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ABSTRACT

The freshwater lamprey genus Ichthyomyzon is restricted to eastern North America. It consists of six species, which can be separated into three sympatric pairs each made up of a parasitic stem species and a nonparasitic satellite species. The three pairs are the following: unicuspis-fossor, castaneus-gagei and bdellium-greeleyi.

The taxonomy of the ammocoetes, which has not been investigated previously, was studied in detail. A total of 323 specimens were examined. The pigmentation patterns on the caudal fin and the different sections of the head, and the number of trunk myomeres proved to be the characters most important to separate the species. These were used in a taxonomic key, accompanied by a series of illustrations. The morphometric characters, on the other hand, proved to be of little taxonomic value.

The taxonomy of the adults was revised through the study of 278 specimens. A detailed analysis, including a key to the adults and principal components analyses, was done. The values of meristic and morphometric characters previously studied by Hubbs and Trautman (1937) showed larger ranges. New morphometric characters were investigated.

I. hubbsi (Raney, 1952) was synonymized with greeleyi.

The geographic distribution of the genus was compiled from the literature, and museum, university and private collections. The range was extended for all the species, especially the nonparasitic ones, whose ranges were extended to include, on the average, three drainage basins. The range of the parasitic species was extended within the drainage basins where they were already known to occur.

RESUME

Les lamproïes dulçaquicoles du genre Ichthyomyzon sont restreintes aux bassins de drainage de l'est de l'Amérique du Nord. Le genre comprend six espèces réparties en trois paires sympatriques. Chaque paire est composée d'une espèce souche parasite et d'une espèce satellite non-parasite: unicuspis-fossor, castaneus-gagei et bdellium-greeleyi.

La taxonomie des ammocètes, qui n'avait pas été examinée auparavant, est étudiée en détail. La répartition de la pigmentation sur la nageoire caudale et sur différentes parties de la tête, ainsi que le nombre de myomères sont les caractères les plus importants dans l'identification des espèces. Ils sont utilisés dans une clé taxonomique accompagnée d'illustrations. Les caractères morphométriques ont peu de valeur taxonomique.

La taxonomie des adultes, étudiée par Hubbs et Trautman (1937) est révisée. On procède à une étude plus détaillée, incluant une nouvelle clé taxonomique et des analyses de composantes principales. Les écarts de variabilité des caractères méristiques et morphométriques déjà étudiés sont élargis. De nouveaux caractères morphométriques sont aussi étudiés.

L'aire de distribution géographique du genre est compilée à partir de publications et données provenant de musées, d'universités et de collections privées. L'aire de distribution de toutes les espèces est étendue, particulièrement celle des espèces non-parasites dont les aires sont étendues à trois nouveaux bassins de drainage, en moyenne. Les aires des espèces parasites s'étendent à l'intérieur des bassins de drainage où elles étaient déjà présentes.

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## INTRODUCTION

The freshwater lamprey genus Ichthyomyzon Girard, 1858 is restricted to the tributaries of the Gulf of Mexico, the Gulf of St. Lawrence and the Hudson Bay in Eastern North America. It belongs to the order Petromyzontiformes, which is characterized by the presence of seven gill openings on each side of the branchial region, a single median nostril, a suctorial disc and an eel-like shape. Scales, paired fins, gill covers, jaws and backbone are absent. The life-cycle consists of the ammocoete, or larval, stage and the adult, or transformed, stage.

The genus Ichthyomyzon, whose diagnostic character is the presence of a continuous dorsal fin, comprises six species. Three of these are parasitic and after metamorphosis, feed mainly on teleost fishes. These are unicuspis, castaneus and bdellium. The other three species, which do not feed as adults, are fossor, gagei and greeleyi. A seventh nonparasitic species, hubbsi, was described by Raney (1952), but it is synonymized with greeleyi in this study.

Until now, only the adult stage has been studied in detail, mainly in the revision of the genus by Hubbs and Trautman (1937). Their revision was based on the number of trunk myomeres, the number, form and arrangement of both the oral and lingual disc-tooth series and the proportionate measurements of body parts. But neither dentition nor some of the body measurements most useful in separating the adults of the species can be used in distinguishing the ammocoetes as they do not possess a disc, but instead have a horseshoe-shaped mouth with a fleshy hood overhanging it. The main purpose of this research was to find

new diagnostic features and develop a taxonomic key to the ammocoetes, using modifications of the taxonomic identification system developed by Vladykov (1950) for the ammocoetes of the species with two dorsal fins. Prior to the present study, it was not possible to identify the larvae. The pigmentation patterns on the caudal fin and sections of the head and body, the number of myomeres, total length and body proportions were recorded from representative samples of ammocoetes. Characters found to be of taxonomic value were summarized in a key to the species.

The second object of this research was to revise the taxonomy of the adults and improve the key to the species first drawn up by Hubbs and Trautman (1937). Complete data on total length, body proportions, number of myomeres and teeth counts were recorded from a representative sample of adults of the six species. The data were then used in principal components and phenetic analyses to explore the status and relationships of the species.

In their study of the morphology of the adults, Hubbs and Trautman (1937) postulated a series of phyletic relationships. They interpreted I. unicuspis as the most primitive form, from which were derived sequentially two other progressively smaller parasitic species, I. castaneus and I. bdellium. Each of these three were believed to have given rise to a single nonparasitic species, I. fossor, I. gagei and I. greeleyi, respectively. This derivative species concept, based on different biotypes, was first developed by Hubbs (1925). A similar concept was presented later by Zanandrea (1954). His term "paired species" is applied to the pairs of closely related and morphologically similar lampreys which overlap in their distribution but differ in their life history. Hardisty and Potter (1971) summarized and discussed in

detail the current view on paired species. The discovery of new species of both biotypes and the extension of the geographical distribution of several species brought Vladykov and Kott (1979) to describe the relationship in terms of "stem" and "satellite" species. Under that classification system, the genus Ichthyomyzon has three pair-complexes: unicuspis-fossor, castaneus-gagei and bdellium-greeleyi. In this study, these complexes will be referred to as sympatric stem-satellite pairs, without necessarily implying that they are immediate relatives or sister-groups.

Literature subsequent to Hubbs and Trautman's (1937) revision of the genus deals mainly with the distribution and ecology of individual species rather than taxonomy. Raney (1939) reported on the spawning behavior of greeleyi in Pennsylvania. Leach (1940) reported the first occurrence of fossor in Indiana and discussed the larval life history, external and internal changes during transformation, changes in behavior, sexual maturity, spawning and early embryological development. Vladykov and Roy (1948) reported on the meristics, morphometrics, growth and sexual maturity of unicuspis in the St. Lawrence River, Quebec. Vladykov (1949) discussed meristics, morphometrics and general biology of unicuspis and fossor in Quebec. Dendy and Scott (1953) described the habitat of larvae and the spawning areas of gagei, recorded observations on spawning habits and fecundity, and adult morphological variations within the species in the southern states. Hall and Moore (1954) reported on the abundance, distribution, habitat and adult meristics and morphometrics of castaneus and gagei in Oklahoma. Schwartz (1959) reported the first occurrence of greeleyi in West Virginia and discussed its meristics and morphometrics. Starrett et al. (1960) reported on the distribution, adult geographic

variation and hybridization of unicuspis and castaneus in Illinois. Hall (1960, 1963) studied the reproduction, feeding, vital statistics and the impact of predation of castaneus upon populations of rainbow and brown trout in Michigan. Nist (1967) studied the growth and behavior of immature bdellium while McBath (1968) did a meristic and morphometric study of a population of the same species in Pennsylvania. Branson (1970) reported on the proportionate measurements, myomere and teeth counts and commented on pigmentation of adult bdellium and unicuspis in Kentucky. Case (1970) reported on the spawning behavior of castaneus in Manitoba. Purvis (1970) studied the growth, age at metamorphosis and sex ratio of fossor in Lake Superior. Moshin and Gallaway (1977) reported on the seasonal abundance, distribution, food habits and condition of gagei in Texas.

Taxonomic work on the ammocoetes of any lamprey genus is scarce. Raney (1941) separated ammocoetes of Lampetra aeopytera, Petromyzon marinus and Entosphenus (Lethenteron) lamottenii using a single character, the number of myomeres. Vladykov (1950) developed an identification system for ammocoetes over 60 mm total length using the pattern and extent of pigmentation of the different sections of the head and body as diagnostic characters to separate the above species. Other characters that he studied were the number of myomeres, the shape of the caudal fin and the pigmentation of the precursor of the tongue. MacDonald (1958) identified Lampetra fluviatilis, L. planeri and Petromyzon marinus in British waters mainly on the basis of myomere number; he also studied the shape of the caudal fin and the pigmentation of the branchial region and caudal fin. This taxonomic work was strongly criticized by Potter and Osborne (1975). Vladykov (1960) based his

identification of ammocoetes of P. marinus and E. lamotteni (19-68 mm total length) on the pigmentation of the dorsal surface of the head and trunk, the lateral side of the head, the tail region, the peritoneum and the precursor of the tongue. Hardisty (1961) identified female larvae of L. planeri and L. fluviatilis using oocyte counts. Branson (1970) reported on the pigmentation and morphometrics of ammocoetes believed to be I. unicuspis collected in Kentucky. A major taxonomic study on ammocoetes of L. planeri, L. fluviatilis and P. marinus by Potter and Osborne (1975) was based on the number of trunk myomeres, proportionate body measurements and patterns of external and internal pigmentation.

A survey of the literature and museum and university collections of specimens was made in order to compile and document complete distributional records for each species. The data are summarized in the form of maps for each species. These maps, part of the thesis, were published by the author in Lee et al. (1980). Complete and detailed documentation for the localities can be obtained from the author.

MATERIALS AND METHODS

A detailed list of the specimens examined is given in Appendix I. A total of 323 larval and 278 adult specimens were studied. Apart from specimens loaned from museums, private collections and universities, specimens of unicuspis, bdellium and greeleyi were obtained by electrofishing in streams and rivers of eastern Canada and the United States.

The ammocoetes of unicuspis were collected in the Ottawa River, in the Ottawa-Hull area, Ontario and Quebec. Samples were taken using a backpack Type VII Electrofisher (Smith-Root Inc., Vancouver) from the sandbars and shoreline around Upper Duck Island ( $45^{\circ}28'N$ ,  $75^{\circ}37'W$ ), Lower Duck Island ( $45^{\circ}28'N$ ,  $75^{\circ}35'W$ ) and Kettle Island ( $45^{\circ}28'N$ ,  $75^{\circ}39'W$ ). The substrate and the vegetation were described by Ericksson (1974).

Specimens of bdellium and greeleyi were collected using an AC electroshocker in French Creek ( $41^{\circ}52'N$ ,  $79^{\circ}59'W$ ) and Woodcock Creek ( $41^{\circ}43'N$ ,  $80^{\circ}00'W$ ), both tributaries of the Allegheny River ( $40^{\circ}27'N$ ,  $80^{\circ}00'W$ ) in northwestern Pennsylvania. The habitat was described by Nist (1967).

Specimens examined were preserved in 4-5% formalin. This preservative is superior to isopropanol in retaining the original color pattern. The effect of preservation on the shrinkage of the specimen was not determined, although it is believed that, in general, the length of preserved specimens is from 1% to 3% shorter than fresh specimens (Churchill, 1945; Vladykov, 1955).

