, may well occur. In fact we venture to predict that the geographic forms *bdellium* and *castaneus* will be found to intergrade where their ranges meet near the mouth of the Ohio River (see Map 1). At present, however, we have no clear indication of intergradation between these two forms.

It is improbable that any regular intergradation occurs between *castaneus* and *unicuspis,* or between *bdellium* and *unicuspis,* for these forms remain essentially typical over their wide ranges (Table II, and tables of characters given under each species). That real populations of *unicuspis* occur in the upper Mississippi Valley is indicated by the rather large series of typical specimens of *unicuspis* at hand from Lake Pepin, a widened portion of the Mississippi River between Wisconsin and Minnesota; from this lake we have seen 39 specimens of *unicuspis,* but only 1 of *castaneus.*

[1] Wajgel (1884), Lönnberg (1893), Smitt (1895: 1188), Creaser and Hubbs (1922: 13), Hubbs (1925: 589), Weissenberg (1925–1927), Rauther (1925), Cotronei (1927), and Berg (1931, 1935, and other papers).

TABLE II

SHOWING THAT *ICHTHYOMYZON UNICUSPIS* AND *I. CASTANEUS* REMAIN AS DISTINCT WHERE OCCURRING TOGETHER AS EACH DOES WHERE OCCURRING ALONE

The values given are all averages. The number of specimens on which each average for a count was computed is indicated as an inferior figure. The number of specimens on which each average measurement was computed is given in the last row; in the larger series an occasional specimen was not measured for one of the characters.

SPECIES	*UNICUSPIS*											*CASTANEUS*					
DRAINAGE BASIN	L. Champlain	L. Erie	Detroit–St. Clair	Saginaw Bay	L. Huron	L. Michigan*	L. Superior	Hudson Bay	L. of the Woods	Upper Mississippi R.*	Ohio R.	L. Michigan*	L. Manitoba	Red R. of the North	Upper Mississippi R.	Lower Mississippi R.	Alabama R.
CHARACTERS: Myomeres	50.5_{2}	51.0_{123}	50.5_{4}	49.9_{29}	49.2_{9}	50.6_{23}	51.3_{13}	49.5_{2}	48.7_{4}	50.0_{47}	49.9_{22}	52.9_{55}	51.5_{2}	52.0_{4}	52.6_{27}	51.7_{9}	52.4_{7}
Supraoral cusps	2.0_{2}	2.1_{123}	2.0_{4}	2.0_{29}	1.9_{11}	1.9_{23}	1.3_{3}	2.0_{2}	2.0_{4}	2.1_{47}	1.7_{3}	2.4_{43}	2.0_{2}	2.8_{4}	2.4_{27}	2.4_{7}	2.1_{7}
Infraoral cusps	8.0_{2}	8.0_{123}	7.3_{4}	8.0_{29}	7.5_{11}	8.1_{23}	7.3_{3}	6.5_{2}	7.3_{4}	7.3_{47}	7.6_{3}	8.4_{43}	9.0_{2}	8.2_{4}	8.4_{27}	8.6_{7}	7.9_{7}
Teeth in row:																	
Circumoral	18.0_{2}	19.1_{110}	21.0_{1}	19.4_{28}	19.6_{10}	19.5_{22}	19.3_{3}	....	....	18.9_{42}	19.3_{8}	21.0_{31}	....	....	20.6_{20}	20.7_{3}	22.0_{2}
Anterior	3.5_{2}	3.1_{110}	3.0_{1}	3.1_{28}	2.9_{10}	3.1_{22}	3.0_{3}	....	....	3.4_{42}	3.0_{8}	4.4_{31}	....	....	4.8_{20}	4.3_{3}	5.0_{2}
Lateral	6.5_{4}	6.6_{246}	6.6_{8}	6.4_{58}	6.4_{22}	6.7_{46}	6.3_{6}	6.0_{4}	6.1_{8}	6.9_{93}	6.0_{6}	8.3_{84}	8.2_{4}	8.1_{8}	8.7_{54}	8.9_{14}	9.2_{13}
Bicuspid circumorals	**0.0_{2}**	**0.0_{123}**	**0.0_{4}**	**0.1_{29}**	**0.2_{11}**	**0.0_{23}**	**0.0_{3}**	**0.0_{2}**	**0.0_{4}**	**0.0_{47}**	**0.0_{3}**	**6.4_{43}**	**4.0_{2}**	**6.0_{4}**	**7.0_{27}**	**6.0_{7}**	**6.7_{7}**
Length of tail	291	298	305	306	293	307	321	302	280	306	295	283	282	286	284	271	276
Length of snout	90	89†	96	94	98	92	93	98	97	111	102	89	79	87	89	97	98
Length of disk	90	78†	94	87	90	84	88	89	92	102	96	76	76	73	76	83	83
Length over gill-openings	94	103	96	97	97	97	90	95	99	101	95	95	92	93	93	97	95
No. of specimens measured	2	122	4	29	9	23	3	2	4	47	3	41	2	4	25	6	7

* Regions where both species occur.
† Average reduced by the puckering of the mouth by recent preservation of live specimens in strong preservative.

The claim of Forbes and Richardson (1909 and 1920: 9–10) that *concolor* [*unicuspis*] and *castaneus* are impossible of separation, although fully concurred with by Creaser and Hubbs (1922: 8) and other recent workers, and the suggestion advanced by Huntsman (1917: 25) that these forms "are evidently only geographical varieties," therefore now appear to have been erroneous. It is obvious that Forbes and Richardson had both species, and that they failed to appreciate their differential characters. Theirs was a natural conclusion, because there is an overlap in each individual character difference, because previous workers whom Forbes and Richardson followed in systematic treatment had laid chief stress on the very poor character of the number of infraoral cusps, and especially because Forbes and Richardson virtually confined their study to the region where the problem is confused by the occurrence together of the two species.

Table II further shows that *unicuspis* and *castaneus* maintain their distinctness, not only in the areas where they occur separately, but also in the broad area where their ranges overlap, namely in the Lake Michigan drainage and the upper Mississippi Valley. This is strikingly true of the most sharply distinctive feature, the number of bicuspid circumoral teeth, the average values for which are given in bold face type. In this and almost all other respects, the adequate material shows that *unicuspis* remains as typical in the region of overlap as in the extensive area to the northeast where it is the only parasitic species of *Ichthyomyzon* (see Map 1 and Fig. 6). Similarly, *cas-*

TABLE III

NUMBER OF MYOMERES AND OF BICUSPID CIRCUMORALS IN *ICHTHYOMYZON UNICUSPIS* AND *I. CASTANEUS*, SHOWING THE DISTINCTNESS OF THE SPECIES

A correlation table for the 2 characters and a frequency table for each. The figures for *unicuspis* are given in bold face type, those for *castaneus* in roman type.

		NUMBER OF BICUSPID CIRCUMORALS											NUMBER OF MYOMERES*	
		0	1	2	3	4	5	6	7	8	9	10	*unicuspis*	*castaneus*
NUMBER OF MYOMERES	47	1	......	......	......	......	......	......	......	......	......	......	1	......
	48	11	1	......	......	......	......	......	......	......	......	......	15	......
	49	38	1	1	......	......	......	......	......	......	......	......	47	1
	50	77	2	......	......	1	1	......	......	1	......	......	86	3
	51	56	......	......	......	2	......	3	2	5	1	......	62	15
	52	39	1+1	......	2	3	......	10	3	8	......	......	46	31
	53	15	......	1	......	2	......	12	7	4	3	1	16	32
	54	2	......	......	......	......	......	3	2	2	1	1	2	12
	55	3	......	......	......	1	......	3	......	......	......	......	3	9
	56	......	......	......	......	......	......	......	......	1	......	......	......	2
Number of bicuspids†													Average 50.5	52.6
unicuspis		245	5	1	......	......	......	......	......	......	......	......	0.0	
castaneus ...		......	1	1	2	9	1	32	15	23	5	2	6.5	

* Including a few specimens on which the count of bicuspid circumorals could not be made.
† Including a few specimens on which the myomere count could not be made.

taneus shows about the same averages for bicuspid circumorals and for other characters, in the area of overlap, as it does in the areas to the west and south where it alone occurs; for this species, however, the material from the area of exclusive occurrence is meager.

Table III shows that the number of bicuspid circumorals almost invariably distinguishes *unicuspis* and *castaneus,* for in these counts only a very slight overlap is apparent. Since a greater overlap occurs in respect to every other character, for instance the number of myomeres, it is difficult to determine whether the two forms intergrade. The problem becomes one of determining whether the usual character combinations are consistent. This seems to be true. Referring again to Table III, we note that 5 of the 6 specimens of *unicuspis* with 1 or 2 bicuspid circumorals, in a total of 243 counted for both characters, have only 48 to 50 myomeres. These myomere counts lie within the range of usual variation for *unicuspis* but below the usual range for *castaneus* (only 4 specimens of *castaneus* have 49 or 50 myomeres, while 100 have 51 to 56 myomeres). Similarly the 4 specimens of *castaneus* showing only 1 to 3 bicuspid laterals, and the 9 showing 4, have the myomeres about as numerous on the average as in typical *castaneus.* Thus by combining the myomere and bicuspid circumoral counts, almost all individual specimens are identifiable.

In Table IV we present the individual characters of all specimens of *Ichthyomyzon unicuspis* and *I. castaneus* examined which have from 1 to 5 bicuspid circumoral teeth. This includes, in addition to 2 specimens which we treat below as possible hybrids, only 6 examples identified as *unicuspis,* with 1 or 2 bicuspids; only 1 of *castaneus* with 1 bicuspid, 1 with 2 bicuspids, and 12 with 3 to 5. In most respects other than the number of bicuspid circumorals, these specimens agree with one or the other species. Some of them come from areas where only one of the two species is known to occur. We interpret them all as probably specimens of one or the other form, with an unusual number of bicuspid circumorals. It is possible, however, that they represent intergradation or hybridization, past or present. Although *castaneus* is not known to occur at present in the Saginaw Bay–Lake Huron drainage, it may have penetrated into this area in postglacial time. If so it has probably been absorbed there by the dominant *unicuspis* population, leaving only occasionally appearing characters, such as 1 or 2 bicuspid circumorals, as indications of its unsuccessful invasion of the area. Of 123 specimens from Lake Erie, only 1 has a bicuspid circumoral.

Two specimens of adult *Ichthyomyzon,* out of more than 600 examined, seem unidentifiable specifically. They combine the characters of two species in such a way as to suggest their doubtful identification as interspecific hybrids. The characters of these possible hybrids are also given in Table IV. One of these specimens, combining the characters of *bdellium* and *unicuspis,* came from the lower part of the Scioto River, well within the range of *bdellium* and not far from the Ohio River, which is the only stream in the upper Ohio Valley from which specimens of *unicuspis* have been taken. The other, combining characters of *castaneus* and *unicuspis,* was taken with specimens of *unicuspis* near Gladstone, Michigan, in an arm of Green Bay (of Lake Michigan), where *unicuspis* abounds but *castaneus* is not known to occur. The Scioto River specimen may be an aberrant individual of *bdellium,* and the Green Bay specimen may be an unusual example of *castaneus* or more probably of *unicuspis;* yet the total characters of each (see Table IV) make the hybrid theory rather plausible. When dealing with such species distinguished by combinations of overlapping differences, however, we find it very difficult to interpret any individual with much assurance as a hybrid.

GENUS *ICHTHYOMYZON* GIRARD

Ichthyomyzon.—*Girard, 1858: 381 (original description). Troschel, 1860: 314 (diagnosis, after Girard). Günther, 1870: 506 (in part; confounded with *Entosphenus*). Jordan, 1875: 228 (misspelled *Icthyomyzon*). Bean, 1882: 119 (recognized, though stated to be a probable synonym of *Petromyzon*). Gill, 1883: 523 (correction of Günther's error). Jordan and Gilbert, 1883*a*: 9 and 868; and 1883*b*: 208. Jordan and Fordice, 1886: 280; and Jordan, 1888: 10, etc. (as subgenus of *Petromyzon*). *Jordan and Evermann, 1896*a*: 9, 10. Jordan, 1899, 1904, 1914: 34). *Regan, 1911: 194, 199. Huntsman, 1917: 24. Jordan, 1919: 291. Borri, 1921: 167. *Creaser and Hubbs, 1922: 3. Rauther, 1924: 678. Hubbs, 1926: 6. Berg, 1931: 89. Holly, 1933: 16. Walls, 1935: 136–146 (visual cells). Pratt, 1935: 25. Pietschmann, 1935: 540.

Scolecosoma.—*Girard, 1858: 384 (based on *Ammocoetes concolor, A. unicolor,* and *A. borealis,* all larvae of *Ichthyomyzon*). *Troschel, 1860: 314 (indicated as based on larvae). *Jordan, 1882: 757, 1001 (accepted and redescribed; then rejected in favor of *Ichthyomyzon*).

Reighardina.—*Creaser and Hubbs, 1922: 4 (as new subgenus). *Jordan, 1929: 7; and Jordan and Evermann, 1929: 9 (as genus). Pratt, 1935: 25 (as genus).

* Important references in the synonymies are starred.

The type species of these 3 nominal genera or subgenera have been designated. Girard recognized no type species for either *Ichthyomyzon* or *Scolecosoma.* After describing *Ichthyomyzon* he definitely referred *Petromyzon planeri, P. lamottenii, P. argenteus,* and *P. appendix* to the genus, then described the two new species *I. castaneus* and *I. hirudo.* These 6 eligible type species are now referred to 3 genera, *Lampetra* (*planeri*), and *Entosphenus* (*lamottenii* = *appendix*), as well as *Ichthyomyzon.* Jordan and Gilbert (1877*b*) somehow forgot this genus in selecting type species for American fresh-water fish genera, but Jordan (1882: 1001), Bean (1882: 119), and Jordan and Gilbert (1883*a*: 9) all selected *Petromyzon argenteus* Kirtland as the type of *Ichthyomyzon.* Jordan and Evermann (1896: 9) and Jordan (1919: 291) have recently confirmed this selection. Therefore

TABLE IV

CHARACTERS OF THE PARASITIC SPECIES OF *ICHTHYOMYZON* AND OF TWO POSSIBLE INTERSPECIFIC HYBRIDS AND OF THE TWENTY OTHER SPECIMENS WITH AN ABERRANT NUMBER OF BICUSPID CIRCUMORALS

The minimum, maximum, and, in bold face type, average values are given for each of the 3 species. The actual determinations are given for all specimens having 1 to 5 bicuspid circumorals, namely the 2 possible interspecific hybrids, respectively *bdellium* × *unicuspis* and *unicuspis* × *castaneus;* 6 specimens of *unicuspis* with 1 or 2 bicuspid circumorals and 13 specimens of *castaneus* with 1 to 5 bicuspids.

SPECIES	*BDELLIUM*	HYBRID?	*UNICUSPIS*							HYBRID?	*CASTANEUS*														
DRAINAGE BASIN	All	Scioto R.	All	L. Erie	Saginaw B.	Saginaw B.	L. Huron	Upper Mississippi R.	Upper Mississippi R.	L. Michigan	L. Michigan	L. Michigan	Upper Mississippi R.	Upper Mississippi R.	L. Michigan	L. Michigan	L. Michigan	L. Michigan	L. Manitoba	L. Manitoba	Upper Mississippi R.	Lower Mississippi R.†	Lower Mississippi R.	L. Michigan	All
CHARACTERS: Myomeres	53 **56.9** 62	55	47 **50.5** 55	50	49	48	09	52	50	51	52	53	52	52	53	55	52	53	52	51	51	52	50	50	49 **52.6** 56
Supraoral cusps	2 **2.6** 3	2	1 **2.0** 4	2	2	2	2	2	2	2	2	2	3	3	2	2	3	2	2	2	2	3	3	2	2 **2.4** 3
Infraoral cusps	7 **8.4** 10	8	5 **7.8** 11	8	9	8	8	6	8	8	8	8	9	8	7	6	9	9	9	9	9	7	9	9	6 **8.3** 11
Teeth in row:																									
Circumoral	19 **20.8** 22	18	15 **19.2** 25	19	20	18	17	18	18	21	21	21	......	22	21	19	21	20	......	......	17	......	......	......	17 **20.8** 25
Anterior	4 **4.3** 5	3	2 **3.2** 4	3	2	3	3	4	3	3	4	5	......	5	4	4	5	5	......	......	4	......	......	......	3 **4.6** 5
Lateral	7 **8.3** 10	7–7	5 **6.6** 8	6–6	6–6	7–8	6–6	6–6	6–7	6–6	9–9	8–8	9–9	9–10	10–10	8–8	8–8	8–8	8–7	9–9	7–7	9–10	8–8	7–7	6 **8.5** 11
Bicuspid circumorals	5 **7.8** 10	3	0 **0.0** 2	1	1	1	2	1	1	4	1	2	3	3	4	4	4	4	4	4	4	4	4	5	1 **6.5** 10
Length of tail	214 **274** 311	310	258 **302** 350	299	297	310	289	310	320	299	287	268	266	266	265	281	276	304	315	250	315	264	......	253	250 **282** 335
Length of snout	75 **86** 94	91	73 **95** 130	111	111	93	98	126	98	91	76	84	81	90	104	84	99	90	82	76	85	103	......	82	75 **90** 109
Length of disk	62 **69** 77	79	59 **86** 118	99	103	88	91	110	90	86	67	75	75	78	88	67	84	82	81	70	82	85	......	72	63 **77** 91
Length over gill openings	77 **89** 107	85	80 **101** 122	98	105	100	96	111	90	103	95	96	100	100	97	95	98	90	89	96	92	92	......	100	83 **94** 114

* Type of *I. castaneus.*
† Type of *I. hirudo.*

Gill's (1883: 523) selection of *Ichthyomyzon castaneus* Girard as the type was invalid. The type of *Scolecosoma* was once indicated by Jordan and Henshaw (1878: 187) as "(*argenteus* Kirt.)," but otherwise always has been designated as *Ammocoetes concolor,* by Jordan and Gilbert (1877*b*: 92), Jordan (1882: 757), Jordan and Evermann (1896*a*: 10), and Jordan (1919: 291; *concolor* wrongly stated to be haplotypic in this reference). The type of *Reighardina* is *Ichthyomyzon fossor* Reighard and Cummins, by original designation.

Scolecosoma was indicated as a synonym of *Ichthyomyzon* by Jordan in 1875 (p. 228), and again in 1882 (p. 1001) in the "Errata" to his *Report on the Fishes of Ohio,* after he had for some unaccountable reason adopted the name *Scolecosoma* for the species of *Ichthyomyzon* while synonymizing *Ichthyomyzon* with *Ammocoetes,* in the body of the text (p. 756), as well as in Jordan and Henshaw (1878: 187). Jordan's act of synonymizing *Scolecosoma* with *Ichthyomyzon* in 1882 was definite and final, for he stated that both genera were based on the same species, and that *Ichthyomyzon* should supersede *Scolecosoma.*

Reighardina appeared to represent a very distinct subgenus when originally described, and it was purely a matter of opinion whether it be recognized as a genus or as a subgenus. The discovery of 2 additional nonparasitic species, however, makes it now appear undesirable to recognize *Reighardina* even as a subgenus. In the first place, the gap between the parasitic and nonparasitic types has been very greatly narrowed, because *I. greeleyi* is much more similar to the already considerably degenerate *I. bdellium,* the type species of *Ichthyomyzon,* than *I. fossor* is to *I. unicuspis.* In the second place, the probably independent origin of the 3 nonparasitic species virtually destroys the apparent value for generic classification of the differences associated with the parasitic habit or lack thereof. *Reighardina* if recognized as either a subgenus or genus for these species would be, on present evidence, a polyphyletic and therefore unnatural assemblage.

Ichthyomyzon appears to us to be a well-defined, homogeneous unit, and probably the most primitive genus among the northern lampreys. From its nearest relative *Petromyzon,* with which it agrees in having the buccal tooth rows radiating in all directions from the esophageal opening and deflected backward toward the margin of the disk, *Ichthyomyzon* differs in the following known respects:

1. The dorsal fin is continuous in both the ammocoetes and adults, often more or less deeply emarginate but never divided into 2 distinct fins as it is in all other lampreys.
2. The dorsal fin is not separated by a sharp notch from the caudal fin.
3. The caudal fin is a broadly oval instead of a rather angular lobe.

4. The lateral circumoral teeth (innermost of disk teeth) are often unicuspid, at least in part, instead of being consistently bicuspid.

5. The bases of the disk teeth are less strongly developed than in *Petromyzon,* and the outer disk teeth show a greater tendency to degenerate.

6. The myomeres are less numerous (fewer than 63 instead of more than 65 between last gill-opening and anus).

7. The body is not definitely mottled.

8. The lateral line sense organs are at least in part blackened (except in *I. fossor*), rather than being entirely colorless.

9. A large size is never attained (the largest specimen examined by us is 328 mm. long to caudal).

Although the genus *Ichthyomyzon* seems well differentiated, it has not been consistently recognized. The history of the recognition and rejection of the genus has been largely that of Jordan's actions, for he was followed closely by ichthyologists in general. *Ichthyomyzon* was first accepted by Jordan as a distinct genus (1875: 228; 1876: 315; and 1877*b*: 377), and was promptly synonymized with *Petromyzon* (1877*a*: 46) and with *Ammocoetes* (1878 *a–e*). In Jordan and Henshaw (1878: 187) he also synonymized *Ichthyomyzon* with *Ammocoetes,* but referred the species of *Ichthyomyzon* to *Scolecosoma.* In 1880 the name *Ichthyomyzon* was once more validated by Jordan (1880: 349), but the species were again referred by him to *Scolecosoma* two years later (1882: 757), though in the addenda to the same work he synonymized *Scolecosoma* with *Ichthyomyzon,* as explained above. In 1883 he (with Gilbert) used *Ichthyomyzon,* then *Petromyzon* for this group, in the same *Synopsis.* In 1884 he returned to *Ichthyomyzon;* in 1885, 1886, etc., to *Petromyzon.* He permanently reverted to *Ichthyomyzon* in 1896, since which time that name has been in general use.

CONFUSION OF *ICHTHYOMYZON* WITH OTHER GENERA

Ichthyomyzon has been confused with *Petromyzon* not only through the synonymizing of *Ichthyomyzon* with *Petromyzon,* but also, occasionally, through erroneous identifications. Thus the records of *Petromyzon concolor* by Wright (1892: 439, Fig. 11) and of *Ichthyomyzon concolor* by Nash (1908: 9; and 1913: 249), from the "Great Lakes" or "Lake Ontario," were based on *Petromyzon marinus,* as shown by Huntsman (1917: 25) and Coventry (1922: 129). Wright's figure of dentition was obviously drawn from a specimen of *Petromyzon marinus.* The provisional reports of *Petromyzon marinus* from Georgian Bay by Bensley (1915: 10) and Toner (1933: 133) were probably based on *Ichthyomyzon unicuspis* (see p. 56). The records of *Petromyzon marinus* from the Mississippi River at Muscatine, Iowa, by Regan (1911: 199) and by Creaser and Hubbs (1922: 10) are now indicated through a further examination of the material to have been based on *Ichthyomyzon castaneus.* The lampreys recorded from sluggish streams of the Ottawa district as *Petromyzon nigricans* by Small (1883: 47) were probably ammocoetes of *Ichthyomyzon unicuspis.* Pratt (1923: 26, Fig. 10; and 1935: 25, Fig. 10), confused by the reference of the name *unicolor* to both *Petromyzon* and *Ichthyomyzon,* employed (see p. 65) a figure of the dentition of "*Petromyzon marinus unicolor*" to illustrate *Ichthyomyzon unicolor = fossor;* this error has been pointed out by Hubbs (1935: 158).

The synonymies of the species of *Ichthyomyzon* and *Entosphenus* have also been confused. That *Petromyzon nigrum* Rafinesque (1820: 84) was based not only on *Entosphenus lamottenii* (*E. appendix*) but also on some *Ichthyomyzon,* probably *I. bdellium,* is indicated by the few significant items in the original description: "Dorsal fins shallow, and distant from each other and the tail"; "A very small species, from four to five inches long"; "It torments sometimes the Buffaloe fish and Sturgeons, upon which it fastens itself." That the name *niger* should not be associated with *Ichthyomyzon* is clear from the circumstance that the name is preoccupied by *Petromyzon niger* Lacépède (1789: 667, Pl. 15, Fig. 2), a synonym of *Lampetra planeri,* as well as from the subsequent history of Rafinesque's name. Kirtland (1838: 170, 197) took no action of consequence, because he based his account of *Petromyzon niger* solely on Rafinesque's description. Jordan (1876: 315; and 1877*c*: 46, etc.) accepted that name for "the common little Black Lamprey of the West," not realizing that there are 3 or 4 such species. Although referred to various genera, the specific name *niger* was thereafter used for some time to designate the supposedly single species of brook lamprey in the United States. Thus *Ammocoetes niger* was the combination used by Jordan and Gilbert (1883: 9), Jordan (1886: 756), and others, to accompany a description best fitting *Entosphenus lamottenii* (*E. appendix*), except for the statement that the dorsals are connected. The name *niger,* however, has never been transferred to or used for a species of *Ichthyomyzon.* In the hope of anticipating any possible exigency, we definitely interpret *Petromyzon nigrum* Rafinesque as a compound of *Entosphenus lamottenii* and *Ichthyomyzon bdellium,* and select *E. lamottenii* as the unit of this complex with which to synonymize Rafinesque's name. In the original description of the genus, Girard referred to *Ichthyomyzon* not only *I. castaneus* and *I. hirudo,* but also *Petromyzon* [*Entosphenus*] *Lamottenii, Petromyzon* [*Lampetra*] *planeri,* and *Petromyzon* [*Entosphenus*] *appendix.* For some unaccountable reason Vaillant (1896: 33) referred "*Petromyzon argenteus* (Kirtland) Jordan and Gilbert" to the synonymy of *Petromyson* [*sic*] *Lamottenii.*

Lampetra has also been confused with *Ichthyomyzon.* Cope (1883: 110) included *Ichthyomyzon* in *Lampetra. Ammocoetes aepyptera* Abbott (1860:

327) was for many years included in the synonymy of *Ichthyomyzon argenteus* [*unicuspis*], as by Jordan (1876: 315), Jordan and Gilbert (1883: 10), and Jordan and Evermann (1896*a*: 11). In his first re-examination of the type specimen Fowler (1901: 328) similarly referred *Ammocoetes aepytera* [*sic*] to *Ichthyomyzon concolor.* On a second re-examination of the type (1908: 465, Fig. 2), he recognized it as representing a distinct species, *Lampetra aepytera* [*sic*]. Evermann and Clark (1920: 306) referred to *Lampetra aepyptera* some ammocoetes from the Lake Maxinkuckee region, which on re-examination prove to refer to *Ichthyomyzon* and presumably to *I. bdellium,* as they are from the Ohio Valley and have 55 or 56 myomeres (not 53 to 55 as counted by Evermann and Clark). The larval lampreys reported from Knox County, Ohio, by Parker, Williamson, and Osburn (1899: 21), and again by Osburn (1901: 15), as *Ichthyomyzon concolor,* on the other hand were presumably *Lampetra aepyptera,* for that species abounds there to the probable exclusion of *Ichthyomyzon.* Both the large larvae from Big Jelloway Creek and the small ones from Sawmill Run were probably *L. aepyptera,* which species closely approaches *Ichthyomyzon* in the low number of segments and in the approximation of the dorsal fins. The two "lampreys" only 2 or 3 inches long, seen by a Mr. J. D. Parker attached to a black bass in Big Jelloway Creek, were more likely leeches, for no lamprey is parasitic at such a size.

The Nomenclature of the Brook Lampreys of Eastern North America Referable to Genera Other than *Ichthyomyzon*

In the preceding paragraphs some alterations from current practice are indicated in the nomenclature of two species of nonparasitic ("brook") lampreys of eastern North America which are not referable to *Ichthyomyzon.* These alterations require explanation.

In their revision of the holarctic lampreys, Creaser and Hubbs (1922) showed that, in addition to the species of *Ichthyomyzon,* there are two nonparasitic species of lamprey in eastern North America, referable respectively to *Entosphenus* and *Lampetra.* For the species of *Entosphenus,* before then usually known as *Lampetra wilderi,* they employed the older and obviously applicable name of *Entosphenus appendix* (De Kay). For the true *Lampetra* they resurrected the name *Lampetra lamottenii* (LeSueur). This application of the name *lamottenii* was apparently justified at that time, when *lamottenii* was known only from LeSueur's plate of *Petromyzon Lamottenii* reproduced by De Kay (1842: 382, Pl. 79, Fig. 249) and Vaillant (1896: 19, Pl. 34); but now our attention is called by Dr. George S. Myers to the hitherto lost original description of *Petromyzon Lamottenii,* published by LeSueur (1827: 9–10, Pl. 6) in one of the rarest works on American ichthyology. We reproduce this description:

PETROMYZON

P. Lamottenii. Body subcylindric, a little dilated in the middle, attenuated towards the tail, rounded and obtuse anteriorly.

Disk circular, margined with many ranges of small, more or less foliaceous appendices; inner surface destitute of teeth in some specimens and having only radiated lines; in others the small teeth are hardly sensible, but are sufficient to indicate the generic affinity; base of the disk with two strong teeth, one above and one below; the former arquated, furnished in some specimens, with two tubercles, obtuse, conical; in others the tubercles are truncated and cutting; inferior tooth arquated, larger than the superior one, mutic or crenulated according to the age of the individual or to the state of the subcorneous substance which covers it. In the male the small, lateral teeth are bi- or trituberculate.

Tongue bilobated; *aperture of the nostril* frontal, in advance of the eyes in the center of a small disk.

Dorsal fins arquated; in the male second dorsal, more elevated, furnished with small rays, united with the caudal and in both sexes leaving a small emargination at the junction with the first dorsal; *anal* less elevated, originating at the anus; *vulva* exterior; *penis* distinct and prominent.

Branchiae enclosed in a sack, open at its extremities; each with 30 lamellae, which are attached by the middles to the inner opening, whilst the remaining part flotes towards the exterior opening; back yellow, marbled with olive; sides and belly white.

Length from 5 to 5 and a half inches.

This species is allied to the present genus by the form of the body and by the seven lateral branchial apertures, but it differs by its long anal fin and by the junction of the two dorsals which are separate in other species. It approaches the *P. argenteus*, BlXII. 415.

It inhabits briskly running waters, attaching itself to rocks which receive cascades; whence it immediately recedes when approached. As its vision is very good, it is necessary to be quick in attempting to seize it, in order to secure it. Of seven individuals which we obtained, but one was a male; the others contained numerous eggs. The water over the rocks on which we observed them, was from 2 inches to 7 feet deep; in a cave formed by the rapid current and secluded from the rays of the sun. We designated this cave by the name of the proprietor, Mr. Wilkinson, it consists of a superposition of sand stone, on scienite and diabase, and will receive a more particular description in an account of an excursion made in April 1820 by Dr. Troost and myself to the Lamotte mine in Missouri. My specific name is that of Lamotte, one of the companions of Renault, who discovered this mine in 1720 when the French possessed that country.

The figure respresents the natural size. The Disk is that of an individual destitute of the small teeth.

A variety of reasons makes it now seem extremely probable that LeSueur's "*Petromyzon Lamottenii*" was based on the species of *Entosphenus* currently known as *E. appendix* (or *Lampetra wilderi*):

1) The *Lampetra* is known only from the upper Ohio Valley, where it is common, and from one locality (Laurel Run) in eastern Maryland; in Ohio it is even confined to the Appalachian foothills. The *Entosphenus* occurs through the West. The type locality of *Petromyzon Lamottenii,* the cave designated by Troost and LeSueur as Wilkinson Cave, is obviously (from

the context) near "the Lamotte mine in Missouri," now Mine Lamotte, Jackson County, Missouri, in the St. Francis River system. Gray (1851*a*: 238 and 1851*b*: 142) erred in attributing *Lampetra Lamottenii* to New York.

2) The date of April for a spawning population fits better for the *Entosphenus* than for the *Lampetra,* which would likely spawn in March if it occurred in Missouri.

3) Some specimens of the *Entosphenus,* especially poorly preserved ones, show tooth scars very poorly, while the disk is marked by radiating lines, more distinctly than in the *Lampetra* specimens examined. These lines, extending across the posterior field of the disk, run between the teeth of the posterior ring series as well as between the marginals. Therefore the specimen figured by LeSueur now appears to have lost its corneous teeth before it was pictured. In LeSueur's male specimen the "lateral teeth are bi- or trituberculate"—as LeSueur would hardly have been expected to observe in the *Lampetra.*

4) The fins as described fit *breeding* specimens of the *Entosphenus* as well as those of the *Lampetra.*

5) The mottled color, as figured and described by LeSueur, we have now found in the *Entosphenus* as commonly as in the *Lampetra.*

6) The statement on habits applies much better to the *Entosphenus* than to the little *Lampetra.*

Consequently *Entosphenus appendix* (De Kay) becomes *E. lamottenii* (LeSueur), and *Lampetra lamottenii* (LeSueur) becomes *L. aepyptera* (Abbott).

SPECIFIC NAMES BASED ON THE AMMOCOETE STAGES OF *ICHTHYOMYZON*

It now seems inadvisable to adopt for any of the 6 species of *Ichthyomyzon* either of the 2 names in current use, *concolor* or *unicolor,* despite the fact that those specific names, and *borealis* as well, were obviously based on some species of *Ichthyomyzon,* and are all older than any of the 6 names adopted. These names are left unused because they were based on the ammocoete (larval) stage, in which none of the specific features of mouth structure are apparent. Even if the types were found, a re-examination would not likely yield definite identification. Now that 6 instead of 2 or 3 species of *Ichthyomyzon* are recognized, it becomes very difficult or impossible to indicate what species is represented, from distributional reasoning. More accurate delineation of range in the future can hardly furnish decisive evidence, because we cannot be sure what the distribution was in the period from 1841 to 1850, when these names were proposed. The earliest name, *concolor,* is particularly doubtful, because it was named from the Ohio Valley where at least 3 species (*unicuspis, bdellium,* and *greeleyi*) occur. The second name, *unicolor,* was based on specimens from Lake Champlain, which *unicuspis* alone is now known to inhabit, though *fossor* may occur or might have occurred there. The type locality of *borealis* is Michipicoten, Ontario, in the Lake Superior basin from which both *unicuspis* and *fossor* are known. Creaser and Hubbs (1922: 8–11) thought that these names could be identified on the basis of distribution, size attained as ammocoetes, presence or absence of black spots, and shape, but fuller evidence now available does not indicate that these criteria are really determinative.