Measurements were made using Wild calipers to the nearest 0.5 mm, on the left side of the specimen. Total length was measured on a metric measuring board. The methods follow Vladykov and Follett (1965)

except that the tail length (a-C) was measured from the anterior edge of cloaca as in Hubbs and Trautman (1937), Kan (1975) and Potter and Osborne (1975), instead of the posterior edge. Therefore, the total of  $d-B_1$ ,  $B_1-B_7$ ,  $B_7-a$  and  $a-C$  is the total length. The following abbreviations are used (Fig. 1):

- $d-B_1$ : head length- the distance from the anterior edge of the disc (in adults) or of the upper lip (in ammocoetes) to the anterior edge of the first branchial opening;
- $B_1-B_7$ : branchial length- the distance from the anterior edge of the first branchial opening to the posterior edge of the last (seventh) gill opening;
- $B_7-a$ : trunk length- the distance from the posterior edge of the last gill opening to the anterior edge of the cloacal slit;
- $a-C$ : tail length- the distance from the anterior edge of the cloacal slit to the tip of the caudal fin;
- O: orbit diameter- the horizontal length of the orbit (in adults);
- d: disc length- longitudinal diameter, with the oral fimbriae included, measured with the disc compressed laterally (in adults);
- $B_1-B_2$ : inter-branchial length- the distance between the first and the second branchial opening (in adults);
- $B_1-O$ : post-orbital length- the distance from the posterior edge of the orbit to the anterior edge of the first branchial opening (in adults);
- hD: dorsal fin height- the point at which the dorsal fin is the highest (in adults);
- TL: total length- the distance from the anteriormost oral fimbriae (in adults) or the tip of the upper lip (in ammocoetes) to the tip of

Fig. 1. Method of measuring adults and ammocoetes using Wild calipers for the body proportions and a metric measuring board for the total length. Abbreviations are as follows:

d-B<sub>1</sub>: head length

B<sub>1</sub>-B<sub>7</sub>: branchial length

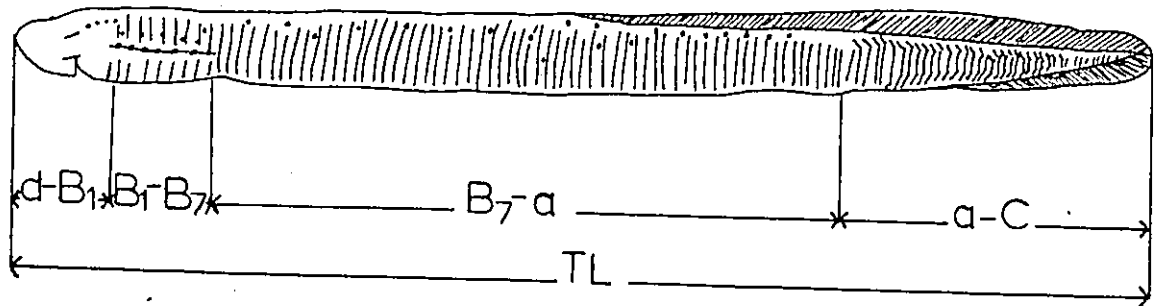
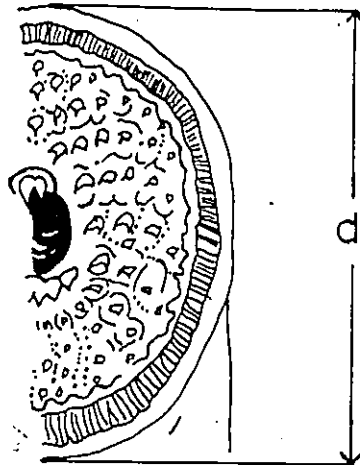
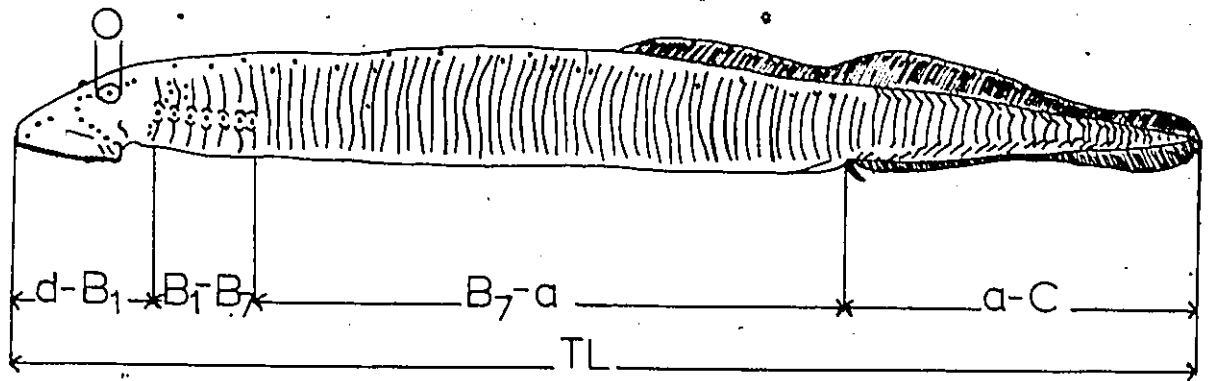
B<sub>7</sub>-a: trunk length

a-C: tail length

O: orbit diameter

d: disc length

TL: total length



the caudal fin.

The number of trunk myomeres is a very important taxonomic character, particularly in ammocoetes. Certain European authors (Cotronei, 1927; D'Ancona, 1930) add to the trunk myomeres those of the branchial region, as they count all preanal myomeres situated between the cloaca and the eye. As myomeres of the branchial region are not always distinguishable, and because they unnecessarily raise the total number of myomeres, they were not counted.

Hubbs and Trautman (1937) counted the number of myomeres in the following way: "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.....The last myomere counted is the one whose lower posterior angle lies in part or wholly above the cloacal slit." Vladykov (1949) followed the same system in his key to the species of adult Quebec lampreys. In this study, the number of trunk myomeres were counted in basically the same fashion, but with more precise and consistent limits. The first myomere counted is the one whose anterior septum passes entirely and distinctly behind the seventh gill opening. The last myomere is the one whose posterior septum lies directly anterior to the cloacal slit when looking at the specimen from a ventral view.

#### Dentition

The terminology of the different types of teeth follows that of Vladykov and Follett (1967) and Hubbs and Potter (1971). The teeth considered of most taxonomic value in the genus Ichthyomyzon are the inner laterals, or endolaterals, referred to as circumorals by Hubbs and Trautman (1937) and lateral circumorals by Hubbs and Potter (1971). These

can be unicuspid or bicuspid, or very rarely, tricuspid. All bicuspid inner laterals on both sides of the oesophageal opening are given in the single count for each specimen to account for specimens with unequal numbers on each side. The number of cusps on the supraoral and infraoral laminae were also counted. Teeth in the anterior, lateral and posterior fields were not counted as they exhibited wide overlap in frequencies between all species (Hubbs and Trautman, 1937). Teeth on the lingual laminae were too minute to be counted.

#### Sexual maturity

Sex of the adults was determined by dissecting the specimens on the right side for a length of about 3 cm in the middle section of the trunk. Examination of the gonads was done using a dissection microscope.

The testis consists of creamy-white flattened lobes, with some surface indentations. It is supported by a mesentery extending downward from the median dorsal line (Hardisty, 1965). It is found, at the immature stage, lying between the opisthonephros in the pleuro-peritoneal cavity. When spawning time approaches, the milt can be extruded by slight pressure on the ventral surface. The ovary is elongate and coiled, and is gray-colored in both fresh and formalin-preserved specimens. At the immature stage, the oocytes can most easily be seen at the anterior end of the pleuroperitoneal cavity at the level of the mesonephros. When mature, the oocytes are free from the mesentery and fill the entire body cavity.

Two stages of development have been recognized for adults, taking into account their degree of sexual maturity. The nonparasitic

species, which do not feed after transformation to the adult stage, can be classified as either

stage 1: early maturity- sexual products are small and retained within the gonads; no secondary sexual characters apparent; or

stage 2: spawning stage- sexual products free in body cavity; secondary sexual characters apparent: genital papilla in male and anal fin-fold in female (spent specimens are also included).

The parasitic species, which feed after transformation up to the spawning period, at which time feeding stops, can be classified as either

stage 1: feeding stage- teeth sharp and intestine functional; sexual products small and retained within the gonads; or

stage 2: spawning stage- intestine non-functional and secondary sexual characters apparent; sexual products free in body cavity (spent specimens are also included).

#### Pigmentation

The variation in the pattern and distribution of pigmentation on the upper lip, suborbital, prebranchial and suprabranchial areas and on the caudal fin of the ammocoetes (Fig. 2a,b) was recorded as belonging to one of the following categories:

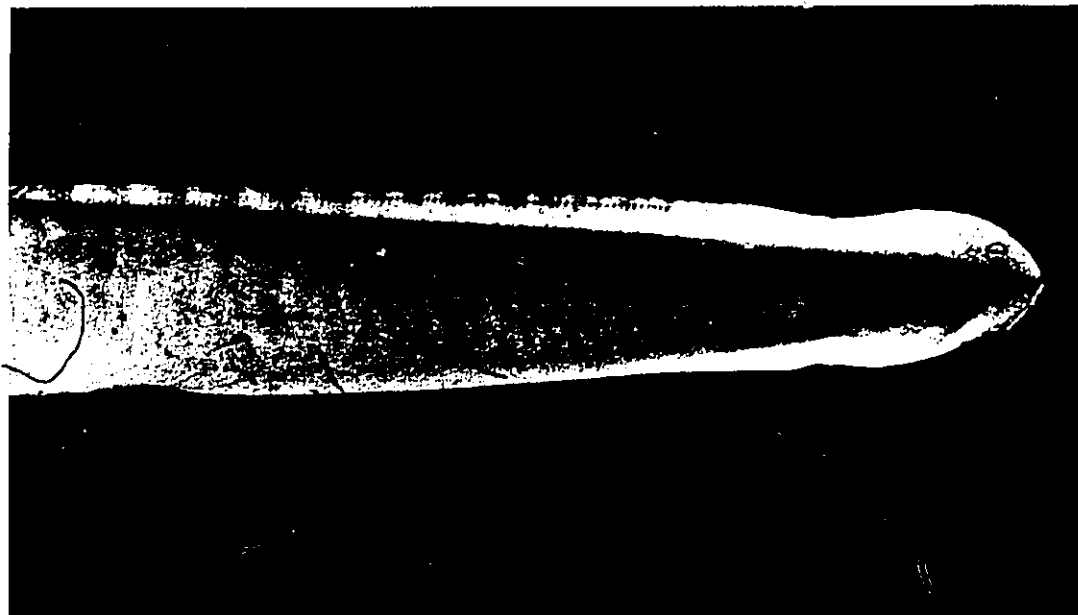
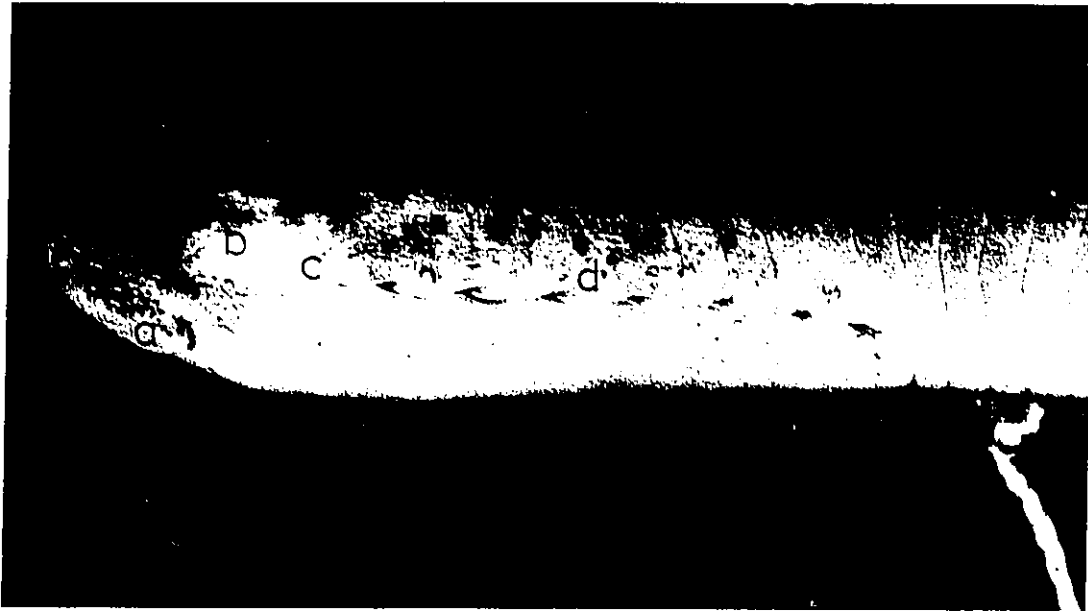
- : pigment absent
- + : pigmentation weak
- ++ : pigmentation moderate
- +++ : pigmentation strong

The different degrees of pigmentation found on the upper lip, or maxillary, of the ammocoetes were of two types:

- ++ : pigment on the lower part of the upper lip does not reach the margin

Fig. 2 (a,b). Areas where the variation in the pattern and distribution of pigmentation were recorded in the ammocoete:

- a- upper lip or maxillary
- b- suborbital area
- c- prebranchial area
- d- suprbranchial area
- e- caudal fin



of the lip, leaving a narrow white band (Fig. 3a);

+++ : pigment reaches the margin of the lower part of the upper lip (Fig. 3b).

Three degrees of pigmentation are recognized on the suborbital area:

+ : presence of a few dispersed melanophores, giving the area an irregularly spotted appearance (Fig. 4a);

++ : melanophores widely distributed, but leaving a white blotch on the cheek (Fig. 4b);

+++ : melanophores covering the whole area (Fig. 4c).

The prebranchial area can be either nonpigmented (-) (Fig. 5a) or pigmented. This pigmentation, forming a prebranchial blotch, can be of the (++) or (+++) type (Fig. 5b,c).

Three degrees of pigmentation are recognized in the upper portion of the branchial region, situated above the horizontal groove joining the branchial openings:

- : presence of a nonpigmented band above the branchial openings, about 1 mm wide (Fig. 6b);

= : presence of a wide nonpigmented band above the branchial openings, about 3 mm wide (Fig. 6a);

+ : pigmentation reaches the level of the branchial openings (Fig. 6c).

The different degrees of pigmentation found on the caudal fin can be defined as follows:

+ : pigment is restricted to the region next to the dorsal and ventral surfaces (Fig. 7a);

++ : pigment covers most of the caudal fin, except for a narrow white band along the outer margin (Fig. 7b);

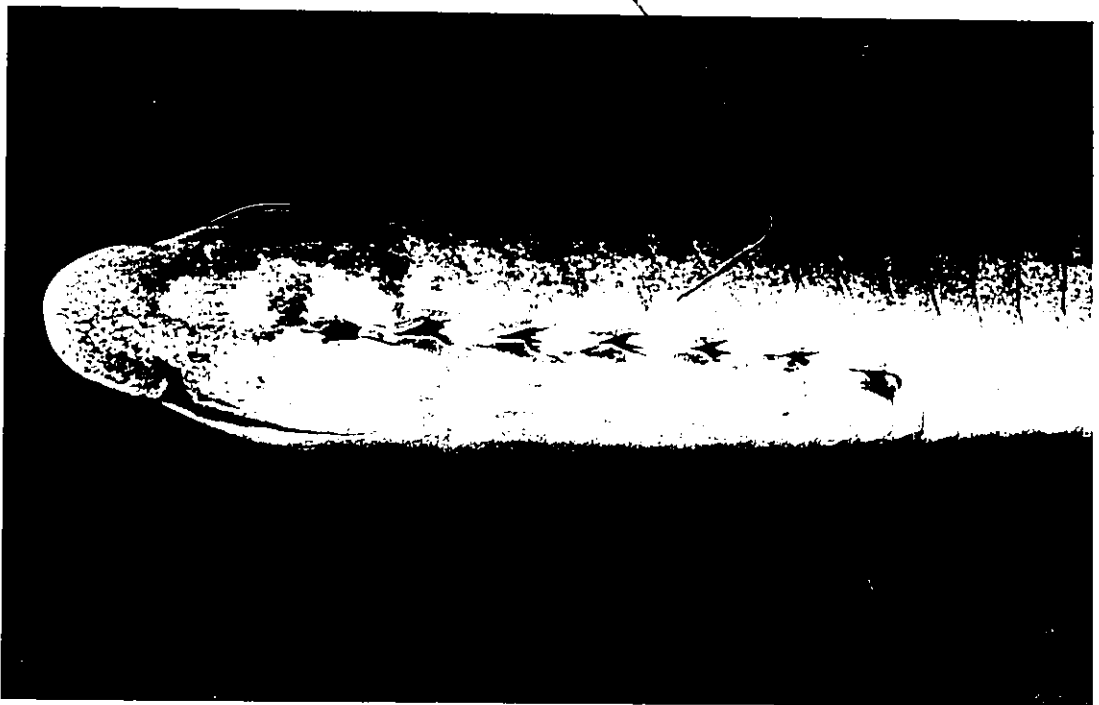
Fig. 3. Variation in the degree of pigmentation of the upper lip of ammocoetes of Ichthyomyzon:

a (++): unicuspis- 97 mm TL; Upper Duck Island, at Ottawa, Ontario; June 7, 1979; J. Lanteigne, J.M. Hanson.

b (+++): fossor- 115 mm TL; Whitemouth River, 105 km E Winnipeg, Manitoba; May 10, 1977; H. Smart. NMC 78-0106.



a



b

Fig. 4. Variation in the degree of pigmentation of the suborbital area of ammocoetes of Ichthyomyzon:

a (+): gagei- 122 mm TL; Choclafula Creek, Macon Co., Alabama; June 15, 1951; J.S. Dendy.

b (++): bdellium- 162 mm TL; French Creek, 3.2 km W Mill Village, Erie Co., Pennsylvania; May 14, 1977; E.L. Cooper, E. Kott, J. Lanteigne.

c (+++): castaneus- 144 mm TL; Prairie River, below Dudley, Lincoln Co., Wisconsin; September 3, 1976; G. and K. Becker. UWSP collection.



a



b



c

Fig. 5. Variation in the degree of pigmentation of the prebranchial area of ammocoetes of Ichthyomyzon:

- a (-): greeleyi- 153 mm TL; French Creek, 3.2 km W Mill Village, Erie Co., Pennsylvania; May 14, 1977; E.L. Cooper, E. Kott, J. Lanteigne.
- b (++): bdellium- 162 mm TL; same collection data as greeleyi.
- c (+++): castaneus- 144 mm TL; Prairie River, below Dudley, Lincoln Co., Wisconsin; September 3, 1976; G. and K. Becker. UWSP collection.

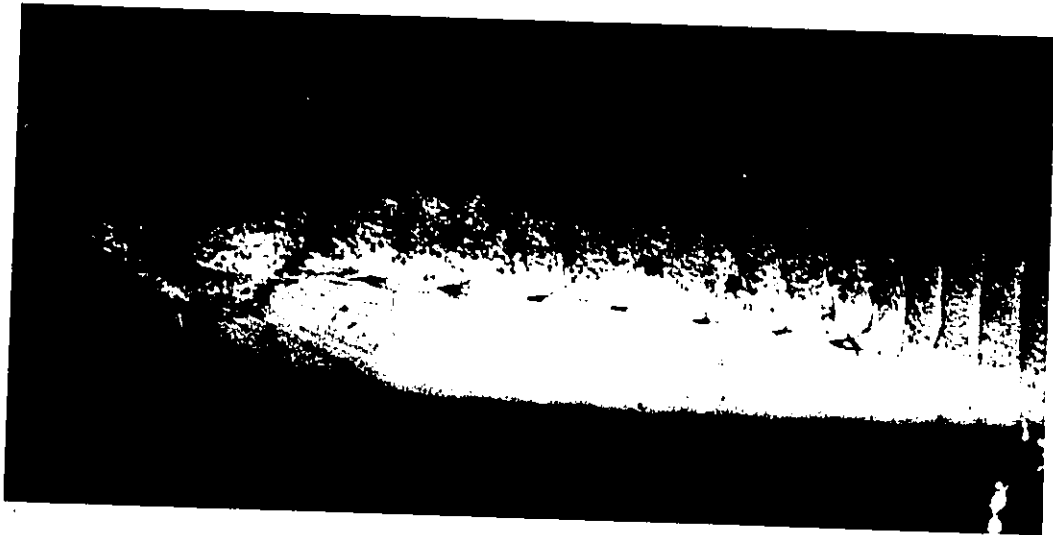
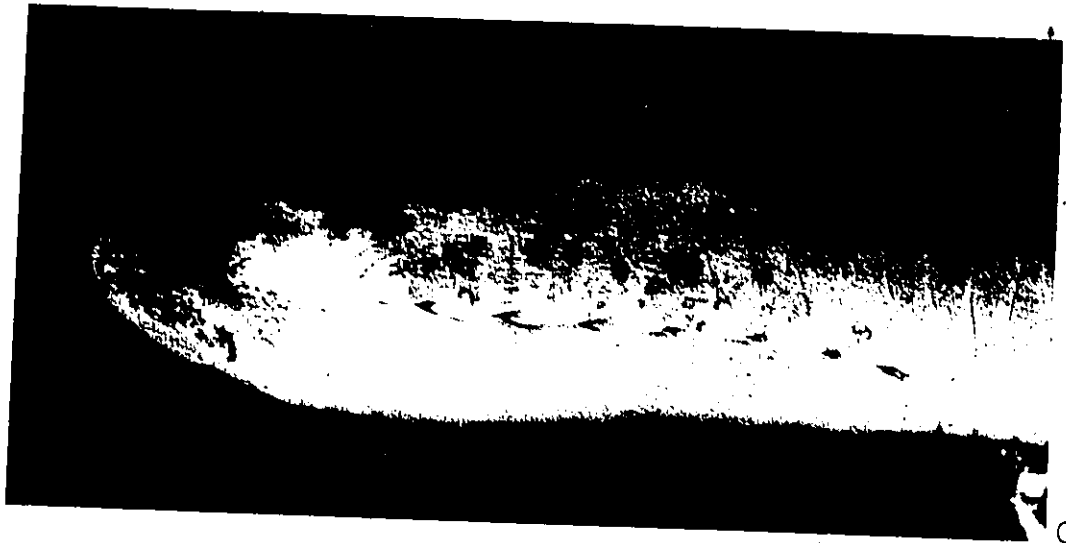


Fig. 6. Variation in the degree of pigmentation on the suprabranchial area of ammocoetes of Ichthyomyzon:

- a (=): unicuspis- 97 mm TL; Upper Duck Island, at Ottawa, Ontario; June 7, 1979; J. Lanteigne, J.M. Hanson.
- b (-): bdeillum- 162 mm TL; French Creek, 3.2 km W Mill Village; Erie Co., Pennsylvania; May 14, 1977; E.L. Cooper, E. Kott, J. Lanteigne.
- c (+): castaneus- 144 mm TL; Prairie River, below Dudley, Lincoln Co., Wisconsin; September 3, 1976; G. and K. Becker: UWSP collection.



a



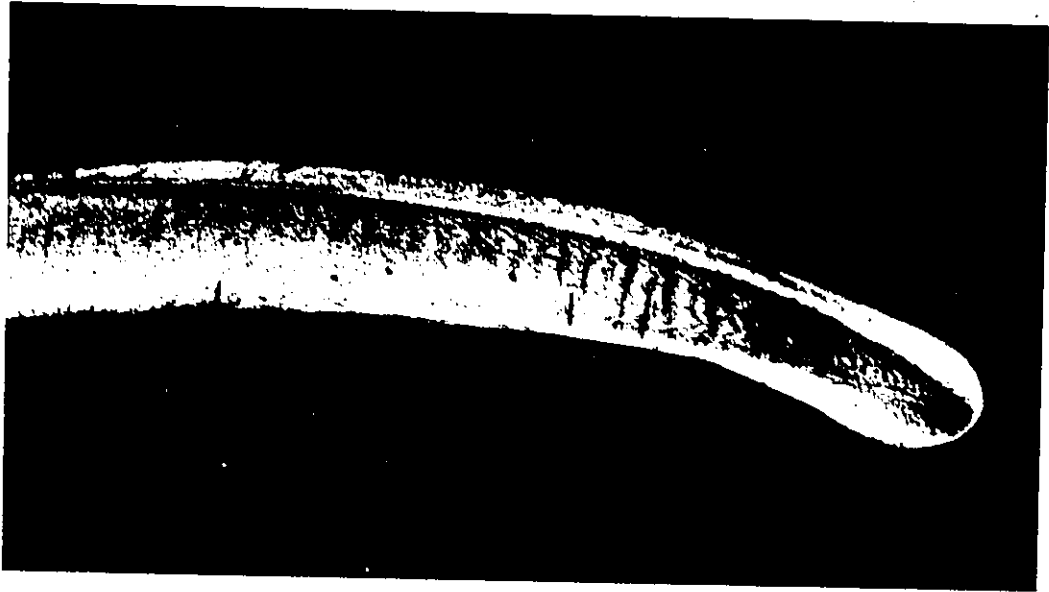
b



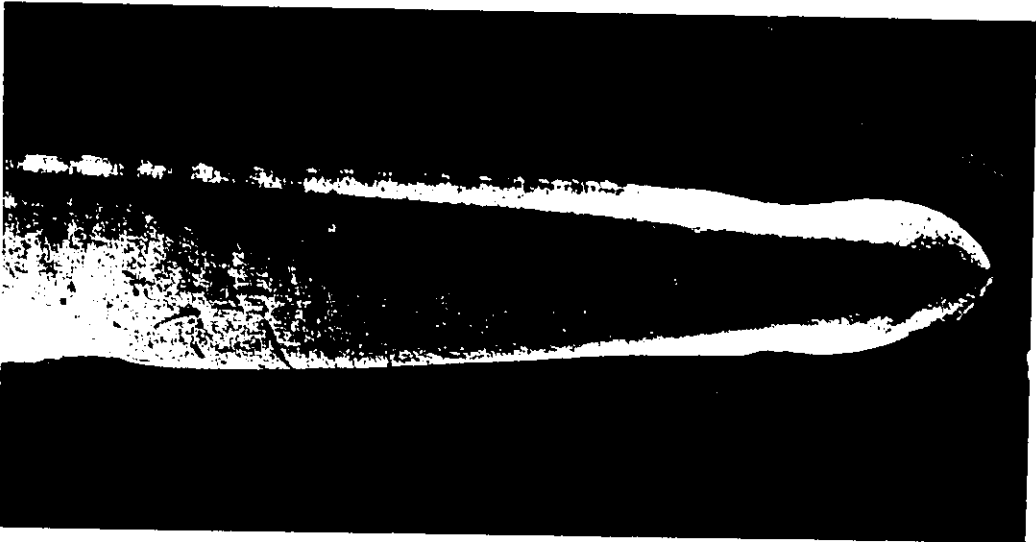
c

Fig. 7. Variation in the degree of pigmentation on the caudal fin of ammocoetes of Ichthyomyzon:

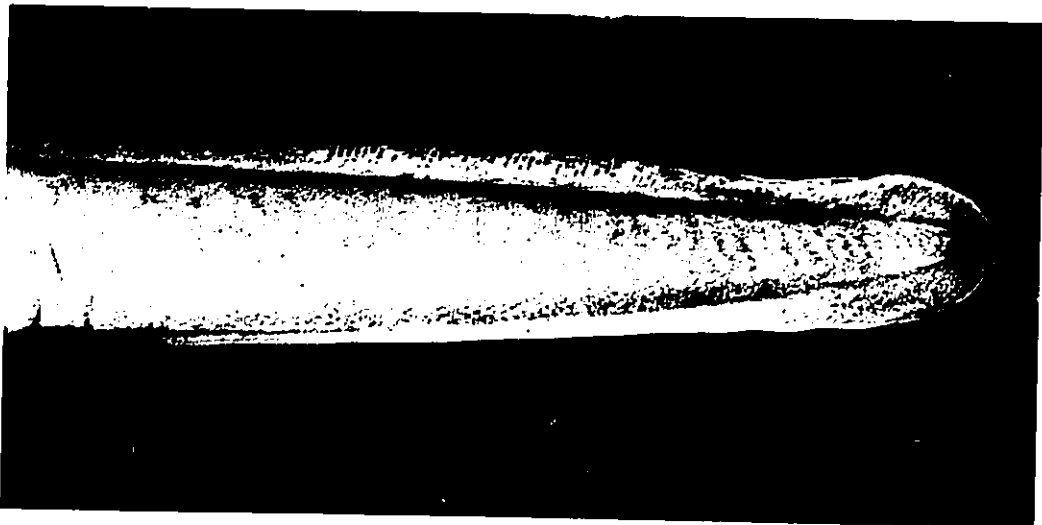
- a (+): fossor- 115 mm TL; Whitemouth River, 105 km E Winnipeg, Manitoba; May 10, 1977; H. Smart. NMC 78-0106.
- b (++): castaneus- 144 mm TL; Prairie River, below Dudley, Lincoln Co., Wisconsin; September 3, 1976; G. and K. Becker. UWSP collection.
- c (+++): bdellium- 162 mm TL; French Creek, 3.2 km W Mill Village, Erie Co., Pennsylvania; May 14, 1977; E.L. Cooper, J. Lanteigne, E. Kott.



a



b



c

+++ pigment follows the fin rays outward to the margin of the caudal fin (Fig. 7c).

#### Treatment of data

Throughout the study, when the different body parts are mentioned, their values are not given in absolute figures, but as percentages of the total length of the specimen. The disc length ( $d$ ) is also expressed as a percentage of the branchial length ( $B_1-B_7$ ). Hubbs and Trautman (1937) and McBath (1968) expressed measurements in thousandths of the total length. However, as the author believed that this procedure would not make a significant contribution to the analysis of the data, it was not used.

Ranges, means and 95% confidence interval of the means were calculated for the number of trunk myomeres, the teeth and the proportionate body measurements. The confidence interval of the mean was calculated using the following formula:

$$L_1 = \bar{X} - t_{\alpha(n-1)} s_{\bar{X}} \quad \text{and} \quad L_2 = \bar{X} + t_{\alpha(n-1)} s_{\bar{X}} \quad \text{where}$$

$s$  = standard error and  $t$  =  $t$ -distribution at 95% confidence level given number of degrees of freedom =  $n-1$  (Sokal and Rohlf, 1973).

The larval pigmentation differences between the species were evaluated using chi-square tests. Characters thus selected were used to prepare a taxonomic key to the ammocoetes.

The morphometric and meristic characters recorded from the adults were used in a revised key to the adults. The raw data recorded for disc length and branchial length were also used in a regression analysis by the least squares method (Ricker, 1975). Furthermore, the data were used in principal components analyses, using a dispersion

(variance-covariance) matrix and a BASIC program translated from the FORTRAN program in Davies (1971). The raw data were also logged and standardized, and used in a phenetic analysis using a correlation matrix. Data obtained from Potter et al. (1974) for Petromyzon marinus were also included in that analysis. These analyses were computed with a Hewlett-Packard 9830A minicomputer.

In addition to the distributional data obtained for the specimens studied and from the published literature, collection records were obtained from the following museums and universities:

- API: Alabama Polytechnic Institute
- ASUMZ: Arkansas State University, Museum of Zoology
- AU: Auburn University
- CU: Cornell University
- EKU: Eastern Kentucky University
- FSU: Florida State University
- KFW: Kentucky Department of Fish and Wildlife Resources
- KU: Kansas University
- MCZ: Museum of Comparative Zoology, Harvard University
- NMC: National Museums of Canada
- OAM: Oklahoma Agricultural and Mechanical College
- OSU: Ohio State University
- PSU: Pennsylvania State University
- ROM: Royal Ontario Museum
- SIUC: Southern Illinois University at Carbondale
- TAM: Texas Agricultural and Mechanical College
- TU: Tulane University
- UA: University of Alabama

UBC: University of British Columbia

UG: University of Georgia

UL: University of Louisville

UMMZ: University of Michigan, Museum of Zoology

UOMZ: University of Oklahoma, Museum of Zoology

USNM: United States National Museum

UT: University of Texas

UWSP: University of Wisconsin, Stevens Point

These data are presented as maps for each species. Complete and detailed documentation for the localities can be obtained from the author.

## TAXONOMY OF THE AMMOCOETES

### Results

#### Pigmentation

The pigmentation patterns on the caudal fin and the different sections of the head are summarized for each species in Table 1 as percentage of occurrence and as absolute numbers. They are used as the basis for the diagnoses, the key and the description of each species. The percentage of specimens showing a given state is also included in the description of each species. The values of the chi-square tests and probability calculated from the values in Table 1 for each pigmentation character for each pair of species are given in Table 4. All species pairs are significantly different in at least two pigment characters.

#### Meristics

Table 2 is a summary of the myomere counts for each species of larval Ichthyomyzon. The mean and its 95% confidence interval for each species is also included. All species are significantly different in mean myomere number at a probability of 0.05, except bdellium and greeleyi.

#### Morphometrics

The values of the morphometric characters are presented as ratios, each expressed as a percentage of the total length. Table 3 gives the number of specimens, the range and the mean  $\pm$  95% confidence interval of the various body proportions of the six species. As environmental differences may influence the processes determining meristic and morphometric characters in fishes, the data have been pooled over the

complete total length range in order to represent the variation of body proportions of a representative sample of specimens, collected from localities within the range of each species.

Diagnoses and descriptions

Ichthyomyzon fossor

northern brook lamprey

Reighard and Cummins, 1916

lamproie de ruisseau septentrionale

Fig. 9a,b

Diagnosis

Ammocoetes of fossor can be distinguished from the other species of the genus, except unicuspis, by its low number of trunk myomeres (usually 50-53) and its lack of pigmented lateral line organs. It can be distinguished from unicuspis by the following combination of pigmentation characters: suborbital area is weakly to moderately pigmented, with melanophores evenly distributed over the area; prebranchial area is moderately to well pigmented with the melanophores forming a well-defined spot; suprbranchial area is pigmented to within 1 mm of the level of the branchial openings. No melanophores are found below the level of the branchial openings.

Description

Pigmentation (Table 1)

Upper lip with moderate (76.7%) to well-developed (23.3%) pigmentation. Suborbital area weakly (21.9%) to moderately (74.0%) pigmented. Prebranchial area with moderate (75.3%) to well-developed (15.1%) pigmentation. Melanophores in suprbranchial area reaching down to 1 mm above branchial openings (91.8%). (Note: no melanophores found below branchial openings.). Caudal fin with weak (30.1%) to moderate (67.1%)

pigmentation. Lateral line organs nonpigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 73 specimens (total length range: 68-167 mm): myomeres: 48-53;  $50.62 \pm 0.27$ ; head length: 6.3-9.6;  $7.59 \pm 0.13$ ; branchial length: 9.9-13.4;  $11.52 \pm 0.15$ ; trunk length: 48.3-55.6;  $52.11 \pm 0.28$ ; tail length: 24.0-31.9;  $28.96 \pm 0.32$ .

Ichthyomyzon unicuspis

silver lamprey

Hubbs and Trautman, 1937

lamproie argentée

Fig. 10a,b

Diagnosis

Ammocoetes of unicuspis can be distinguished from the other species of the genus, except fossor, by their low number of trunk myomeres (usually 50-53) and their lack of pigmented lateral line organs. It can be distinguished from fossor by the following combination of characters: suborbital area with pigmentation absent or weak; prebranchial area with pigmentation absent or weak; suprabranchial area with dispersed melanophores reaching down to level of branchial openings, but a 3 mm wide band clearly visible. A few dispersed melanophores are found below the level of the branchial openings.

Description

Pigmentation (Table 1)

Upper lip with moderate (100%) pigmentation. Suborbital area with weak (36.1%) to moderate (63.9%) pigmentation. Prebranchial area nonpigmented (48.6%) or weakly (47.2%) pigmented. Suprabranchial area with dispersed melanophores reaching down to level of branchial openings, but a 3 mm

wide band clearly visible. (Note: a few dispersed melanophores are found below the branchial openings ). Caudal fin with weak (25%) to moderate (75%) pigmentation. Lateral line organs nonpigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 72 specimens (total length range: 73-138 mm): myomeres: 48-54;  $51.65 \pm 0.25$ ; head length: 6.5-8.7;  $7.50 \pm 0.09$ ; branchial length: 9.3-12.8;  $10.76 \pm 0.12$ ; trunk length: 50.0-54.5;  $52.29 \pm 0.24$ ; tail length: 26.2-32.6;  $29.46 \pm 0.26$ .

Ichthyomyzon gagei

southern brook lamprey

Hubbs and Trautman, 1937

lamproie de ruisseau méridionale

Fig. 11a,b

Diagnosis

Ammocoetes of gagei can be distinguished from ammocoetes of fossor and unicuspis by the presence of pigmented lateral line organs, especially on the head and suprbranchial areas. Gagei larvae differ from those of greeleyi and bdellium by a lower number of trunk myomeres (usually 51-54), and from those of castaneus, which have a similar number of trunk myomeres, by the following combination of pigmentation characters: suborbital area is devoid of pigment or weakly pigmented; prebranchial area with pigmentation absent or weak.

Description

Pigmentation (Table 1)

Upper lip with moderate (92.6%) pigmentation. Suborbital area devoid of pigment (19.0%) or weakly (69.5%) pigmented. Prebranchial area devoid of pigment (41.1%) or weakly pigmented (55.8%). Melanophores in suprbranchial

area reaching down to 1 mm above branchial openings (100%). Caudal fin with weak (45.3%) to moderate (54.8%) pigmentation. Lateral line organs pigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 95 specimens (total length range: 56-150 mm): myomeres: 49-56;  $52.35 \pm 0.25$ ; head length: 5.9-9.3;  $7.73 \pm 0.13$ ; branchial length: 10.1-13.8;  $11.3 \pm 0.14$ ; trunk length: 50.5-57.7;  $54.11 \pm 0.25$ ; tail length: 24.2-31.2;  $27.27 \pm 0.25$ .

Ichthyomyzon castaneus

chestnut lamprey

Girard, 1858

lamproie brune

Fig. 12a,b

Diagnosis

Ammocoetes of castaneus can be distinguished from ammocoetes of fossor and unicuspis by the presence of pigmented lateral line organs, especially on the head and suprabranchial areas. It differs from ammocoetes of greeleyi and bdellium by a lower number of trunk myomeres (usually 51-54). It differs from those of gagei, which have a similar number of trunk myomeres, by the following combination of pigmentation characters: sub-orbital area is moderately to well-pigmented; prebranchial area is moderately to well-pigmented.

Description

Pigmentation (Table 1)

Upper lip with moderate (50%) to strong (50%) pigmentation. Suborbital area moderately (77.3%) to well (18.2%) pigmented. Prebranchial area with moderate (68.2%) to well (27.3%) developed pigmentation. Melanophores in

suprabranchial area reaching down to 1 mm above branchial openings (54.5%) or reaching down to level of branchial openings (45.5%). Caudal fin moderately (95.5%) pigmented. Lateral line organs pigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 22 specimens (total length range: 75-165 mm): myomeres: 50-56;  $54.21 \pm 0.60$ ; head length: 6.4-8.3;  $7.32 \pm 0.21$ ; branchial length: 8.9-12.4;  $10.9 \pm 0.29$ ; trunk length: 52.0-56.6;  $53.89 \pm 0.48$ ; tail length: 25.0-30.3;  $27.98 \pm 0.55$ .

Ichthyomyzon greeleyi

Allegheny brook lamprey

Hubbs and Trautman, 1937

lamproie de ruisseau d'Allegheny

Fig. 13a,b

Diagnosis

Ammocoetes of greeleyi can be distinguished from ammocoetes of fossor and unicuspis by the presence of pigmented lateral line organs, especially on the suprabranchial area. It differs from those of gagei and castaneus in the higher number of trunk myomeres (usually 57-59). It differs from those of bdellium, which have a similar number of trunk myomeres, by the following combination of pigmentation characters: upper lip moderately pigmented; suborbital area weakly to moderately pigmented.