The first mention of any ammocoete of *Ichthyomyzon,* or indeed of any specimen of this genus, was by Kirtland (1838: 170, 197), who recorded from the Mahoning River, Ohio, under the name of *Ammocoetes bicolor,* some larval specimens which were presumably those that later served as part of the types of *Ammocoetes concolor* (1841: 473, Pl. 27, Fig. 1). The specimen figured by Kirtland in 1841 was stated to be one of a lot from the vicinity of Columbus, Ohio, a locality later more specifically given by Kirtland (1851: 213) as "a small pond on the farm of Joseph Sullivant, Esq., near Franklinton, in Franklin Co., Ohio" (now within the city of Columbus, on the lowlands on the west side of the Scioto River). This specimen, probably no longer extant, we designate as the type, thus restricting the type locality to the vicinity of Columbus. Judging from present distributional evidence the species of *Ichthyomyzon* which most probably would have been taken there almost a century ago is *I. bdellium,* but it might well have been either *I. unicuspis* or *I. greeleyi*; there is no means of deciding now which species was represented. The species most likely to have been taken in the Mahoning River is *I. greeleyi,* for most of our specimens of that species come from the same stream system in Pennsylvania, only a few miles away. *I. bdellium* probably also occurred in the Mahoning in 1838, and *I. unicuspis* might well have penetrated upstream that far. The only seemingly logical course is to regard the name *concolor* as specifically unidentifiable.

Plummer (1848: 54) also reported, as *Ammocoetes bicolor,* some lamprey larvae from near Richmond, Indiana. The original *Ammocoetes bicolor* LeSueur, 1818 (see LeSueur, 1827: 41, Pl.; De Kay, 1842: 383, Pl. 79, Fig. 248; or Vaillant, 1896: 19, Pl. 35), from the Connecticut River at or near Northampton, was presumably the ammocoete of *Petromyzon marinus,* but possibly the larva of *Entosphenus lamottenii* (geographical distribution and the separation of the dorsal fins exclude other possibilities). Incidentally, the name *bicolor* is preoccupied in *Petromyzon* by *P. bicolor* Shaw (1804: 263), a synonym of *Lampetra planeri.*

The subsequent history of the name *concolor* may be recited. Thompson (1842: 150) described from Winooski River, a Vermont tributary of Lake Champlain, under the name *Ammocoetes concolor,* some larvae of *Ichthyomyzon* which have subsequently been identified as *Ichthyomyzon concolor* [meaning *unicuspis*] by Evermann and Kendall (1896: 580, 584; and 1902*a*:

219, 222) and by Kendall (1908: 2). Storer (1846: 519) and Gray (1851*a*: 241; and 1851*b*: 146) accepted *Ammocoetes concolor* on the basis of Kirtland's original account. Later it became known that the forms of *Ammocoetes* merely represent the larval stage of the several genera of lampreys. Jordan (1885: 792), expressing his opinion that names based on ammocoetes of *Ichthyomyzon* are not definitely identifiable, avoided using *concolor* in place of *argenteus,* then shown to be preoccupied. In the addenda to the same work (on p. 973), however, Jordan unfortunately reversed his opinion and adopted the name *Petromyzon concolor* in favor of his substitute name *P. bdellium.* Subsequently the name *concolor* was generally used for 1, 2, or 3 of the parasitic species of *Ichthyomyzon,* except by Regan (1911: 199)[2] and Huntsman (1917: 25).

The second larval *Ichthyomyzon* to be distinctively named was *Ammocoetes unicolor* De Kay (1842: 383, Pl. 79, Fig. 250), from Lake Champlain. Referring to this form Kirtland (1851: 213) remarked rather prophetically:

> Can any person point out an essential specific difference between the above species [*Ammocoetes concolor*] and the *A. unicolor,* which De Kay has described several years subsequent to the publication of our description?

Gray (1851*a*: 241; and 1851*b*: 146) accepted *A. unicolor* as a distinct species. The resurrection of the name *unicolor* by Jordan (1885: 973) for the landlocked form of the sea lamprey, in the combination *Petromyzon marinus unicolor,* was obviously erroneous, although followed by most subsequent authors. In the first place the sea lamprey is unknown in Lake Champlain (see Evermann and Kendall, 1902*a*; and Kendall, 1908: 2), where the occurrence of *Ichthyomyzon* [*unicuspis*] is now well authenticated (Greeley, 1930: 73). In the second place De Kay's account and figure almost certainly indicate that he had a species of *Ichthyomyzon,* with connected dorsal fins. Evermann and Kendall (1896: 580, 584), specifically treating the records by De Kay and by Thompson, referred *Ammocoetes unicolor* De Kay to *Petromyzon marinus unicolor* and *Ammocoetes concolor* Thompson to *Ichthyomyzon concolor,* despite the fact that the type of *unicolor* was almost certainly one of the specimens identified by Thompson as *concolor. Ammocoetes unicolor* was later identified by Evermann and Kendall (1902: 218) with *Ichthyomyzon concolor.* Huntsman (1917: 26) also disclaimed the pertinence of *unicolor* to *Petromyzon.* Kendall (1908: 2) reverted approximately to the views expressed by Evermann and him in 1896, referring *Ammocoetes unicolor* De Kay to *Petromyzon unicolor* and *Ammocoetes concolor* Thompson to *Ichthyomyzon concolor.*

Since Creaser and Hubbs (1922: 9) identified *unicolor* with another species of *Ichthyomyzon,* namely *I. fossor* Reighard and Cummins, that non-

[2] Regan, however, went entirely too far in stating that no differences are evident between the larva described by Kirtland as *Ammocoetes concolor* and that of *Lampetra planeri.*

parasitic species has generally been known as *I. unicolor*. We now believe, however, that there is no sound reason for associating the name *unicolor* with that species. Records of *Ichthyomyzon unicolor* based on ammocoetes from Madrid, New York (Creaser and Hubbs, 1922: 8), and from Maple River, Michigan (Creaser and Brown, 1927: 101) are not definitely identifiable. The application of the name *unicolor* to species of 2 genera, *Petromyzon* and *Ichthyomyzon* is confusing. Pratt (1923: 26, Fig. 10; and 1935: 25, Fig. 10), for instance, used a figure of the dentition of *Petromyzon marinus unicolor* to illustrate "*Ichthyomyzon unicolor.*"

The third name applied to an ammocoete of *Ichthyomyzon* was *Ammocoetes borealis* Agassiz (1850*a*: 252), from Michipicoten, Ontario, on the northeast shore of Lake Superior. The description of the dorsal fin as continuous assures the accuracy of the reference of *borealis* to *Ichthyomyzon*, but whether the types were larvae of *fossor*, as thought by Creaser and Hubbs (1922: 9), or of *unicuspis*, now seems indeterminable. *Ammocoetes borealis* Agassiz is not to be confused with *Petromyzon borealis* Girard (1858: 377), which was based on *Petromyzon fluvialis* Richardson (1823: 705, and 1836: 294). The relationships of that species were indicated by Richardson's statement that it looks like Bloch's figure of *Petromyzon argenteus* [=*Lampetra fluviatilis*] and that it has the dentition of *Petromyzon fluvialis* [=*Lampetra fluviatilis*]. Bean (1881: 159) referred *P. borealis* doubtfully to the synonymy of his *Ammocoetes aureus*, which Creaser and Hubbs (1922: 9) indicated as a synonym of *Entosphenus japonicus* (Martens, 1858). The best provisional disposition of *Petromyzon borealis* Girard, 1858, is to place it also in the synonymy of *Entosphenus japonicus*.

Ammocoetes surely or probably of *Ichthyomyzon* have been identified as *Lampetra aepyptera* as explained on page 22, and as *Ammocoetes brachialis*, for instance by Meek (1891*a*: 116). Woolman (1895: 369) even recorded adults of *Ichthyomyzon* (*castaneus*, and perhaps *unicuspis* in part) as *Ammocoetes brachialis*, the name used for European ammocoetes.

Ammocoetes from Wisconsin unidentifiable as to species have recently been recorded by Greene (1935: 21) as *Ichthyomyzon*. In the same category we now place the ammocoete from Whitcomb Creek, near Symco, Wisconsin, recorded by Greene (p. 22) as *I. castaneus*.

Methods of Counting and Measuring, and an Evaluation of the Characters Used, with a Comparison of the Species on the Basis of Each Character

We have found 19 characters or sets of characters to be of greater or lesser value in distinguishing between the 6 species of *Ichthyomyzon*. We here define each of these characters; describe the method by which each was counted, measured, or otherwise determined; point out difficulties and sources of error in the determinations; discuss individual variability in each character; make clear the variations which occur with stage of development; and evaluate each character from the standpoint of systematics.

Nearly all of the counts and measurements were made by the junior author.

NUMBER OF MYOMERES (Fig. 1).—The muscle bands (myomeres = myo-

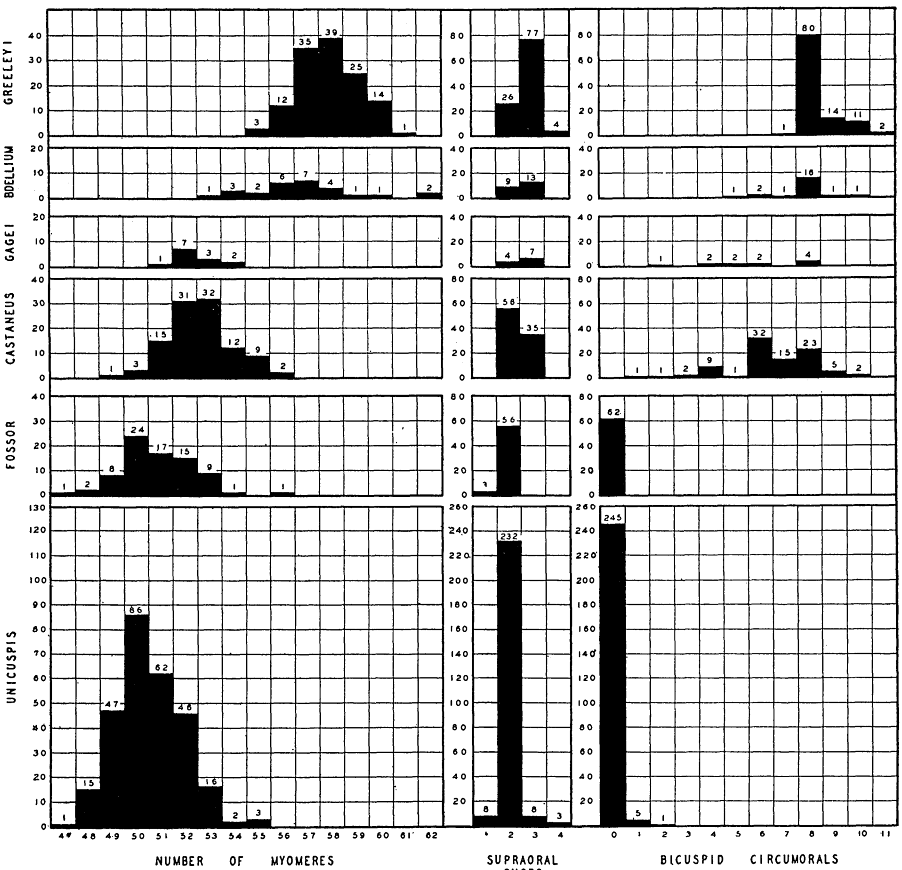


FIG. 1. Myomere and tooth characters in the species of *Ichthyomyzon*. The histograms and the figures for each species show the frequency distribution of the given counts.

tomes), not the intermuscular septa (myocommata), were counted between the last gill-opening and the cloaca. The first myomere counted is the one whose posterior septum passes distinctly and entirely behind the groove which surrounds the fringed margin of the last gill-opening, so as to leave a definite though often narrow band of muscle between the groove and the septum. The last myomere counted is the one whose lower posterior angle lies in part or wholly above the cloacal slit.

The myomeres are often difficult to count in preserved specimens because they tend to become hidden by the thick skin or by mucous secretions, especially in larger specimens; in that event the myomere boundaries can be made more distinct by scraping the skin toward the tail. The myomere count is often made difficult also by the shriveling of the body to produce subvertical creases down the middle of some or all of the myomeres; manipulating the specimen and keeping in mind the normal width of a myomere makes it possible to count specimens showing these false creases. Due to these various difficulties, a source of error exists which may lead to a miscount of 1 myomere, or possibly 2, in some specimens.

The number of myomeres exhibits rather wide individual variations in each species, but seems to show no significant age variations. The count in ammocoetes, which can be made with more facility than in the adult, appears to be identical with that of the adult in all species. The average and the usual numbers of myomeres (Fig. 1) are of prime importance in the separation of the 3 pairs of species of *Ichthyomyzon,* but do not serve to distinguish the parasitic and nonparasitic members of each pair.

Supraoral Cusps (Fig. 1).—The number of cusps on the supraoral lamina usually is easy to determine, but care is occasionally required in counting a small cusp lying along the side or at the base of a large cusp, on one or both sides. Such small cusps are counted, even though they appear irregular and supernumerary. A cusp distinctly divided at its tip is counted as 2. Most of the specimens of *unicuspis* with more than 1 or 2 supraoral cusps show some degree of irregularity in this character. No age variations are indicated, except for the tendency, shared with all of the teeth, for the supraoral cusps to become blunt in the spawning season. The lack of age variation in the number of cusps on the supraoral, and also the infraoral lamina and other teeth, is due to the method of tooth replacement in the lampreys: each new tooth, formed as the core of its predecessor, is the image of the former tooth which is sloughed off as a hollow corneous structure. The number of cusps is a good though only average specific character.

Infraoral Cusps (Fig. 2).—The number of cusps on the infraoral lamina is usually easy to determine, though care is needed to observe all the tips, as for the supraoral cusps. The count is very difficult to obtain, however, in specimens which are not completely transformed, and in all examples of *fossor*. In such specimens the count is most readily made while a jet of compressed air is played on the disk, for during the early stages of desiccation the tooth tips become visible, even though buried in the gum. (This method of examination is valuable in examining all of the teeth, especially in detecting all of the distal teeth in the anterior and lateral rows.) Considerable individual variation, but no age variation, was noted in the number of infraoral cusps (Fig. 2). This character, in contradiction to the claims of earlier workers, proves to be of only very slight average significance.

TEETH IN CIRCUMORAL ROW (Fig. 2).—The innermost disk teeth forming the circumoral row as counted include the 4 (sometimes 5) laterals of each side, which are at the edge of the esophageal opening (a small accessory tooth, occasionally developed at the edge of the esophageal opening inside the laterals, is not counted); the 1 to 4 teeth connecting the anteriormost lateral of each side in an arc just in advance of the supraoral cusp; and the

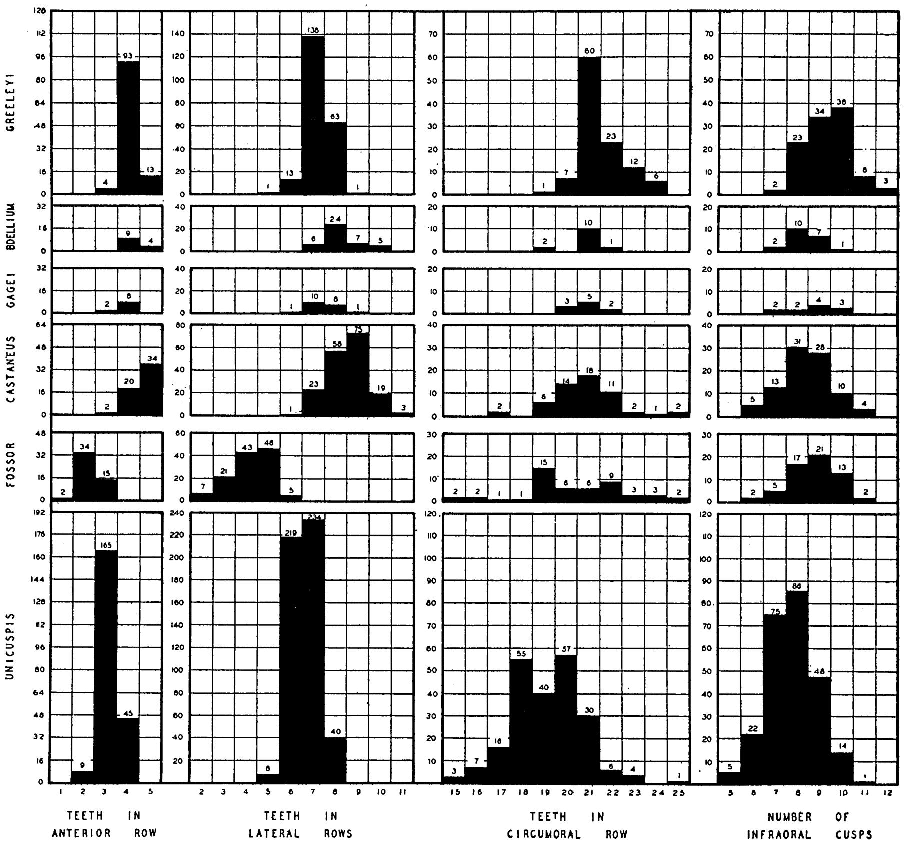


FIG. 2. Tooth characters in the species of *Ichthyomyzon*. The histograms and the figures for each species show the frequency distribution of the given counts.

several teeth forming a similar posterior connective arc lying close to and paralleling the infraoral lamina. The basic number of circumorals seems to be 15, including 1 anterior tooth, 4 laterals on each side, and 6 in the posterior connective series. Increases in the number of teeth in the posterior series are brought about either by an increase in the number of rows which end in these posterior circumorals or by a complete doubling of the base of 1 or more of the teeth. Increases in the number of teeth in the anterior connective series are brought about by the interpolation of new rows from the anterior end of the disk. As new teeth are added here, the V-shaped rows of the anterior field (see Pl. II) move backward. The first step comes when the apex of the V, represented by a median tooth, moves behind the supraoral lamina so as to eliminate this median tooth, causing the tooth on either side in the V to come in contact with the supraoral, and to enter into the circumoral count. The next step is accomplished when the median tooth representing the apex of the next anterior V becomes interpolated between the 2, so as to give a count of 3 in the anterior portion of the circumoral row, when the interpolation has proceeded far enough to bring the posterior edge of this median tooth behind the arc connecting the centers of the circumoral teeth. When this median tooth becomes eliminated by a further increase in the number of rows, the count is increased to 4.

In all fields of the disk only those circumorals are counted which lie at the inner end of a tooth row, thus avoiding the inclusion of 2 teeth aligned in any one row, even though both seem at first sight to lie next to the esophageal opening; this criterion needs especially to be applied about the ends of the infraoral lamina; an exception to this criterion is made of the rare circumoral teeth the bases of which are doubled. Constant consideration of this method of tooth increase, and of the criteria stated above, has allowed this count of the teeth in the circumoral row to be made with small possible error. Considerable individual variation but no age variation seems to occur in the number of teeth in this or any other row: the whole tooth pattern is permanently laid down at the metamorphosis. Although exhibiting wide overlapping in frequencies the number of teeth in the circumoral row of the several species (Fig. 2) shows good average differences, significantly separating *unicuspis, fossor, castaneus,* and *greeleyi*; the few counts for *gagei* and *bdellium* are similar to those for *castaneus.*

TEETH IN ANTERIOR ROW (Fig. 2).—The teeth counted as the anterior disk row are those which lie along the mid-line and thus form the apexes of the **V**-shaped rows of the anterior field (1 or 2 of the anteriormost teeth in the row often lie in advance of the apex of the first **V**). The posterior tooth of the anterior row as counted is not enumerated as one of the circumoral series, when the teeth in the anterior connective portion of the circumoral row form an even (paired) number; but when a median anterior tooth in the circumoral series is developed, to complete a **V**, it is also counted in the anterior row. The chief difficulty in making an accurate count of the teeth in the anterior row lies less in any irregularity of the **V**-pattern than in the tendency of the anteriormost (outermost) tooth to degenerate so far as to lie concealed in the gum. Unless the anterior tooth became visible under the microscope when a jet of compressed air was used, it was not counted; that is, dissection was not employed to detect rudimentary outer teeth wholly invisible on external examination. Occasional dissections showed that such hidden teeth are sometimes developed in all species, normally so in the very degenerate *fossor*. This character also shows much individual but apparently no age variations. It yields average numbers (Fig. 2) of considerable systematic value.

TEETH IN LATERAL ROWS (Fig. 2).—The lateral rows chosen to represent the number of the teeth at the side of the disk are those rows which originate in the circumoral tooth of each side that lies opposite the supraoral lamina, ordinarily the anteriormost lateral. Since the row of each side is counted separately, twice as many counts are obtained for this character as for any other. Care is necessary to include all of the outermost teeth, not only because they tend to degenerate just as do the outermost teeth of the anterior series (see discussion above), but also because the outer end of the row is often so sharply deflected backward as to appear a part of the next posterior row (these deflected ends of the lateral rows comprise the marginals in *Ichthyomyzon*). The number of teeth in the lateral rows shows considerable individual variation, but provides average numbers which are distinctive of the several species.

BICUSPID CIRCUMORALS (Fig. 1).—A variable number of circumoral teeth in *Ichthyomyzon,* unlike any of the other teeth with the exception of the supraoral, often show 2 cusps instead of the usual single cusp. Ordinarily the double cusps are confined to 4 pairs of laterals, occasionally to 5 pairs of laterals; more rarely the circumoral just behind the last lateral or the one just before the first lateral (rarely both of these on one side) is also bicuspid. The number of bicuspid circumorals varies from 0 to 11 (all bicuspids of both sides are given in the single count for each specimen). Teeth are enumerated as bicuspid even when the second cusp is only a slight projection at the base or side of a main cusp, or when an essentially single cusp is distinctly, though only slightly, divided at its tip. It is necessary to determine that the 2 cusps arise from a common base, to avoid enumerating pairs of closely adjacent unicuspid teeth as bicuspids. In examining these and other teeth it is well to first remove excess mucus, then to examine the teeth under a binocular microscope while a jet of compressed air is used. There is every reason to believe that the number of bicuspid teeth is fixed when the teeth are formed during metamorphosis. The outstanding systematic value of the number of bicuspid circumorals has already been indicated (pp. 14–18).

TRANSVERSE LINGUAL LAMINA (Fig. 3).—The form of the transverse lingual lamina,[3] its size and degree of cornification, and the size, number, and degree of development of the cusps on this lamina, best observed under a rather high magnification as air is blown into the mouth, provide a set of

[3] This is the tongue plate, usually known as the anterior lamina. It does lie in advance of a pair of longitudinal ("posterior") laminae when the tongue is retracted in the mouth, but is the more posterior when the tongue is protruded as it is when functioning as a rasping organ. Contrary to the statement of Reighard and Cummins (1916: 11), copied by Creaser and Hubbs (1922: 4), lingual laminae are essentially alike in number and position in all species of *Ichthyomyzon*.

characters of outstanding value in the distinction of the species of *Ichthyomyzon.* In *unicuspis,* typically, the lamina is definitely bilobed, since the base of the plate as well as the cuspidate edge is usually strongly angled forward on the median line; this feature is usually so marked that the tooth edge appears to consist of 2 separated crescents, although close inspection shows that the 2 arcs are connected along a complete though narrow U-shaped line; rarely the lamina is only weakly bilobed in *unicuspis,* and is almost strictly linear in 1 specimen; the lamina of *unicuspis* is relatively large and strongly cornified, and bears a very large number of relatively

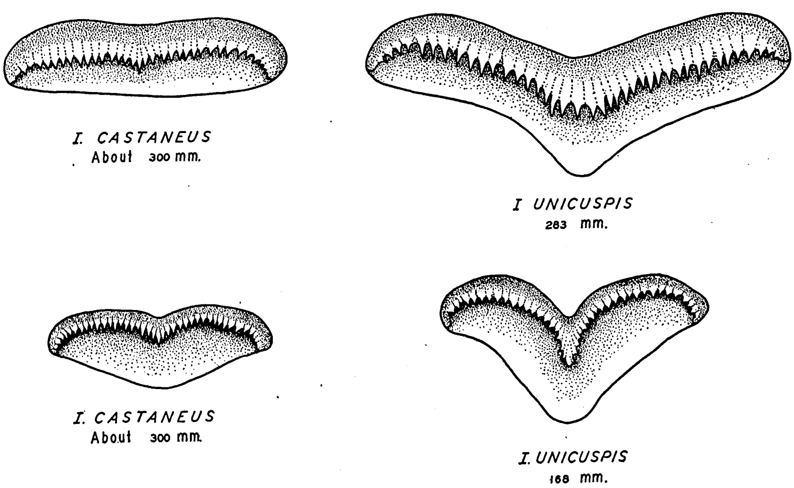


FIG. 3. Transverse lingual lamina in the species of *Ichthyomyzon.* There are illustrated an average and a rather strongly-curved lamina for *castaneus,* and a rather weakly-curved and a strongly-curved one for *unicuspis.* Note relatively larger size of lamina in *unicuspis.* Drawn by Luis Howell Rivero; × 20.

short, needle-like cusps. The transverse lingual lamina of *castaneus* is usually weakly bilobed or almost strictly linear, very rarely deeply indented along the mid-line (the difference in form is sufficiently consistent to distinguish about three-fourths of the specimens of each form on the basis of this character alone); the lamina is usually much smaller and weaker than in *unicuspis* (see figures), and the teeth tend to be fewer and longer. The lamina of *bdellium,* in contrast with that of *castaneus,* is bilobed, often as deeply as in the average *unicuspis;* the plate is rather weaker and narrower than in *unicuspis,* and has fewer though longer cusps.

The transverse lingual laminae of the 3 nonparasitic species show differences comparable and parallel to those exhibited by the parasitic species. That of *fossor* is consistently bilobed, as usually in *unicuspis,* but is extremely small and weak, often without cusps and sometimes even without any apparent cornification, never with such a strong horny sheath as in the parasitic species; the cusps when developed are small and numerous, likewise as in *unicuspis*. The lamina of *gagei* is linear or very weakly bilobed, indicating relationship with *castaneus;* it is very small, scarcely or not at all cornified and bears no apparent cusps (at least in the few specimens in the Michigan collection). The lamina of *greeleyi* is the least degenerate of any possessed by a nonparasitic species, for it is consistently more or less strongly cornified and denticulate; the lamina in this species is always bilobed, as in *bdellium* and *unicuspis;* the denticulations are relatively few and long, suggesting relationship with *bdellium* rather than *unicuspis*.

Form and Strength of Disk Teeth (Pl. II).—The form and strength of the teeth are determined by inspection under a binocular microscope. The teeth of course are first formed during metamorphosis. They remain sharp (except in the extremely degenerate *fossor*) until the spawning period, during which they become blunter. The teeth vary in strength and length as well as in form. In *unicuspis* they are strongest, but tend to be rather short and not very acutely pointed, and are usually only slightly bent backward. On the average they are slenderer, longer, sharper, and more curved in *castaneus,* and this tendency is carried to an extreme in *bdellium*. In *fossor* the teeth are extremely weak, low, blunt, and not curved, often are concealed in the gum, and are obsolescent on the posterior part of the disk. In *gagei* the teeth resemble those of *castaneus,* but are much weaker, tending to become obsolescent posteriorly. In *greeleyi* the teeth are remarkably sharp, long, slender, and strongly curved for a nonparasitic species, often showing no very striking degeneration from the condition observed in *bdellium,* except on the outer and posterior parts of the disk, where tooth degeneration is greatest in lampreys. Usually, therefore, the form and strength of the teeth provide good specific characters.

Total Length.—The total length is employed instead of the standard length, because the notochord and flesh extend almost to the end of the caudal fin, and because the total length can be the more easily and accurately obtained. In taking this over-all measurement, care is observed to manipulate the specimen so as to compensate for any twisting or unusual shriveling caused by preservation. Without resorting to an undesirable though readily accomplished stretching of the specimens, it seems impossible to compensate for the very considerable shrinkage undergone by these boneless creatures. This shrinkage during initial hardening in formalin and subsequent preservation in alcohol amounts, according to a few test measurements, to about 10 mm. in a 300 mm. lamprey. The decrease in length seems due almost equally to a relatively uniform shrinkage in the trunk and tail region and to a greater shriveling and puckering of the disk region. In consequence most of the length measurements given are smaller than in life. Some specimens, originally preserved in alcohol, or kept for years in weakened alcohol, or preserved in formalin after the lamprey had died or become weakened, are on the contrary very flabby, and perhaps are as long or even longer than in life. To make the measurements as comparable as possible, we have allowed practically all specimens to remain in alcohol a month or more before measuring. It would have been much more satisfactory to have anesthetized the specimens before a very careful hardening and preservation. All other measurements are expressed as thousandths of the total length. The total length measurements in themselves (Fig. 4) are of value in distinguishing between the species, especially between the parasitic and nonparasitic species in each of the 3 pairs.

LENGTH OF TAIL (Fig. 4).—The tail length is measured in a straight line

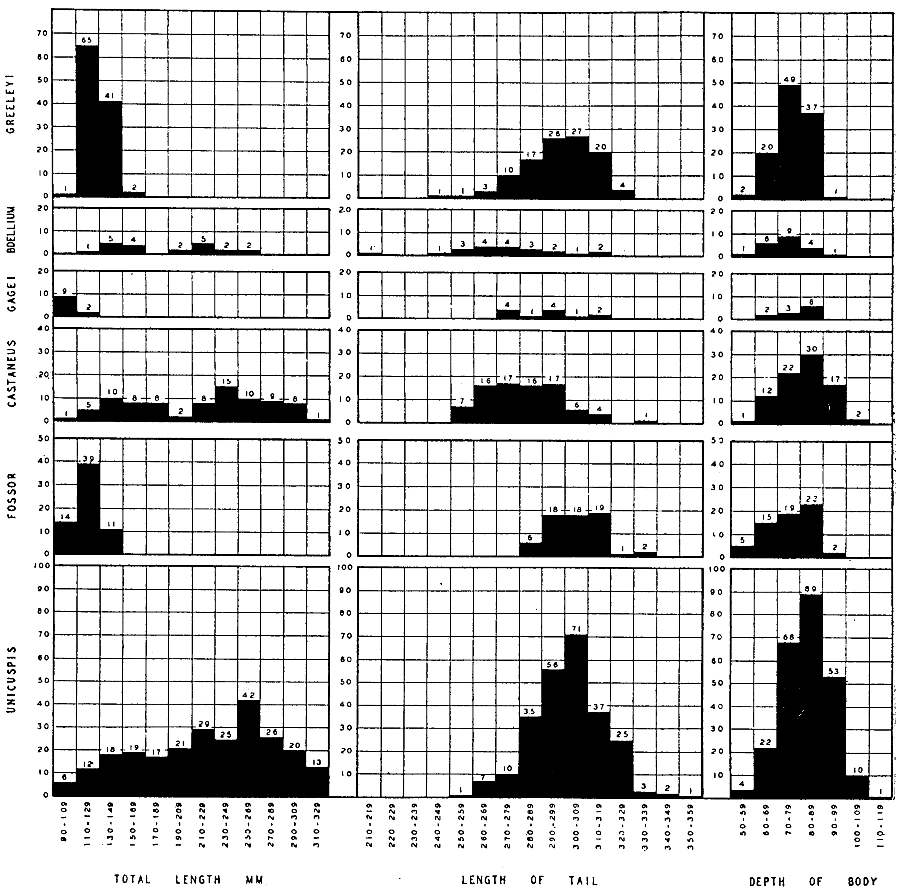


FIG. 4. Total length measurements, and length of tail and depth of body in thousandths of total length, in the species of *Ichthyomyzon*. The histograms and the figures for each species show the frequency distribution of the measurements, for adult specimens.

from the inner anterior edge of the cloacal slit (in advance of the genital papilla when evident) to the extreme tip of the caudal fin. This measurement is made with ease and with small probable error. The tail length shows much individual variation, but the average values seem to be of specific significance.

DEPTH OF BODY (Table V; Fig. 4).—The depth of the body is the greatest vertical measurement just anterior to the origin of the first dorsal fin. The measurement is readily made, but is subject to marked individual fluctuation. Heavily fed lampreys, turgid with blood, are much deeper than ones empty of food. The depth becomes greater with age (Table V). Gravid individuals are about one-fourth to one-third deeper than immature or spent ones. The differences in depth due to age and maturity very largely overshadow the specific differences. (Compare data in Table V with that in Fig. 4.)