Description

Pigmentation (Table 1)

Upper lip with moderate (100 %) pigmentation. Suborbital area with weak (73.1%) to moderate (19.2%) pigmentation. Prebranchial area weakly (30.8%) to moderately (53.8%) pigmented. Melanophores in suprabranchial area reaching down to 1 mm above branchial openings (100%). Lateral line organs

pigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 26 specimens (total length range: 110-160 mm): myomeres: 55-60;  $57.77 \pm 0.38$ ; head length: 6.7-7.7;  $7.27 \pm 1.0$ ; branchial length: 9.6-11.4;  $10.43 \pm 1.40$ ; trunk length: 54.4-57.8;  $55.7 \pm 2.99$ ; tail length: 24.5-29.2;  $26.83 \pm 0.41$ .

Ichthyomyzon bdellium

Ohio lamprey

(Jordan, 1885)

lamproie de l'Ohio

Fig. 14a,b

Diagnosis

Ammocoetes of bdellium can be distinguished from ammocoetes of fossor and unicuspis by the presence of pigmented lateral line organs, especially on the suprabranchial area. It differs from those of gagei and castaneus in the higher number of trunk myomeres (usually 56-59). It differs from those of greeleyi, which have a similar number of trunk myomeres, by the following combination of pigmentation characters: upper lip moderately to well-pigmented; suborbital area moderately pigmented.

Description

Pigmentation (Table 1)

Upper lip moderately (68.6%) to well (31.4%) pigmented. Suborbital area with weak (5.7%) to moderate (88.6%) pigmentation. Prebranchial area with moderate (65.7%) to strong (17.1%) pigmentation. Melanophores in supra-branchial area reaching down to 1 mm above branchial openings (100%). Caudal fin moderately (85.7%) pigmented. Lateral line organs pigmented.

Meristics and morphometrics (Tables 2 and 3)

Range, mean and 95% confidence interval of trunk myomeres and body proportions for 35 specimens (total length range: 110-169 mm): myomeres: 55-59;  $57.37 \pm 0.33$ ; head length: 5.7-8.2;  $7.13 \pm 1.65$ ; branchial length: 8.8-11.8;  $10.36 \pm 2.16$ ; trunk length: 53.0-62.6;  $56.09 \pm 0.48$ ; tail length: 22.7-30.0;  $26.8 \pm 0.41$ .

Table 1: Variation in the degree of pigmentation on the caudal fin and the different sections of the head of ammocoetes of Ichthyomyzon (in percentage and in absolute numbers).

Species	N	Upper lip	Suborbital area			Prebranchial area			Suprabranchial			Caudal fin							
		-	+	++	+++	-	+	++	+++	+	=	-	+	++	+++				
<u>I. fossor</u>	73	76.7 12 56	23.3 17	-	21.9 16	74.0 54	4.1 3	4.1 3	4.1 3	2.7 2	6.9 5	75.3 55	15.1 11	-	91.8 67	8.2 2	30.1 22	67.1 49	2.7 2
<u>I. unicuspis</u>	72	100 72	-	36.1 26	63.9 46	-	-	-	-	48.6 35	47.2 34	4.2 3	-	-	2.8 2	97.2 70	25.0 18	75.0 54	-
<u>I. kareli</u>	95	82.1 84.7 86	7.4 7	19.0 18	69.5 66	11.6 11	-	-	-	41.1 39	55.8 53	3.2 3	-	-	100 95	-	45.3 43	54.8 52	-
<u>I. castaneus</u>	22	50.0 11	50.0 11	-	4.5 1	77.3 17	18.2 4	-	-	4.5 1	68.2 15	27.3 6	-	45.5 10	54.5 12	-	-	95.5 21	4.5 1
<u>I. greeleyi</u>	26	100.0 96.1 96	-	7.7 2	73.1 19	19.2 5	-	-	-	11.5 3	30.8 8	53.8 14	3.9 1	-	100 26	-	-	96.1 25	3.9 1
<u>I. bdellium</u>	35	68.6 24	31.4 11	5.7 2	88.6 31	-	-	-	-	8.6 3	8.6 3	65.7 23	17.1 6	-	100 35	-	-	85.7 30	14.3 5

Note: see Materials and Methods for definition of degrees of pigmentation

Table 2. Myomere counts in the six species of larval Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	48	49	50	51	52	53	54	55	56	57	58	59	60	Mean $\pm$ 95% C.I.
<u>fossor</u>	73	9	3	19	24	12	6	-	-	-	-	-	-	-	50.62 $\pm$ 0.27
<u>unicuspis</u>	72	1	3	8	18	23	16	3	-	-	-	-	-	-	51.65 $\pm$ 0.25
<u>gajei</u>	95	-	3	4	18	31	22	9	4	4	-	-	-	-	52.35 $\pm$ 0.25
<u>castaneus</u>	22	-	-	2	6	5	1	7	-	1	-	-	-	-	54.21 $\pm$ 0.60
<u>greeleyi</u>	26	-	-	-	-	-	-	-	2	1	4	14	4	1	57.77 $\pm$ 0.38
<u>bdeillum</u>	35	-	-	-	-	-	-	-	1	9	7	12	6	-	57.37 $\pm$ 0.33

Table 3. Morphometric characters (as a percentage of total length) of larval Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	TL (mm)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$
<u>fossor</u>	73	68-167	6.3-9.6	9.9-13.4	48.3-55.6	24.0-31.9
<u>unicuspis</u>	72	73-138	7.59 $\pm$ 0.13	11.52 $\pm$ 0.15	52.11 $\pm$ 0.28	28.96 $\pm$ 0.32
<u>gagei</u>	95	56-150	6.5-8.7	9.3-12.8	50.0-54.5	26.2-32.6
<u>castaneus</u>	22	75-165	7.50 $\pm$ 0.09	10.76 $\pm$ 0.12	52.29 $\pm$ 0.24	29.46 $\pm$ 0.26
<u>greeleyi</u>	26	110-160	5.9-9.3	10.1-13.8	50.5-57.7	24.2-31.2
<u>bellium</u>	35	110-169	7.73 $\pm$ 0.13	11.30 $\pm$ 0.14	54.11 $\pm$ 0.25	27.27 $\pm$ 0.25
			6.4-8.3	8.9-12.4	52.0-56.6	25.0-30.3
			7.32 $\pm$ 0.21	10.9 $\pm$ 0.29	53.89 $\pm$ 0.48	27.98 $\pm$ 0.55
			6.7-7.7	9.6-11.4	54.4-57.8	24.5-29.2
			7.27 $\pm$ 0.10	10.43 $\pm$ 0.14	55.70 $\pm$ 0.30	26.83 $\pm$ 0.41
			5.7-8.2	8.8-11.8	53.0-62.6	22.7-30.0
			7.13 $\pm$ 0.17	10.36 $\pm$ 0.22	56.09 $\pm$ 0.48	26.80 $\pm$ 0.41

Table 4. Calculated chi-square values, degrees of freedom (in brackets) and probability of larval pigmentation characters of species x species of Ichthyomyzon.

	<u>unicuspis</u>	<u>gagai</u>	<u>castaneus</u>	<u>greeleyi</u>	<u>bdellium</u>
<u>fossor</u> 1.	18.8(1)***	8.9(1) *	5.7(1)	7.3(1)*	2.3(1)
2.	97.5(3)***	78.4(3)***	7.4(2)*	30.5(3)***	9.7(3)*
3.	108.6(3)***	130.1(3)***	2.3(3)	14.6(3)**	2.2(3)
4.	115.1(1)***	8.1(1)**	84.4(2)***	2.3(1)	3.1(1)
5.	2.6(2)	6.1(2)*	8.7(2)*	10.1(2)**	16.5(2)***
<u>unicuspis</u> 1.		12.5(2)**	40.8(1)***	2.8(1)	25.2(1)***
2.		13.1(2)**	88.5(3)***	19.5(2)***	89.9(2)***
3.		1.2(2)	74.6(3)***	37.9(3)***	69.9(3)***
4.		159.0(1)***	37.8(2)***	88.5(1)***	98.4(1)***
5.		7.3(1)**	6.5(1)*	10.3(2)**	19.4(2)***
<u>gagai</u> 1.			24.7(1)***	2.0(1)	12.3(1)**
2.			66.8(3)***	2.5(2)	69.7(2)***
3.			94.2(3)***	48.6(3)***	87.9(3)***
4.			47.2(1)***	--	--
5.			19.0(2)***	20.9(2)***	33.3(2)***
<u>castaneus</u> 1.				24.2(2)***	3.6(1)
2.				28.6(3)***	7.9(3)**
3.				11.8(3)**	2.9(3)
4.				14.9(1)***	19.3(1)***
5.				0.02(1)	1.4(1)
<u>greeleyi</u> 1.					10.0(1)**
2.					31.9(2)***
3.					6.9(3)
4.					--
5.					1.8(1)

Legend for characters: 1- upper lip

2- suborbital area

3- prebranchial area

4- suprabranchial area

5- caudal fin

Legend for probabilities:

\*: 0.01 < p < 0.05

\*\* : 0.001 < p < 0.01

\*\*\*: p < 0.001

## Discussion

The first character used for primary separation of the ammocoetes of the genus Ichthyomyzon is the presence or absence of pigmentation of the lateral line organs. The lateral line system comprises several rows of sense organs on the head and body. In the genera possessing two dorsal fins, pigmentation of the lateral line organs is typically absent (Vladykov, 1955).

A definite dark pigmentation with melanin develops in ammocoetes of gagei, castaneus, greeleyi and bdellium. In fossor and unicuspis, they are nonpigmented. In the adult stage, they become pigmented in unicuspis but remain nonpigmented in fossor. The absence of pigmentation on the lateral line organs, plus the low number of trunk myomeres (usually 50-53) were therefore the criteria to separate the ammocoetes of the sympatric stem-satellite pair unicuspis-fossor from the remaining four species.

Secondary separation between the pairs of ammocoetes with pigmented lateral line organs was achieved through the number of trunk myomeres. The sympatric stem-satellite pair castaneus-gagei usually has from 51-54 myomeres; castaneus has a mean number of 54, and gagei, 52. The sympatric stem-satellite pair bdellium-greeleyi usually has 56-59; bdellium has 57, and greeleyi, 58.

Separation between members of each sympatric stem-satellite pair was achieved by using a combination of the pigmentation patterns on the caudal fin and the different sections of the head. The calculated chi-square values (Table 4) of each pigmentation character for each pair of species demonstrated that there was a significant difference at the 95% confidence level or higher between the pigmentation patterns found

on each member of a pair: unicuspis-fossor: upper lip, suborbital, prebranchial and suprabranchial areas; castaneus-gagei: all pigmentation patterns; bdellium-greeleyi: upper lip and suborbital area. Even ignoring the pigmentation of the lateral line organs and the number of trunk myomeres as primary and secondary characters to separate the species, it can be seen from the calculated chi-square values of the pigmentation patterns that the ammocoetes are significantly different at the species level and can usually be distinguished on that basis. Thus, the other possible combinations of species can be separated by using a combination of the following pigmentation patterns: fossor-gagei: all pigmentation patterns; fossor-castaneus: suborbital area, caudal fin; fossor-greeleyi: upper lip, suborbital and prebranchial areas, caudal fin; fossor-bdellium: suborbital area, caudal fin; unicuspis-gagei: upper lip, suborbital and suprabranchial areas, caudal fin; unicuspis-castaneus: upper lip, suborbital and prebranchial areas, caudal fin; unicuspis-greeleyi: suborbital, prebranchial and suprabranchial areas, caudal fin; unicuspis-bdellium: all pigmentation patterns; gagei-greeleyi: prebranchial and suprabranchial areas, caudal fin; gagei-bdellium: all pigmentation patterns; castaneus-greeleyi: upper lip, suborbital, prebranchial and suprabranchial areas; castaneus-bdellium: suborbital and suprabranchial areas.

Potter (1980) emphasized the fact that, since the various body proportions undergo changes during larval life, particularly in the early stages, it was important to make comparisons between values obtained for animals of similar lengths. But even when the data for body proportions are pooled over the complete total length range, certain general trends can be noticed:

a- fossor and unicuspis have smaller trunk lengths but longer tail lengths

- than gagei, castaneus, greeleyi and bdellium;
- b- gagei and castaneus have smaller trunk lengths than bdellium and greeleyi, but longer than fossor and unicuspis;
  - c- gagei and castaneus have shorter tail lengths than fossor and unicuspis, but longer than greeleyi and bdellium;
  - d- greeleyi and bdellium have longer trunk lengths but shorter tail lengths than fossor, unicuspis, gagei and castaneus;
  - e- fossor, unicuspis and gagei have longer head lengths than greeleyi and bdellium;
  - f- unicuspis and castaneus have shorter head lengths than gagei;
  - g- unicuspis, castaneus, greeleyi and bdellium have shorter branchial lengths than fossor; greeleyi and bdellium are also shorter than unicuspis, gagei and castaneus, but gagei is longer than unicuspis.