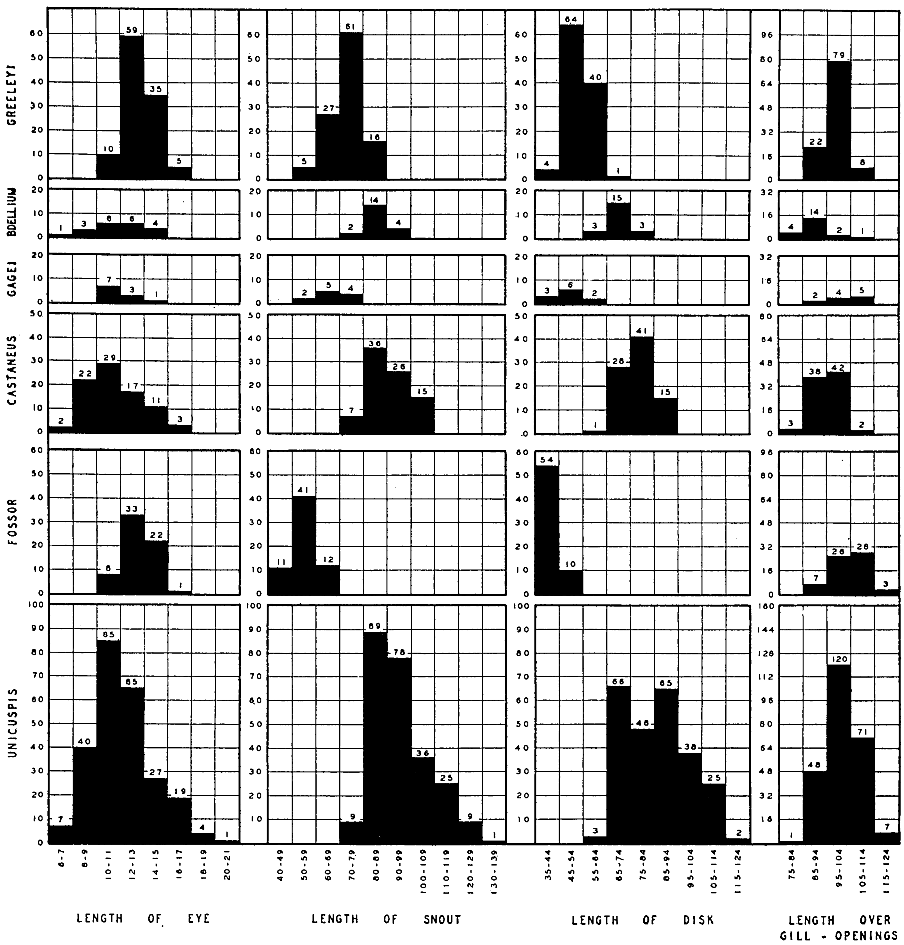


FIG. 5. Proportionate measurements, in thousandths of total length, in the species of *Ichthyomyzon*. The histograms and the figures for each species show the frequency distribution of the measurements.

TABLE V

AGE VARIATION IN DEPTH OF BODY IN THE SIX SPECIES OF *ICHTHYOMYZON*

Measurements in thousandths of total length. For each 30-mm. size class of each species there is given the minimum, maximum, and (in italics) the average value, and the number of specimens as the inferior figure.

Length, mm.	*unicuspis*	*fossor*	*castaneus*	*gagei*	*bdellium*	*greeleyi*
91–120	56–88 $\mathit{67}_{14}$	50–93 $\mathit{75}_{40}$	60–75 $\mathit{66}_{5}$	63–85 $\mathit{78}_{10}$	....	60–85 $\mathit{75}_{14}$
121–150	54–89 $\mathit{71}_{21}$	52–91 $\mathit{71}_{25}$	59–81 $\mathit{70}_{11}$	.... $\mathit{67}_{1}$	55–92 $\mathit{69.5}_{6}$	59–90 $\mathit{76}_{93}$
151–180	64–84 $\mathit{74}_{29}$	....	66–88 $\mathit{75}_{12}$	....	67–72 $\mathit{69}_{14}$	84–88 $\mathit{86}_{2}$
181–210	65–105 $\mathit{83}_{29}$	....	69–92 $\mathit{82}_{5}$	....	72–73 $\mathit{72.5}_{2}$	....
211–240	70–105 $\mathit{87}_{36}$	....	64–109 $\mathit{88}_{16}$	....	64–84 $\mathit{75}_{5}$	....
241–270	65–115 $\mathit{87}_{51}$	....	74–100 $\mathit{87}_{17}$	....	76–83 $\mathit{80}_{4}$	....
271–300	78–103 $\mathit{86}_{37}$	....	73–97 $\mathit{86}_{11}$	....	....	....
301–330	72–103 $\mathit{87}_{19}$	....	80–90 $\mathit{85}_{7}$	....	....	....

LENGTH OF EYE (Table VI; Fig. 5).—The horizontal diameter of the eye is rather easy to measure in breeding adults of the nonparasitic species, but is difficult to measure in the parasitic ones, in which the eye not only lacks any orbital rim, but also is flattened out and apparently overgrown with skin. The eye, as usual in fishes, decreases in relative size with age (Table VI). The age variation is greater than the species differences (Fig. 5). The eyes of the adults of the nonparasitic species are proportionately larger than those of the adults of the parasitic species, but are no larger, probably on the average smaller, than those of young of the latter, which are of the same size as the adults of the nonparasitic species. *I. gagei* seems to have slightly smaller eyes than either *fossor* or *greeleyi*. At comparable sizes, the eyes of the 3 parasitic species are of the same average size (Table VI).

LENGTH OF SNOUT (Table VII; Fig. 5).—The length of the snout is measured with dividers from the front of the eye to the anteriormost point of the snout. The measurement is readily taken, but is subject to enormous fluctuations caused by differential shriveling in preservation, particularly in *I. unicuspis,* the species with the longest snout. Live individuals and specimens preserved in weak alcohol show extremely long snouts, those preserved in rather strong formalin have markedly shortened snouts. The high average value for the proportionate snout length shown by the unshrunken specimens from the Upper Mississippi Valley, namely 0.111 of the total length, contrasts sharply with the value of 0.089 for the rather shriveled specimens from the

TABLE VI

AGE VARIATION IN LENGTH OF EYE IN THE SIX SPECIES OF *ICHTHYOMYZON*

Measurements in thousandths of total length. For each 30-mm. size class of each species there is given the minimum, maximum, and (in italics) the average value, and the number of specimens as the inferior figure.

Length mm.	*unicuspis*	*fossor*	*castaneus*	*gagei*	*bdellium*	*greeleyi*
91–120	8–18	10–16	10–17	11–14	......	12–16
	$\mathit{14}_{14}$	$\mathit{13}_{40}$	$\mathit{14}_{4}$	$\mathit{11}_{10}$	......	$\mathit{14}_{14}$
121–150	8–18	11–15	9–17	......	12–15	10–16
	$\mathit{14}_{21}$	$\mathit{13}_{25}$	$\mathit{14}_{12}$	$\mathit{12}_{1}$	$\mathit{13.5}_{6}$	$\mathit{13}_{93}$
151–180	9–17	......	9–14	......	11–14	10–13
	$\mathit{14}_{29}$	......	$\mathit{12}_{13}$	......	$\mathit{12.5}_{4}$	$\mathit{11.5}_{2}$
181–210	10–16	......	8–14	......	9–12	......
	$\mathit{12}_{28}$	......	$\mathit{11}_{5}$	......	$\mathit{10.5}_{2}$	......
211–240	9–14	......	8–13	......	10–11	......
	$\mathit{11}_{37}$	......	$\mathit{10}_{16}$	......	$\mathit{10.5}_{4}$	......
241–270	8–15	......	7–15	......	6–11	......
	$\mathit{11}_{62}$	......	$\mathit{10}_{16}$	......	$\mathit{9}_{4}$	......
271–300	7–13	......	7–11	......	......	......
	$\mathit{9}_{38}$	......	$\mathit{10}_{11}$	......	......	......
301–330	7–14	......	8–11	......	......	......
	$\mathit{10}_{17}$	......	$\mathit{10}_{7}$	......	......	......

TABLE VII

AGE VARIATION IN LENGTH OF SNOUT IN THE SIX SPECIES OF *ICHTHYOMYZON*

Measurements in thousandths of total length. For each 30-mm. size class of each species there is given the minimum, maximum, and (in italics) the average value, and the number of specimens as the inferior figure.

Length, mm.	*unicuspis*	*fossor*	*castaneus*	*gagei*	*bdellium*	*greeleyi*
91–120	83–105	41–65	82–102	57–74	......	62–84
	$\mathit{95}_{14}$	$\mathit{56}_{40}$	$\mathit{92}_{4}$	$\mathit{67}_{10}$	......	$\mathit{73}_{14}$
121–150	96–130	47–63	75–109	......	85–91	51–88
	$\mathit{111}_{20}$	$\mathit{54}_{25}$	$\mathit{91}_{12}$	$\mathit{60}_{1}$	$\mathit{88}_{6}$	$\mathit{73}_{93}$
151–180	87–126	......	82–104	......	84–94	63–77
	$\mathit{110}_{29}$	......	$\mathit{95}_{13}$	......	$\mathit{87}_{3}$	$\mathit{70}_{2}$
181–210	80–125	......	82–106	......	83–84	......
	$\mathit{100}_{29}$	......	$\mathit{96}_{6}$	......	$\mathit{83}_{2}$	......
211–240	83–115	......	75–108	......	75–89	......
	$\mathit{95}_{37}$	......	$\mathit{90}_{16}$	......	$\mathit{84}_{4}$	......
241–270	77–106	......	79–96	......	77–91	......
	$\mathit{90}_{62}$	......	$\mathit{88}_{16}$	......	$\mathit{83}_{3}$	......
271–300	73–100	......	76–98	......	......	......
	$\mathit{86}_{36}$	......	$\mathit{85}_{10}$	......	......	......
301–330	78–91	......	76–85	......	......	......
	$\mathit{84}_{19}$	......	$\mathit{82}_{7}$	......	......	......

Lake Erie drainage basin. This shrinking makes the snout appear almost as small in the latter series as in average *castaneus.* Inclusion of measurements made on the large series of shrunken specimens from the Lake Erie basin produces a false skewness in the frequency curve for snout length in *unicuspis* (Fig. 5). Efforts are made to force the shrunken snouts back to their normal shape, but do not by any means fully compensate for the shrinking. There also seems to be a very considerable individual variation in length of snout. At least in all the parasitic species, the snout, after greatly increasing in length during metamorphosis, decreases in relative size with increasing total length (Table VII). Despite the great fluctuations due to preservation, the average snout measurements (Fig. 5) provide one of the best characters distinguishing the 6 species of the genus.

LENGTH OF DISK (Table VIII; Fig. 5).—The size of the disk as measured

TABLE VIII

AGE VARIATION IN LENGTH OF DISK IN THE SIX SPECIES OF *ICHTHYOMYZON*

Measurements in thousandths of total length. For each 30-mm. size class of each species there is given the minimum, maximum, and (in italics) the average value, and the number of specimens as the inferior figure.

Length mm.	*unicuspis*	*fossor*	*castaneus*	*gagei*	*bdellium*	*greeleyi*
91–120	76–97 $\mathit{88}_{14}$	35–49 $\mathit{41}_{40}$	77–82 $\mathit{80}_{5}$	38–58 $\mathit{49}_{10}$	....	48–58 $\mathit{54}_{14}$
121–150	79–118 $\mathit{103}_{21}$	36–49 $\mathit{41}_{25}$	68–93 $\mathit{82}_{11}$	.... $\mathit{39}_{1}$	70–77 $\mathit{72}_{6}$	43–65 $\mathit{53}_{93}$
151–180	80–112 $\mathit{102}_{29}$	....	72–89 $\mathit{83}_{13}$	....	62–75 $\mathit{69}_{4}$	48–51 $\mathit{49.5}_{2}$
181–210	74–111 $\mathit{94}_{29}$	....	65–90 $\mathit{81}_{5}$	....	68–68 $\mathit{68}_{2}$	....
211–240	68–101 $\mathit{85}_{36}$	....	66–88 $\mathit{77}_{16}$	....	64–76 $\mathit{70}_{5}$	....
241–270	67–98 $\mathit{79}_{62}$	....	67–80 $\mathit{74}_{17}$	....	66–70 $\mathit{66.5}_{4}$	....
271–300	65–91 $\mathit{73}_{36}$	....	69–88 $\mathit{75}_{11}$	....	....	....
301–330	66–86 $\mathit{72}_{19}$	....	66–73 $\mathit{69}_{7}$	....	....	....

is the longitudinal diameter, between the outer bases of the marginal fimbriae. This measurement, especially in the big-mouthed *unicuspis,* is subject to even greater fluctuations than that of the snout, due likewise to differential shriveling. By firm preservation the disk may be compressed into a longitudinal slit, or puckered into a disk hardly more than half its normal diameter. Specimens taken fresh from the water and dropped directly into a rather strong formalin solution show this puckering to an extreme, while those long pickled in weak alcohol, or hardened and preserved after they have died or nearly died from exposure on a boat or fish house floor, show the huge mouth which the species consistently shows in life. The differences in size of disk shown by the specimens from the Lake Erie and the Upper Mississippi drainage basins (averaging respectively 0.078 and 0.102 of the standard length) we believe to be due to preservation, for the Lake Erie specimens also have huge mouths in life. Inclusion of the measurements made on the large series of shrunken specimens from the Lake Erie basin is responsible for the abnormal, bimodal frequency curve for the disk measurements of *unicuspis.* Efforts are of course made, but with very incomplete success, to force shrunken disks back into their normal expansiveness. The disk, after enormously increasing in size during metamorphosis, gradually decreases in proportionate size with increasing total length in all of the parasitic species (Table VIII). Despite great fluctuations due to preservation and to individual variation, the disk measurements yield average figures of prime importance in separating the species of *Ichthyomyzon.* We feel convinced that better preserved specimens would show even sharper contrasts in disk size, especially as between *unicuspis* and *castaneus.*

LENGTH OVER GILL-OPENINGS (Fig. 5).—This measurement is made with dividers from the front of the first gill-opening to the groove just behind the fimbriae on the posterior edge of the last opening. Manipulation of the specimen avoids errors in measurement due to a crooking of the neck in preservation. Large fluctuations, not compensated for, are caused by differences in the form of the branchial basket on preservation. These differences are due to the mechanical relation between the expansion of the disk and the contraction of the gill region. When the disk is greatly contracted on preservation, as in the specimens from the Lake Erie drainage, the gill regions are expanded. There is an analogous negative correlation between the size of the disk and the length of the gill region which is of racial significance, for the nonparasitic species with reduced disks have somewhat larger gill regions than their respective parasitic ancestors (Fig. 5). The character, however, is not of great systematic use.

COLOR.—The general color is difficult to determine, because of changes on preservation and large individual variations. Nonspawning adults tend to vary from light yellow-tan to bluish slate. Spawning lampreys of this and other genera become progressively darker, until a bluish black color is attained by the spent individuals soon before death. Despite these differences due to individual variation and condition of maturity, average differences in color tone also appear to distinguish the species. Before spawning, *I. unicuspis* is usually a light yellow-tan, gradually changing from dark on the back to light on the belly, with a tendency toward a mottled admixture of these shades on the sides; occasional specimens are slaty. *I. castaneus,* judging from our rather meager material, appears to average somewhat darker. *I. bdellium* seems to be the darkest of the parasitic species, and the most sharply bicolored: the slaty back and sides tend to contrast sharply with the whitish belly. The nonparasitic species seem to show a parallel series: *fossor,* like *unicuspis,* is usually light grayish brown, and not sharply bicolored; *gagei* appears to be intermediate in color tone; *greeleyi,* even more than *bdellium,* tends toward a very dark slate color, with strongly contrasting light lower surfaces.

PIGMENTATION OF LATERAL LINE ORGANS (Table IX).—The very irregular lateral line system in *Ichthyomyzon,* as in other lampreys, comprises a row of sense organs along the base of the dorsal fin, and a separate overlapping row running from below the middle of the dorsal fin forward, along the upper sides, to the head; a row of organs along the upper edge of the gill-openings, and 2 parallel rows above the gill region; also a pair of strongly arched rows, one on either side of the snout, curving backward on each side behind the disk, almost to the mid-ventral line, on either side of which they are continued backward as a pair of parallel rows on the ventral surface of the branchial region. No specific differences are observed in the distribution of these sense organs, but marked differences are evident in the degree to which they are pigmented with melanin. Since the degree of pigmentation of the dorsal and ventral sense organs is often independent, separate observations and records are made for each region. The dorsal sense organs particularly studied in this connection are those on the upper side of the median part of the body. The ventral organs studied are those on the lower surface of the branchial region.

The degree of blackening of the lateral line sense organs varies with age as well as with the individual and the species (Table IX). The dorsal organs, which darken first, may even be blackened in ammocoetes, as in the type of Kirtland's *Ammocoetes concolor.* In the immature adults of the parasitic species, the black dorsal specks are usually either absent or weakly developed, commonly becoming apparent at a length of about 150 mm. Further blackening of these spots with maturity is slight in *unicuspis,* more marked on the average in *castaneus* and *bdellium.* The ventral sense organs in the 3 parasitic species tend to remain unpigmented or only weakly pigmented through the immature period of adult life, but usually become intensely blackened during the spawning season.

The 3 nonparasitic species, in which the immature adult stage of development has been eliminated, differ sharply in the degree of blackening of the sense organs. In *fossor,* in correlation with its extreme degeneracy, none of the organs, either dorsal or ventral, are ever blackened. In *greeleyi* the dorsal organs are moderately to very intensely pigmented, while the ventral organs remain as free of pigment as in *fossor.* In *gagei* the dorsal organs are strongly pigmented, and the ventral ones either remain colorless or develop a moderate amount of pigment. *I. gagei,* according to the few specimens

TABLE IX

SPECIFIC DIFFERENCES AND AGE VARIATIONS IN THE INTENSITY OF THE BLACK PIGMENTATION OF THE LATERAL LINE ORGANS

The intensity of the pigmentation is indicated by numbers with the following significance: 0 = no trace of blackening, 1 = very weakly blackened, 2 = rather weakly blackened, 3 = moderately blackened, 4 = rather strongly blackened, 5 = very strongly blackened.

SPECIES AND STAGE OF DEVELOPMENT (No. of Specimens Indicated in Parenthesis)	INTENSITY OF PIGMENTATION OF LATERAL LINE ORGANS													
	Dorsal Sense Organs (Upper Side of Median Part of Body)							Ventral Sense Organs (Lower Surface of Branchial Region)						
	0	1	2	3	4	5	(Ave.)	0	1	2	3	4	5	(Ave.)
I. unicuspis														
Immature adults (104)	27	32	17	14	9	5	(1.6)	73	18	5	6	......	2	(0.5)
Maturing and mature adults (96)	8	23	37	19	8	1	(2.0)	......	3	7	12	16	58	(4.2)
I. fossor														
Maturing and mature adults (54)	54	......	......	......	......	......	(0.0)	54	......	......	......	......	......	(0.0)
I. castaneus														
Immature adults (16)	3	8	2	1	2	......	(1.4)	14	1	......	1	......	......	(0.3)
Maturing and mature adults (36)	1	6	7	6	5	11	(3.1)	......	1	2	1	6	26	(4.5)
I. gagei														
Maturing and mature adults (10)	......	......	......	2	2	6	(4.4)	5	......	4	1	......	......	(1.1)
I. bdellium														
Immature adults (4)	1	......	2	......	1	......	(2.0)	3	1	......	......	......	......	(0.3)
Maturing and mature adults (4)	......	......	......	1	3	......	(3.7)	......	......	......	......	1	3	(4.7)
I. greeleyi														
Maturing and mature adults (109)	......	......	2	9	41	57	(4.4)	109	......	......	......	......	......	(0.0)

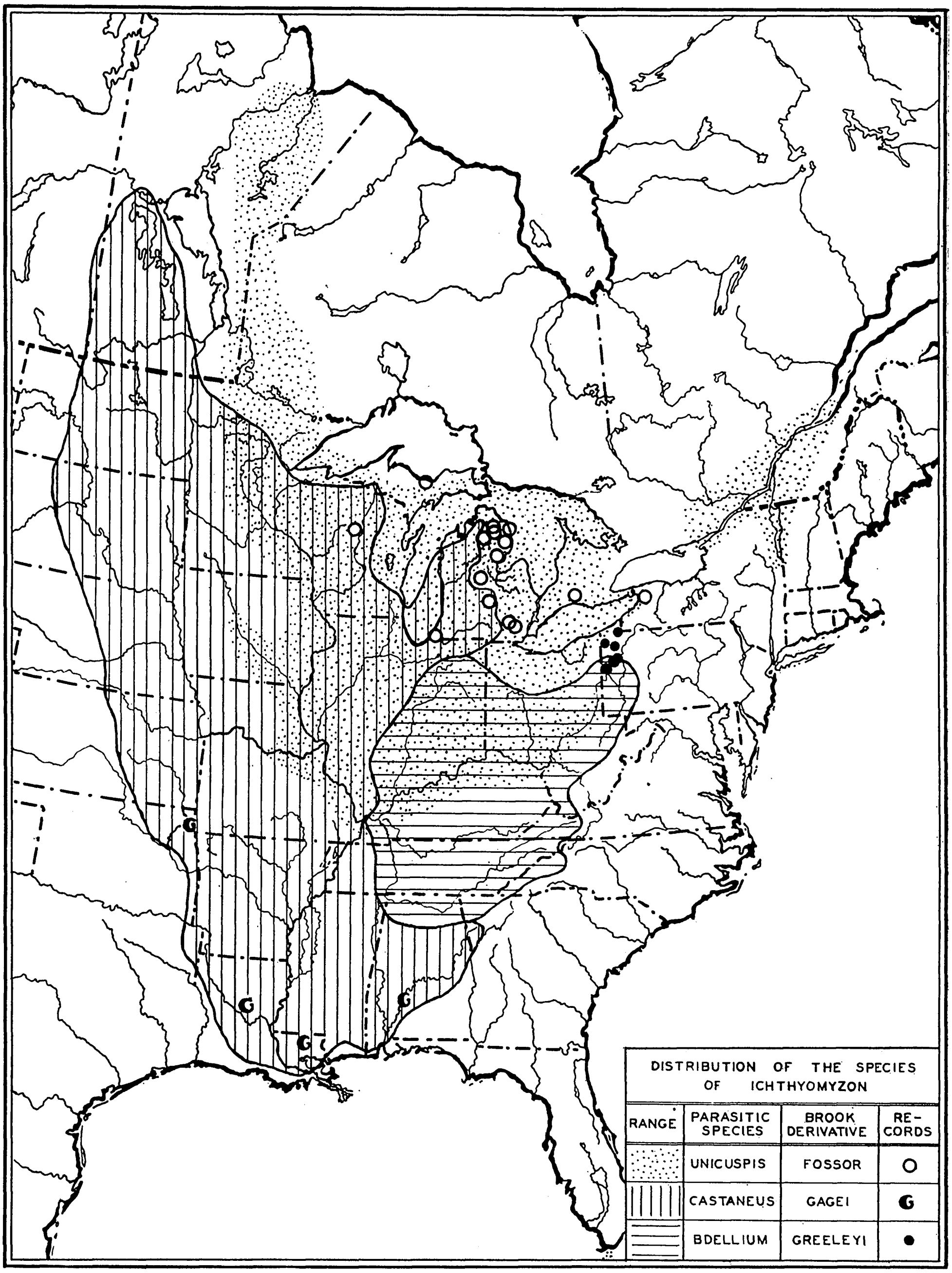
at hand, differs from the other species of the genus in the definite intensification of the row of dots around and just behind the mouth, and in the usual blackening of the organs connecting this row about the mouth with the corresponding ventral row.

LIFE HISTORY.—The contrasting life history types (see p. 9) sharply distinguish the parasitic species *unicuspis, castaneus,* and *bdellium,* from their respective nonparasitic derivatives, *fossor, gagei,* and *greeleyi.* The latter omit the feeding and growing period of life, which in the parasitic types intervenes between the ammocoete and the mature stages. All adults of the nonparasitic species belong in the maturing or mature category. In fact, the gonads very definitely show approaching maturity before the transformation of the ammocoetes into the adult stage is indicated by any external evidence, and thus often provide a ready means for the identification of some large ammocoetes. The possibility should be explored of distinguishing the ammocoetes of the parasitic and nonparasitic forms before the enlargement of the gonads, by microscopic study of sections of the gonads. Weissenberg (1927) showed that pre-maturing larvae of *Lampetra fluviatilis* and *L. planeri* may be distinguished by the number of oocytes for each cross section of ovary, and, less readily, by microscopic differences in the testes.

GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION OF THE SPECIES

Differential distribution, considered from the standpoint of either area or habitat, virtually provides an additional or twentieth characteristic by which to distinguish between the 6 species of *Ichthyomyzon.* As already noted (p. 7), it was the correlation between distribution and structural characters which first led us to appreciate that the genus contains 6 instead of only 2 or 3 forms. The distributional evidence also bears on the problem of the possible intergradation or hybridization between the forms (pp. 14–18).

The geographical distribution of the 3 parasitic species (Fig. 6) is largely complementary. The range of *I. unicuspis,* it is true, overlaps that of both *castaneus* and *bdellium,* but to a very large extent lies beyond the known limits of either of the other parasitic species—northeast of the range of *castaneus* and north of the range of *bdellium. I. unicuspis* is the only one of the parasitic species known to occur in the Saint Lawrence River and Lake Champlain, and their tributaries; in Lakes Erie, Huron, Superior, and the northern and western parts of Lake Michigan, or the tributaries thereto, or connecting waters; and in Lake of the Woods and Hayes River, which are tributary waters of Hudson Bay in Ontario and eastern Manitoba. *I. unicuspis* as well as *castaneus* occurs in the upper Mississippi River and main tributaries at least as far south as St. Louis; it lives with *bdellium* in the Ohio and its main affluents, at least as far east as Portsmouth, Ohio.



MAP 1. Distribution of the species of *Ichthyomyzon*.

I. castaneus appears to be replaced in the Ohio River system, including the Wabash and the Tennessee river drainage divisions, by *I. bdellium,* which is confined to that area. *I. castaneus* appears to be the only parasitic species over a large area lying to the west and south of the range of *unicuspis.* The area of exclusive occurrence appears to include Lakes Winnipegosis and Manitoba, and Assiniboine River in the western part of Manitoba; the western and southern parts of the Mississippi River systems; and the Gulf drainage east to the Alabama River system.

The ranges of the 3 nonparasitic species appear to be entirely complementary and relatively local (Fig. 6). *I. fossor* is known only from streams in the drainage basins of Lakes Erie, Huron, Michigan, and Superior, in New York, Ontario, and Michigan, and of the upper Mississippi River in Wisconsin. *I. gagei* is known only from the southern part of the Mississippi Valley, in Alabama, Louisiana, and probably Oklahoma. *I. greeleyi* is known only from the upper Ohio River system, in Pennsylvania.

In terms of glacial distribution and postglacial redispersal (see Greene, 1935), the several species of *Ichthyomyzon* appear to have had very different histories. *I. unicuspis* presumably inhabited the upper Mississippi and very likely also the Ohio River system during the Late Wisconsin glaciation, after which time this species apparently moved northward into regions freed of ice, *via* all of the glacial lake outlet connectives, with the probable exception of the westernmost or Lake Agassiz outlet. The occurrence of this species in Lake of the Woods and Hayes River, but not so far as known in western Manitoba, suggests the use of a glacial connective in the Rainy River region. The other glacial lake outlets probably used by *I. unicuspis* were the St. Croix, Fox, Chicago, Maumee outlets, and possibly connectives still farther east. *I. castaneus* was apparently a resident of the lower Mississippi Valley during the time of the Late Wisconsin ice sheet; it seems to have used only the Agassiz and Chicago lake outlets in its northward postglacial redispersal. *I. bdellium* was with little doubt forced into the southern part of the Ohio drainage basin by the last advance of the ice, and seemingly used none of the postglacial redispersal routes. *I. fossor,* presumably, had a glacial range not far south of the edge of the Wisconsin ice sheet, and retreated entirely or almost entirely from the nonglacial regions, using the Chicago and Maumee outlets and perhaps some of the adjacent outlets as well, in its northward redisposal. *I. greeleyi* has apparently moved northward but little after the recession of the ice, only slightly penetrating the area of the last glaciation and not reaching the Saint Lawrence drainage basin. The range of *I. gagei* was probably too far south during the ice age to be greatly disturbed by glacial history.

In their ecological distribution the species of *Ichthyomyzon* are also to a large degree complementary. The mutual avoidance is probably due chiefly to competition and the resulting population pressure. The operation of this factor is perhaps most plausibly indicated by the apparent absence of *Ichthyomyzon unicuspis* in the waters of Lake Ontario and the Finger Lakes, where it is replaced by the abundant, landlocked form of *Petromyzon marinus;*[4] *I. unicuspis* occurs commonly east and west of Lake Ontario. Considering the distribution of the nonparasitic species of lampreys it is evident that *Ichthyomyzon gagei* occurs beyond the known limits of any other brook lamprey, and that *I. greeleyi* seems to occur almost exclusively above the range of *Lampetra aepyptera,* the other common brook lamprey of the Ohio Valley. Even if *greeleyi* and *aepyptera* should be found to occur in the same minor stream system, all evidence indicates that they would still be found to avoid one another, for both the adults and ammocoetes of *aepyptera* undoubtedly inhabit smaller brooks while *greeleyi* occurs in the larger creeks and smaller rivers. In Michigan, where *Ichthyomyzon fossor* and *Entosphenus lamottenii* are both abundant and widespread, competition is avoided in the same way, for *fossor* usually inhabits larger streams than the other species. Even when they occur together, a partial avoidance is attained by the circumstance that *I. fossor* tends to spawn later than *E. lamottenii,* usually in May rather than March and early April in southern Michigan, and in June rather than May in the northern part of the State.

The parasitic and nonparasitic species of *Ichthyomyzon* where occurring in the same region show a similar avoidance, for the nonparasitic types usually keep to the smaller waters. None of the nonparasitic species of the genus occur together. *I. castaneus* and *I. bdellium* of the parasitic series have a sharp line of segregation (see p. 45 and Fig. 6). Even *I. unicuspis* and *I. castaneus,* which overlap widely in distribution, show a strong tendency toward mutual avoidance. *I. unicuspis* tends to inhabit the larger, quieter, and cooler waters. Thus in the Lake Michigan watershed, *I. unicuspis* alone is known from the northern and western part of the lake and of its watershed, whereas almost all our specimens from the streams tributary to Lake Michigan in Michigan are *castaneus.* In the base-level lakes at the mouths of these streams *castaneus* greatly predominates, whereas in the open waters of Lake Michigan *unicuspis* appears to be the common species, although *castaneus* occurs along the east shore of the lake and seems to be the common form along the shallow, relatively warm, southern shore. In the upper Mississippi system, *castaneus* seems to be widespread, extending even into medium-sized streams, whereas *unicuspis* seems to be chiefly confined to the main river and the chief tributaries. From Lake Pepin, a deep

[4] Now that *Petromyzon marinus* has penetrated into Lake Erie *via* the Welland Canal, and is becoming established not only in that lake but also in Lakes Huron and Michigan, it will be interesting to observe whether it will partially or wholly replace *Ichthyomyzon* there.

TABLE X

SUMMARY COMPARISON OF THE CHARACTERS OF THE SPECIES OF *ICHTHYOMYZON*

	UNICUSPIS	*FOSSOR*	*CASTANEUS*	*GAGEI*	*BDELLIUM*	*GREELEYI*
Myomeres in trunk (Fig. 1)						
Range	47–55	47–56	49–56	51–54	53–62	55–61
Average	*50.5*	*50.9*	*52.6*	*52.3*	*56.9*	*57.9*
Supraoral cusps (Fig. 1)						
Range	1–4	1–2	2–3	2–3	2–3	2–4
Average	*2.0*	*2.0*	*2.4*	*2.6*	*2.6*	*2.8*
Infraoral cusps (Fig. 2)						
Range	5–11	6–11	6–11	7–10	7–10	7–12
Average	*7.8*	*8.7*	*8.3*	*8.7*	*8.4*	*9.4*
Teeth in circumoral row (Fig. 2)						
Range	15–25	15–25	17–25	20–22	19–22	19–24
Average	*19.2*	*20.3*	*20.8*	*20.9*	*20.8*	*21.5*
Teeth in anterior row (Fig. 2)						
Range	2–4	1–3	3–5	3–4	4–5	3–5
Average	*3.2*	*2.2*	*4.6*	*3.8*	*4.3*	*4.1*
Teeth in lateral rows (Fig. 2)						
Range	5–8	2–6	6–11	6–9	7–10	5–9
Average	*6.6*	*4.7*	*8.5*	*7.4*	*8.3*	*7.2*
Bicuspid circumorals (Fig. 1)						
Range	0–2	0	1–10	2–8	5–10	7–11
Average	*0.0*	*0.0*	*6.5*	*5.9*	*7.8*	*8.4*

TABLE X—(*Continued*)

	UNICUSPIS	*FOSSOR*	*CASTANEUS*	*GAGEI*	*BDELLIUM*	*GREELEYI*
Transverse lingual lamina (Fig. 3)						
Shape usually	Moderately to strongly bilobed	Strongly bilobed	Linear to weakly bilobed	Linear to weakly bilobed	Moderately to strongly bilobed	Moderately to strongly bilobed
Cornification	Very strong	Lacking or weak	Strong	Lacking or very weak	Strong	More or less strong
Denticulations usually	Small, numerous	Lacking or numerous	Fewer, slenderer, longer	Lacking	Rather few, very long and slender	As in *bdellium*
Form and strength of disk teeth (Pl. II)						
Backward curvature	None to moderate	None	Rather strong	Slight	Strong	Strong
Length of teeth	Rather short	Very short	Rather long	Rather short	Very long	Rather long
Tendency to degenerate	None	Extreme*	None	Moderate*	None	Slight*
Form of teeth	Relatively robust	Tubercular	Relatively slender	Rather slender	Very slender	Very slender
Total length in mm. (Fig. 4)						
Maximum	328	146	310	126	259	161
Average, all adults	*224*	*119*	*216*	107	*189*	*128*
Range of breeders	205–328	94–146	200?–310	99–126	200?–259	105–161

* Teeth often greatly degenerated on posterior field of disk.

TABLE X—(*Continued*)

	UNICUSPIS	*FOSSOR*	*CASTANEUS*	*GAGEI*	*BDELLIUM*	*GREELEYI*
Length of tail (Fig. 4)						
Range	258–350	281–334	250–335	272–310	214–311	245–325
Average	*302*	*304*	*282*	*292*	*274*	*297*
Depth of body (Fig. 4)						
Range	54–115	50–93	59–109	63–85	55–92	59–90
Average	*82*	*74*	*82*	*77*	*73*	*76*
Length of eye (Fig. 5)						
Range	7–21	10–16	7–17	11–14	6–15	10–16
Average	*11*	*13*	*11*	*12*	*11*	*13*
Length of snout (Fig. 5)						
Range	73–130	41–65	75–109	57–74	75–94	51–88
Average	*95*	*55*	*90*	*66*	*86*	*73*
Length of disk (Fig. 5)						
Range	59–118	36–49	63–91	38–58	62–77	43–65
Average	*86*	*41*	*77*	*48*	*69*	*53*
Length over gill-openings (Fig. 5)						
Range	80–122	92–119	83–114	92–109	77–107	88–110
Average	*101*	*104*	*94*	*102*	*89*	*98*

TABLE X—(*Concluded*)

	UNICUSPIS	*FOSSOR*	*CASTANEUS*	*GAGEI*	*BDELLIUM*	*GREELEYI*
Color of mature adults (Pl. I)						
Usually	Tan, darker above; scarcely bicolored	Grayish grown; slightly bicolored	Somewhat darker; scarcely bicolored	Rather dark; somewhat bicolored	Rather dark; somewhat bicolored	Very dark; strongly bicolored
Pigmentation of lateral line organs (Table IX)						
In immature adults						
Dorsal and ventral organs	Usually absent to moderate	....	Usually absent to moderate	....	Usually absent or weak	....
In maturing and mature adults						
Dorsal organs	Usually moderate	Entirely lacking	Usually moderate to strong	Moderate to very strong	Moderate	Moderate to very strong
Ventral organs	Moderate to very strong	Entirely lacking	Moderate to very strong	Lacking to moderate	Very strong	Entirely lacking
Life history type (p. 9)	Parasitic	Non-parasitic	Parasitic	Non-parasitic	Parasitic	Non-parasitic
Range (Fig. 6)	St. Lawrence, Great Lakes, Hudson Bay, Upper Mississippi R., Ohio R.	Great Lakes and Upper Mississippi River basins	Hudson Bay, L. Michigan, and Gulf basins	Lower Mississippi Valley	Ohio River system	Upper Ohio R. system
Usual habitat	Large lakes and large rivers	Small rivers and large creeks	Large to medium rivers	Creeks	Large to medium rivers	Large to small creeks

enlargement of the Mississippi River, we have seen a rather large series of *unicuspis* but only a single example of *castaneus.*

The possible bearing of the differential habitat selection of the several species of *Ichthyomyzon* on the problem of the phylogeny of the group, and on the problem of the origin of the nonparasitic types, is discussed on pages 13 and 14.

Analysis of the Species

On the preceding pages the characters of the 6 species of *Ichthyomyzon* are variously compared. In Table X the distinctive characteristics are briefly summarized. A careful comparison of the characters of any specimen with this table, with few exceptions, should definitely indicate the species involved. To facilitate the identification of typical specimens, the following artificial key is offered. The characters of the genus are described on pages 19 and 20.

ARTIFICIAL KEY TO THE SPECIES OF *ICHTHYOMYZON*

1*a*.—Parasitic species: adults retaining a functional digestive tract, with a wide lumen, until a length of more than 175 mm. is attained; gonads and secondary sexual characters, inconspicuous at sizes smaller than 175 mm.; length of disk contained 7.7 to 16.9 times in total length; teeth well developed even on posterior field of disk.

2*a*.—Circumoral teeth (with rare exceptions) all unicuspid; supraoral cusps 1 to 4, very rarely more than 2; teeth in anterior row 2 to 4, usually 3; teeth in lateral rows 5 to 8, usually 6 or 7. Disk usually larger, decidedly wider than branchial region when expanded, especially in half-grown; length of disk usually contained more than 12.5 times in total length (except when shrunken). Myomeres between last gill-slit and anus usually 49 to 52 (extreme range 47 to 55).

3*a*.—Transverse lingual lamina (with rare exceptions) moderately to strongly bilobed. *Drainage areas of Lake Champlain, Saint Lawrence River, the Great Lakes, Lake of the Woods, Hudson Bay, upper Mississippi River, and Ohio River.* .... 1. *Ichthyomyzon unicuspis*

2*b*.—Circumoral teeth in part (1 to 11, usually 6 to 8) bicuspid; supraoral cusps 2 or 3, about as commonly 3 as 2; teeth in anterior row 3 to 5, seldom 3; teeth in lateral rows 6 to 11, usually 8 or 9. Disk usually smaller, little wider to narrower than branchial region; length of disk usually contained more than 12.5 times in total length. Myomeres between last gill-slit and anus usually 51 to 58 (extreme range 49 to 62).

3*b*.—Transverse lingual lamina usually linear or weakly bilobed.—Myomeres between last gill-slit and anus usually 51 to 54 (extreme range 49 to 56). Disk usually of moderate size; its length usually less than 14.3 times in the total length (except when shrunken). Bicuspid circumorals usually 6 to 8. *Drainage areas of Assiniboine River and upper Mississippi River (excluding Ohio River drainage basin), and lower portion of Gulf drainage basin.* .... 3. *Ichthyomyzon castaneus*

3*c*.—Transverse lingual lamina moderately to strongly bilobed.—Myomeres between last gill-slit and anus usually 56 to 58 (extreme range 53 to 62).

Disk usually rather small; its length usually contained more than 13.3 times in total length. Bicuspid circumorals usually 8. *Ohio River drainage basin.* .... 5. *Ichthyomyzon bdellum*

1*b*.—Nonparasitic species: adults with nonfunctional intestinal tract, reduced to a strand; not reaching a total length of 175 mm.; adults with well-developed gonads and secondary sexual characters (ova showing marked enlargement even before metamorphosis); length of disk contained 15.4 to 27.7 times in total length; teeth more or less degenerate, at least on posterior field of disk (not greatly degenerated in some specimens of *greeleyi*).

2*c*.—Circumoral teeth invariably all unicuspid; supraoral cusps 2 (rarely 1); visible teeth in anterior row 1 to 3, usually 2; visible teeth in lateral rows 2 to 6, usually 3 to 5 (all disk teeth greatly degenerate). Length of disk contained 20.4 to 27.7 times in total length (average 24.4). Myomeres between last gill-slit and anus usually 50 to 52 (extreme range 47 to 56).

3*d*.—Transverse lingual lamina moderately to strongly bilobed, often without cornification or denticulations. *Great Lakes drainage basin, and upper Mississippi basin in Wisconsin.* .... 2. *Ichthyomyzon fossor*

2*d*.—Circumoral teeth in part (2 to 11, usually 4 to 10) bicuspid; supraoral cusps 2 to 4, most frequently 3; teeth in anterior row 3 to 5, most frequently 4; teeth in lateral rows 5 to 9, usually 7 or 8 (teeth, except of posterior field, usually not greatly degenerate). Length of disk contained 15.4 to 26.3 times in total length. Myomeres between last gill-slit and anus usually 52 to 60 (extreme range 51 to 61).

3*e*.—Transverse lingual lamina linear to weakly bilobed, with slight or no cornification, without denticulations.—Myomeres between last gill-slit and anus 51 to 54. Length of disk contained 17.2 to 26.3 times in total length. Bicuspid circumorals 2 to 8, commonly 8. *Lower portion of Mississippi Valley* .... 4. *Ichthyomyzon gagei*

3*f*.—Transverse lingual lamina moderately to strongly bilobed, definitely cornified, and provided with long denticulations.—Myomeres between last gill-slit and anus 55 to 61. Length of disk contained 15.4 to 23.3 times in total length. Bicuspid circumorals 7 to 11 (rarely 7).
6. *Ichthyomyzon greelegi*

The Species of *Ichthyomyzon*

For each species we have attempted to gather together synonymies as complete as possible, in the hope of thus referring to all that is known regarding each of the species. The subject matter, except in mere lists of names, and the locality records, if any, are briefly given in parentheses, for each reference in each synonymy. The outstandingly important references are starred with an asterisk. The identification of many of the literature references is open to serious doubt, and is so indicated. With the aid of our data on geographical distribution we have been able to place all literature references under 1 or 2 or 3 of the species, with a greater or lesser degree of assurance, except for most records based on ammocoetes (see pp. 24–27).

Under each species we list all specimens which we have examined, with the exception of ammocoetes entirely unidentified as to species. All species listed are adults, except as otherwise stated. The order of each entry is:

1) Name of museum, abbreviated as follows:
   - Am. Mus., American Museum of Natural History
   - Field Mus., Field Museum of Natural History
   - Mich., Museum of Zoology, University of Michigan
   - Milwaukee, Milwaukee Public Museum
   - Ohio, Ohio State Museum
   - U. S. Bur. Fish., United States Bureau of Fisheries Reserve Collection
   - U. S. N. M., United States National Museum
   - Univ. Wisc., University of Wisconsin collection, made by the Wisconsin Geological and Natural History Survey.
2) Catalogue number in the given museum.
3) Locality, briefly stated.
4) Collector.
5) Date of collection.
6) Host species on which the given specimens were taken; or indication that specimens are ammocoetes, with myomere count and statement of doubt as to identification. These items when called for are given in parentheses.

1. ICHTHYOMYZON UNICUSPIS, N. SP.

Northern Lamprey

(Pl. I, Fig. A, and Pl. II, Figs. A and B, dentition)

Petromyzon argenteus (misidentifications; not *Petromyzon argenteus* Kirtland, 1841 = *Ichthyomyzon bdellium* (Jordan), 1885).—*Kirtland, 1841: 343 nontype L. Erie specimens only;[5] *1851: 205 (Lake Erie and streams in vicinity of Cleveland, spawning in May).[5] Milner, 1874: 36, 75 (effect on sturgeon; Great Lakes).[5] Jordan and Copeland, 1876: 161 (Great Lakes and Ohio Valley; this and other references by Jordan and his early associates are referred to *unicuspis* largely because Jordan later listed these references in the synonymy of his *Petromyzon concolor*, which was clearly the species here described as *unicuspis*).[5] (?) Jordan, 1877*a*: 46, and 1877*b*: 377 (White River system near Indianapolis).[5] Jordan and Gilbert, 1877*a*: 2 (Indiana rivers; in part only?).[5] Goode, 1883: 353 (Great Lakes, after Milner, 1874).[5] Hoy, 1883: 435 (Racine, Wisconsin).[5]

Ichthyomyzon argenteus.—Jordan, 1875: 228 (Lake Erie and Ohio River; see note under Jordan and Copeland, above);[5] *1876: 315 (unidentifiable description: Great Lakes and Ohio Valley, E. to New York; *Ammocoetes aepyptera* wrongly synonymized).[5] Nelson, 1876: 52 (Lake Michigan and large rivers, Illinois; in part).[5] Jordan, 1882: 1001 (Ohio; in part).[5] Jordan and Gilbert, 1883*a*: 10 (description hardly identifiable; Great Lakes and Mississippi Valley);[5] 1883*b*: 208 (supraoral bicuspid). Small, 1883: 47 (as *Ichthyomyzon Argenteus;* Rideau, Gatineau, and Lievres rivers, and tributaries, Ottawa district).[5] Forbes, 1884: 86 (Illinois; in part).[5]

[5] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

(?)*Ammocoetes argenteus.*—Jordan, 1878*a*: 120 (Lake Erie; White River; Ohio River;[6] 1878*b*: 70 (Illinois River, Pekin, Illinois);[6] 1878*c*: 369 (Indiana rivers; in part only?);[6] and 1878*d*: 349; 1878*e*: 413. Jordan and Brayton, 1878: 87 (Ohio and Illinois river basins).[6]

Scolecosoma argenteum.—Jordan, 1882: 757 (Ohio; in part).[6]

Lampetra argentea.—Cope, 1883: 110 (after Jordan, 1876; no records).[6]

Petromyzon.—Fortin, 1864 (Saint Lawrence River, below Quebec; identified as *I. bdellium,* meaning *unicuspis*, by Huntsman, 1917; description definitely indicates *Ichthyomyzon*). Nelson, 1878: 791, 794 (Lake Michigan at Chicago, with sturgeon, and Calumet Lake, Indiana; either *unicuspis* or *castaneus* or both).[6]

Petromyzon hirudo (misidentification; not *Ichthyomyzon hirudo* Girard, 1858 = *I. castaneus* Girard, 1858).—Jordan and Copeland, 1876: 161 (Lake Erie only).[6] (?)Jordan and Gilbert, 1877*a*: 2 (lakes and Ohio River, Indiana).[6]

(?)*Ammocoetes hirudo.*—Jordan, 1878*a*: 120 (Lake Erie only);[6] 1878*c*: 369 (lakes and Ohio River, Indiana);[6] 1878*d*: 350 (Great Lakes only);[6] and 1878*e*: 413 (Lake Erie only).[6] Jordan and Brayton, 1878: 87 (Ohio River Basin).[6]

Ichthyomyzon castaneus (presumably a misidentification, not *I. castaneus* Girard, 1858).—Provancher, 1876: 262 (Saint Lawrence River).[6]

(?)*Petromyzon castaneus.*—Garman, 1889: 22; and 1891: 148 (Wood Slough on Ohio River bottoms, near Quincy, Illinois; sight record of very doubtful identity).[6]

Lampetra fluriatitis [*sic*] or *P. Nigricans* (misidentification; neither *Lampetra fluviatilis* (Linnaeus), 1758, nor *Petromyzon nigricans* Le Sueur, 1818 = *Petromyzon marinus* Linnaeus, 1758).—Ward, 1878: 222 (Detroit River).[6]

Lampern.—[Hallock,] 1878: 222 (Winnebago Lake, Wisconsin).[6] Clarke, 1878: 259 (Lake Pepin, Minnesota).[6]

Petromyzon concolor (probably not *Ammocoetes concolor* Kirtland, 1841 = *Ichthyomyzon,* species indeterminate).—*Jordan and Fordice, 1886: 282 (good characterization for *unicuspis*; Ohio River, New Albany; Ohio; White River; Mississippi River: Lake Erie; Lake Michigan; some records perhaps based on other species).[6] (?)Evermann and Jenkins, 1888*a*: 43, 52, 54; and 1888*b*: 109, 120, 123 (Wabash River at Delphi; New Albany; White River, Indianapolis, Indiana; identified as *unicuspis,* because the authors were students of Jordan who then used *concolor* in the sense of *unicuspis*, satisfactorily distinguishing this species from *castaneus*). *Jordan, 1888, 1891, 1894, 1899, 1904, 1910, 1914, 1916: 11 (Lake Erie to Missouri and north; species well distinguished); 1890: 162 (Wabash River, New Harmony; identified from circumstantial evidence).[6] McCormick, 1890: 126; and 1892: 9 (Vermillion River, Ohio).[6] Bean, 1893: 3 (description applies to *unicuspis;* no records). (?)Hay, 1894: 151 (same records as given by Eigenmann and Beeson, same year). (?)Garman, 1894: 63. Kirsch, 1894: 36 (Blue River at Columbia City, Whitley Co., Indiana: identified by circumstantial evidence).[6] (?)Surber, 1913: 114 (presumably Mississippi River near Fairport, Iowa; identified from locality and because author also listed *castaneus*).[6]

Ichthyomyzon concolor.—(?)Eigenmann and Beeson, 1894: 78 (literature records for Indiana, and Blue River at Wyandotte Cave, Indiana; identified from circumstantial evidence, and because authors involved were Jordan and his students who distinguished *unicuspis*, as ''*concolor*'').[6] (?)Eigenmann, 1896: 253 (Indiana). *Jordan and Evermann, 1896*a*: 11; and 1896*b*: 212

[6] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

(except synonymy in part; Rainy River included in range). Cox, 1897: 9 (Lake of the Woods; identified by description and re-examination of specimens). Osburn, 1901: 15 (Ohio literature records; in part). Evermann, 1902: 95 (Great Lakes; in part; species erroneously starred as confined to Great Lakes basin).[7] Evermann and Kendall, 1902*b*: 235 (Saint Lawrence River at Cape Vincent, New York; also Fortin's record).[7] Huard, 1902: 169 (Saint Lawrence River, below Montreal).[7] (?)Large, 1902: 7 (Illinois River, Illinois only?).[7] Bean, 1903: 14 (New York state).[7] Dawson, 1905: 100 (Detroit River).[7] (?)Eigenmann and Beeson, 1905: 116 (same as 1894: 78).[7] Michael, 1906: 6 (Detroit River at Ecorse and at Belle Isle, identified respectively by re-examination and locality).[7] Meek, 1908: 134 (Indiana; in part).[7] Wagner, 1908: 26 (Mississippi River, in Lake Pepin; re-examined). Evermann and Goldsborough, 1908: 90 (Fortin's record; Hill River, Manitoba, re-examined). *Forbes and Richardson, 1909: 9 (Illinois; in part; material re-examined in part). Evermann and Latimer, 1910: 126 (Garden Island, Lake of the Woods; re-examined). Leathers, 1911: 248 (Sand Point region, Saginaw Bay, Michigan).[7] Halkett, 1913: 11, 38 (Hill River, Hudson Bay region; range). Herrick, 1913: 635 (Lake Erie; brain structure; reference to previous papers on same material).[7] *Bensley, 1915: 9, Pl. 1, Fig. 5 (Go Home River below first falls, Ontario; good description and figure of teeth). Jordan, 1918: 93 (synonymy). Conger, 1920: 5 (Michigan; in part).[7] Evermann and Clark, 1920: 311 (quotation of Wagner only refers to this species). *Forbes and Richardson, 1920: 9 (same as 1909: 9). Surber, 1920: 9 (Minnesota records; in part only?).[7] Pearse, 1921: 35 (generic name spelled *Icthyomyzon;* Lake Pepin, Wisconsin).[7] *Creaser and Hubbs, 1922: 8 (in part; material re-examined). Dymond, 1922: 58, 59, 60 (Lake Erie at Point Pelee, Merlin, and Rondeau, Ontario).[7] Pratt, 1923: 25 (in part). Pearse, 1924: 183 (same as 1921: 35). Rauther, 1924: 678 (in part). Jackson, 1924: 3 (name spelled *concolour;* Hudson Bay drainage).[7] Hubbs, 1925: 588, 589, 590 (in part), and 1926: 7 (Great Lakes; in part). Greene, 1927: 304 (in part; re-examined). Bajkov, 1928: 97 (Hudson Bay drainage).[7] Hubbs and Greene, 1928: 385 (Great Lakes; in part). (?)Potter and Jones, 1928: 342 (literature records for Iowa; possibly some records based on this species rather than on *castaneus*). Greeley, 1929: 166 (Lake Erie, New York).[7] Hubbs and Brown, 1929: 17 (Lake Erie). Jordan, 1929: 7 (in part). Jordan, Evermann, and Clark, 1929: 9 (in part). (?)Hankinson, 1929: 445 (literature records for North Dakota; perhaps in part of this species).[7] Coker, 1930: 214 (Mississippi River in Lake Pepin and from Fairport to Keokuk; presumably in part).[7] *Greeley, 1930: 53, 71, 73, Col. Pl. 1 (records in Lake Champlain basin; breeding habits; part of material reexamined; identification of larvae doubtful). Osburn, Wickliff, and Trautman, 1930: 170 (Ohio; in part). *Berg, 1931: 90 (in part; not the figure). Greeley and Greene, 1931: 79, 81 (Salmon River, Fort Covington, New York).[7] Greeley and Bishop, 1932: 75, 77 (Saint Lawrence River, off Ogdensburg).[7] Luce, 1933: 87, 95 (Mississippi River and Kaskaskia River, near junction, Illinois; presumably both *unicuspis* and *castaneus*).[7] Holly, 1933: 16 (in part). Toner, 1933: 133 (Go Home River and Georgian Bay, Ontario).[7] Greeley, 1934: 96, 97 (lower Raquette River and Saint Lawrence

[7] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

River near Raquette River, New York).[8] Walls, 1935: 135–141 (generic name spelled *Icthyomyzon;* in part; visual cells). Pratt, 1935: 25 (in part). O'Donnell, 1935: 475 (Illinois; in part).

Lamprey.—Wagner, 1904: 555 (as parasite of *Polyodon;* Lake Pepin; material examined).

Ichthyomyzon.—Forbes, 1909: 384, 393, 403 (Illinois; records by river systems; in part re-examined). Gage, 1928: 161 (New York state).[8] Greene, 1935: 21 (Winnebago Lake and Lake Michigan off Jacksonport, Wisconsin; material examined).

Ichthyomyzon bdellium (misidentification; not *I. bdellium* (Jordan), 1885).—*Regan, 1911: 199 (Louisville, Kentucky; description refers to *unicuspis*). *Huntsman, 1917: 24 (Canadian synonymy and records; Brigham's Creek, Hull, Quebec; "North River, Ottawa"; Point Pelee, Lake Erie; Lake Saint Clair; Mitchell Bay, Lake Saint Clair; specimen "of doubtful origin" excepted).[8] Coventry, 1922: 129.

(?)*Petromyzon marinus unicolor* (probably an erroneous identification, based on fishermen's report of a lamprey 15 inches long; possibly a correct report, for *Petromyzon* has recently penetrated into Lake Michigan).—Bensley, 1915: 10 ("upper lakes"; Georgian Bay apparently meant).

(?)*Petromyzon marinus* (probably an erroneous identification, based on Bensley's report). —Toner, 1933: 133 (Georgian Bay).

Ichthyomyzon unicuspis.—*Greene, 1935: 21 (*nomen nudum;* range stated jointly with that of *I. castaneus;* postglacial redispersal; Wisconsin records; material reexamined).

NOMENCLATURE.—In describing *Petromyzon argenteus* (= *bdellium*), Kirtland (1841: 343) mentioned that Lake Erie specimens [no doubt *unicuspis*] are larger than typical *argenteus* from the Ohio River drainage, thus indicating one of the features of *unicuspis* in the first published record of specimens referable to our new species. In a later paper Kirtland (1851: 205) elaborated on the distinction of the Lake Erie type, indicating a difference in color as well as size:

> The above description was made out many years since, from a specimen found adhering to a Lucio-perca in the Ohio River [meaning Big Miami River near its mouth]. Since that period we have found it very abundant in the waters of Lake Erie. Here it attains a larger size, and is of 12 to 15 inches in length, and is most commonly of a waxen yellow color [in contrast with the color of true *argenteus* = *bdellium*, described as "back, ash-gray; sides and beneath, silvery gray"].

This species was distinguished nomenclatorially by Jordan, in the first edition of the *Manual of the Vertebrates* (1876: 315), and in other papers of about the same date.[9] He recorded it under the preoccupied name of *Ichthyomyzon* (or *Ammocoetes* or *Scolecosoma*) *argenteus* (Kirtland) [= *I. bdellium* (Jordan)]. Apparently Jordan used the name *argenteus* in the sense of *unicuspis,* for Jordan and Fordice (1886: 282) and Jordan

[8] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

[9] See synonymy.

(1888: 11) placed his earlier references to *argenteus* in the synonymy of *Petromyzon concolor,* under which name they gave the first unequivocal distinction of *I. unicuspis.* In their early use of the name *hirudo,* Jordan and his associates apparently confused *unicuspis* and *castaneus.*

The name *concolor,* based on an ammocoete, is not used by us for *unicuspis,* for reasons advanced on page 24. This name was distinctively applied to the species here termed *unicuspis* from 1886 until 1909, when Forbes and Richardson (1909: 9–10), impressed with the variability of the number of cusps on the supraoral and infraoral laminae and on the "extraoral" [circumoral] teeth, synonymized *castaneus* with *concolor.* Forbes and Richardson had both species (we have re-examined part of their material), but they failed to notice the correlation of variable characters which definitely indicate the existence of 2 species. This confusion probably arose from the circumstance that they confined their studies to material from Illinois, which is in the zone of overlap between the ranges of *unicuspis* and *castaneus.* Creaser and Hubbs (1922: 8) followed Forbes and Richardson in uniting these 2 species. It was not until we had studied a large amount of new material from regions where these species do not overlap in range, that we appreciated their specific distinctness. Overlooking the contribution by Forbes and Richardson, Regan (1911: 199) recognized and diagnosed this species as distinct from *castaneus,* but erroneously applied to it the name *bdellium.* Huntsman (1917: 24) followed Regan in applying the name *bdellium* to this species, for which he gave diagnostic characters, although he regarded it and the older-named *castaneus* as "evidently only geographical varieties," having a "transition region" in Illinois.

Material Examined

Lake Champlain, New York

- Mich. 95656 (1)—South Bay, near extreme southern end of lake; F. J. Trembly 2; June 5, 1930.
- Mich. 101992 (1)—Monte Bay, Chazy Landing; C. Willard Greene; July 10, 1929.

Lake Erie and Tributaries

- Am. Mus. 7607 (1)—Lake Erie (in New York market).
- Mich. 85828 (1)—New York: Lake Erie, 3 miles west of Dunkirk: C. Willard Greene; Aug. 4, 1928.
- Ohio F492 (2)—Ohio: Lake Erie, about islands; spring, 1929.
- Ohio F434 (1)—Ohio: Lake Erie; Scacht Fish Co.; Nov. 23, 1927.
- Mich. 101628 (1)—Ohio: Lake Erie; U. S. Bur. Fish.; 1927 (feeding on *Catostomus c. commersonnii* and *Ameiurus nebulosus*).
- Ohio F498 (1)—Ohio: Ashtabula Co.; Apr., 1930.
- Mich. 101644 (2)—Ohio: Lake Erie, 21 miles N. ½ E. of Vermillion; John Van Oosten; Aug. 27, 1927.
- U.S.N.M. 65294 (1)—Ohio: Wakeman [on Vermillion River], Huron Co.; Rollin S. Barnes.
- Mich. 101643 (1)—Ohio: Lake Erie, 18 miles NNW. of Vermillion; John Van Oosten; Aug. 23, 1927.

Mich. 101639 (2)—Ohio: Lake Erie, 17 miles N. by W. ½ W. of Vermillion; John Van Oosten; Aug. 21, 1927.

Mich. 55306 (1)—Ohio: Lake Erie, off Sandusky; Walter Koelz; Nov. 29, 1920 (taken on *Coregonus clupeaformis*).

U.S.N.M. 11060 (1)—Ohio: Sandusky; J. W. Milner.

Am. Mus. 1550 (2)—Ohio: Sandusky Bay.

Field Mus. 6307–6309 (4)—Ohio: Sandusky Bay; 1904 to 1907.

Ohio F673 (1)—Ohio: Sandusky Bay; Milton B. Trautman; Apr. 14, 1931.

Mich. 85892 (1)—Ohio: off Kellys Island or Bass Island; Ben Hill; Nov. 29, 1928.

Ohio F438 (1)—Ohio: Put-in-Bay; E. L. Wickliff; Apr. 12, 1929.

Mich. 75493–75495 (13), 102952–102955 (13), 102980–102981 (32), 107040 (1), 107041 (16), and 108242–108244 (15)—Ohio: Swan Creek, Toledo; Bernard R. and Louis W. Campbell; Apr. 26 to June 2, 1934 and 1935 (breeding).

Mich. 55307 (2)—Ohio: Maumee River; Alexander Winchell.

Mich. 55304 (1)—Michigan: Lake Erie, off Monroe; Carl L. Hubbs; autumn, 1920 (on *Ameiurus nebulosus*).

DETROIT AND SAINT CLAIR RIVERS, MICHIGAN

U.S.N.M. 12518 (2)—Ecorse: J. W. Milner.

Mich. 60620 (1)—Clinton River, above Utica; O. E. Fisher; May 31, 1915.

U.S.N.M. 68725 (1)—Saint Clair River at Fort Gratiot; U. S. Fish Commission (not counted or measured).

U.S.N.M. 7479 (1)—Fort Gratiot.

SAGINAW BAY AND VALLEY, MICHIGAN

U.S.N.M. 68914 (1)—Lake Huron [about mouth of Bay], off Port Austin, 14 to 17 fathoms; U. S. Fish. Comm.; June 22, 1894.

Mich. 91158 (1)—Saginaw Bay, ¼ mile S. of Lone Tree Island; Carl L. Hubbs and Canuto G. Manuel; July 9, 1930.

Mich. 87323 (2)—Saginaw Bay (Mich. Dept. Conservation); Dec. 31, 1929.

Mich. 91533 (4)—Saginaw Bay; Canuto G. Manuel; July 11, 1930.

Mich. 101767 (5)—Saginaw Bay; T. H. Langlois; Nov., 1928.

Mich. 55309 (8)—near head of Saginaw Bay; U. S. Bur. Fish.; Oct. 26–28, 1921 (taken on *Catostomus commersonnii* and *Ameiurus nebulosus*).

Mich. 107046 (1)—Saginaw River, Saginaw; Joe Woods; Aug. 1, 1934.

Mich. 81810 (5)—Saginaw River, 1 mile below and 1 mile above Zilwaukee; Jan Metzelaar; Mar. 23, 1927.

Mich. 80806 (1)—Saginaw River, Zilwaukee; T. H. Langlois; Apr. 20, 1926.

Mich. 55426 (1)—Pine River, near St. Louis; A. Garlick; 1915.

LAKE HURON, IN MICHIGAN NORTH OF SAGINAW BAY

Mich. 66772 (2)—Van Etten Lake; T. H. Langlois; June 19, 1924 (on *Esox lucius*).

———— Pierces Point, Van Etten Lake; Jan Metzelaar; Aug. 6, 1927 (field No. 702; specimen apparently lost; identification presumptive).

———— Au Sable River, just above Foote Dam, Iosco Co.; report of one seen on pike prior to 1934 (identification presumptive).

Mich. 67321 (1)—Lake Huron, near shore N. of South Point of Thunder Bay or about Scare Crow Island, Alpena Co.; Norman Jones (for Carl L. Hubbs); Aug. 29, 1925.

Mich. 55654 (7)—Lake Huron, 12 miles SE. by S. ½ S. off Alpena; Walter Koelz; Sept. 22, 1922 (on *Coregonus clupeaformis*).

——————— Sturgeon River, just below dam at Wolverine, 2 seen on *Salmo gairdnerii irideus* on Aug. 18, 1921 (identification presumptive).

Mich. 112354 (1)—Hongore Bay, Black Lake, Cheboygan Co.; L. A. Golczynski; summer, 1936.

Mich. 103297 (1)—Lake Huron, near Cheboygan; C. W. Creaser; July 10, 1929.

U.S.N.M. 68726 (1)—Bois Blanc Island, Straits of Mackinac; J. T. Scovell; July 30, 1894.

LAKE MICHIGAN AND TRIBUTARIES

Mich. 72625 (1)—Michigan: Lake Michigan, near Isle aux Calets (Skilligallee), E. of Beaver Islands; probably 10 to 12 fathoms; John McCann; Oct. 15, 1925.

Mich. 68622 (1)—Michigan: Blodgett Creek, Sec. 8, Grant Township, Mecosta Co. (Muskegon River drainage); Jan Metzelaar; May 9, 1925 (possibly an aberrant specimen of *I. castaneus* with no bicuspid circumorals).

(?)Mich. 63051 (2)—Indiana: Turkey Creek, W. J. Moenkhaus; July 21, 1895 (ammocoetes, with 51 myomeres in each; perhaps *fossor;* an adult lamprey from Turkey Lake, Syracuse, Indiana, collected June 24, 1911, was in the Indiana University collection, now in California Academy of Sciences).

Field Mus. 8960 (1)—Illinois: Jackson Park Lagoon, Chicago; Wm. Welch; June 7, 1915.

Milwaukee 807 (1)—Wisconsin: [Lake Michigan] Jacksonport, Door Co.; A. C. Bender; Oct. 16, 1913.

Mich. 55308 (1)—Wisconsin: Green Bay, off Washington Harbor, 5 miles W. of Boyer Bluff, Walter Koelz; Aug. 18, 1920 (on *Cristivomer namaycush*).

Milwaukee 4750 (1)—Wisconsin: Sturgeon Bay, Door Co.; F. G. Dooley, Apr. 29, 1934 (attached to pickerel).

Mich. 103374 (1)—Wisconsin: Green Bay, 2 miles N. of Door Bluff, Door Co.; Glenn Weborg, for Edward Schneberger; Nov. 7, 1935 (from lake trout).

Milwaukee 4770 (1)—Wisconsin: Lake Poygan, Winnebago Co.; A. E. Tellefson, May 31, 1936 (attached to rock bass; record and identification furnished by T. E. B. Pope).

Milwaukee 4178 (1)—Wisconsin: Lake Winnebago; Albert Dettman; Jan. 1933 (attached to pickerel).

Milwaukee 4179 (1)—Wisconsin: Appleton [on Fox River], Outagamie Co.; Herman Poyler; Jan. 1933.

Milwaukee 3710 (1)—Wisconsin: Wolf River, Winnebago Co.; June 22, 1931.

Univ. Wisc. 4010–4013 (4)—Wisconsin: Wolf River, Winnebago Co.

Mich. 55477 (4)—Wisconsin: Green Bay, off Oconto; John N. Lowe; Aug. 6, 1920.

Mich. 55427 (3 counted and measured)—Michigan: arm of Green Bay, Gladstone; Fred Holmberg; winter, 1921–1922.

LAKE SUPERIOR DRAINAGE BASIN, WISCONSIN

Mich. 80066 (4)—mouth of Amnicon River, Douglas Co.; Carl L. Hubbs and Leonard P. Schultz; June 3, 1926 (young adults; clinging to stones on riffle).

Mich. 80059 (10)—Amnicon River, Douglas Co.; Carl L. Hubbs and Leonard P. Schultz; June 3, 1926 (ammocoetes, with myomeres 50 to 53).

HUDSON BAY DRAINAGE, MANITOBA

U.S.N.M. 32663 (1)—York Factory, Hudson Bay; Dr. Robert Bell.

U.S.N.M. 63029 (1)—Hill River, branch of Hays River; Edward A. Preble.[10]

[10] Dr. Preble writes that this very interesting specimen was found attached just behind the gill region of a pike, *Esox lucius,* about 33 inches long, caught at the Rock Portage of Hill River, July 9, 1900, and that it is the only lamprey he ever found in his extensive travels in the Hudson Bay region, although he caught hundreds of fish with hook.

LAKE OF THE WOODS, MINNESOTA

U.S.N.M. 67009 (2)—at Warroad; S. E. Meek.

U.S.N.M. 64833 (2)—Garden Island; A. J. Woolman; Aug. 10, 1894.

UPPER MISSISSIPPI RIVER DRAINAGE

Univ. Wisc. 1712 (39)—Minnesota: Lake Pepin, Lake City; George Wagner; July 22, 1908 (on *Polyodon spathula*).

Mich. 76813 (1)—Wisconsin: Mississippi River, Cassville, Grant Co.; C. Willard Greene and L. C. Stuart; Aug. 10, 1927.