As a general rule, proportionate body measurements of ammocoetes cannot be used as characters to separate the parasitic and nonparasitic members of a pair. When non-overlapping confidence intervals are taken as prima facie evidence of significant differences, it can be seen that only gagei and castaneus, in their head length, and fossor and unicuspis, in their branchial length, differ significantly. No body proportions in the pair greeleyi-bdellium differ significantly.

The characters most useful to separate ammocoetes at the species level are, therefore, the number of trunk myomeres and the pigmentation patterns on the caudal fin and the different sections of the head. To aid in identification of specimens, the following key was constructed. It is accompanied by a series of illustrations. The pigmentation patterns are described on pages 11, 12 and 13.

Key to species of larval Ichthyomyzon

- 1 One dorsal fin; notch absent, or if notch present, membrane below notch with horny rays (Fig. 8a).  
 Genus Ichthyomyzon.....2
- 2 Two dorsal fins, separated by a wide notch or if fleshy extension unites them, it does not possess horny rays (Fig. 8b).  
 All other lamprey genera.
  
- 2 Mouth with teeth; its rim encircled with fringe-like fimbriae (Fig. 28); mouth used as an adhesive and sucking organ; eyes functional and well-developed; free-swimming.  
 Transforming ammocoetes or adults.....(see key to adults)
- 2 Mouth without teeth and fimbriae; horseshoe-shaped mouth with fleshy hood overhanging it; eyes non-functional; living in burrows in stream bottoms and banks; not free-swimming (Fig. 9).  
 Ammocoetes.....3
  
- 3 Nonpigmented, whitish lateral line organs; myomeres between 7<sup>th</sup> gill opening and anterior part of cloacal slit 48-54 (usually 50-53).  
 .....4
- 3 Darkly pigmented lateral line organs, especially on head region; myomeres 49-60.  
 .....5

Suborbital and prebranchial areas moderately pigmented;  
suprabranchial area with melanophores reaching down to 1 mm  
above branchial openings (Fig. 9a,b).

4 .....fossor

Suborbital and prebranchial areas weakly pigmented;  
suprabranchial area with dispersed melanophores, leaving a  
3 mm whitish band apparent (Fig. 10 a,b).

.....unicuspis

5 Myomeres 49-56 (usually 51-54).

.....6

Myomeres 55-60 (usually 56-59).

.....7

6 Prebranchial area weakly pigmented, with very little pigment on  
the cheek; caudal fin with weak to moderate pigmentation  
(Fig. 11 a,b).

.....gagei

Prebranchial blotch present and strong pigmentation on the cheek;  
caudal fin with well-developed pigmentation (Fig. 12 a,b).

.....castaneus

Suborbital area weakly pigmented, with white blotch on cheek; weak pigmentation in prebranchial area; weak to moderate pigmentation on caudal fin (Fig. 13 a,b).

7

.....greeleyi

Suborbital and prebranchial areas strongly pigmented; no white blotch on cheek; well-developed pigmentation on caudal fin (Fig. 14 a,b).

.....bdellium

In their key to ammocoetes of the Great Lakes, Vladykov and Kott (1980) separated unicuspis from fossor on the basis of heavy pigmentation on the caudal fin and head in unicuspis and weak pigmentation on these areas in fossor. As shown in this study, fossor has moderately pigmented suborbital and prebranchial areas, whereas unicuspis has weak pigmentation on those areas. The pigmentation on the caudal fin was not significantly different in the two species. No data were presented in their study to support their statements.

#### Range and habitat

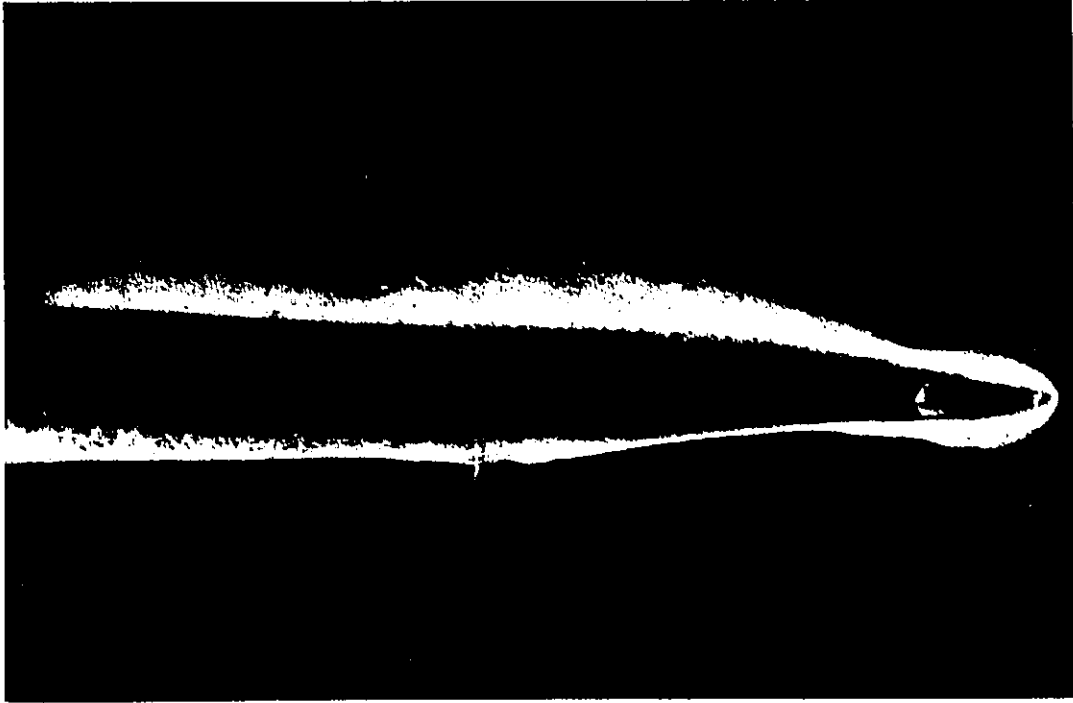
The geographical distribution of the ammocoetes of each species is the same as that of the adults, and will be discussed in the section on the distribution of the genus.

The ammocoetes live buried in sandbars and mudbanks of rivers and streams where the adults spawned on the gravel riffles in the shallows. Dendy and Scott (1953) found ammocoetes believed to be gagei most abundant in accumulation of leaves and other organic debris on the

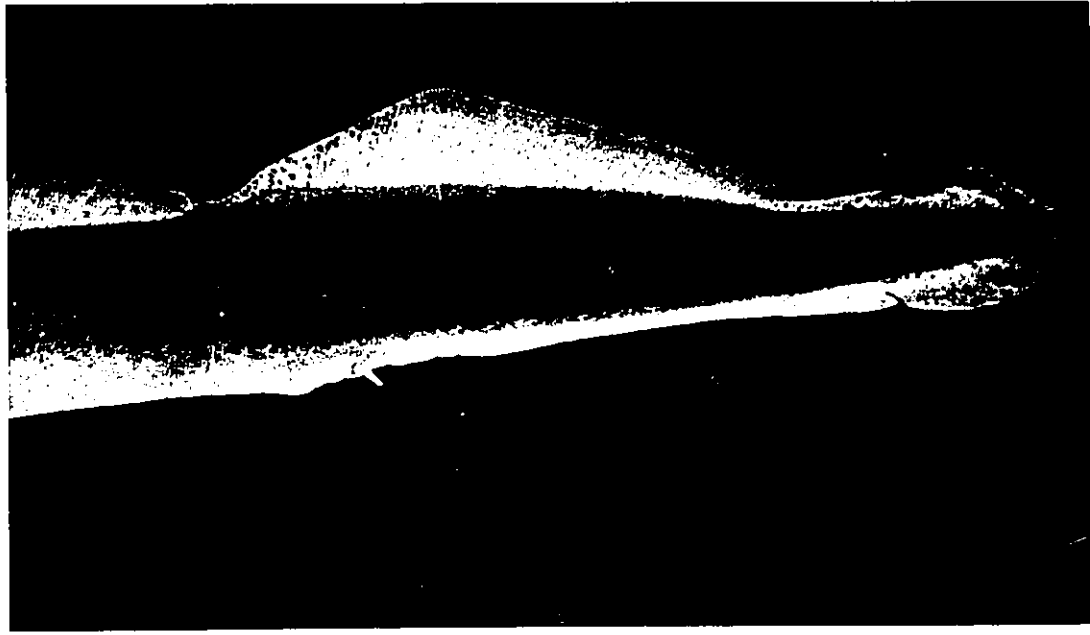
Fig. 8. Presence or absence of two dorsal fins:

a: Ichthyomyzon greeleyi- ♂, 143 mm TL; French Creek, 3.2 km  
W Mill Village, Erie Co., Pennsylvania; May 14, 1977;  
E.L. Cooper, J. Lanteigne, E. Kott.

b: Lampetra pacifica- ♂, 126 mm TL; Crystal Springs Creek,  
tributary to Columbia River, near Portland, Oregon; June 13,  
1956; R.W. Phillips.

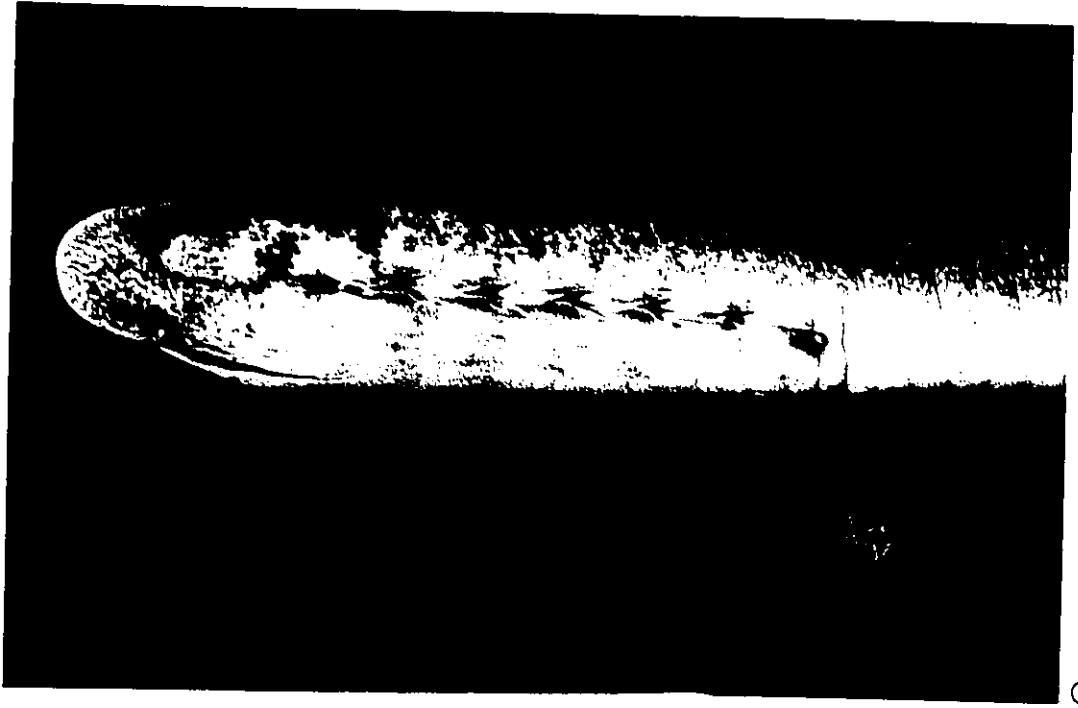


a

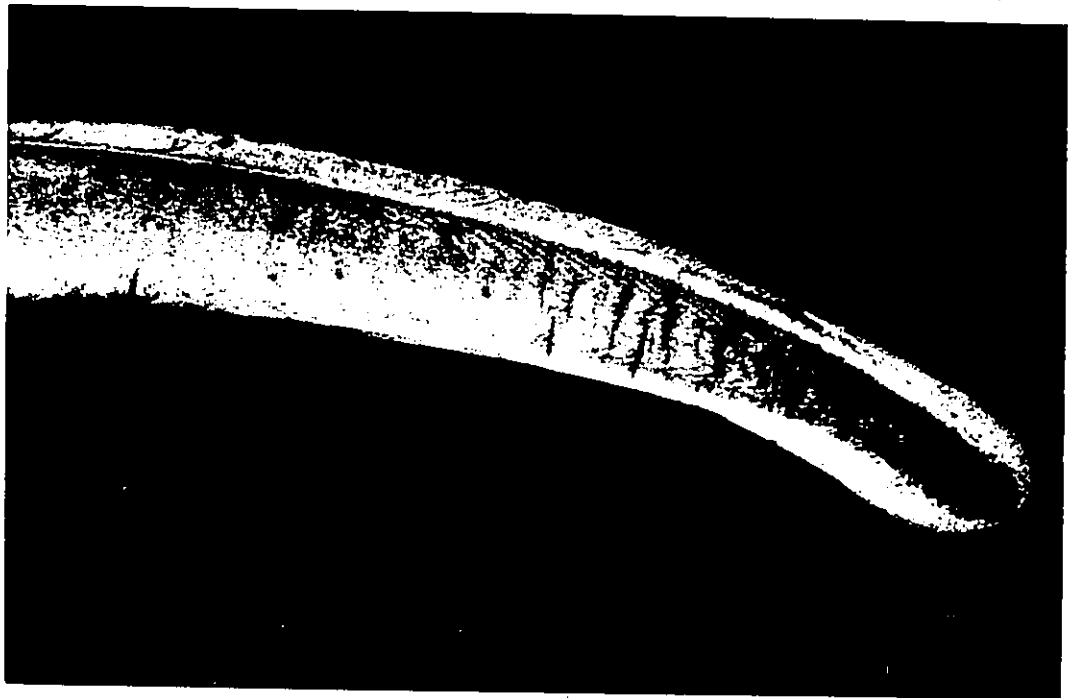


b

Fig. 9 (a,b). Ichthyomyzon fossor: 115 mm TL; Whitemouth River, 105 km  
E Winnipeg, Manitoba; May 10, 1977; H. Smart; NMC 78-0106.