Mich. 55320 (1)—Illinois: Seelis Lake; Havana; Illinois St. Lab. Nat. Hist.; Apr. 18, 1896.

Mich. 55323 (1)—Illinois: Grafton; Illinois St. Lab. Nat. Hist.; July 6, 1904.

Field Mus. 6462 (3)—Illinois: Illinois River, Meredosia; S. E. Meek and Heim; Sept. 1908.

U.S.N.M. 78162 (1)—Missouri: Mississippi River, St. Louis; T. Hurter; 1908.

Mich. 107038 (1)—Illinois: Mississippi River, Chester; Illinois Nat. Hist. Surv.; Feb. and Mar., 1930.

OHIO RIVER DRAINAGE

Mich. 55337 (1)—Illinois: Embarrass River, Newtown; T. L. Hankinson; May 1, 1917.

U.S.N.M. 17762 (1)—Illinois: Mount Carmel [on Wabash River]; Samuel Turner.

Mich. 97208 (8)—Indiana: Tippecanoe River, Warsaw; W. J. Leach; Sept. 30, 1931 (ammocoetes, with myomeres 49 to 52; possibly *I. fossor*).

Mich. 92100 (3)—Indiana: Tippecanoe River, Warsaw; W. J. Leach; Mar. 31, 1931 (ammocoetes, with myomeres 49 to 52; possibly *I. fossor*).

U.S.N.M. 64915 (8)—Indiana: outlet of Lost Lake; Barton W. Evermann and H. Walton Clark; Oct. 7, 1901 (ammocoetes, with myomeres 48 to 52; possibly *I. fossor*).

Ohio F725—Ohio: Ohio River, Manchester, Adams Co.; Milton B. Trautman (on *Ictiobus niger*).

NO LOCALITY

U.S.N.M. 7442 (3).

RANGE AND HABITAT.—*Ichthyomyzon unicuspis* is the northeasternmost of the parasitic species, as already mentioned (p. 43). It occurs throughout the Saint Lawrence River, from the vicinity of Quebec to the outlet end of Lake Ontario, including Lake Champlain and other tributary waters at relatively low elevations, below the uplands where the fish fauna is of a more relict nature. In Lake Ontario and the Finger Lakes of New York it is apparently replaced by the abundant, land-locked form of *Petromyzon marinus*. The center of abundance of *unicuspis* seems to be Lake Erie, Lake Huron, and the northern and western parts of Lake Michigan, and connecting waters; it occurs also in the larger streams tributary to these lakes, and runs into smaller streams to spawn. From Lake Superior waters it is known only from the Amnicon River, Wisconsin, near the western end of the lake. From the Hudson Bay drainage it is reported only for Lake of the Woods and Hayes River. In the Gulf drainage it occurs in the Mississippi River and main tributaries as far south as St. Louis, and up the Ohio River at least as far as Portsmouth, Ohio. The tendency of the adults of *I. unicuspis* to inhabit very large waters, except when engaged in spawning activities, and thus to be largely segregated from the other species of the genus, is discussed on page 46.

TYPE SPECIMENS.—The holotype, No. 107040, Mus. Zool. Univ. Mich., a breeding male 319 mm. in total length, was collected in Swan Creek, 3 miles above its confluence with the lower Maumee River, at the South Avenue dam in the city of Toledo, Ohio, on May 20 to 22, 1934, by Bernard Roi Campbell. Numerous paratypes were taken at the same point during the spawning runs of 1934 and 1935. The other adult specimens examined, as listed above, are almost all designated as paratypes, for the counts and measurements taken on these specimens have been used in characterizing the species.

CHARACTERS OF HOLOTYPE.—Myomeres between last gill-opening and anus, 50. Supraoral cusps, 2; infraoral cusps, 7; teeth in circumoral row, 18; teeth in anterior row, 3; teeth in lateral row (outward from supraoral lamina), 7–7; bicuspid circumorals, 0; transverse lingual lamina strongly bilobed; disk teeth broadly triangular in cross section, with heavy bases, rather low, mostly rather blunt, only a few definitely recurved, well developed and distinct on all fields of disk. Proportionate measurements of parts, in thousandths of total length (319 mm.): length of tail, 297; depth of body, 76; length of eye, 11; length of snout, 84; length of disk, 76 (value too low due to puckering in preservation); length over gill-openings, 91. General color in alcohol, light, slightly darkened above, becoming gradually lighter toward the belly; life color a light yellow-tan. Lateral line organs all moderately blackened, somewhat more conspicuous on lower surface of branchial region than on side of body.

CHARACTERS (Tables XI and XII), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—*Ichthyomyzon unicuspis* appears to be most closely related to its presumed nonparasitic derivative *I. fossor* (see p. 9 and Table I), although it diverges most strikingly from that little dwarf in characters related to feeding and life history (see p. 12). It is very similar to *castaneus* in numerous characters, but apparently maintains its specific distinctness even in the area where the ranges of the forms overlap (see pp. 14–18, and Tables II to IV). It differs from *bdellium* more strikingly than from *castaneus,* in each of the characters by which *bdellium* differs from *castaneus,* except in the shape of the transverse lingual lamina (p. 33, and Fig. 3), and in the scarcely or insignificantly different average number of infraoral cusps and of teeth in the circumoral, anterior, and lateral rows. The distinction of *unicuspis* from *gagei* and *greeleyi* is so great as to require no further comment.

MYOMERES IN TRUNK (Fig. 1).—47 to 55, usually 49 to 52; averaging 50.5, very slightly lower than in *fossor,* about 2 fewer than in *castaneus* or *gagei,* about 6.5 fewer than in *bdellium* or *greeleyi.*

SUPRAORAL CUSPS (Fig. 1).—1 to 4, almost always 2; averaging 2.0 as in *fossor,* rather than 2.4 to 2.8 as in the other species; the cusps large and strong.

INFRAORAL CUSPS (Fig. 2).—5 to 11; averaging 7.8, slightly lower than in all the other species (8.3 to 9.4); the cusps well developed; the lamina strongly cornified.

TEETH IN CIRCUMORAL ROW (Fig. 2).—15 to 25; averaging 19.2, slightly lower than in all the other species (20.3 in *fossor,* 20.8 to 21.5 in others).

TEETH IN ANTERIOR ROW (Fig. 2).—2 to 4, usually 3; averaging 3.2, more than are externally visible in *fossor* (1 to 3, averaging 2.2), but fewer than in other species (3 to 5, seldom 3, averaging 3.8 to 4.6).

TEETH IN LATERAL ROWS (Fig. 2).—5 to 8, usually 6 or 7; averaging 6.6, about 2 more than in *fossor,* but about 1 or 2 fewer than in the other species.

BICUSPID CIRCUMORALS (Fig. 1).—0 to 2, very rarely 1 or 2 (Tables II to IV); averaging 0.0 as in *fossor,* 5.9 to 8.4 fewer than in the other species. This is one of the outstandingly distinctive features of the species, and the one from which the specific name *unicuspis* is derived.

TRANSVERSE LINGUAL LAMINA (Fig. 3).—With rare exceptions moderate to very strongly bilobed, very wide and strong, heavily cornified, with very numerous though short denticulations along margin. This is one of the most definitely diagnostic of the characters of this new species, as indicated by the descriptions and comparisons on pages 32 to 34, and in Table X.

FORM AND STRENGTH OF DISK TEETH (Pl. II, Figs. A and B).—Broadly triangular in cross section, with heavy bases; rather low and hence usually not very acutely pointed, not at all or only moderately recurved; well developed and distinct on all fields of disk. In these characters *unicuspis* differs only on the average from *castaneus* and *bdellium,* but invariably from *fossor, gagei,* and *greeleyi,* most sharply from *fossor* (see p. 34, and Table X).

TOTAL LENGTH (Fig. 4).—Adults examined, 103 to 328 mm. long, averaging 224 mm.; mature adults 205 to 328 mm. long, apparently averaging slightly larger than those of *castaneus* and distinctly larger than those of *bdellium;* probably always larger than in *fossor, gagei,* or *greeleyi.* Kirtland (1851: 205) gave the length of Lake Erie specimens of *Petromyzon argenteus,* that is, of *I. unicuspis,* as 12 to 15 inches, and Luce (1933: 95) stated that "*I. concolor*" (*unicuspis* or *castaneus*) reaches a length of 16 inches, but we have seen none as long as 15 inches.

PROPORTIONATE SIZE OF PARTS, IN THOUSANDTHS OF TOTAL LENGTH (Figs. 4 and 5).—Length of tail, 258 to 350; averaging 302, about as in *fossor,* considerably to slightly higher than in the other species (270 to 297). Depth

TABLE XI

SUMMARY OF MYOMERE AND TOOTH COUNTS FOR *ICHTHYOMYZON UNICUSPIS*

For each character there is given the minimum and maximum count, the average in italics, and the number of counts as an inferior figure.

DRAINAGE BASIN	MYO-MERES	SUPRA-ORALS	INFRA-ORALS	CIRCUM-ORALS	ANTE-RIOR ROWS	LATERAL ROWS	BICUSPID CIRCUM-ORALS
Lake Champlain	50–51 $\mathit{50.5}_{2}$	2–2 $\mathit{2.0}_{2}$	7–9 $\mathit{8.0}_{2}$	17–19 $\mathit{18.0}_{2}$	3–4 $\mathit{3.5}_{2}$	6–7 $\mathit{6.5}_{4}$	0–0 $\mathit{0.0}_{2}$
Lake Erie	48–55 $\mathit{51.0}_{123}$	1–4 $\mathit{2.1}_{123}$	6–10 $\mathit{8.0}_{123}$	15–25 $\mathit{19.1}_{110}$	2–4 $\mathit{3.1}_{110}$	5–8 $\mathit{6.6}_{246}$	0–1 $\mathit{0.0}_{123}$
Detroit–Saint–Clair	49–53 $\mathit{50.5}_{4}$	2–2 $\mathit{2.0}_{4}$	7–8 $\mathit{7.3}_{4}$	.... $\mathit{21}_{1}$	.... $\mathit{3}_{1}$	6–7 $\mathit{6.6}_{8}$	0–0 $\mathit{0.0}_{4}$
Saginaw Bay	48–52 $\mathit{49.9}_{29}$	1–2 $\mathit{2.0}_{29}$	6–11 $\mathit{8.0}_{29}$	17–22 $\mathit{19.4}_{28}$	2–4 $\mathit{3.1}_{28}$	5–8 $\mathit{6.4}_{58}$	0–1 $\mathit{0.1}_{29}$
Lake Huron	47–52 $\mathit{49.2}_{9}$	1–2 $\mathit{1.9}_{11}$	6–9 $\mathit{7.5}_{11}$	17–21 $\mathit{19.6}_{10}$	2–3 $\mathit{2.9}_{10}$	6–8 $\mathit{6.4}_{22}$	0–2 $\mathit{0.2}_{11}$
Lake Michigan	48–53 $\mathit{56.6}_{23}$	1–2 $\mathit{1.9}_{23}$	6–10 $\mathit{8.1}_{23}$	16–23 $\mathit{19.5}_{22}$	3–4 $\mathit{3.1}_{22}$	6–8 $\mathit{6.7}_{46}$	0–0 $\mathit{0.0}_{23}$
Lake Superior	50–53 $\mathit{51.3}_{13}$	1–2 $\mathit{1.3}_{3}$	7–8 $\mathit{7.3}_{3}$	18–21 $\mathit{19.3}_{3}$	3–3 $\mathit{3.0}_{3}$	6–7 $\mathit{6.3}_{6}$	0–0 $\mathit{0.0}_{3}$
Hudson Bay	49–50 $\mathit{49.5}_{2}$	2–2 $\mathit{2.0}_{2}$	6–7 $\mathit{6.5}_{2}$	....	....	6–6 $\mathit{6.0}_{4}$	0–0 $\mathit{0.0}_{2}$
Lake of the Woods	48–50 $\mathit{48.7}_{4}$	2–2 $\mathit{2.0}_{4}$	7–8 $\mathit{7.3}_{4}$	....	....	5–7 $\mathit{6.1}_{8}$	0–0 $\mathit{0.0}_{4}$
Upper Mississippi R.	48–53 $\mathit{50.0}_{47}$	2–4 $\mathit{2.1}_{47}$	5–10 $\mathit{7.3}_{47}$	17–22 $\mathit{18.9}_{42}$	2–4 $\mathit{3.4}_{42}$	6–8 $\mathit{6.9}_{93}$	0–1 $\mathit{0.0}_{47}$
Ohio River	48–52 $\mathit{49.9}_{22}$	1–2 $\mathit{1.7}_{3}$	7–9 $\mathit{7.6}_{3}$	18–22 $\mathit{19.3}_{8}$	3–3 $\mathit{3.0}_{8}$	6–6 $\mathit{6.0}_{6}$	0–0 $\mathit{0.0}_{3}$
Grand Total	47–55 $\mathit{50.5}_{278}$	1–4 $\mathit{2.0}_{251}$	5–11 $\mathit{7.8}_{251}$	15–25 $\mathit{19.2}_{226}$	2–4 $\mathit{3.2}_{226}$	5–8 $\mathit{6.6}_{501}$	0–2 $\mathit{0.0}_{251}$

of body, 54 to 115, tending to increase with age (Table V); averaging 82, about as in *castaneus,* considerably to slightly more than in the other species (72 to 77). Length of eye, 7 to 21, decreasing with age (Table VI); averaging 11, as in *castaneus* and *bdellium,* somewhat lower than in *fossor* (13), *gagei* (12), and *greeleyi* (13). Length of snout, 73 to 130, tending to decrease with age (Table VII); averaging 95 according to our measurements, which tend to be decreased by shrinkage; since this shrinkage has especially affected the large series of *unicuspis* from the type locality, the larger average size of the snout in *unicuspis* is incompletely indicated by the available data; the average for *castaneus* is 90 and for *bdellium* 85; the 3 nonparasitic species usually have much shorter snouts, averaging 55 to 73; between *unicuspis* and *fossor* no overlap in relative snout length is indicated, for the range of variation is 73 to 130 rather than 41 to 65. Length of disk, 59 to 118, tending to decrease with age (Table VIII); averaging 86 (a value even more affected by shrinkage than the snout length); despite a greater average

TABLE XII

SUMMARY OF MEASUREMENTS FOR *ICHTHYOMYZON UNICUSPIS*

Total length in mm., and other measurements in thousandths of total length; range of variation, and averages in italics.

DRAINAGE BASIN	NUMBER OF SPECIMENS*	TOTAL LENGTH	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL-OPENINGS LENGTH OVER ALL
Lake Champlain	2	114–162 *138*	282–299 *291*	63–81 *75*	10–13 *11*	87–93 *90*	87–92 *90*	93–96 *94*
Lake Erie	122	119–328 *258*	258–331 *298*	58–115 *85*	7–15 *10*	77–124 *89*	59–113 *78*	90–122 *103*
Detroit–Saint Clair	4	138–288 *215*	286–323 *305*	67–93 *84*	9–12 *11*	73–118 *96*	79–111 *94*	80–104 *96*
Saginaw Bay	29	103–301 *216*	274–350 *306*	59–105 *85*	7–16 *11*	76–111 *94*	73–106 *87*	87–109 *97*
Lake Huron	9	114–246 *182*	263–313 *293*	54–105 *82*	10–17 *12*	93–113 *98*	81–109 *90*	87–107 *97*
Lake Michigan	23	112–327 *227*	277–344 *307*	69–101 *85*	8–17 *12*	78–113 *92*	67–108 *84*	87–118 *99*
Lake Superior	3	104–116 *110*	313–328 *321*	56–65 *60*	15–18 *16*	87–104 *93*	83–94 *88*	87–94 *90*
Hudson Bay	2	108–169 *139*	301–303 *302*	60–67 *63*	9–9 *9*	95–101 *98*	80–97 *89*	88–103 *95*
Lake of the Woods	4	182–222 *209*	267–311 *280*	78–96 *87*	9–13 *10*	92–104 *97*	87–99 *92*	96–100 *99*
Upper Mississippi R.	47	106–264 *172*	267–340 *306*	63–100 *76*	10–21 *15*	94–130 *111*	84–118 *102*	88–114 *101*
Ohio River	3	104–121 *112*	274–318 *295*	61–65 *64*	14–18 *16*	96–107 *102*	87–108 *96*	94–95 *95*
Grand Total	248	103–328 *224*	258–350 *302*	54–115 *82*	7–21 *11*	73–130 *95*	59–118 *86*	80–122 *101*

* In the larger series one of the measurements could not be secured in an occasional specimen.

degree of shrinkage in *unicuspis,* the disk proportion averages distinctly higher than in either *castaneus* (77) or *bdellium* (69), much higher than in *gagei* (48) and *greeleyi* (53), and more than twice as high as in *fossor* (average 41, range 36 to 49). Length over gill-openings, 80 to 122; averaging 101, very slightly lower than in *fossor* and *gagei,* slightly higher than in *greeleyi,* considerably higher than in *castaneus* and *bdellium.*

COLOR.—Adults usually light yellow-tan, very light on belly, gradually darkening toward the back; scarcely bicolored; the darker and lighter colors tending to become mottled on sides; occasionally exhibiting a more slaty phase at any age; darkening to a blue-black after spawning, that is, soon before death.

PIGMENTATION OF LATERAL LINE ORGANS.—The lateral line organs on the side of the body and on the ventral surface of the branchial region, as in *castaneus* and *bdellium*, are scarcely or not at all blackened at the time of transformation. The dorsal (and lateral) spots commonly become evident at a length of about 150 mm.; further blackening of these organs is slight in *unicuspis*, greater in *castaneus* and *bdellium*. The ventral organs, as in *castaneus* and *bdellium*, remain unpigmented or only slightly blackened through the immature period of adult life, but blacken intensely during the spawning season. In this character *I. unicuspis* contrasts with *fossor*, which never shows blackened organs, either dorsal or ventral; with *gagei*, which has the dorsal spots moderate to strong but the ventral spots lacking to moderate; and with *greeleyi*, which has moderate to very strong dorsal spots but absolutely no trace of blackened pores on the ventral surface (data in Table IX).

LIFE HISTORY.—This is one of the parasitic species of *Ichthyomyzon*, retaining a long feeding and growing stage between the ammocoete and the mature adult period (see p. 9).

VARIATION.—There seems to be some geographical variation within this species (Tables XI and XII), but not enough to call for subspecific distinctions. The possible intergradation and hybridization between *unicuspis* and *castaneus*, and between *unicuspis* and *bdellium*, is discussed on pages 14 to 18.

2. *ICHTHYOMYZON FOSSOR* REIGHARD AND CUMMINS

Northern Brook Lamprey

(Pl. I, Fig. D, and Pl. II, Figs. C and D, dentition)

Ichthyomyzon fossor.—*Reighard and Cummins, 1916: 1, Pls. 1–2 (original description and figures; breeding habits; Mill Creek at Dexter and Huron River at Ann Arbor, Michigan; types re-examined). Huntsman, 1917: 25 (casual reference). Greene, 1935: 22 (distribution; Scott Creek, Wisconsin; material re-examined). Hubbs, 1935: 158 (*Reighardina unicolor* as synonym; Pratt's misuse of figure of *Petromyzon marinus* for this species pointed out).

Ichthyomyzon sp.—Hankinson, 1920: 5 (Galien River, Berrien Co., Michigan; re-examined).

Ichthyomyzon unicolor (name based on *Ammocoetes unicolor* De Kay, 1842, now regarded (see p. 24) as not definitely identifiable).—*Creaser and Hubbs, 1922: 8 (names based on larvae, *unicolor* and *borealis*, thought referable to this species; Michigan; ammocoete record for Madrid, New York, unidentifiable). Pratt, 1923: 26 (but not Fig. 10, which represents *Petromyzon marinus*—see p. 21). *Okkelberg, 1922: 5 (life history; Thunder Bay River near Atlanta, Gilchrist Creek in same system, Mill Creek near Dexter, Michigan; ammocoetes; re-examined; identified as *fossor* chiefly because parasitic lampreys are unknown in the waters listed). Rauther, 1924: 678. *Creaser, 1925: 34 (range and records; material re-examined). *Hubbs, 1925: 588, 589, 599–602 (life history; Thunder Bay River, Gilchrist Creek, and Rifle River, Michigan; ammocoetes, from streams in which parasitic lampreys are unknown); and 1926: 7. Hubbs and Greene, 1928: 385. Greeley, 1929: 166 (Little Buffalo Creek, Lake Erie drainage, New York; re-examined). Hubbs and Brown, 1929: 5 (distribution). Berg, 1931: 90.

Hankinson, 1932: 420 (Saline River, Saline, Michigan; breeding habits). Holly, 1933: 17. Walls, 1935: 134–142 (generic name spelled *Icthyomyzon;* visual cells).

Reighardina unicolor.—*Jordan, 1929: 7. Jordan, Evermann, and Clark, 1929: 9. Pratt, 1935: 25 (same as *I. unicolor* Pratt, 1923: 26; not Fig. 10).

NOMENCLATURE.—This species was first recognized by Reighard and Cummins (1916), who accurately and fully described it, giving it the name to which we now return. Since 1922 the species has been called *Ichthyomyzon* or *Reighardina unicolor,* on the assumption of Creaser and Hubbs (1922: 8) that *Ammocoetes unicolor* De Kay, based on an ammocoete, should be identified with this species. Present evidence renders this assumption unjustified (see p. 24).

MATERIAL EXAMINED

LAKE ERIE DRAINAGE, NEW YORK

Mich. 91544 (1)—Little Buffalo Creek, near Elma; T. L. Hankinson; June 12, 1928.

LAKE ERIE DRAINAGE, MICHIGAN

Mich. 55344 (6)—Saline River, York; Carl L. Hubbs; Sept. 1, 1921 (large ammocoetes, myomeres 50, 51, 51, 52, 53, 56; identification not fully certain).

Mich. 110153 (9)—Saline River, Saline; T. L. Hankinson; May 13, 1930 (breeding).

Mich. 60612 (1)—Huron River, Ann Arbor; Wood and Reighard; Apr. 23, 1916 (paratype).

Mich. 60617 (formerly 48388) (1)—same locality; Harold Cummins, Apr. 23, 1916 (ammocoete; paratype).[11]

Mich. 56221 (4)—Mill creek, near Dexter, Washtenaw Co.; Carl L. Hubbs and Charles W. Creaser; May 13, 1922 (ammocoetes).[11]

Mich. 56232 (12)—same locality; Carl L. Hubbs and party; Dec. 10, 1921 (ammocoetes).[11]

Mich. 56233 (27)—same locality; Peter Okkelberg and Carl L. Hubbs; Apr. 22, 1922 (25 ammocoetes and 2 adults).[11]

Mich. 56234 (24)—same data; May 27, 1922 (ammocoetes).[11]

Mich. 56235 (16)—same data; May 5, 1922 (15 ammocoetes and 1 adult).[11]

Mich. 56236 (26)—same locality; Dec. 10, 1922; Carl L. Hubbs and party (26 ammocoetes and 1 subadult).[11]

Mich. 55325 (22) and Am. Mus. 7972 (1)—same locality; Jacob Reighard and Peter Okkelberg; May 20, 1918 (15 counted and measured).

Mich. 56237 (5)—same locality; Peter Okkelberg; June, 1918 (also 1 ammocoete not counted).

Mich. 60611 (48392) (6)—same locality; F. E. Wood; May, 1905 (6 ammocoetes; paratypes).[11]

Mich. 60613 (48369–48376) (8)—same locality; Wood and Reighard; May, 1905 (6 restudied; 2 now in British Museum; paratypes).

Mich. 60614 (48378–48383) (6)—same data (paratypes).

Mich. 60615 (48384) (1)—same locality; Harold Cummins; Apr. 23, 1916 (ammocoete; paratype).[11]

[11] These specimens were counted and examined for identification, but the counts are not included in the tabulations.

Mich. 60616 (48385–48387) (3)—same data; May, 1905 (ammocoetes; paratypes).[12]

Mich. 60618 (48389–48391) (3)—same locality; Reighard and Cummins; May, 1916 (ammocoetes; paratypes).[12]

Mich. 60619 (2)—same locality; Jacob Reighard (one remeasured; paratypes).

Mich. 107045 (48377) (1)—same locality; Jacob Reighard; May, 1905 (holotype).

Mich. 64942 (1)—Mill Creek, near Lima Center; T. L. Hankinson, Carl L. Hubbs, and Jan Metzelaar; Apr. 23, 1924 (one large ammocoete).[12]

THAMES RIVER, ONTARIO

Univ. Toronto (2)—Thames River, London (adults studied and identified by Hubbs, but not counted or measured for present paper).

LAKE HURON DRAINAGE, MICHIGAN

(?) Mich. 82151 (4)—Kearsley Creek, Genesee Co.; Jan Metzelaar; July 11, 1927 (ammocoetes, with myomeres 51, 52, 52, 53; perhaps *I. unicuspis*).[12]

Mich. 101686 (1)—Pine River, between Alma and St. Louis; John Delevan; Oct., 1933 (held over winter in aquarium).[12]

(?) Mich. 55341 (7)—Pine River, at Riverdale; C. W. Creaser; Sept. 21, 1921 (ammocoetes, one with 50 myomeres; perhaps *I. unicuspis*).[12]

Mich. 55342 (94)—Rifle River, 9 miles NW. of Prescott; Carl L. Hubbs and Charles W. Creaser; Aug. 27, 1921 (ammocoetes, and one transforming and maturing specimen with 51 myomeres; this count only included in tabulations).

Mich. 66745 (1)—Au Sable River, just below Five Channels Dam; Charles W. Creaser and T. H. Langlois; June 13, 1924 (adult, from stomach of *Ambloplites rupestris*).[12]

Mich. 66773 (1)—same locality; C. W. Creaser; June 21, 1924.

Mich. 61836 (10)—East Branch, Au Sable River, near Grayling; Jan Metzelaar and Carl L. Hubbs; June 19, 1924 (9 ammocoetes and 1 adult).[12]

Mich. 61381 (11)—East Branch, Au Sable River, Crawford Co.; Metzelaar and Hubbs; June 23, 1924 (9 counted and measured).

Mich. 67432 (90)—North Branch, Devil River, Alpena Co.; Carl L. Hubbs; Sept. 2, 1925 (ammocoetes, and 4 transforming and maturing specimens with 50, 51, 51, and 53 myomeres; these counts only tabulated).

Mich. 55345 (136)—Thunder Bay River, 4 miles E. of Atlanta; Carl L. Hubbs and Charles W. Creaser; Aug. 25, 1921 (ammocoetes, and 2 transforming and maturing specimens with 50 and 53 myomeres; these counts only tabulated).

Mich. 55346 (95)—Gilchrist Creek, tributary of Thunder Bay River; Hubbs and Creaser; Aug. 26, 1921 (ammocoetes, and 1 transforming and maturing specimen with 51 myomeres; this count only tabulated).

(?) Mich. 55358 (8)—Maple River, Cheboygan Co., Hubbs and Creaser; Aug. 10, 1921 (ammocoetes; one with 50 myomeres; perhaps *I. unicuspis*).[12]

Mich.————Numerous other collections of *Ichthyomyzon*, including only ammocoetes, from the Au Sable and Thunder Bay river systems, where this species occurs and where evidence is extensive that parasitic lampreys are absent.

LAKE MICHIGAN DRAINAGE, MICHIGAN

(?) Mich. 71392 (2)—Winnepasang Creek, Newaygo Co.; T. H. Langlois and Erwin Moody; July 20, 1926 (ammocoetes, with 50 and 52 myomeres; very possibly *I. unicuspis*).[12]

Mich. 55313 (7)—Red Cedar River, East Lansing; A. C. Conger; spring, 1920.

Mich. 80611 (2)—Portage Creek, Kalamazoo Co.; H. R. Becker; July, 1926 (ammocoetes, with 49 myomeres in each; perhaps *I. unicuspis*).[12]

[12] These specimens were counted and examined for identification, but the counts are not included in the tabulations.

Mich. 102044 (7)—same data; Aug., 1933 (ammocoetes, with myomeres 49, 50, 51, 53 in 4).[13]

Mich. 55339 (1)—Galien River, Berrien Co.; T. L. Hankinson; June 2, 1919.

LAKE SUPERIOR DRAINAGE, MICHIGAN

Mich. 102278 (1)—Au Train River; Alger Co.; V. D. LaBaw; June, 1934.

(?) Mich. 68706 (1)—East Branch, Fox River, Luce Co.; Jan Metzelaar; May 23, 1925 (ammocoete, with 52 myomeres; possibly *unicuspis*).[13]

MISSISSIPPI RIVER DRAINAGE, WISCONSIN

Mich. 75552 (1)—near mouth of Scott Creek, 2 miles north of Marathon, Marathon Co.; C. Willard Greene and L. C. Stuart; June 18, 1927.

RANGE AND HABITAT.—This species is very abundant throughout Michigan, occurring in all of the lake drainages of the State (Erie, Huron, Michigan, and Superior). Outside of Michigan it has been taken, so far as definitely known, only once in each of 3 regions:[14] Scott Creek in the Mississippi River drainage of Wisconsin; Thames River, tributary to Lake Saint Clair, at London, Ontario; Little Buffalo Creek, near Elma, in the Lake Erie drainage of New York. The numerous record stations comprise a compact range (Fig. 6). Future collecting may extend this range, particularly to the northward and eastward. Definite search for it in Ohio has been unavailing, and there is no trace of its occurrence in Indiana or Illinois.

I. fossor lives throughout its life in creeks and small rivers, apparently largely avoiding both small brooks and large rivers. It has never been taken in lakes, either small or large.

TYPE SPECIMENS.—The holotype is a spawning male 121 mm. in total length, No. 48377, recatalogued as No. 107045, Mus. Zool., Univ. Mich., collected by Jacob Reighard, May, 1905, in Mill Creek, tributary to Huron River (Lake Erie drainage), Washtenaw County, Michigan. The paratypes are designated in the original description of *fossor,* and also above, in the list of material examined.

CHARACTERS OF HOLOTYPE (as determined by us).—Myomeres between last gill-opening and anus, 49; supraoral cusps, 2; infraoral cusps, 10, dull, widened, irregular, difficult to count (1 or 2 more cusps might be counted); teeth in circumoral row, 24 (these teeth on posterior field are so degenerate as to be very difficult to count accurately, but the count of 24 is a minimum); teeth in anterior row, 3, none well developed, the anteriormost scarcely evident; teeth in lateral rows (outward from supraoral lamina), 5–6; bicuspid circumorals, 0; transverse lingual lamina bilobed, extremely weak, scarcely cornified along edge, with indistinct denticulations; disk teeth greatly degenerate, discernible with difficulty except near the sides of the mouth, obsolescent toward edge of disk and on posterior field of disk. Proportionate measurements of parts, in thousandths of total length (121 mm.): length of

[13] These specimens were counted and examined for identification, but the counts are not included in the tabulations.

[14] For published records see synonymy.

tail, 315; depth of body, 81; length of eye, 12; length of snout, 62; length of disk, 49 (not markedly puckered); length of over gill-openings, 102. General color in alcohol, light, slightly darkened above, slightly bicolored. Lateral line organs entirely without black pigment.

CHARACTERS (Tables XIII and XIV), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—*Ichthyomyzon fossor* is obviously the nonparasitic derivative of *unicuspis* (see p. 9 and Table I), but diverges greatly from that species in characters related to life history and to feeding (p. 12). The several distinctive characters which it shares with *unicuspis,* as indicated below, set it off sharply from all other species. It is sufficiently distinguished from the two other nonparasitic forms, *gagei* and *greeleyi,* in the key to the species (p. 52).

MYOMERES IN TRUNK (Fig. 1).—47 to 56, usually 50 to 52; averaging 50.9, very slightly higher than in *unicuspis,* somewhat lower than in *castaneus* (52.6) and *gagei* (52.3), about 6 fewer than in *bdellium* or *greeleyi.*

SUPRAORAL CUSPS (Fig. 1).—1 to 2, seldom 1; averaging 2.0 as in *unicuspis,* rather than 2.4 to 2.8 as in the other species.

INFRAORAL CUSPS (Fig. 2).—6 to 11; averaging 8.7, slightly higher than in *unicuspis;* the number of cusps less distinctive than their extreme bluntness and smallness, often leading to obsolescence.

TEETH IN CIRCUMORAL ROW (Fig. 2).—15 to 25; averaging 20.3, slightly higher than in *unicuspis* (19.2), slightly lower than in the other species (20.8 to 21.5).

TEETH IN ANTERIOR ROW (Fig. 2).—1 to 3, usually 2; averaging 2.2, fewer than in any other species (3.2 to 4.6), largely because the outer teeth are obsolete.

TEETH IN LATERAL ROWS (Fig. 2).—2 to 6, usually 4 or 5; averaging 4.7, about 2 fewer than in *unicuspis,* still fewer than in the other species.

BICUSPID CIRCUMORALS (Fig. 1).—Invariably 0; showing agreement only with *unicuspis,* for all other species have from 1 to 11 bicuspid circumorals.

TRANSVERSE LINGUAL LAMINA.—Strongly bilobed, as usually in *unicuspis, bdellium,* and *greeleyi;* not weakly bilobed or linear as in *castaneus* and *gagei;* the lamina small and weak, weakly or not at all cornified; with denticulations lacking or weak, small and numerous as in *unicuspis* when developed.

FORM AND STRENGTH OF DISK TEETH (Pl. II, Figs. C and D).—Tubercular, minute, obsolescent outward and on posterior field of disk; obsolete toward edge of disk, readily evident only near sides of mouth; not at all recurved.

TOTAL LENGTH (Fig. 4).—Adults 94 to 146 mm.; averaging 119 mm.; always smaller than mature adults of *unicuspis, castaneus,* and *bdellium;* averaging slightly larger than *gagei* and slightly smaller than *greeleyi.*

TABLE XIII

SUMMARY OF MYOMERE AND TOOTH COUNTS FOR *ICHTHYOMYZON FOSSOR*

For each character there is given the minimum and maximum count, the average in italics, and the number of counts as an inferior figure.

DRAINAGE BASIN AND STATE	MYOMERES	SUPRA-ORALS	INFRA-ORALS	CIRCUM-ORALS	ANTERIOR ROWS*	LATERAL ROWS*	BICUSPID CIRCUM-ORALS
Lake Erie New York	$\mathit{49}_{1}$	$\mathit{2}_{1}$	....	$\mathit{22}_{1}$	$\mathit{3}_{1}$	....	....
Lake Erie Michigan	48–56 $\mathit{51.1}_{50}$	2–2 $\mathit{2.0}_{41}$	6–11 $\mathit{8.8}_{42}$	15–25 $\mathit{20.6}_{31}$	1–3 $\mathit{2.2}_{32}$	2+ –6+ $\mathit{4.2}+_{86}$	0–0 $\mathit{0.0}_{41}$
Lake Huron Michigan	49–53 $\mathit{50.8}_{18}$	1–2 $\mathit{1.8}_{10}$	7–10 $\mathit{8.7}_{9}$	18–22 $\mathit{19.6}_{10}$	2–3 $\mathit{2.3}_{10}$	2+ –5+ $\mathit{3.8}+_{20}$	0–0 $\mathit{0.0}_{10}$
Lake Michigan Michigan	47–52 $\mathit{50.0}_{7}$	1–2 $\mathit{1.9}_{7}$	8–11 $\mathit{9.0}_{7}$	17–22 $\mathit{19.9}_{7}$	2–3 $\mathit{2.3}_{7}$	3+ –6+ $\mathit{4.4}+_{14}$	0–0 $\mathit{0.0}_{8}$
Lake Superior Michigan	$\mathit{50}_{1}$	....	$\mathit{8}_{1}$	....	....	....	$\mathit{0}_{1}$
Mississippi R. Wisconsin	$\mathit{50}_{1}$	$\mathit{2}_{1}$	$\mathit{6}_{1}$	$\mathit{19}+_{1}$	$\mathit{2}_{1}$	$\mathit{4}+_{2}$	$\mathit{0}_{1}$
Grand Total	47–56 $\mathit{50.9}_{78}$	1–2 $\mathit{2.0}_{59}$	6–11 $\mathit{8.7}_{60}$	15–25 $\mathit{20.3}_{50}$	1–3 $\mathit{2.2}_{51}$	2+ –6+ $\mathit{4.7}+_{122}$	0–0 $\mathit{0.0}_{62}$

* Since in this species the outer disk teeth are vestigial, only the visible, exposed teeth were counted.

TABLE XIV

SUMMARY OF MEASUREMENTS FOR *ICHTHYOMYZON FOSSOR*

Total length in mm., and other measurements in thousandths of total length; range of variation for series, and averages in italics.

DRAINAGE BASIN AND STATE	NUMBER OF SPECIMENS*	TOTAL LENGTH	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL-OPENINGS, LENGTH OVER ALL
New York Lake Erie	1	*133*	*296*	*53*	*11*	*52*	*39*	*93*
Michigan Lake Erie	44	100–146 *122*	281–334 *304*	52–93 *75*	10–16 *13*	44–65 *56*	36–49 *41*	92–119 *105*
Lake Huron	10	94–119 *110*	288–318 *308*	65–85 *78*	11–14 *13*	51–60 *56*	36–48 *41*	92–108 *101*
Lake Michigan	8	99–143 *117*	281–317 *304*	50–81 *67*	13–15 *14*	41–63 *54*	38–45 *41*	96–108 *103*
Lake Superior	1	*117*	*295*	*60*	*12*	*41*	*37*	*103*
Wisconsin Mississippi R.	1	*100*	*300*	*62*	*11*	*59*	*42*	*100*
Grand Total	65	94–146 *119*	281–334 *304*	50–93 *74*	10–16 *13*	41–65 *55*	36–49 *41*	92–119 *104*

* All measurements made on all specimens, with exception of length of tail on one specimen from Lake Michigan drainage.

Proportionate Size of Parts in Thousandths of Total Length (Figs. 4 and 5).—Length of tail, 281 to 334; averaging 304, about as in *unicuspis,* considerably to slightly higher than in the other species (274–297). Depth of body, 50 to 93; averaging 74, somewhat lower than in *unicuspis* and *castaneus* (82), almost the same as in the other species; about the same as in young of *unicuspis* and *castaneus* (see Table V). Length of eye, 10 to 16; averaging 13, about as in *gagei* and *greeleyi,* slightly higher than in *unicuspis, castaneus,* and *bdellium* (11), but about the same as, or even lower than in young of the same size of those species (see Table VI). Length of snout, 41 to 65; averaging 55; so foreshortened that the disk usually stands at an angle of about 30° (see Pl. I, Fig. D); always shorter than in *unicuspis, castaneus,* and *bdellium* (73 to 130); usually shorter than in *gagei* (57 to 74) and *greeleyi* (51 to 88). Length of disk, 36 to 49; averaging 41; always smaller than in *unicuspis, castaneus,* and *bdellium* (59 to 118); usually smaller than in *gagei* (38 to 58) and *greeleyi* (43 to 65); the small measurement of the disk in *fossor* is not attributable to puckering, for little shrinkage of the muzzle takes place in this species. Length over gill-openings, 92 to 119; averaging 104, about as in *unicuspis* (101) and *gagei* (102), somewhat longer than in the other species (89 to 98).

Color.—Grayish brown in alcohol, somewhat darker on the average than in *unicuspis,* especially on back; slightly bicolored.

Pigmentation of Lateral Line Organs.—Entirely lacking on all parts of body and on the lower surface of the head and branchial region; this is a very salient character (Table IX).

Life History (Okkelberg, 1922, and Hubbs, 1925).—This is one of the nonparasitic lampreys, not growing after metamorphosis; the gut degenerates during transformation and the gonads enlarge, females showing rather large ova before metamorphosis.

Variation.—No trustworthy indication of significant geographical variation exists for *fossor* (Tables XIII and XIV), although the few specimens taken away from the center of abundance of the species indicate that some regional variation may be demonstrated when more material from the outlying localities is available.

3. *ICHTHYOMYZON CASTANEUS* GIRARD

Western Lamprey

(Pl. I, Fig. B, and Pl. II, Fig. E, dentition)

Ichthyomyzon castaneus.—*Girard, 1858: 381 (original description; "Galena, Minnesota"; type re-examined). *Suckley, 1860: 368 (characters; "Galena, Illinois?"). Troschel, 1860: 314 (after Girard). Günther, 1870: 507 (after Girard). Jordan, 1876: 315 (after Girard). *Bean, 1882: 117 (Forlorn Hope, Louisiana; re-examined; type of *castaneus* redescribed). Jordan and Gilbert, 1883*a*: 10 (from Girard); and 1883*b*: 208 (teeth). (?)Cox, 1896: 608 (Minnesota River, Mankato, Minnesota).[15] Evermann and Cox, 1896: 363, 384, 426 (after Cragin).[15] *Jordan and Evermann, 1896*a*: 11; and 1896*b*: 212. *Cox, 1897: 9 (Red Lake River and Minnesota River at Mankato, Minnesota; identification respectively certain and somewhat doubtful, from evidence given).[15] (?)Thompson, 1898: 214 (Assiniboine River at Portage la Prairie).[15] Large, 1902: 7 (Pekin, Illinois).[15] Evermann and Goldsborough, 1908: 90 (after Thompson, 1898).[15] Wagner, 1908: 27 (Mississippi River at Lake Pepin; presumably correct though all specimens preserved were identified as *concolor* and are *unicuspis;* a specimen of *castaneus* from Lake Pepin has been examined). Prince, 1909: 235 (Manitoba).[15] *Regan, 1911: 199. Jordan, 1918: 94 (teeth and range). Evermann and Clark, 1920: 306 (size at transformation). Surber, 1920: 9 (Red Lake River and Mankato, Minnesota; after Cox).[15] Bissett, 1927: 127 (Manitoba).[15] Bajkov, 1928: 97 (Hudson Bay drainage).[15] Jackson, 1924: 3 (named spelled *castaneous;* Hudson Bay drainage).[15] Greene, 1935: 22 (postglacial dispersal; Wisconsin records; material re-examined; record for Whitcomb Creek now considered unidentifiable).

Petromyzon castaneus.—Jordan and Copeland, 1876: 161 (Minnesota). Goode and Bean, 1882: 240 ("Gulf of Mexico"—record probably based on specimen reported by Bean, 1882, as *I. castaneus,* from Forlorn Hope, Louisiana). Jordan and Gilbert, 1883: 868 (after Bean, 1882). *Cragin, 1885*a*: 100 (Mill Creek, Shawnee Co., Kansas; presumably a correct identification because all supraorals were tricuspid); 1885*b*: 106 (Mill Creek, Wabaunsee Co., Kansas, on buffalo fish).[15] Jordan, 1885: 792. *Jordan and Fordice, 1886: 281 (first definite diagnosis; *hirudo* doubtfully synonymized). *Jordan, 1888, 1891, 1894, 1899, 1904, 1910, 1914, 1916: 10 (good diagnosis; range; *hirudo* definitely synonymized). Meek, 1892: 11 (Mississippi River, Iowa; re-examined). Hay, 1894: 151 ("not yet known from Indiana"). Young, in Brannon, 1912: 21 (Red River between Fargo and Pembina, North Dakota).[15] Surber, 1913: 114 (presumably from Missisippi River near Fairport, Iowa; *concolor* also listed).[15]

Ammocoetes castaneus.—Jordan, 1878*b*: 413 (upper Mississippi).

Ichthyomyzon hirudo.—*Girard, 1858: 382 (original description; Fort Smith, Arkansas; type re-examined). Troschel, 1860: 314 (after Girard). Günther, 1870: 507 (after Girard). Jordan, 1876: 315 (after Girard). (?)Nelson, 1876: 52 (Ohio River at Cairo, Illinois).[15] *Bean, 1882: 119 (dentition of type). Jordan and Gilbert, 1883*b*: 208.

Petromyzon hirudo.—*Jordan and Copeland, 1876: 161 (Arkansas only). Jordan and Gilbert, 1883: 868 (after Bean, 1882). Jordan, 1885: 792.

(?)*Ammocoetes hirudo.*—Jordan, 1878*a*: 120 (Lake Michigan and Mississippi River only); 1878*b*: 70 (Mississippi River, and Ohio River at Cairo, Illinois)[15]; 1878*d*: 350 (Mississippi Valley only); 1878*e*: 413 (Arkansas only).

Ichthyomyzon argenteus (misidentification; not *Petromyzon argenteus* Kirtland, 1841 = *Ichthyomyzon bdellium* (Jordan), 1885).—Cope, 1864: 276 (Michigan; specimen collected by Professor Miles, now in University of Michigan); Nelson, 1876: 52 (Lake Michigan and large rivers, Illinois; in part);[15] Forbes, 1884: 86 (Illinois; in part).[15]

Petromyzon argenteus.—(?)Wheeler, 1878: 34 (Marais des Cygnes, Ottawa, Kansas).[15] (?) Cragin, 1885*b*: 106 (Osage River, after Wheeler).[15] Graham, 1885: 70 (Cottonwood River, Kansas; reference of this record to *concolor* = *unicuspis* by Evermann and Cox, 1896: 365, was unwarranted, for Graham

[15] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

gave no description and included *hirudo* in the synonymy of *argenteus*).[16]

Ichthyomyzon argenteum.—Jordan, 1880 and 1884: 349 (in part).

(?)*Anguilla vulgaris* (misidentification in field, based on lost specimens less than half an inch long).—Jordan, 1877*b*: 352 (Etowah or Oostanaula River, Georgia).

Petromyzon.—Nelson, 1878: 791, 794 (Lake Michigan at Chicago, with sturgeon, and Calumet Lake, Indiana; either *unicuspis* or *castaneus* or both).[16]

(?)*Ammocoetes niger* (misidentification; not *Petromyzon nigrum* Rafinesque, 1820: 84).—Graham, 1885: 70 (on red-horse from Wild Cat Creek, near Manhattan, Kansas).[16] Cragin, 1885: 106 (Kansas River, Lawrence, Kansas).[16]

Petromyzon concolor (presumably a misidentification; not *Ammocoetes concolor* Kirtland, 1841 = *Ichthyomyzon*, species indeterminable, based on an ammocoete from beyond the known range of *castaneus*).—Bollman, 1891: 221 (Wilder Creek, outlet of Brace Lakes, Calhoun Co., Michigan; on dead *Catostomus;* re-examined). Meek, 1889: 162 (Iowa); 1891*b*: 3 (Cedar and Mississippi rivers, Iowa); 1892*a*: 11 (Mississippi River, Iowa); 1892*b*: 221, 223, 228, 231 (Mississippi River near Muscatine, Des Moines River at Des Moines, Iowa River, and Cedar River, Iowa; Muscatine and Des Moines specimens re-examined; others probably also *castaneus*).[16] Call, 1892: 45 (Des Moines River at Des Moines, Iowa; probably based on Meek's specimens which have been re-examined). Meek, 1893: 221 (Arkansas and other southern records); 1894: 84, 89, 92 (ammocoete from Sallisaw River near Makey's Ferry, Oklahoma, probably of this species, and type of *hirudo* from Fort Smith, Arkansas; both re-examined).

Ichthyomyzon concolor.—Evermann and Cox, 1896: 363, 384, 426 (Crow Creek, Chamberlain, South Dakota (not re-examined), and Kansas literature records; all or in part *castaneus*).[16] Evermann, 1902: 95 (Great Lakes; in part).[16] Michael, 1906: 6 (Cope's and Bollman's records from Michigan only). Meek, 1908: 134 (Indiana; in part).[16] *Forbes and Richardson, 1909: 9 (Illinois; in part; material re-examined in part). Meek and Hildebrand, 1910: 232 (Lake Michigan at Whiting and Edgemoor, Indiana; re-examined). Halkett, 1913: 11, 38 (Assiniboine River, Portage la Prairie; range). Fowler, 1918: 2 (Michigan, after Cope). Conger, 1920: 5 (Michigan; in part).[16] Forbes and Richardson, 1920: 9 (same as 1909: 9). Creaser and Hubbs, 1922: 8 (in part). Pratt, 1923: 25 (in part). Rauther, 1924: 678 (in part). Hubbs, 1925: 588–590 (in part); 1926: 7 (in part). Greene, 1927: 304 (Wisconsin; in part; re-examined). Hubbs and Greene, 1928: 385 (Great Lakes; in part). Potter and Jones, 1928: 342 (Iowa literature records; at least in part).[16] Jordan, 1929: 7 (in part). Jordan, Evermann, and Clark, 1929: 9 (in part); Hankinson, 1929: 445 (North Dakota literature records; presumably in part).[16] Coker, 1930: 214 (Mississippi River in Lake Pepin and from Fairport to Keokuk; presumably in part).[16] *Gudger, 1930: 145 (Coosa River, Rome, Georgia; re-examined). *Berg, 1931: 90, Pl. I, Fig. 1, and Pl. II, Fig. 3 (in part; specimens figured, from Illinois, is clearly *castaneus,* as also the Alabama River record, after Gudger). Luce, 1933: 87, 95 (Mississippi River and Kaskaskia River, near junction, Illinois); presumably both *unicuspis* and *castaneus*).[16] Holly, 1933: 16, Figs. 17–18 (in part; figures from Berg, 1931). Walls, 1935: 135–141 (generic name spelled *Icthyomyzon;* probably in part; visual cells). Pratt, 1935: 25 (in part). O'Donnell, 1935: 475 (Illinois; in part).

[16] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

Ammocoetes branchialis (misidentification; not *Petromyzon branchialis* Linnaeus, 1758, now thought to be unidentifiable, though certainly belonging to *Petromyzon marinus, Lampetra fluviatilis,* or *L. planeri*).—Woolman, 1895: 369 (at least in part; Minnesota specimens satisfactorily identified as *castaneus* by Cox, 1897: 9; specimen from Cheyenne River at Lisbon, North Dakota, not re-examined).

Ichthyomyzon.—Forbes, 1909: 384, 393, 403 (Illinois records by river systems; in part; re-examined in part).[17] Greene, 1935: 21 (Wisconsin River at Prairie du Sac, Wisconsin; material examined).

Petroymyzon marinus (misidentification; not *Petromyzon marinus* Linnaeus, 1758.)—Regan, 1911: 199; Creaser and Hubbs, 1922: 10; and Gudger, 1930: 146 (record for Mississippi River at Muscatine, Iowa, only; on further re-examination of shriveled specimens collected by Meek at Muscatine, the identification is now made as *Ichthyomyzon castaneus,* thus eliminating these troublesome records of the sea lamprey from the Mississippi River).

Ichthyomyzon bdellium (misidentification; not *P. bdellium* Jordan, 1885.).—Huntsman, 1917: 25 (specimen "of doubtful origin," with some bicuspid circumorals, only).

NOMENCLATURE.—The pertinence of the names *castaneus* and *hirudo* to this species is confirmed by our re-examination of the type specimens. Of these names, proposed in the same publication, *castaneus* is to be employed, for the first revisers as well as all subsequent authors who have regarded these names as synonymous chose to use it; Jordan and Fordice (1866: 281) doubtfully synonymized *hirudo* with *castaneus,* and Jordan (1888: 10) definitely followed the same course. The specific name *argenteus* (= *bdellium*) has been wrongly applied to this species by a few authors, as also the specifically unidentifiable name *concolor* (see p. 24) by those who recognized but 1 species of *Ichthyomyzon.* Other published misidentifications of specimens of this species are clarified in the synonymy given above.

MATERIAL EXAMINED

LAKE MICHIGAN DRAINAGE, MICHIGAN AND INDIANA

Mich. 55305 (1)—Michigan: Lake Manistee, Manistee; Mrs. W. D. Tuxbury; Mar., 1916.

Mich. 111323 (1)—Michigan: Manistee River, Kalkaska Co.; A. S. Hazzard; June 11, 1936 (on *Salvelinus fontinalis*).

Grayling Fish Hatchery (3)—Michigan: Manistee River; Phil Zalsman.

Grayling Fish Hatchery (1)—Michigan: Lake Margrethe, Crawford Co.; Phil Zalsman; Feb. 13, 1931.

——————— Michigan: Manistee River, Kalkaska Co., 9 miles E. of Grayling; Reuben S. Babbitt (reported common, attacking trout).

Mich. 103551 (1)—Michigan: Manistee River, Wexford Co. near Missaukee Co. line; I. A. Rodeheffer; July 8, 1936 (small adult, on *Salvelinus fontinalis*).

Mich. 71454 (1)—Michigan: Big South Branch, Pere Marquette River, Newaygo Co.; T. H. Langlois and Erwin Moody; July 17, 1926 (ammocoete, with 54 myomeres, presumably of this species).

[17] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

Mich. 79510 (1) and 79973 (1)—Michigan: West Branch, Muskegon River, Missaukee Co.; Jan Metzelaar; May 14, 1926.

Mich. 70761 (1)—Michigan: McDuffy Creek, Newaygo Co.; T. H. Langlois; July 9, 1926 (good *castaneus,* but measurements not taken because of injured tail).

Mich. 71869 (7)—Michigan: Brooks Creek, Newaygo Co.; Langlois and Moody; Sept. 3, 1926 (ammocoetes, presumably of this species, with myomeres 51, 52, 52, 54, 55, 55, 55).

Mich. 55312 (1)—Michigan: Red Cedar River, East Lansing; A. C. Conger; spring, 1920.

Mich. 109989 (1)—Presumably the specimen from "Michigan" listed by Cope; perhaps from vicinity of Lansing; Manly Miles.

Field Mus. 13100 (1)—Michigan: Black Lake, Holland; Julius Friesser; May 30, 1925.

Mich. 101722 (19)—Michigan: Black Lake, Ottawa Co.; Jan Metzelaar; Mar. 1, 1929.

Mich. 103549 (2)—Michigan: Black Lake, Holland; Wendell H. Krull; 1930 (on *Cyprinus carpio*).

Mich. 72535 (1)—Michigan: South Branch, Kalamazoo River, 2 miles SW. of Albion; Leonard P. Schultz and Parris; Aug. 27, 1925.

Mich. 60544 (1)—Michigan: Rice Creek, Marshall, Calhoun Co.; Carl L. Hubbs; Oct. 8, 1923 (on *Catostomus c. commersonnii*).

Mich. 102956 (1)—Michigan: Battle Creek, Convis Twp., Calhoun Co.; Lawrence N. Walkinshaw; May 12, 1935 (on *Esox lucius*).

Mich. 82704 (1)—Michigan: Wolf Lake, Van Buren Co.; Jan Metzelaar; Nov. 11, 1927.

U.S.N.M. 40704 (1)—"Michigan, Bollman" [no doubt from Wilder Creek, outlet of Brace Lakes, Calhoun Co., collected by Charles H. Bollman, in 1888].

Mich. 60621 (1)—Michigan: South Haven; C. D. Nelson; May 15, 1911.

Mich. 55381 (1)—Michigan: Lake Michigan, near South Haven; R. E. Ellsworth; June 11, 1911.

Mich. 55338 (2)—Michigan: Lake Michigan, at Saint Joseph; T. L. Hankinson; June 8, 1915 (satisfactorily identified, though in too poor condition for counting or measuring).

Field Mus. 16538 (1)—Indiana: Saint Joseph River, 5 miles E. of South Bend; Oct. 15, 1930.

U.S.N.M. 66881 (2)—Indiana: Elkhart River, Goshen; Ridgley and Blatchley; 1890.

Mich. 60610 (5)—Michigan: White Pigeon River, S. of White Pigeon; A. S. Pearse; Apr. 13, 1909 (ammocoetes, presumably of this species, with myomeres, 51, 52, 53, 55, 55).

Field Mus. 7288 (1)—Indiana: Lake Michigan, Whiting; S. E. Meek.

Field Mus. 7289 (2)—Indiana: Lake Michigan, Edgemoor; S. E. Meek.

LAKE MANITOBA, MANITOBA

U. S. Bur. Fish. 757 (1)—C. W. Nash; May 15, 1894.

U. S. Bur. Fish. 2786 (1)—E. T. Seton; Jan. 2, 1904.

RED RIVER OF THE NORTH

U.S.N.M. 8338 (1)—Kennicott (collector).

U. S. Bur. Fish. 249–251 (3)—North Dakota: Grand Forks; S. Oftedal; (?) Oct., 1908.

UPPER MISSISSIPPI DRAINAGE

Mich. 77869 (2)—Wisconsin: Clam River, 7 miles W. of Webster, Burnett Co.; Leonard P. Schultz and Clarence M. Tarzwell; Aug. 13, 1928 (ammocoetes, with 54 and 56 myomeres).

Field Mus. 9088 (1)—Minnesota: channel of Mississippi River, Lake Pepin; Carl L. Hubbs and Leon L. Pray; Oct. 15, 1917.

Field Mus. 21833 (1)—Wisconsin: Okee [on Wisconsin River]; Thomas K. Birks; Sept. 3, 1933.

Milwaukee 763 (1)—Wisconsin: Wisconsin River, Prairie du Sac; E. D. Ochsner; May 4, 1914.

Mich. 55317 (1)—Illinois: Seelis Lake, Havana; Apr. 18, 1896; Illinois St. Lab. Nat. Hist.

U.S.S.R. Mus. Zool. 23164 (1)—Illinois: Pekin; Nov., 1882; Illinois St. Lab. Nat. Hist. (specimen sent from University of Michigan; counts and measurements taken from Berg's figure).

Mich. 55321 (1)—Illinois: no definite data; Illinois St. Lab. Nat. Hist.

U.S.N.M. 979 (1)—"Galena, Minn." [presumably Galena, Illinois]; G. Suckley (type of *I. castaneus*).

Mich. 101709 (16)—Illinois: Mississippi River, Chester; Illinois St. Lab. Nat. Hist.

Field Mus. 1009 (2)—Iowa: Muscatine [Mississippi River]; S. E. Meek (in poor condition; counted but not measured; another specimen of this lot was in the Indiana University collection, Cat. No. 8358, now in California Academy of Sciences).

Field Mus. 963 (1)—Iowa: Des Moines [Des Moines River]; S. E. Meek.

U.S.N.M. 78161 (1)—Missouri: Mississippi River, St. Louis; T. Hurter; 1908.

LOWER MISSISSIPPI DRAINAGE

Mich. 102613 (1)—Missouri: Carter Creek, 2 miles SE. of Van Buren; E. P. Creaser and E. B. Williamson; Aug. 11, 1930 (ammocoete, with 52 myomeres, perhaps of this species).

U. S. Bur. Fish. 2 (1)—Indian Territory [= Oklahoma]: Sallisaw River, Makey Store; S. E. Meek; 1891 (ammocoete, with 53 myomeres; perhaps of this species).

Univ. Okla. (1)—Oklahoma: Glover River, near Broken Bow, McCurtain Co.; Oklahoma Biol. Surv.; Apr., 1931.

U. S. N. M. 980 (1)—Arkansas: Fort Smith [Arkansas River]; George Shumard (type of *I. hirudo*).

Mich. 81314 (1)—Louisiana: Monroe; Max Hardware Co. (received from Southern Biological Supply Co.).

Mich. 81315 (1)—Louisiana: Natchitoches; A. Gregory (received from Southern Biological Supply Co.).

U. S. N. M. 89481 (1)—Louisiana: Trout; T. M. Butter.

U. S. N. M. 30334 (1)—Louisiana: Forlorn Hope; N. B. Moore.

Mich. 72135 (2)—Louisiana: Beechwood Fish Hatchery; Percy Viosca, Jr.

ALABAMA RIVER SYSTEM, GEORGIA

Am. Mus. 10104 (5) and Mich. 97135 (2)—Coosa River, Rome; C. F. O'Keefe; Apr. 18, 1930.

NO LOCALITY

U. S. N. M. 9019 (1).

RANGE AND HABITAT.—*Ichthyomyzon castaneus* seems to finds its northeastern limit in the Lake Michigan drainage of Michigan and Indiana, not penetrating into the waters of Lake Huron, Lake Erie, and the Saint Lawrence River, which are inhabited by *unicuspis*. In the Hudson Bay drainage it occurs in Lake Manitoba and Assiniboine River, and the Red River of the North, in Manitoba, North Dakota, and Minnesota, farther west than the known range of *unicuspis*. It occurs in the Mississippi Valley in Wisconsin, Minnesota, and presumably the Dakotas,[18] Illinois, Iowa, Kansas, Missouri, Oklahoma, Arkansas, Louisiana, and presumably the western edge of Kentucky and Tennessee; probably also through Mississippi and Alabama. It reaches the southeastern limit of the genus in the Alabama River system in Georgia. It is represented in the entire Ohio River system, including the Wabash and Tennessee basins, by the closely related *I. bdellium*.

TYPE SPECIMENS.—The single type specimens of *Ichthyomyzon castaneus* and of its synonym *I. hirudo* are extant. The type of *castaneus*, No. 979, U. S. National Museum, is an adult male 248 mm. in total length, catalogued and generally recorded as from Galena, Minnesota. This locality seems to have been erroneously given by Girard (1858: 381), who was very careless in stating localities, for we find no town of that name in Minnesota; the type was probably taken at Galena, in the northwestern corner of Illinois, for Suckley (1860: 368) recorded the locality as "Galena, Illinois?" The type of *hirudo*, No. 980 in the same museum, is a small adult 125 mm. long, from Fort Smith, Arkansas (on the Arkansas River near the western boundary of the state).

CHARACTERS OF TYPE SPECIMENS.—Oddly, the type specimens of *castaneus* and *hirudo* are aberrant in having only 3 and 4 bicuspid circumorals, respectively, but their other characters indicate them to represent the species we call *castaneus* (see Table IV). The only characters of the type specimens taken by us but not listed in that table are the depth of the body and the length of the eye, which are respectively 0.088 and 0.008 of the total length in the type of *castaneus*, and 0.081 and 0.014 of the total length in the type of *hirudo*.

CHARACTERS (Tables XV and XVI), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—As indicated in the account of *I. unicuspis* (pp. 56 and 61), we now find good evidence that this essentially western and southern species is distinct from the form which has generally been called *argenteus* and *concolor*, but which we find it necessary to name as a new species (*unicuspis*). The original descriptions of *castaneus* (and *hirudo*) were insufficient to set this form apart, so that later workers either doubted

18 The westernmost record for the genus is Missouri River, North Dakota. A specimen in the U. S. National Museum, catalogued as No. 76583 as from that locality, is apparently lost. It was probably *I. castaneus*.

its distinctness or were unable to assign it any valid characters. Cragin (1885*a*: 100) was apparently responsible for fixing the rather vague idea that *castaneus* is distinguished by a high number of supraoral and of infraoral cusps; all of his specimens happened to have a tricuspid supraoral, and a high number of infraoral cusps. Jordan and Fordice (1886: 281), followed by Jordan (1888: 10), added the more trenchant feature of the bicuspid circumorals, and thus gave the first really acceptable diagnosis of the species *castaneus* (including *hirudo*). The character of the many infraoral cusps has generally been overemphasized, a circumstance which was partially responsible for the synonymizing of *castaneus* with "*concolor*" by Forbes and Richardson and by Creaser and Hubbs (see discussion under *I. unicuspis*). The specific distinctness of *castaneus* and *unicuspis* is indicated in the discussion on pages 14 to 18, and in Tables II to IV. *I. castaneus* and *I. bdellium* are compared under the head of the latter form (pp. 91–92). The distinctness of *castaneus* from *unicuspis* and *bdellium,* as well as from the 3 nonparasitic species (*fossor, gagei,* and *greeleyi*) is indicated in Table X and the key to the species.

Myomeres in Trunk (Fig. 1).—49 to 56, usually 51 to 54; averaging 52.6, about as in *gagei,* about 2 more than in *unicuspis,* 1.5 more than in *fossor,* about 4.5 to 5.5 fewer than in *bdellium* and *greeleyi,* respectively.

Supraoral Cusps (Fig. 1).—2 to 3, about as commonly 3 as 2; averaging 2.4, rather than 2.0 (*unicuspis* and *fossor*), or 2.6 to 2.8 (other species); cusps strong, but averaging slenderer than in *unicuspis.*

Infraoral Cusps (Fig. 2).—6 to 11; averaging 8.3, only slightly higher than in *unicuspis* (7.8), about the same as in *bdellium,* slightly lower than in the other species. This character is much less trenchant than formerly thought. The cusps are usually long and sharp.

Teeth in Circumoral Row (Fig. 2).—17 to 25; averaging 20.8, slightly higher than in *unicuspis* (19.2) or *fossor* (20.3), about the same as in *gagei* and *bdellium,* slightly lower than in *greeleyi* (21.5).

Teeth in Anterior Row (Fig. 2).—3 to 5, usually 4 or 5; averaging 4.6, slightly higher than in *gagei, bdellium,* and *greeleyi* (3.8 to 4.3), and definitely higher than in *unicuspis* (3.2) and *fossor* (2.2).

Teeth in Lateral Rows (Fig. 2).—6 to 11, usually 8 or 9; averaging 8.5, very slightly higher than in *bdellium* (8.3), considerably higher than in *gagei* (7.4) and *greeleyi* (7.2), much higher than in *unicuspis* (6.6) and *fossor* (4.7).

Bicuspid Circumorals (Fig. 1).—1 to 10, usually 6 to 8; averaging 6.5, somewhat lower than in *bdellium* (7.8) and *greeleyi* (8.4), slightly higher than in *gagei* (5.9), much higher than in *unicuspis* and *fossor* (0.0). This character probably provides the sharpest difference between *castaneus* and *unicuspis,* but is not quite invariably distinctive (see Table IV).

TRANSVERSE LINGUAL LAMINA (Fig. 3).—Linear to weakly bilobed, rarely rather strongly bilobed; usually smaller and weaker than in *unicuspis;* strongly cornified; denticulations averaging fewer and longer than in *unicuspis,* but not so long as in *bdellium* or *greeleyi.*

FORM AND STRENGTH OF DISK TEETH (Pl. II, Fig. E).—More or less narrowly and sharply triangular in cross section, with bases averaging less heavy than in *unicuspis*; rather long, slender, and sharply pointed, tending to be rather strongly curved backward; showing no tendency to degenerate, well developed on all fields of disk. In these characters *castaneus* is intermediate between *unicuspis* and *bdellium,* and differs only on the average from either.

TOTAL LENGTH (Fig. 4).—Adults examined 105 to 310 mm. long; averaging 216 mm., probably slightly smaller than in *unicuspis* and slightly higher than in *bdellium* (189 mm.); adults becoming mature as small as about 200 mm.; mature adults always larger than in *fossor, gagei,* and *greeleyi.*

PROPORTIONATE SIZE OF PARTS IN THOUSANDTHS OF TOTAL LENGTH (Figs. 4 and 5).—Length of tail, 250 to 335; averaging 282, slightly higher than in *bdellium* (274), slightly lower than in *gagei* and *greeleyi* (292 and 297), considerably lower than in *unicuspis* and *fossor* (302 and 304). Depth of body, 59 to 109, tending to increase with age (Table V), averaging 82, as in *unicuspis,* considerably to slightly higher than in the other species (72 to 77), but scarcely different when specimens of like size are compared. Length of eye, 7 to 17, decreasing with age (Table VI), averaging 11 as in *unicuspis* and *bdellium,* somewhat lower than in *gagei* (12), *fossor* and *greeleyi* (13), but higher than in those 3 species when specimens of like size are compared. Length of snout, 75 to 109, tending to decrease with age (Table VII); averaging 90, lower than in *unicuspis,* but higher than in the other species (see p. 37). Length of disk, 63 to 91, tending to decrease with age (Table VIII); averaging 77, lower than in *unicuspis* but higher than in the other species (see p. 39). Length over gill-openings, 83 to 114; averaging 94, slightly lower than in *unicuspis, fossor, gagei,* and *greeleyi* (98 to 104), slightly higher than in *bdellium* (89).

COLOR.—Adults averaging somewhat darker than *unicuspis*; the color grading from light on belly to darker above, with scarcely any bicolored effect; sides sometimes mottled; occasionally slaty at any stage, becoming blue-black after spawning, prior to death.