a

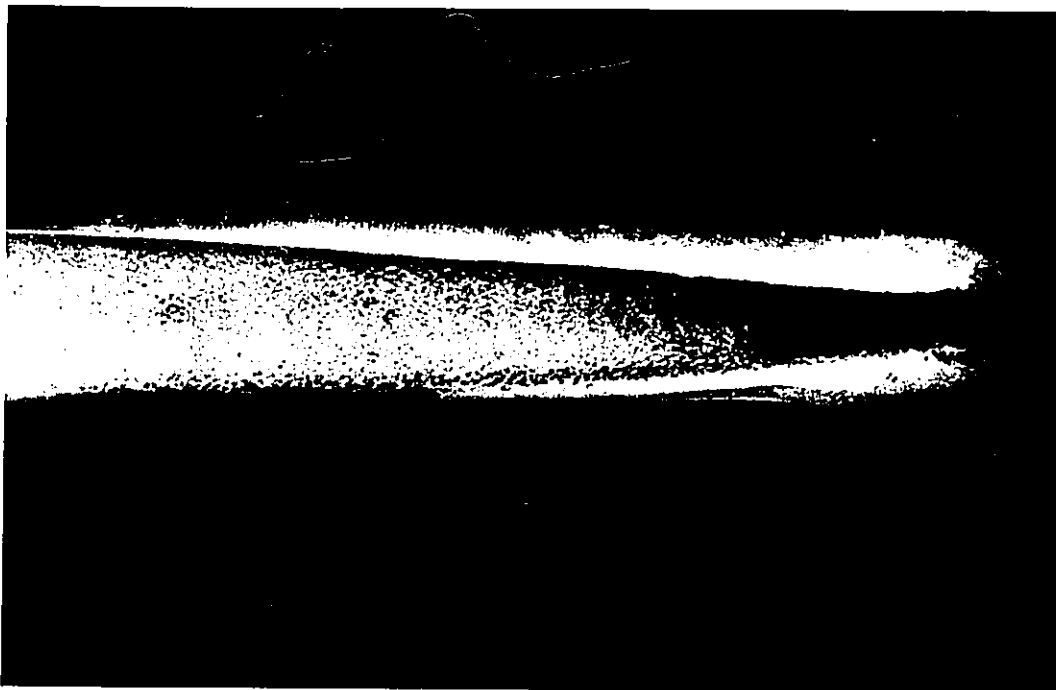


b

Fig. 10 (a,b). Ichthyomyzon unicuspis: 97 mm TL; Upper Duck Island,  
Ottawa River, at Ottawa, Ontario; June 7, 1979;  
J. Lanteigne, J.M. Hanson. 5

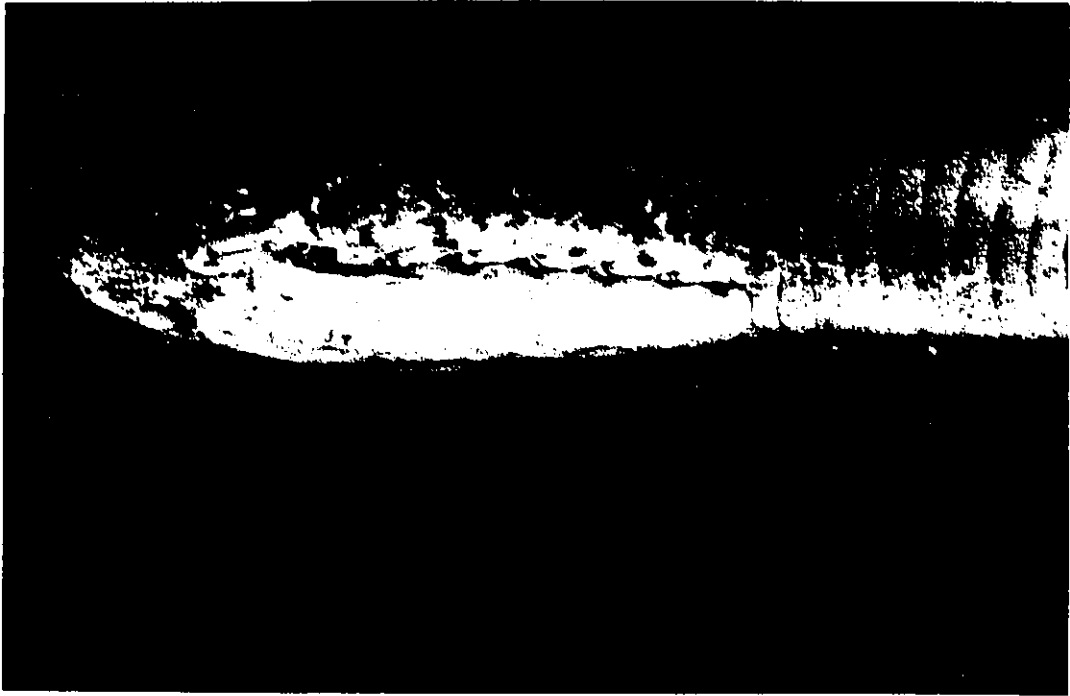


a

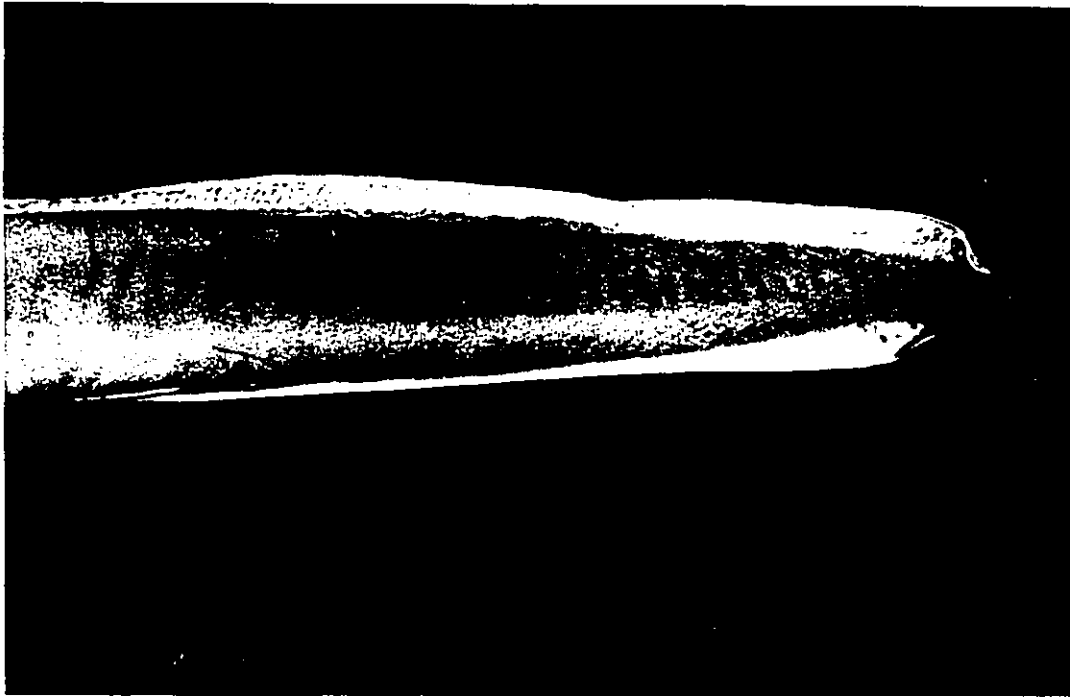


b

Fig. 11 (a,b). Ichthyomyzon gagei: 122 mm TL; Choclafaula Creek,  
Macon Co., Alabama; June 15, 1951; J.S. Dendy.



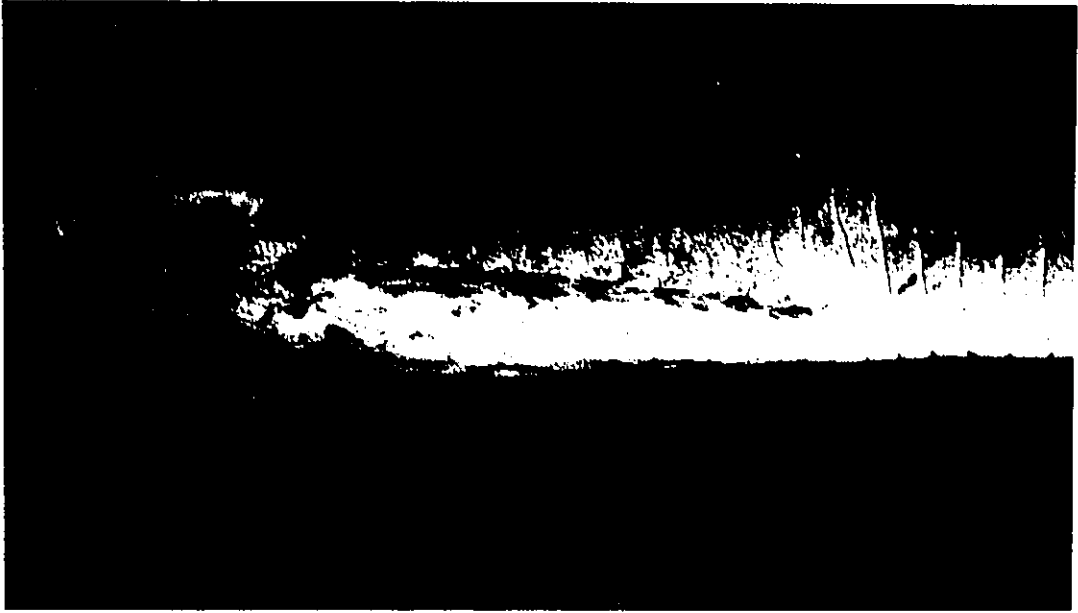
a



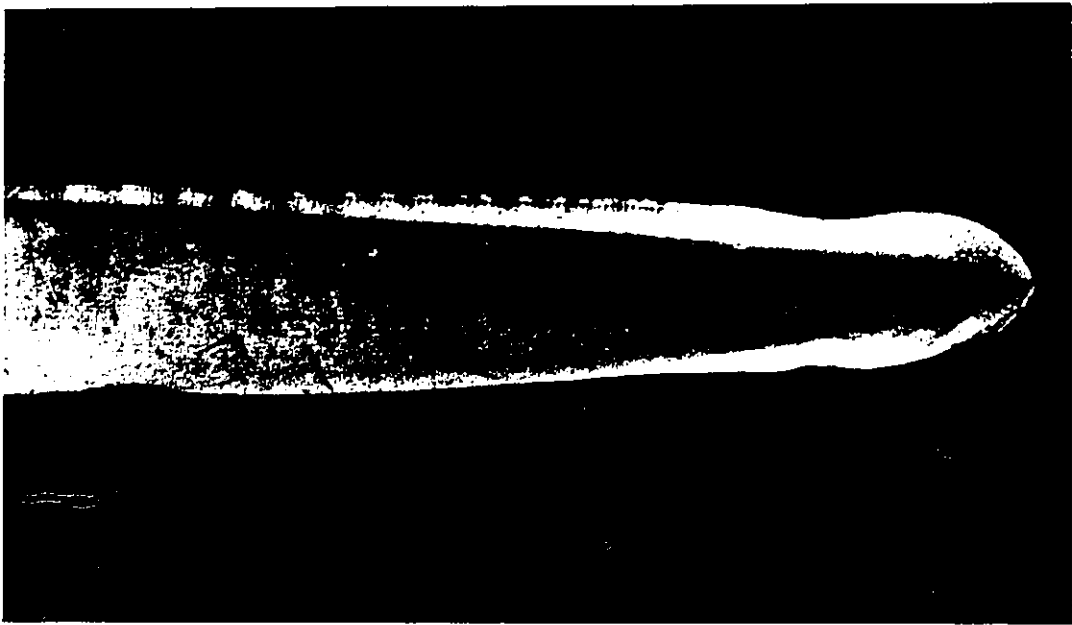
b

P'