PIGMENTATION OF LATERAL LINE ORGANS.—As in *castaneus* and *bdellium,* the sense organs of the lateral line system in the side of the body, on the head, and on the lower surface of the branchial region, are scarcely pigmented in the very small adults, but become more or less blackened at a length of about 150 mm. The dorsal and lateral organs continue to darken thereafter, becoming, as in *bdellium,* blacker on the average than in *unicuspis.* As in both of those species the ventral organs become intensely black with maturity. The evidence for these statements is given in Table IX, which further indicates distinctions in this character between *castaneus* and the 3 nonparasitic species, *fossor, gagei* (difference slight), and *greeleyi.*

LIFE HISTORY.—This is one of the parasitic species, retaining a long feeding and growing period between the ammocoete stage and the mature adult (see p. 9).

VARIATION.—Tables XV and XVI indicate that this species probably varies considerably in different parts of its wide range. Evidence on the possible intergradation or hybridization of *castaneus* with *unicuspis* is given on pages 14 to 18.

4. ICHTHYOMYZON GAGEI, N. SP.

Southern Brook Lamprey

(Pl. I, Fig. E, and Pl. II, Fig. F, dentition)

MATERIAL EXAMINED

Mich. 103163 (2 ammocoetes with developing gonads, one a female with fairly well-developed ova; identification somewhat doubtful)—Oklahoma: Elk River, Turkey Ford, Delaware Co.; Carl L. Hubbs and Milton B. Trautman; Sept. 13, 1935.

Mich. 107042 (holotype) and 107043 (6 paratypes)—Louisiana: stream ¼ mile south of Dry Prong, Grant Parish; presumably a secondary tributary of Little River; Donald J. Ameel, Leslie R. Hedrick, and E. P. Creaser; May 29, 1932.

Mich. 64494 (3 paratypes)—Louisiana: spring-fed brook tributary to Tangipahoa River, near Kentwood; Mrs. L. L. Travis (received from Percy Viosca, Jr., of the Southern Biological Supply Co., through Professor Simon H. Gage; collected before May 1, presumably in late April, 1930).

U.S.N.M. 92300 (1 paratype)—Alabama: Rockwood Creek, small tributary to Alabama River, Wilcox Co.; B. H. Williams; May 11, 1934.

RANGE AND HABITAT.—The range of this species is definitely indicated by the few type series as the Gulf drainage of Louisiana and Alabama. It probably ranges more widely in the lower Mississippi Valley. In fact, the 2 ammocoetes recently taken by us in Elk River, Oklahoma, indicate with high probability that it occurs as far north as northwestern Oklahoma. It seems, like the other nonparasitic species of *Ichthyomyzon,* to be a species of creeks and small rivers. It apparently lives in brooks as well.

TYPE SPECIMENS.—The holotype, No. 107042, Mus. Zool., Univ. Mich., is a breeding male 103 mm. in total length. It was collected in a stream ¼ mile south of Dry Prong, Grant Parish, Louisiana, presumably a secondary tributary of Little River, on May 29, 1932, by Donald J. Ameel, Leslie R. Hedrick, and E. P. Creaser. The 3 series of paratypes are specified in the list of material examined.

TABLE XV

SUMMARY OF MYOMERE AND TOOTH COUNTS FOR *ICHTHYOMYZON CASTANEUS*

For each character there is given the minimum and maximum counts, the average in italics and the number of counts as an inferior figure.

DRAINAGE BASIN	MYO-MERES	SUPRA-ORALS	INFRA-ORALS	CIRCUM-ORALS	ANTERIOR ROWS	LATERAL ROWS	BICUSPID CIRCUM-ORALS
Lake Michigan	50–55 $\mathit{52.9}_{55}$	2–3 $\mathit{2.4}_{43}$	6–11 $\mathit{8.4}_{43}$	17–25 $\mathit{21.0}_{31}$	3–5 $\mathit{4.4}_{31}$	7–11 $\mathit{8.3}_{84}$	1–10 $\mathit{6.4}_{34}$
Lake Manitoba	51–52 $\mathit{51.5}_{2}$	2–2 $\mathit{2.0}_{2}$	9–9 $\mathit{9.0}_{2}$	....	....	7–9 $\mathit{8.2}_{4}$	4–4 $\mathit{4.0}_{2}$
Red River of the North...	51–54 $\mathit{52.0}_{4}$	2–3 $\mathit{2.8}_{4}$	7–10 $\mathit{8.2}_{4}$	....	....	7–9 $\mathit{8.1}_{8}$	6–6 $\mathit{6.0}_{4}$
Upper Mississippi R.	49–56 $\mathit{52.6}_{27}$	2–3 $\mathit{2.4}_{27}$	6–10 $\mathit{8.4}_{27}$	17–23 $\mathit{20.6}_{20}$	4–5 $\mathit{4.8}_{20}$	6–11 $\mathit{8.7}_{54}$	3–10 $\mathit{7.0}_{27}$
Lower Mississippi R.	50–53 $\mathit{51.7}_{9}$	2–3 $\mathit{2.4}_{7}$	7–11 $\mathit{8.6}_{7}$	20–22 $\mathit{20.7}_{3}$	4–5 $\mathit{4.3}_{3}$	8–11 $\mathit{8.9}_{14}$	3–8 $\mathit{6.0}_{7}$
Alabama River	51–53 $\mathit{52.4}_{7}$	2–3 $\mathit{2.1}_{7}$	6–10 $\mathit{7.9}_{7}$	21–23 $\mathit{22.0}_{2}$	5–5 $\mathit{5.0}_{2}$	8–10 $\mathit{9.2}_{13}$	6–9 $\mathit{6.7}_{7}$
Grand Total*	49–56 $\mathit{52.6}_{105}$	2–3 $\mathit{2.4}_{91}$	6–11 $\mathit{8.3}_{91}$	17–25 $\mathit{20.8}_{56}$	3–5 $\mathit{4.6}_{56}$	6–11 $\mathit{8.5}_{179}$	1–10 $\mathit{6.5}_{91}$

* Including some determinations made on 1 specimen without locality.

TABLE XVI

SUMMARY OF MEASUREMENTS FOR *ICHTHYOMYZON CASTANEUS*

Total length in mm., and other measurements in thousandths of total length; range of variation and averages in italics.

DRAINAGE BASIN	NUMBER OF SPECIMENS*	TOTAL LENGTH	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL-OPEN-INGS, LENGTH OVER ALL
Lake Michigan	41	114–305 *215*	253–335 *283*	59–109 *82*	8–17 *11*	75–108 *89*	67–89 *76*	83–114 *95*
Lake Manitoba	2	114–276 *195*	250–315 *282*	60–77 *69*	7–12 *9*	76–82 *79*	70–81 *76*	89–96 *92*
Red River of the North	4	179–257 *218*	255–304 *286*	74–79 *77*	7–11 *9*	81–98 *87*	65–79 *73*	87–97 *93*
Upper Mississippi R.	25	117–310 *244*	256–315 *284*	64–100 *82*	8–15 *11*	75–103 *89*	63–90 *76*	84–100 *93*
Lower Mississippi R.	6	105–256 *172*	264–283 *271*	62–90 *77*	9–17 *13*	90–103 *97*	77–91 *83*	92–101 *97*
Alabama River	7	130–199 *162*	265–290 *276*	68–92 *82*	9–14 *12*	89–109 *98*	77–90 *83*	92–102 *95*
Grand Total......		105–310 *216*	250–335 *282*	59–109 *82*	7–17 *11*	75–109 *90*	63–91 *77*	83–114 *94*

* All measurements made on all specimens listed, excepting one from Louisiana, for which only total length, disk length, and length over gill-openings were taken.

CHARACTERS OF HOLOTYPE.—Myomeres between last gill-opening and anus, 51. Supraoral cusps, 2, very distinct; infraoral cusps, 9, very weak and tubercular, difficult to see, the lamina very weakly cornified; teeth in circumoral row, 20, very weak posteriorly; teeth in anterior row, 4, the most anterior one barely discernible; teeth in lateral rows (outward from supraoral lamina), 8–8, extremely difficult to count owing to obsolescence of teeth outward (outer teeth countable with aid of high power only, as dark spots in the gum); bicuspid circumorals, 6 (3 on each side), fairly well developed, larger than the other disk teeth, the cusps arising almost independently from the very base of the teeth; transverse lingual lamina almost linear, weakly bilobed, small and fleshy, without evident cornification or denticulation; disk teeth rather short but slender, with small bases, slightly curved backward, moderately degenerate on sides of disk, very weak on posterior field. Proportionate measurements of parts, in thousandths of total length (103 mm.), indicated in the third row of Table XVIII. Color in formalin, olive, becoming very dark on body posteriorly; darkened also on snout; dorsal fin pale olive with tinge of orange; black specks conspicuous. Color in alcohol rather dark, rather distinctly bicolored. Lateral line organs of back and sides of body distinctly blackened; those around posterior part of disk somewhat blackened, but lighter than the spots on the body; those on ventral surface of branchial region very slightly blackened; mature at a very small size.

CHARACTERS (Tables XVII and XVIII), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—For reasons given on page 10, *I. gagei* is regarded as the nonparasitic, dwarfed derivative of *I. castaneus*. It certainly seems to be much more closely related to *castaneus* than to any other species of the genus, though in general appearance it is more similar to *fossor* and *greeleyi*. The characters by which *gagei* differs from *castaneus*, almost entirely correlated with the dropping out of the parasitic or feeding stage in adult life, include the small maximum size, degenerate intestine in adult, the degenerate teeth, the small size of disk and the short snout.

MYOMERES IN TRUNK (Fig. 1).—51 to 54, most frequently 52; averaging 52.3, about as in *castaneus*, 1.8 higher than in *unicuspis*, nearly 5 fewer than in *bdellium* and *greeleyi*.

SUPRAORAL CUSPS (Fig. 1).—2 to 3, more often 3 than 2; average 2.6, more than 0.5 higher than in *unicuspis* and *fossor*, about the same as in the other species.

INFRAORAL CUSPS (Fig. 2).—7 to 10; averaging 8.7, slightly higher than in *unicuspis*, *castaneus*, and *bdellium*, about as in *fossor*, 0.7 lower than in *greeleyi*; very weak and tubercular; the lamina very weakly cornified.

TEETH IN CIRCUMORAL ROW.—20 to 22; averaging 20.9, about the same as in *castaneus* and *bdellium*, slightly higher than in *unicuspis* (19.2) and

TABLE XVII

MYOMERE AND TOOTH COUNTS FOR *ICHTHYOMYZON GAGEI*

LOCALITY	MUSEUM	CAT. NO.	MYOMERES	SUPRAORALS	INFRAORALS	CIRCUMORALS	ANTERIOR ROWS	LATERAL ROWS	BICUSPID CIRCUMORALS
Oklahoma:	Mich.	103163	53*	......	......	......	......	......	......
Elk River	Mich.	103163	53*	......	......	......	......	......	......
Elk River									
Louisiana:									
Grant Parish	Mich.	107042†	51	2	9	20	4	8–8	6
Grant Parish	Mich.	107043	52	3	9	21	4	8–8	8
Grant Parish	Mich.	107043	52	3	10	20	4	8–8	6
Grant Parish	Mich.	107043	52	3	9	20	4	7–7	6
Grant Parish	Mich.	107043	54	3	7	21	4	8–9	8
Grant Parish	Mich.	107043	54	2	7	21	4	8–7	5
Grant Parish	Mich.	107043	52	3	10	22	4	7–7	8
Averages	......	......	*52.4*	*2.7*	*8.7*	*20.7*	*4.0*	*7.7*	*6.7*
Kentwood	Mich.	64494	52	3	8	21	3	7–7	8
Kentwood	Mich.	64494	53	2	9	21	3	6–7	4
Kentwood	Mich.	64494	52	2	10	22	4	7–7	2
Averages	......	......	*52.3*	*2.3*	*9.0*	*21.3*	*3.3*	*6.8*	*4.7*
Alabama:									
Rockwood Creek	U.S.N.M.	92300	52	3	......	......	......	......	4?
Grand Averages	......	......	*52.3*	*2.6*	*8.7*	*20.9*	*3.8*	*7.4*	*5.9*

* Ammocoetes; identification somewhat doubtful; counts not included in averages.
† Holotype.

fossor (20.3), slightly lower than in *greeleyi* (21.5); the posterior teeth very weak.

TEETH IN ANTERIOR ROW (Fig. 2).—3 to 4, usually 4; averaging 3.8, higher than in *unicuspis* (3.2) and *fossor* (2.2), lower than in the other species (4.1 to 4.6).

TEETH IN LATERAL ROWS (Fig. 2).—6 to 9, usually 7 or 8; averaging 7.4, fewer than in *castaneus* (8.5) or *bdellium* (8.3), almost the same as in *greeleyi* (7.2), somewhat higher than in *unicuspis* (6.6) and much higher than in *fossor* (4.7); lateral teeth extremely weak toward margin of disk.

BICUSPID CIRCUMORALS (Fig. 1).—2 to 8; averaging 5.9, slightly fewer than in *castaneus* (6.5), considerably fewer than in *bdellium* (7.8) and *greeleyi* (8.4); much more than in *unicuspis* and *fossor* (0.0); the cusps, when double, separate to very base of teeth.

TRANSVERSE LINGUAL LAMINA.—Extremely degenerate (more so than in any other species), small, fleshy, without denticulations and with little or no cornification; linear to weakly bilobed, as in *castaneus* as contrasted with all other species.

TABLE XVIII

MEASUREMENTS OF *ICHTHYOMYZON GAGEI* IN THOUSANDTHS OF THE TOTAL LENGTH

LOCALITY	MUSEUM	CAT. NO.	LENGTH, MM.	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL-OPENINGS, LENGTH OVER ALL
Oklahoma:									
Elk River	Mich.	103163	144	....	.....	.....	.....	.....	....
Elk River	Mich.	103163	105	....	.....	.....	.....	.....	....
Louisiana:									
Grant Parish	Mich.	107042*	103	306	81	12	68	51	107
Grant Parish	Mich.	107043	99	310	79	11	72	58	102
Grant Parish	Mich.	107043	100	288	83	11	70	50	109
Grant Parish	Mich.	107043	104	279	82	11	69	52	106
Grant Parish	Mich.	107043	104	296	85	14	67	50	92
Grant Parish	Mich.	107043	107	297	85	11	74	56	105
Grant Parish	Mich.	107043	108	296	82	11	72	49	102
Averages	....	....	*104*	*296*	*82*	*12*	*70*	*52*	*103*
Kentwood	Mich.	64494	107	272	72	12	64	46	103
Kentwood	Mich.	64494	108	278	70	11	57	38	94
Kentwood	Mich.	64494	113	310	63	11	59	44	96
Averages	....	....	*109*	*287*	*68*	*11*	*60*	*43*	*98*
Alabama:									
Rockwood Creek	U.S.N.M.	92300	126	276	67	12	60	39	105
Grand Averages	....	....	*107*	*292*	*77*	*12*	*66*	*48*	*102*

* Holotype.

FORM AND STRENGTH OF DISK TEETH (Pl. II, Fig. F).—Rather short, but slender, with small bases, only slightly curved backward (less so than in *castaneus, bdellium,* and *greeleyi,* more so than in *fossor*), moderately degenerate on sides of disk, very weak on posterior field (considerably more degenerate than usually in *greeleyi,* much less degenerate than in *fossor*).

TOTAL LENGTH (Fig. 4).—Adults examined, all mature, 99 to 126 mm., averaging 107 mm. in total length, somewhat less than in *fossor* and *greeleyi,* much smaller, and always smaller when adult, than in the 3 other species.

PROPORTIONATE SIZE OF PARTS, IN THOUSANDTHS OF TOTAL LENGTH (Figs. 4 and 5).—Length of tail, 272 to 310; averaging 292, somewhat higher than in *castaneus* (282) or *bdellium* (274), slightly lower than in *greeleyi* (297), considerably lower than in *unicuspis* and *fossor* (302 and 304). Depth of body, 63 to 85; averaging 77, about as in *greeleyi* and *fossor,* slightly higher than in *bdellium* (73), and lower than in *unicuspis* and *castaneus* (82) but not lower than in the small adults of those species (Table V). Length of eye, 11 to 14; averaging 12, intermediate between *unicuspis, castaneus,* and *bdellium* (11) on the one side and *fossor* and *greeleyi* (13) on the other; not so low as in small adults of the large species (Table VI). Length of snout (scarcely subject to shrinkage in this species), 57 to 74; averaging 66, intermediate between *fossor* (55) and *greeleyi* (73), much lower than in the others (86 to 95); the difference accentuated by comparing the very small adults of *gagei* with specimens of like size of the 3 large species (Table VII). Length of disk (little subject to shriveling in this species), 38 to 58; averaging 48, intermediate between *fossor* (41) and *greeleyi* (53), much lower than in any of the 3 large species (69 to 86); this difference also is accentuated by comparing specimens of like size (Table VIII). Length over gill-openings, 92 to 109; averaging 102, about as in *unicuspis* and *fossor* (101 to 104), slightly higher than in *castaneus* (94), *bdellium* (89), and *greeleyi* (98).

Color.—Color in formalin as described for holotype. Color in alcohol rather dark above, much darker than in *fossor* or *unicuspis,* or even *castaneus,* and probably somewhat darker than in *bdellium,* but much lighter than in *greeleyi;* moderately bicolored, distinctly more so than *unicuspis, fossor,* and *castaneus,* perhaps somewhat more bicolored than *bdellium,* but less than *greeleyi.*

Pigmentation of Lateral Line Organs.—Dorsal and lateral sense organs moderate to very strong, averaging as strong as in *greeleyi,* somewhat stronger than in *bdellium* and *castaneus,* much stronger than in *unicuspis* or *fossor.* Ventral organs (below gill region) lacking or moderately developed, instead of being consistently lacking as in *fossor* and *greeleyi,* much lighter than in breeding specimens of any of the 3 large species. *I. gagei,* according to the few specimens at hand, differs from the other species of the genus in the definite intensification of the row of dots around and just behind the mouth, and in the usual blackening of the organs connecting this row with the corresponding ventral row.

Life History.—This is one of the 3 degenerate, nonparasitic species of *Ichthyomyzon,* sharing this type of life history with *fossor* and *greeleyi:* the gonads progress well toward maturity before metamorphosis, at which time the gut degenerates and growth ceases. Most of the characters by which this species differs from *castaneus,* as pointed out above, are associated with the abbreviated, nonfeeding adult life.

Variation.—The specimens from Grant Parish in central Louisiana, west of the Mississippi River, are distinctly less degenerate than the few other examples, from Kentwood, Louisiana, and Rockwood Creek, Alabama, both east of the Mississippi River. Though not smaller, the Kentwood and Rockwood Creek specimens are slenderer, have shorter snouts, smaller disks, and weaker teeth. There also seem to be some average differences in number of teeth and of cusps (Table XVII). The intensity of pigmentation of the ventral organs of the lateral line may also differ: these organs below the branchial region are unpigmented in the 3 specimens from Kentwood and the 1 from Rockwood Creek, but are very weakly to weakly pigmented in 5 of the 7 from Grant Parish.

We take pleasure in associating the name of Dr. Simon Henry Gage, one of the foremost students of the lampreys, with this interesting and distinct species, which he first brought to our attention.

5. *ICHTHYOMYZON BDELLIUM* (JORDAN)

Ohio Lamprey

(Pl. I, Fig. C, and Pl. II, Fig. G, dentition)

(?) *Petromyzon nigrum* (preoccupied by *Petromyzon niger* Lacépède, 1798 = *Lampetra planeri* Bloch, 1782).—Rafinesque, 1820: 84 (Ohio River basin as high as Pittsburgh; probably in part; but name preoccupied, and selected on p. 21 as applying to *Entosphenus lamottenii*).[19]

Petromyzon argenteus (preoccupied by *Petromyzon argenteus* Bloch, 1790: Pl. 415, Fig. 2; Bloch and Schneider, 1801: 532, Pl. 102, Fig. 1; Shaw, 1804: 262; and Gray, 1851: 144,—a synonym of *Lampetra fluviatilis* (Linnaeus), 1758).—*Kirtland, 1838: 170, 197 (''Big Miami,'' Ohio; probably to be indicated as original diagnosis, for the few words of description, ''silvery appearance of its sides and abdomen,'' coupled with the locality, provide a reasonable indication that a species of *Ichthyomyzon* was meant); *1841: 342, Pl. 4, Fig. 3; and 1851: 205, 1 fig. (Big Miami River, in 1851 given as ''Ohio River,'' Ohio; attached to ''*Lucio-perca Americana*''; description; the small size of mouth and other features attributed to *argenteus* indicate that Kirtland had the common, small Ohio Valley species here called *bdellium;* not the Lake Erie specimens, which were doubtless *unicuspis*). De Kay, 1842: 382; Storer, 1846: 518; and Gray, 1851*a*: 237; and 1851*b*: 139 (all after Kirtland). Plummer, 1848: 51 (near Richmond, Indiana; identification very doubtful).[19] Jordan and Copeland, 1876: 161 (in part).

Ichthyomyzon argenteus.—Putnam, 1863: 2 (identification extremely doubtful). Jordan, 1882: 1001 (Ohio; in part).[19] (?) Call, 1896: 13 (Falls of the Ohio; species uncertain; so identified because all 3 specimens examined from Louisville are *bdellium*).[19]

Ichthyomyzon argenteum.—Jordon, 1880 and 1884: 349 (in part).

Scolecosoma argenteum.—Jordan, 1882: 757 (Ohio; in part).

(?) *Petromyzon* sp.—Cope, 1869: 239 (Holston River, at Glade Springs, Virginia; sight record).[19]

Petromyzon bdellium (substitute name to replace *P. argenteus* Kirtland, preoccupied).—*Jordan, 1885: 792.

Petromyzon concolor (presumably an unwarranted use of the name *concolor,* based on the unidentifiable *Ammocoetes concolor* Kirtland, 1841—see p. 24).—*Jordan, 1885: 973 (to replace *P. bdellium*). (?) Henshall, 1888: 122 (hydrant pipe, Cincinnati, Ohio).[19]

Ichthyomyzon concolor.—Osburn, 1901: 15 (Ohio; in part). (?) Fowler, 1908: 464 (Clinch River, Tennessee; transforming specimen re-examined). (?) Evermann, 1918: 313, 333, 366 (after Cope, 1869).[19] Creaser and Hubbs, 1922: 8 (in part). (?) Fowler, 1923: 23 (Clinch River, Tennessee; transforming specimen re-examined). Pratt, 1923: 25 (in part). Rauther, 1924: 678 (in part). Hubbs, 1925: 588, 589, 590 (in part). Jordan, 1929: 7 (in

[19] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

part). Jordan, Evermann, and Clark, 1929: 9 (in part). Osburn, Wickliff, and Trautman, 1930: 170 (Ohio; in part; in part re-examined). Berg, 1931: 90 (in part). Hildebrand, 1932: 51 (ammocoetes; Tuckaseegee River, Cullowhee Bridge, North Carolina; identified by reason of distribution and high number of myomeres—we count 55, 56, and 56 in 3 specimens, not 53 as given by Hildebrand).[20] Holly, 1933: 16 (in part). Pratt, 1935: 25 (in part).

(?)*Lampetra aepyptera* (misidentification, not *Ammocoetes aepypterus* Abbott, 1860).—Evermann and Clark, 1920; 306 (Lake Maxinkuckee, Indiana; see p. 22).

NOMENCLATURE.—Kirtland's preoccupied name *Petromyzon argenteus* was obviously based on this species, which since 1851 has not been recognized. His description of the teeth as "inflected" (that is, angled or curved) definitely suggests *bdellium* rather than *unicuspis*. His distinction of Lake Erie specimens from typical *argenteus* of the Ohio River basin, on the basis of their larger size (12 to 15 inches instead of 11) and different color ("waxen yellow," instead of "back ash-gray; sides and beneath, silvery gray"), indicates that he was contrasting *unicuspis* with *bdellium* (see p. 56). The numerous and slender disk teeth, rather small disk, and slender body shown in the type figure of *argenteus* all point likewise toward its identification with the species we call *bdellium*. The taking of the type on a *Stizostedion*, its length (11 inches), and the size of the disk as figured, all prove that Kirtland was not describing *greeleyi* (or *fossor* or *gagei*). Identification of *argenteus* with *castaneus* is apparently precluded on geographical grounds. Since Jordan's name *Petromyzon bdellium* was a simple substitute for *P. argenteus* Kirtland, the name *bdellium* belongs with this species, rather than with the one we call *unicuspis*, as thought by Regan (1911: 199) and Huntsman (1917: 24). The application of other names to this species is explained in the synonymy given above.

MATERIAL EXAMINED

WABASH RIVER SYSTEM, ILLINOIS AND INDIANA

U.S.N.M. 17761 (2)—Illinois: Mount Carmel [on Wabash River]; Samuel Turner.

Mich. 107039 (1)—Illinois: Embarrass River, Newton; T. L. Hankinson; May 1, 1917.

Mich. 55333 (1)—Illinois: Embarrass River, Charleston; Corbin; May 30, 1908.

U.S.N.M. 66882 (1)—Indiana: Wabash River, Terre Haute; Frank Byrns.

Mich. 99957 (1)—Indiana: Tippecanoe River, near Rochester; E. B. Williamson and Carl L. Hubbs; June 1, 1930 (attached to stone, in swift water).

U.S.N.M. 64914 (several)—Lake Maxinkuckee outlet; Barton W. Evermann and H. Walton Clark; June 18, 1901 (ammocoetes; 2 studied carefully).

OHIO RIVER, AT LOUISVILLE, KENTUCKY

U.S.N.M. 7419 (2) and 30733 (1)—no further data.

[20] Identification based on locality, with more or less evidence of a circumstantial, confirmatory nature.

OHIO RIVER DRAINAGE IN OHIO

Ohio F 723 (2)—mouth of White Oak Creek, Higginsport (on *Moxostoma erythrurum* and on *Placopharynx carinatus*); Harry Brookbank; summer, 1932.

Ohio F 724 (2)—Ohio River, Manchester, Adams Co. (on large *Cyprinus carpio*); Milton B. Trautman and T. Preston; Apr. 29, 1931.

Ohio F 443 (1)—small tributary to Ohio River, Adams Co. (clinging to stone in riffle; George T. Watters; Apr. 27, 1929.

UPPER TENNESSEE RIVER SYSTEM

Mich. 103548 (1)—Alabama: Goose Pond on Upper Huntsville Spring Branch, Madison Co.; Tennessee Valley Authority; June 6, 1936.

U.S.N.M. 35384 (1)—Tennessee: Dunning and Stevens.

Mich. 112330 (2)—Tennessee: Clinch River, below Norris Dam; A. R. Cahn; Mar. 4, 1936.

Phila. Acad. 22978 (1)—Tennessee: Coal Creek, Clinch River; E. D. Cope (transforming specimen; possibly *I. greeleyi*).

Mich. 96901 (1)—Virginia: North Fork of Holston River, above Saltville, Smyth Co.; H. R. Becker and party; July 9, 1928.

U.S.N.M. 92527 (several)—North Carolina: Tuckaseegee River, above Cullowhee Bridge; J. S. Gutsell; Aug. 25, 1930 (ammocoetes; 3 restudied; possibly not of this species).

NO LOCALITY

U.S.N.M. 22679 (1).

RANGE AND HABITAT.—*Ichthyomyzon bdellium,* so far as known, is confined to the Ohio River and its tributaries, including the Wabash and the Tennessee rivers. In this basin it appears to represent *I. castaneus.* It ranges upstream in Ohio and Kentucky at least as far as near Portsmouth, Ohio, and presumably still farther, into Pennsylvania, from which state, however, we have satisfactory records for *I. greeleyi* only. In the Wabash River basin it occurs in both Illinois and Indiana. From the Tennessee River basin there are records for Tennessee, Alabama, Virginia, and North Carolina.

The habitat of *bdellium,* to judge from the rather meager available material, is large and medium-sized rivers during the growing period of adult life, and rather small rivers and creeks during the spawning, ammocoete, and recently transformed periods of life.

TYPE SPECIMEN.—Kirtland's type of *Petromyzon argenteus* is no longer extant, so far as we can discover by searching through the collections of all the museums and colleges of Ohio which might once have contained any of his specimens. Since the name *Petromyzon bdellium* was a mere substitute for *P. argenteus,* the type of *bdellium* is, or was, the same as that of *argenteus.*

CHARACTERS (Tables XIX and XX), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—*Ichthyomyzon bdellium* is apparently the terminal form in the evolutionary series of the parasitic species of *Ichthyo-*

myzon, unicuspis → castaneus → bdellium, though in a few characters it resembles *unicuspis* more closely than *castaneus* (see pp. 13–14). Its closest relationship is with its presumed nonparasitic derivative, *greeleyi* (p. 95), to which it is much more similar than *unicuspis* is to *fossor,* and considerably more similar than *castaneus* is to *gagei* (p. 12).

MYOMERES IN TRUNK (Fig. 1).—53 to 62, usually 56 to 58; averaging 56.9, about as in *greeleyi* (57.1), more than 4 higher than in *castaneus* (52.6) or *gagei* (52.3), and much higher than in *unicuspis* (50.5) or *fossor* (50.9); this is probably the sharpest character distinguishing *bdellium* from all species other than *greeleyi.*

SUPRAORAL CUSPS (Fig. 1).—2 or 3; averaging 2.6, slightly lower than in *greeleyi* (2.8), the same as in *gagei,* slightly higher than in *castancus* (2.4), distinctly higher than in *unicuspis* and *fossor* (2.0); the cusps are long and strong.

INFRAORAL CUSPS (Fig. 2).—7 to 10, most frequently 8; averaging 8.4, about as in *castaneus* (8.3), more than in *unicuspis* (7.8), and less than in the 3 other species (8.7 to 9.4); the cusps are well developed.

TEETH IN CIRCUMORAL ROW (Fig. 2).—19 to 22, most frequently 21; averaging 20.8, almost as in *castaneus* and *gagei* (20.8 and 20.9), higher than in *unicuspis* (19.2) and *fossor* (20.3), lower than in *greeleyi* (21.5); the posterior teeth of the row well developed.

TEETH IN ANTERIOR ROW (Fig. 2).—4 or 5, usually 4; averaging 4.3, about as in *greeleyi* (4.1), slightly lower than in *castaneus* (4.6), higher than in *unicuspis* (3.2), *fossor* (2.2), and *gagei* (3.8).

TEETH IN LATERAL ROWS (Fig. 2).—7 to 10, usually 8; averaging 8.3, slightly lower than in *castaneus* (8.5), more or less higher than in the other species (4.7 to 7.4).

BICUSPID CIRCUMORALS (Fig. 1).—5 to 10, usually 8; averaging 7.8, lower than in *greeleyi* (8.4), somewhat higher than in *castaneus* (6.5) and *gagei* (5.9), and much higher than in *unicuspis* or *fossor* (0.0); the cusps largely distinct, but very obviously fused above the slightly bilobed, well cornified bases.

TRANSVERSE LINGUAL LAMINA.—Contrasting with that of *castaneus,* the transverse lingual lamina of *bdellium* is moderately to strongly bilobed, often as deeply cleft medially as usually in *unicuspis;* the plate is rather weaker and smaller than in *unicuspis;* the cusps average fewer, but longer and slenderer than in the other species excepting *greeleyi.*

FORM AND STRENGTH OF DISK TEETH (Pl. II, Fig. G).—Narrowly triangular in cross section, with rather light bases; long, slender, and acutely pointed, strongly recurved; well developed and distinct on all fields of the disk, even toward the margin; in the character of the cusps, *bdellium* differs rather sharply from *unicuspis,* but only on the average from *castaneus;* in

TABLE XIX

MYOMERE AND TOOTH COUNTS FOR *ICHTHYOMYZON BDELLIUM*

DRAINAGE BASIN	STATE	MUSEUM	CAT. NO.	MYOMERES	SUPRA-ORALS	INFRA-ORALS	CIRCUM-ORALS	ANTERIOR ROWS	LATERAL ROWS	BICUSPID CIRCUM-ORALS
Wabash	Illinois	U.S.N.M.	17761	57	3	9	......	......	7–8	8
Wabash	Illinois	U.S.N.M.	17761	56	3	8	......	......	8–9	6
Wabash	Illinois	Mich.	55333	56	2	9	21	5	10–10	8
Wabash	Illinois	Mich.	107039	54	2	8	19	5	10–10	6
Wabash	Indiana	U.S.N.M.	66882	57	2	9	......	......	8–8	8
Wabash	Indiana	Mich.	99957	58	2	8	19	4	8–8	8
Wabash	Indiana	U.S.N.M.	64914*	55	......	......	......	......	......	......
Wabash	Indiana	U.S.N.M.	64914*	56	......	......	......	......	......	......
Averages				*56.1*	*2.3*	*8.5*	*19.7*	*4.7*	*8.7*	*7.3*
Ohio	Kentucky	U.S.N.M.	7419	54	2	8	......	......	8–8	8
Ohio	Kentucky	U.S.N.M.	7419	57	2	7	......	......	9–9	8
Ohio	Kentucky	U.S.N.M.	30733	56	3	7	......	......	8–8	5
Averages				*55.7*	*2.3*	*7.3*	......	......	*8.3*	*7.0*
Ohio	Ohio	Ohio	F 723	58	2	8	22	4	8–8	8
Ohio	Ohio	Ohio	F 723	57	3	8	21	4	8–9	9
Ohio	Ohio	Ohio	F 724	53	2	8	21	4	7–7	8
Ohio	Ohio	Ohio	F 724	57	3	9	21	4	8–8	8
Ohio	Ohio	Ohio	F 443	58	3	9	21	4	7–8	8
Ohio	Ohio	Mich.	103298	62	3	9	21	4	7–7	8
Averages				*57.5*	*2.7*	*8.5*	*21.1*	*4.0*	*7.7*	*8.1*
Tennessee	Alabama	Mich.	103548	54	3	10	21	4	10–9	10
Tennessee?	Tennessee	U.S.N.M.	35384	57	3	8	......	......	8–8	8
Tennessee	Tennessee	Mich.	112330	60	2	9	21	5	8–8	8
Tennessee	Tennessee	Mich.	112330	62	3	9	21	5	8–8	8
Tennessee	Tennessee	Phila.	22978	59?	3	......	......	......	....	8?
Tennessee	Virginia	Mich.	92527*	56	......	......	......	......	....	......
Tennessee	North Carolina	U.S.N.M.	92527*	56	......	......	......	......	....	......
Tennessee	North Carolina	U.S.N.M.	92527*	55	......	......	......	......	....	......
Tennessee	North Carolina	U.S.N.M.	92527	55	......	......	......	......	....	......
Averages				*57.4*	*2.9*	*8.8*	*21.0*	*4.5*	*9.5*	*8.3*
?	?	U.S.N.M.	22679	57	3	8	......	......	8–8	7
Grand Averages				*56.9*	*2.6*	*8.4*	*20.8*	*4.3*	*8.3*	*7.8*

* Ammocoetes; myomere counts included in averages.

TABLE XX

MEASUREMENTS OF *ICHTHYOMYZON BDELLIUM* IN THOUSANDTHS OF THE TOTAL LENGTH

DRAINAGE BASIN	STATE	MUSEUM	CAT. NO.	LENGTH, MM.	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL-OPENINGS, LENGTH OVER ALL
Wabash	Illinois	U.S.N.M.	17762	142	277	70	12	90	70	85
Wabash	Illinois	U.S.N.M.	17761	224	214	80	10	87	76	85
Wabash	Illinois	Mich.	55333	259	295	83	11	91	68	107
Wabash	Illinois	Mich.	55333	158	291	72	12	84	72	83
Wabash	Indiana	U.S.N.M.	66882	206	266	73	9	83	68	85
Wabash	Indiana	Mich.	99957	211	275	64	11	86	64	96
Wabash	Indiana	U.S.N.M.	64914*	124	275	57	......	......	......	......
Wabash	Indiana	U.S.N.M.	64914*	133	265	60	......	......	......	......
Averages				*200*	*270*	*74*	*11*	*87*	*70*	*90*
Ohio	Kentucky	U.S.N.M.	7419	246	256	83	9	......	70	85
Ohio	Kentucky	U.S.N.M.	7419	247	251	76	9	77	66	92
Ohio	Kentucky	U.S.N.M.	30733	229	268	70	......	75	65	77
Averages				*241*	*258*	*76*	*9*	*76*	*67*	*85*
Ohio	Ohio	Ohio	F 723	163	244	70	13	84	62	85
Ohio	Ohio	Ohio	F 723	192	286	72	12	84	68	93
Ohio	Ohio	Ohio	F 724	126	289	55	15	86	70	88
Ohio	Ohio	Ohio	F 724	143	306	69	13	91	70	90
Ohio	Ohio	Ohio	F 443	139	276	67	14	85	73	85
Ohio	Ohio	Mich.	103298	253	253?	79	6	81	62	92
Averages				*169*	*276*	*69*	*12*	*85*	*67*	*89*
Tennessee	Alabama	Mich.	103548	229	311	84	11	89	74	97
Tennessee?	Tennessee	U.S.N.M.	35384	141	286	64	13	85	77	86
Tennessee	Tennessee	Mich.	102330	139	274	92†	14	86	72	91
Tennessee	Tennessee	Mich.	102330	151	310	67	14	85	75	91
Tennessee	Tennessee	Phila.	22978‡	137	287	62	8	29	35	98
Tennessee	Virginia	Mich.	96901	168	268	68	11	94	66	84
Tennessee	North Carolina	U.S.N.M.	92527*	69	....	......	......	......	......	......
Tennessee	North Carolina	U.S.N.M.	92527*	69	....	......	......	......	......	......
Tennessee	North Carolina	U.S.N.M.	92527*	70	....	......	......	......	......	......
Averages				*166*	*293*	*75*	*13*	*88*	*73*	*90*
?	?	U.S.N.M.	22679	216	264	76	10	89	71	83
Grand Averages				*189*	*274*	*73*	*11*	*86*	*69*	*89*

* Ammocoetes; measurements not included in averages.
† Unusually deep, because very turgid with blood.
‡ Transforming specimen; measurements not included in averages.

the degree of development of the teeth, it contrasts with the 3 small species, least strikingly with *greeleyi*.

TOTAL LENGTH (Fig. 4).—Adults examined, 124 to 259 mm. long, averaging 189 mm., maturity probably attained at a minimum length of about 200 mm.; mature adults probably averaging slightly smaller than those of *castaneus,* and considerably smaller than those of *unicuspis,* probably always larger than those of *fossor, gagei,* and *greeleyi.*

PROPORTIONATE SIZE OF PARTS, IN THOUSANDTHS OF TOTAL LENGTH (Figs. 4 and 5).—Length of tail, 214 to 311; averaging 274, lower than in any of the other species (282 to 304); closest to *castaneus* in this character. Depth of body, 55 to 92; averaging 73, lower than in any other form, contrasting most sharply with *unicuspis* and *castaneus* (82); this difference due in part only to the circumstance that a higher percentage of the available specimens of *bdellium* than of *unicuspis* and *castaneus* are small and immature, and hence slenderer on account of age variation (see Table V). Length of eye, 6 to 15, tending to decrease with age (Table VI); averaging 11, as in *castaneus* and *unicuspis,* somewhat lower than in *gagei* (12) and *fossor* and *greeleyi* (13). Length of snout (less subject to shrinkage in this species than in *unicuspis*), 75 to 94; averaging 86, lower than in *castaneus* (90) and *unicuspis* (95), higher on the average than in *greeleyi* (73), consistently higher than in *gagei* (66) and *fossor* (55); length of snout tending to decrease with age (Table VII). Length of disk (showing less tendency to be lowered by puckering than in the other large species), 62 to 77; averaging 69, distinctly lower than in *castaneus* (77), and much lower than in *unicuspis* (average 86, unduly lowered by puckering), consistently larger than in *greeleyi* when specimens of like size are compared (see Table VIII), always larger than in *gagei* or *fossor.* Length over gill-openings, 77 to 107; averaging 89, lower than in any of the other species (94 to 104).

COLOR.—The available specimens of *bdellium* on the average are darker above, more slaty and less yellow, than those of *unicuspis* and *castaneus,* and are more distinctly bicolored, for their darker backs contrast more sharply with their lighter bellies. This species is darker and more bicolored than *fossor,* but definitely lighter, and less bicolored, than *greeleyi.*

PIGMENTATION OF THE LATERAL LINE ORGANS.—In small adults the sense organs of the body and head are unpigmented or only faintly blackened. The dorsal organs become moderately blackened in the half-grown adults, but the ventral organs, on the branchial region, remain unpigmented or nearly so. With maturity the dorsal organs become rather strongly blackened, while the ventral organs become very intensely blackened. In this character, *bdellium* essentially agrees with *unicuspis* and *castaneus,* and contrasts with *fossor, gagei,* and *greeleyi* (see Table IX).

LIFE HISTORY.—Although it is apparently somewhat reduced in size, and has a markedly reduced disk, *I. bdellium* definitely belongs in the parasitic series, preying on fishes and growing after metamorphosis.

VARIATION.—The data in Tables XIX and XX indicate that this species shows little geographical variation. Whether it intergrades with *castaneus* near the mouth of the Ohio River remains to be learned. Possible hybridization between *bdellium* and *unicuspis* is indicated on pages 17 to 18.

6. ICHTHYOMYZON GREELEYI, N. SP.

Allegheny Brook Lamprey

(Pl. I, Fig. F, and Pl. II, Fig. H, dentition)

(?) *Lampetra wilderi* (presumable misidentification; not *Lampetra wilderi* Gage, 1896 = *Entosphenus appendix* (De Kay), 1842 = *E. lamottenii* (LeSueur), 1827).—Fowler, 1906: 595 (Allegheny River above Port Allegany, Pennsylvania); 1907: 6 (Kiskiminitas River, Pennsylvania).[21]

(?) *Ichthyomyzon castaneus* (misidentification; not *Ichthyomyzon castaneus* Girard, 1858).—Fowler, 1908: 464 (Kiskiminitas River, Pennsylvania; reidentification of specimens named *Lampetra wilderi* in 1907).

(?) *Ichthyomyzon concolor* (probably an unwarranted use of name *concolor*).—Fowler, 1910: 345 (Two Licks Creek and Ramsey's Run, basin of Conemaugh River, Pennsylvania); 1919: 52 (Conemaugh River formerly and Two Licks Creek, Indiana and McKean cos., Pennsylvania).[21]

NOMENCLATURE.—Although very distinct this species has never been given a definite name. As indicated above it has probably been recorded, under inapplicable names, by Fowler. It is possible that the type of Kirtland's *Ammocoetes concolor* from Columbus, Ohio, was an ammocoete of *Ichthyomyzon greeleyi*, and probable that the nontype specimens from the Mahoning River were of that species. We consider it inadvisable, however, to apply the name *concolor* to any of the species (see p. 24).

MATERIAL EXAMINED

OHIO RIVER SYSTEM, PENNSYLVANIA

Mich. 108103 and 108105–108112 (98)—Little Neshannock Creek, from 2 miles S. of to 2 miles N. of New Wilmington, Mercer and Lawrence cos.; Edward C. Raney; May 17 to 27, 1935.

Mich. 109085 (3)—Little Neshannock Creek, 2 miles N. of New Wilmington, Mercer Co.; Edward C. Raney and Ernest Lachner; Aug. 24, 1935 (ammocoetes).

Mich. 102390 (1)—tributary of Pymatuming Swamp above Linesville, Crawford Co.; Paul A. Webb; spring, 1933 (from mouth of a *Necturus*).

Mich. 109084 (1)—Big Sandy Creek, near Franklin, Venango Co.; Edward C. Raney; Mar. 23, 1935.

Carn. 8590 (1) and Mich. 106836 (1)—Little Sandy Creek, near Polk, Venango Co.; Edward C. Raney; May 26, 1934.

[21] Identification based on locality, with more or less additional evidence of a circumstantial, confirmatory nature.

Mich. 108104 (3)—South Branch of Little Sandy Creek, near Pearl, Venango Co.; Edward C. Raney; May 29, 1935.

Mich. 91545 (1)—French Creek, near Meadville; Paul A. Webb; Sept. 4–5, 1928.

Mich. 91546 (4)—French Creek, near Wattsburg; Paul A. Webb; Sept. 20, 1928 (ammocoetes).

Mich. 94981 (14)—same locality; John R. Greeley; Sept. 19, 1931 (13 ammocoetes and 1 subadult).

Mich. 92317 (holotype)—French Creek, just above Wattsburg; John R. Greeley; May 30, 1931.

Mich. 102389 (3)—same locality; Carl L. Hubbs and Milton B. Trautman; May 13, 1934.

RANGE AND HABITAT.—*Ichthyomyzon greeleyi* seems to be confined to the upper portion of the Ohio River system. Though all available records pertain to northwestern Pennsylvania, it is almost certain that the species also occurs, or at least formerly lived, in northeastern Ohio, in the Beaver River system, in which the species occurs in Pennsylvania. It presumably also occurs in French Creek within New York limits, for the type was taken in that stream only a few miles from the Pennsylvania–New York boundary. Throughout its life this lamprey seems to occur chiefly in creeks, avoiding small brooks as well as rivers.

TYPE SPECIMENS.—The holotype is a largely spent female collected by Dr. John R. Greeley on May 30, 1931, in French Creek, a tributary of Allegheny River, 1 mile above (east of) Wattsburg, Erie County, Pennsylvania, among large stones on a swift riffle. All other specimens listed above have been used in preparing the following description, and are designated as paratypes.

CHARACTERS OF HOLOTYPE.—Myomeres between last gill-opening and anus, 57. Supraoral cusps, 3; infraoral cusps, 8, so weak as to be almost uncountable; teeth in circumoral rows, 21, very weak posteriorly; teeth in anterior row, 4, the outermost 1 obsolescent; teeth in lateral rows, 7–8, the outermost 2 of each side obsolescent; bicuspid circumorals, 8, the 2 cusps so deeply cleft as to give the appearance of separate teeth; transverse lingual lamina so strongly bilobed that the crest is very narrowly U-shaped medially, weakly cornified, with relatively few denticulations which are lower and blunter than usual in this species; disk teeth rather long and slender, with small bases, curved backward, moderately degenerate on sides of disk, very weak on posterior field. Proportionate measurements of parts in thousandths of the total length (105 mm.): length of tail, 277; depth of body, 68; length of eye, 12; length of snout, 62; length of disk, 52; length over gill-openings, 92. Color in alcohol rather dark brown on back and midsides, abruptly changing to light yellow on lower surface, to give a strongly bicolored appearance. Lateral line organs of back and sides of body moderately blackened, but those of ventral surface of branchial region entirely unpigmented. Life history obviously of the nonparasitic type: size small when breeding, gut degenerated, disk greatly reduced.

CHARACTERS (Tables XXI and XXII), COMPARISONS (Table X, and Key to Species), AND RELATIONSHIPS.—*Ichthyomyzon greeleyi*, according to available indications is most closely related to, and is the nonparasitic derivative of *I. bdellium*, with which it specifically agrees in the very high number of trunk myomeres; the form and number of teeth and tooth cusps; the strongly bilobed transverse lingual lamina with few, long denticulations; the bicolored

TABLE XXI

SUMMARY OF MYOMERE AND TOOTH COUNTS OF *ICHTHYOMYZON GREELEYI*

For each character there is given the minimum and maximum count, the average in italics, and the number of counts as an inferior figure.

LOCALITY	MYOMERES	SUPRAORALS	INFRAORALS	CIRCUMORALS	ANTERIOR ROWS	LATERAL ROWS	BICUSPID CIRCUMORALS
Pennsylvania							
Little Neshannock Creek	55–61	2–4	8–12	19–24	3–5	5–9	7–11
	58.0_{100}	2.8_{96}	9.4_{97}	21.4_{97}	4.1_{97}	7.2_{194}	8.4_{97}
Trib. of Pymatuming Swamp	58_{1}	2_{1}	10_{1}	24_{1}	4_{1}	8_{2}	10_{1}
	57–60	2–3	8–10	....	3–4	6?–8	8–9
French Creek	57.5_{22}	2.8_{5}	8.6_{5}	21_{4}	4.75_{4}	7.6_{10}	8.2_{5}
Sandy creeks, Venango Co.	58–61	2–3	7–10	21–23	3–4	7–8	8–11
	58.5_{6}	2.4_{5}	9.0_{5}	21.4_{5}	3.8_{5}	7.6_{10}	9.4_{5}
Total Range	55–61	2–4	7–12	19–24	3–5	5–9	7–11
Grand Average	57.9_{129}	2.8_{107}	9.4_{108}	21.5_{107}	4.1_{107}	7.2_{216}	8.4_{108}

TABLE XXII

SUMMARY OF MEASUREMENTS FOR *ICHTHYOMYZON GREELEYI*

Total length in mm., and other measurements in thousandths of total length; range of variation, and averages in italics.

LOCALITY	NUMBER OF SPECIMENS	TOTAL LENGTH	TAIL LENGTH	BODY DEPTH	EYE LENGTH	SNOUT LENGTH	DISK LENGTH	GILL OPENINGS, LENGTH OVER ALL
Pennsylvania								
Little Neshannock Creek		111–152	245–325	59–90	10–16	51–88	43–65	88–108
	98	*128*	*299*	*76*	*13*	*73*	*53*	*99*
Trib. of Pymatuming Swamp	1	*161*	*299*	*84*	*10*	*63*	*48*	*92*
		105–142	271–307	68–88	11–12	62–78	45–57	92–98
French Creek	5	*127*	*285*	*78*	*12*	*71*	*52*	*95*
Sandy creeks, Venango Co.		118–134	253–290	74–84	13–16	61–84	47–58	92–110
	5	*125*	*274*	*79*	*14*	*77*	*53*	*100*
Total Range		105–161	245–325	59–90	10–16	51–88	43–65	88–110
Grand Average	109	*128*	*297*	*76*	*13*	*73*	*53*	*98*

pattern; and geographical distribution. It resembles *bdellium* more closely than *castaneus* in every important respect by which *bdellium* differs from *castaneus*. It contrasts strongly with *unicuspis*. It differs from *gagei* and *fossor*, respectively, in the same way that *bdellium* differs from *castaneus* and *unicuspis*, and further differs from *gagei* and especially from *fossor* in being much less degenerate.

MYOMERES IN TRUNK (Fig. 1).—55 to 61, usually 57 to 59; averaging 57.9, slightly higher (1) than in *bdellium*, more than 5 higher than in *castaneus* and *gagei* and 7.4 to 7.0 higher than in *unicuspis* and *fossor*.

SUPRAORAL CUSPS (Fig. 1).—2 to 4, about thrice as often 3 as 2; averaging 2.8, slightly higher than in *castaneus* (2.4) and *gagei* and *bdellium* (2.6), decidedly higher than in *unicuspis* and *fossor* (2.0); the cusps usually rather strong and sharp.

INFRAORAL CUSPS (Fig. 2).—7 to 12, usually 8 to 10; averaging 9.4, higher than in any other species (7.8 to 8.7); the cusps usually discrete and sharp, though occasionally weak and tubercular; the lamina usually well cornified.

TEETH IN CIRCUMORAL ROW (Fig. 2).—19 to 24, usually 21; averaging 21.5, somewhat more than in any of the other species (19.2 to 20.9).

TEETH IN ANTERIOR ROW (Fig. 2).—3 to 5, usually 4; averaging 4.1, about as in *bdellium* (4.3), somewhat lower than in *castaneus* (4.6) but higher than in *gagei* (3.6), distinctly higher than in *unicuspis* (3.2) or *fossor* (2.2).

TEETH IN LATERAL ROWS (Fig. 2).—5 to 9, most frequently 7, often 8; averaging 7.2, about 1 fewer than in *bdellium*, lower than in *castaneus* (8.5) or even *gagei* (7.4), higher than in *unicuspis* (6.6) or *fossor* (4.7).

BICUSPID CIRCUMORALS (Fig. 1).—7 to 11, typically 8; averaging 8.4, slightly higher than in *bdellium* (7.8), considerably higher than in *castaneus* (6.5) and *gagei* (5.9), and of course much higher than in *unicuspis* and *fossor* (0.0).

TRANSVERSE LINGUAL LAMINA.—Moderately to strongly bilobed, the crest often narrowly U-shaped medially, as usually in *unicuspis* and *bdellium*, not linear to weakly bilobed as in *castaneus* and *gagei;* the lamina much better developed than in *fossor* or *gagei*, more or less strongly cornified; the crest with relatively few, usually long and sharp denticulations, as in *bdellium*.

FORM AND STRENGTH OF DISK TEETH (Pl. II, Fig. H).—Usually narrowly triangular in cross section, with rather small bases, contrasting most strongly with *unicuspis* in this respect; rather long, slender, and sharp, usually more so than in *gagei*, and much more so than in *fossor*, rather closely approaching *bdellium* in these respects; more or less strongly curved, also as in *bdellium;* teeth usually less degenerate than in *gagei*, much less than in *fossor*, tending to be well developed except toward margin of disk and on posterior field, where more or less obsolescent as usual in the nonparasitic species. In strength of dentition, *greeleyi* diverges less from its parasitic ancestor *bdellium* than *gagei* does from *castaneus,* much less than *fossor* does from *unicuspis.*

TOTAL LENGTH (Fig. 4).—Adults examined (almost all, including both extremes of size, taken in the spawning season), 105 to 161 mm. long, usually between 110 and 150 mm.; averaging 128 mm.; larger in average or maximum size than either *fossor* or *gagei,* consistently smaller than the mature adults of *unicuspis, castaneus,* and *bdellium.*

PROPORTIONATE SIZE OF PARTS, IN THOUSANDTHS OF TOTAL LENGTH (Figs. 4 and 5).—Length of tail, 245 to 325; averaging 297, slightly higher than in *bdellium* (274), *castaneus* (282), and *gagei* (292), slightly lower than *unicuspis* and *fossor* (302 and 304). Depth of body, 59 to 90; averaging 76, slightly higher than in *bdellium* (73), probably because we have measured few mature specimens of *bdellium,* almost the same as in *fossor* (74) and *gagei* (77), somewhat lower than in *unicuspis* and *castaneus* (82). Length of eye, 10 to 16; averaging 13, as in *fossor,* slightly higher than in *gagei* (12), or in *unicusps, castaneus,* and *bdellium* (11), but not higher than in specimens of like size of the 3 species last named. Length of snout (not subject to marked shrinkage in this species), 51 to 88; averaging 73, lower than in *bdellium* (86), *castaneus* (90), and *unicuspis* (95), higher than *gagei* (66) and *fossor* (55); these distinctions of average significance only, even on comparison of specimens of like size (Table VII). Length of disk (little subject to false reduction by shriveling in this species), 43 to 65; averaging 53, lower than in *bdellium, castaneus,* and *unicuspis* (the distinction consistent when specimens of like size are compared, as in Table VIII), higher (on the average) than in *gagei* (48) and *fossor* (41). Length over gill-openings, 88 to 110; averaging 98, higher than in *bdellium* (89), slightly higher than in *castaneus* (94), slightly lower than in the 3 other species (101 to 104).

COLOR.—In alcohol dark brown above and on mid-sides, darker than in any other species (not considering the post-spawning blackened phase); this color contrasting strongly and abruptly with the pale yellowish lower parts, to produce a more definitely bicolored pattern than in any of the other species of the genus, approaching *bdellium* and *gagei* most closely in this respect.

Specimens after brief preservation in formalin were dark olive green, underlaid with slaty on back, sides, and tail; light muddy yellow, underlaid and mottled with light slate, on the lower surface and lowermost sides of the trunk and branchial region; as dark on the gular region as on the back. The heart-shaped pineal region is very conspicuous, light yellow. The pupil is blue-black; the iris is ringed with light gray around the pupil, and with gray-blue externally. The dorsal fin is very pale gray with a yellowish cast, almost transparent; the somewhat swollen anterior end of the fin is not reddish, as it is in *Entosphenus lamottenii* and *Lampetra aepyptera.* The deeply pigmented area on the end of the body, spreading out on the adjacent parts of the caudal fin, and the pigmentation of the dorsal fin, are scarcely evident in life, becoming apparent after preservation in formalin and conspicuous when the fins have become somewhat desiccated.

This species, although never showing the light yellowish phase characteristic of the immature and early spawning periods in the life of *I. unicuspis,* does very noticeably darken, as do other lampreys, as spawning progresses. The final stage of darkening, attained as the lamprey approaches its inevitable death after spawning, is represented by a fully spent specimen, taken dead in Little Neshannock Creek on May 26; it was a brilliant, dark blue on the back and sides, with a glaucous sheen perhaps due to the usual fungus infection, and bluish white below.

Pigmentation of the Lateral Line Organs.—The dorsal and lateral sense organs in the adult of this species are usually rather strongly to very strongly pigmented with black, are always more or less blackened, but tend to be less conspicuous than in other species because the darker ground color of the body provides less contrast; the ventral organs below the branchial region, in contrast, are entirely unpigmented in all specimens. This character alone invariably separates this species from *unicuspis, castaneus,* and *bdellium,* all of which have the ventral organs very evidently blackened during maturity, and from *fossor,* which develops pigment in neither dorsal nor ventral organs; the distinction from *gagei* is less definite, for that species has more or less blackened dorsal sense organs and often shows some pigmentation in the ventral organs.

Life History.—*Ichthyomyzon greeleyi* is one of the nonparasitic lampreys, definitely commencing to mature before metamorphosis and not growing after that event. Its fine set of teeth of relatively large size for a nonparasitic lamprey and its rather large mouth indicate the relatively recent attainment of this type of life history by this species; its differentiation from *I. bdellium* has apparently been somewhat recent (see p. 13).

Geographical Variation.—This species shows a moderate amount of individual but very little geographical variation in its very restricted known range. Specimens from the Sandy creeks in Venango County, from French Creek (both tributary to the Allegheny River), and from Little Neshannock Creek, of the Beaver River system, yield averages which do not differ greatly, considering the small size of the series from all except the last-named locality. The one relatively large specimen from a tributary of the Pymatuming Swamp (now an artificial lake), in the headwaters of the Shenango-Beaver system, is somewhat aberrant, and possibly represents a slightly differentiated race.

We name this species for its discoverer, Dr. John R. Greeley, who has kindly given us permission to include its description in this revision of the lampreys of the genus *Ichthyomyzon.*

Literature Cited

We have attempted to gather together all references which deal with the genus *Ichthyomyzon,* with any of its species, or with species confused with the forms of this genus. Many of the citations merely list a species or two, or give locality records. Items which have an important bearing on the systematics of *Ichthyomyzon* are marked with an asterisk (*).

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PLATE I

THE SIX SPECIES OF *ICHTHYOMYZON*

The 3 parasitic species are shown above (Figs. A–C), about one-third natural size; the 3 nonparasitic species are shown below (Figs. D–F), slightly reduced. Photographs by F. W. Ouradnik.

FIG. A. *I. unicuspis:* the holotype, a male 319 mm. in total length; Cat. No. 107040, Mus. Zool.

FIG. B. *I. castaneus:* an adult female 301 mm. long, from Black Lake, Ottawa Co., Michigan; Cat. No. 101722, Mus. Zool.

FIG. C. *I. bdellium:* an adult male 253 mm. long, from Ohio River, Adams Co., Ohio; Cat. No. 103298, Mus. Zool.

FIG. D. *I. fossor:* an adult male 116 mm. long, from Red Cedar Creek, East Lansing, Michigan; Cat. No. 55313, Mus. Zool.

FIG. E. *I. gagei:* an adult male paratype, 108 mm. long, from stream near Dry Prong, Louisiana; Cat. No. 107043, Mus. Zool.

FIG. F. *I. greeleyi:* an adult male paratype, 131 mm. long, from Little Neshannock Creek, Pennsylvania; Cat. No. 108105, Mus. Zool.

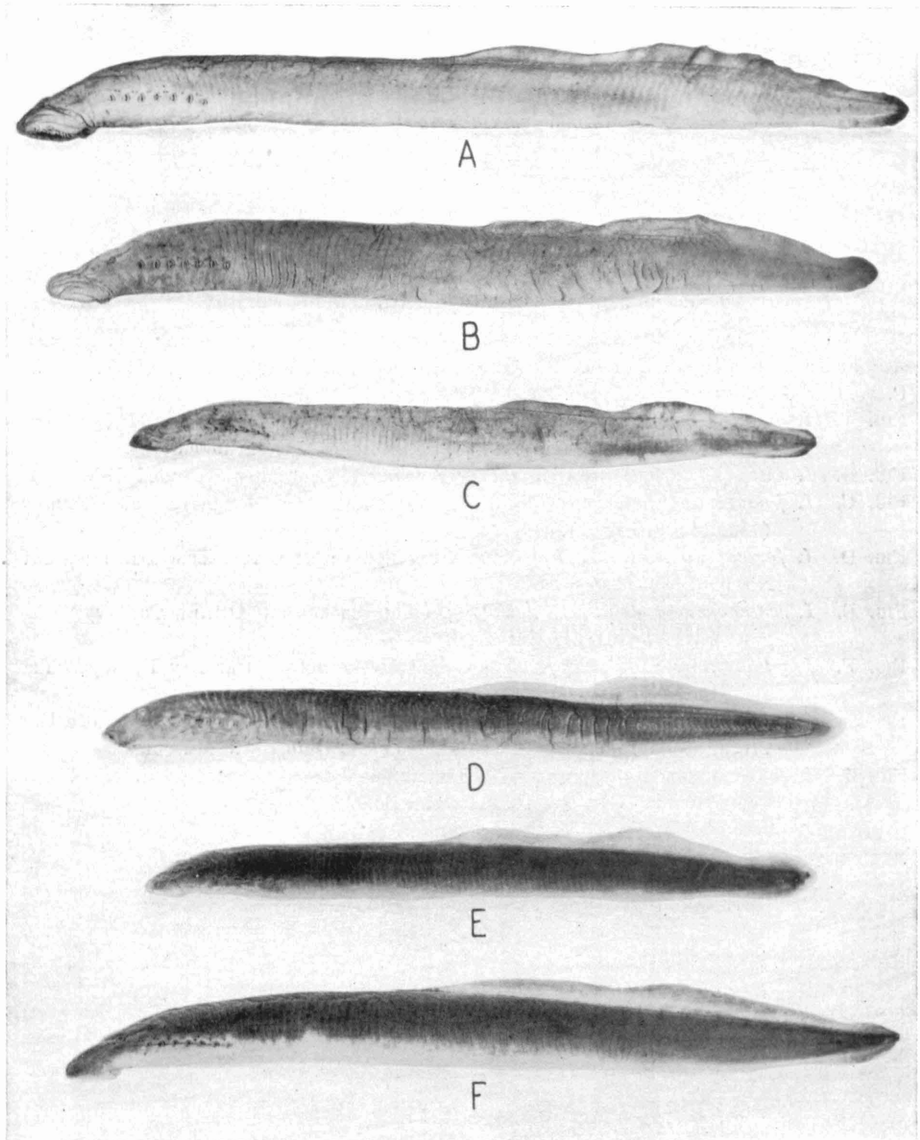


PLATE II

DISK AND DENTITION IN THE SPECIES OF *ICHTHYOMYZON*

The figures are arranged to show the 3 pairs of species, each containing a large parasitic and a small nonparasitic form. All enlarged to the same degree. Photographs by F. W. Ouradnik.

FIG. A. *I. unicuspis:* an adult paratype 302 mm. long, from Lake Erie, off Sandusky, Ohio; Cat. No. 55306, Mus. Zool.; disk somewhat shrunken.

FIG. B. *I. unicuspis:* a half grown paratype showing the normally expanded disk.

FIG. C. *I. fossor:* an adult type specimen; reproduced from Reighard and Cummins (1916, Pl. 2, Fig. 1).

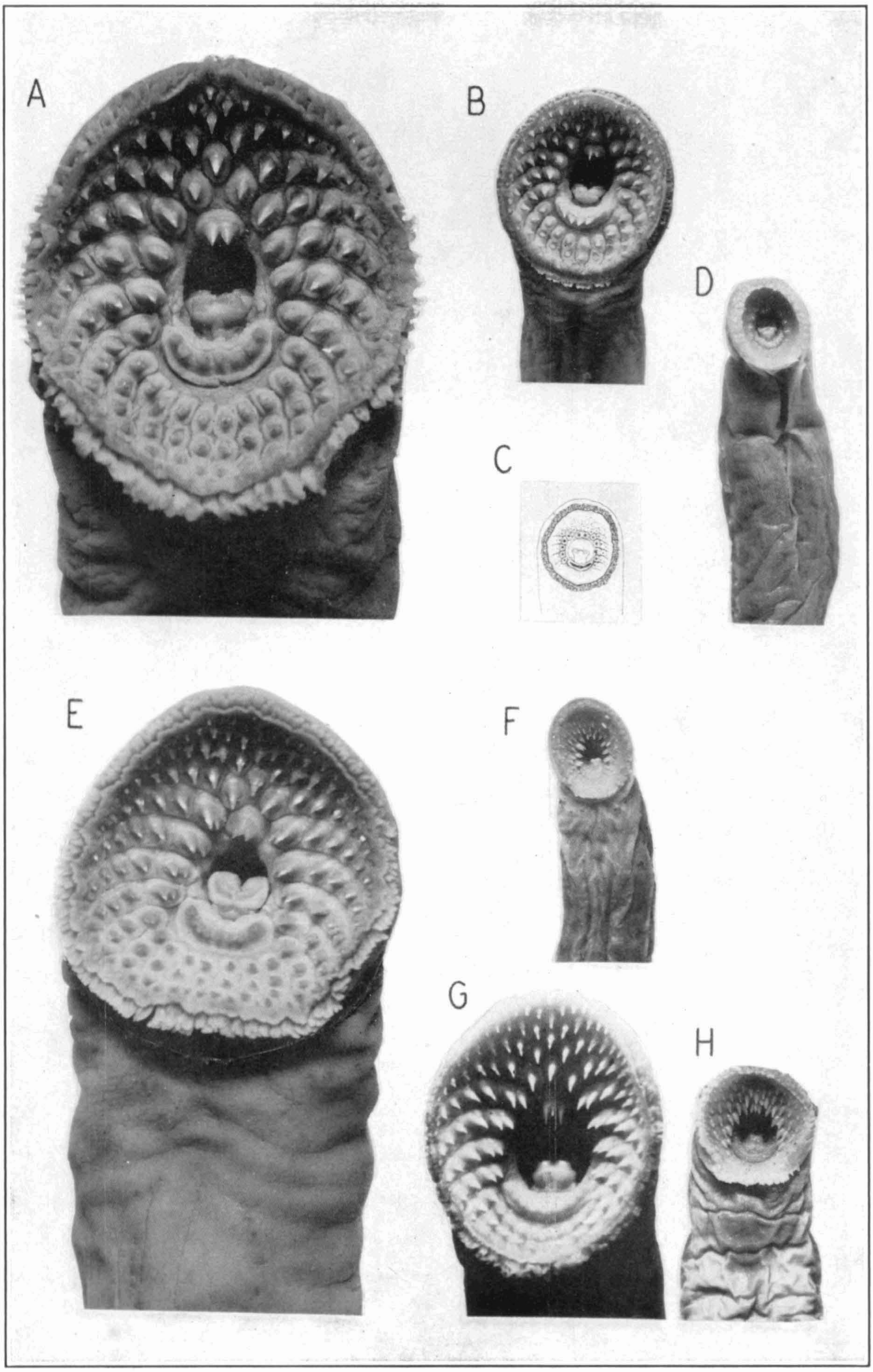
FIG. D. *I. fossor:* an adult 116 mm. long, from Red Cedar Creek, East Lansing; Cat. No. 55313, Mus. Zool.

FIG. E. *I. castaneus:* an adult 275 mm. long, from Black Lake, Ottawa County, Michigan; Cat. No. 101722, Mus. Zool.

FIG. F. *I. gagei:* an adult paratype 99 mm. long, from stream near Dry Prong, Louisiana; Cat. No. 107043, Mus. Zool.

FIG. G. *I. bdellium:* a small adult paratype 163 mm. long, from mouth of White Oak Creek, at Higginsport, Ohio; Cat. No. 723, Ohio State Museum.

FIG. H. *I. greeleyi:* an adult paratype 128 mm. long, from Little Neshannock Creek, Pennsylvania; Cat. No. 108111, Mus. Zool.


A
B
C
D
E
F
G
H

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