Fig. 12 (a,b). Ichthyomyzon castaneus: 144 mm TL; Prairie River, below  
Dudley, Lincoln Co., Wisconsin; September 3, 1976;  
G. and K. Becker; UWSP collection.



a

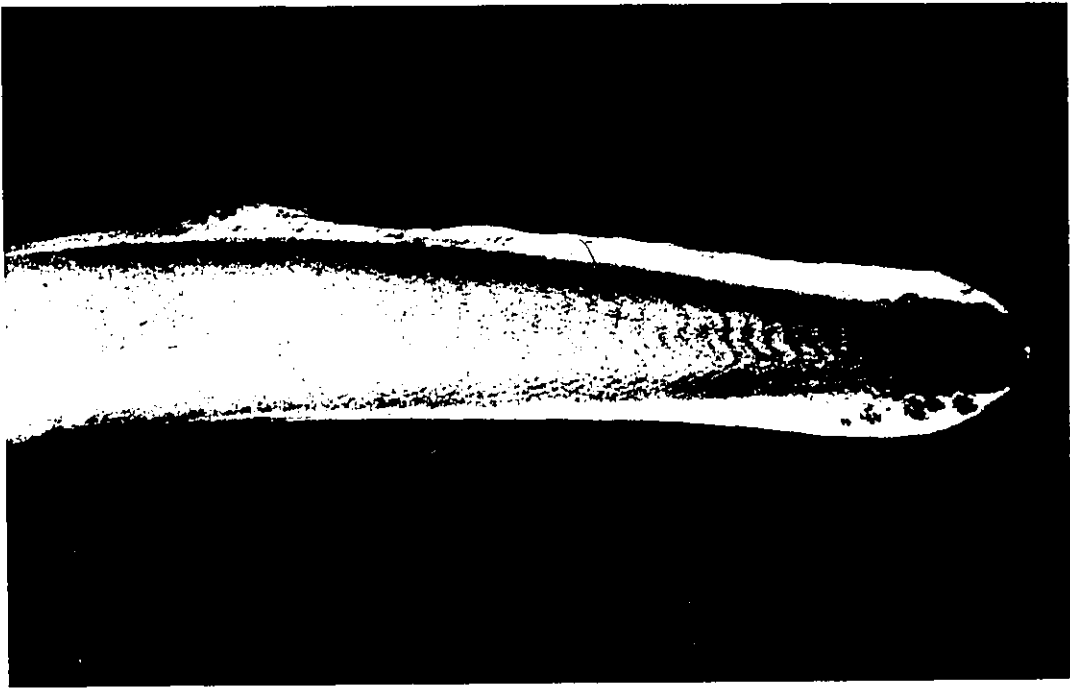


b

Fig. 13 (a,b). Ichthyomyzon greeleyi: 153 mm TL; French Creek, 3.2 km  
W Mill Village, Erie Co., Pennsylvania; May 14, 1977;  
E.L. Cooper, J. Lanteigne, E. Kott.

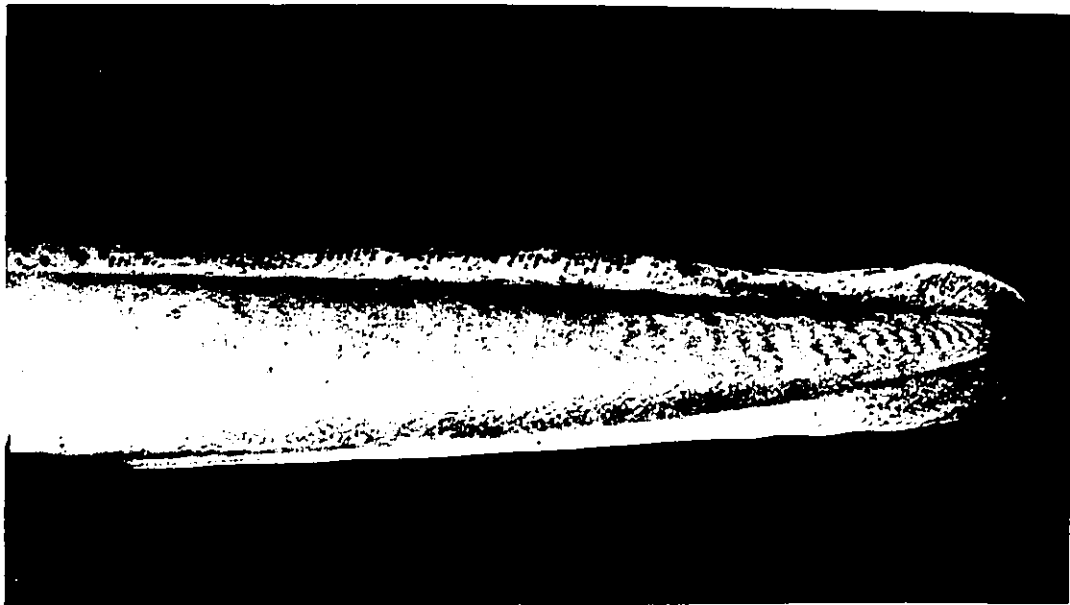


a



b

Fig. 14 (a,b). Ichthyomyzon bdellium: 162 mm TL; French Creek, 3.2 km  
W Mill Village, Erie Co., Pennsylvania; May 14, 1977;  
E.L. Cooper, J. Lanteigne, E. Kott.



bottom, in slack, marginal waters, usually at the downstream end of sandbars. They are not, as a rule, found in firm sand or in the extremely soft mud of the backwaters. The best location, according to Churchill (1945), is a mixture of sand and silt. He found ammocoetes believed to be fossor most numerous in water 12-32 cm deep, among the vegetation. Morman (1979) found that Ichthyomyzon larvae preferred the lowermost, warmwater section of a river, while ammocoetes of Lethenteron lamottenii preferred the uppermost, coldwater section. He also noticed a tendency of the non-parasitic species to occupy headwaters allotopically and main streams syntopically. The parasitic species, particularly I. unicuspis and I. castaneus, avoided small streams and the headwaters and small tributaries of large streams. It is also possible to find the ammocoetes in sandbars along the islands of large rivers in water less than 1.1 m deep (Lanteigne et al., 1981).

TAXONOMY OF THE ADULTS

Results

Meristics

Table 5 summarizes the myomere counts for the adults. The mean and its 95% confidence interval for each species is also included. Tables 6, 7, and 8 summarize the teeth counts: supraorals, infraorals and bicuspid endolaterals, respectively.

I. fossor

Trunk myomeres: 48-55, usually 51-54; averaging 52

Supraorals: 2-4, usually 2; averaging 2.1

Infraorals: 6-10, usually 8; averaging 7.9

Bicuspid endolaterals: 0-1, usually all unicuspid; averaging 0.09

I. unicuspis

Trunk myomeres: 49-54, usually 50-53; averaging 52

Supraorals: 2

Infraorals: 5-10, usually 7-8; averaging 7.6

Bicuspid endolaterals: 0-2, usually all unicuspid; averaging 0.06

I. gagei

Trunk myomeres: 50-56, usually 52-54; averaging 53

Supraorals: 2-4, usually 2; averaging 2.3

Infraorals: 5-10, usually 8-9; averaging 8.3

Bicuspid endolaterals: 1-8, usually 3-7; averaging 4.7

I. castaneus

Trunk myomeres: 51-55, usually 53-55; averaging 54

Supraorals: 1-4, usually 2-3; averaging 2.4

Infraorals: 6-11, usually 7-9; averaging 8.0

Bicuspid endolaterals: 2-8, usually 5-8; averaging 5.9

I. greeleyi

Trunk myomeres: 56-62, usually 57-60; averaging 58

Supraorals: 2-3, usually 3; averaging 2.7

Infraorals: 8-11, usually 9-10; averaging 9.5

Bicuspid endolaterals: 6-10, usually 8-10; averaging 8.6

I. bdellium

Trunk myomeres: 57-60, usually 58-60; averaging 59

Supraorals: 2-3; averaging 2.5

Infraorals: 6-10, usually 7-9; averaging 8.4

Bicuspid endolaterals: 7-10, usually 8-10; averaging 8.6

Morphometrics

The values of the morphometric characters are presented as ratios, each expressed as a percentage of the total length. The disc length is also expressed as a percentage of the branchial length. The number of specimens, the range and the mean  $\pm$  95% confidence interval of the various body proportions of the six species are summarized in Appendix 2, Tables 1 to 9. The nonparasitic species are separated into prespawning and spawning stages and the parasitic species into feeding

Table 5. Myomere counts in the six species of adult Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	Mean $\pm$ 95% C.I.
<u>fossor</u>	59	1	1	4	16	19	7	10	1	-	-	-	-	-	-	-	51.98 $\pm$ 0.30
<u>unicuspis</u>	42	-	2	13	7	9	5	6	-	-	-	-	-	-	-	-	51.48 $\pm$ 0.36
<u>gagei</u>	35	-	-	3	3	5	12	8	2	2	-	-	-	-	-	-	52.94 $\pm$ 0.52
<u>castaneus</u>	41	-	-	-	1	1	12	12	15	-	-	-	-	-	-	-	53.95 $\pm$ 0.32
<u>greeleyi</u>	48	-	-	-	-	-	-	-	-	3	7	16	14	7	7	1	58.40 $\pm$ 0.35
<u>bdeillum</u>	52	-	-	-	-	-	-	-	-	-	7	15	19	11	-	-	58.65 $\pm$ 0.27

Table 6. Number of cusps on the supraoral lamina in the six species of adult Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	1	2	3	4	Mean $\pm$ 95% C.I.
<u>fossor</u>	49	-	47	1	1	2.1 $\pm$ 0.08
<u>unicuspis</u>	43	-	43	-	-	2.0
<u>gagei</u>	29	-	22	6	1	2.3 $\pm$ 0.17
<u>castaneus</u>	36	2	19	14	1	2.4 $\pm$ 0.18
<u>greeleyi</u>	42	-	12	30	-	2.7 $\pm$ 0.12
<u>bdeUium</u>	51	-	28	23	-	2.5 $\pm$ 0.12

Table 7. Number of cusps on the infraoral lamina in the six species of adult Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	5	6	7	8	9	10	11	Mean $\pm$ 95% C.I.
<u>fossor</u>	51	-	2	13	25	9	2	-	7.9 $\pm$ 0.20
<u>unicuspis</u>	43	1	4	15	16	7	-	-	7.6 $\pm$ 0.25
<u>gagei</u>	23	1	-	2	10	8	2	-	8.3 $\pm$ 0.38
<u>castaneus</u>	35	-	2	11	13	3	5	1	8.0 $\pm$ 0.35
<u>greeleyi</u>	40	-	-	-	4	17	15	4	9.5 $\pm$ 0.22
<u>bdeiliium</u>	48	-	2	9	13	15	8	1	8.4 $\pm$ 0.28

Table 8. Number of bicuspid endolaterals in the six species of adult Ichthyomyzon. Number of specimens and mean  $\pm$  95% confidence interval are included.

Species	N	0	1	2	3	4	5	6	7	8	9	10	Mean $\pm$ 95% C.I.
<u>fossor</u>	53	48	5	-	-	-	-	-	-	-	-	-	0.09
<u>unicuspis</u>	43	40	2	1	-	-	-	-	-	-	-	-	0.06
<u>gagai</u>	25	2	2	2	2	4	1	4	3	5	-	-	4.7 $\pm$ 0.91
<u>castaneus</u>	36	-	-	1	2	6	7	5	5	10	-	-	5.9 $\pm$ 0.50
<u>greeleyi</u>	34	-	-	-	-	-	-	1	7	19	5	2	8.0 $\pm$ 0.25
<u>bdeUium</u>	50	-	-	-	-	-	-	-	1	31	5	13	8.6 $\pm$ 0.21

and spawning stages. Within these stages, the males are separated from the females; range and mean of the morphometric characters for the combined sexes are also given.

### I. fossor

There are no significant differences between the males and the females at the prespawning stage (Appendix 2, Table 1). The low number of females in the sample might have introduced a statistical bias. At this stage, fossor attains a greater tail length than gagei at the same stage. No adults at the prespawning stage were available for greeleyi.

At the spawning stage, the females of fossor have a longer trunk length than males; the males have a longer tail length, a greater orbit diameter, and a bigger disc as a proportion of the total length and the branchial length (Appendix 2, Table 2). Males at the spawning stage also have a bigger orbit diameter, a bigger disc as a proportion of the total length and a longer branchial length than males at the prespawning stage.

When both sexes are combined, the spawning adults of fossor have a smaller head length, a smaller disc as a proportion of the total length and the branchial length than gagei and greeleyi at the same stage. Fossor also has a greater total length than gagei, and a longer tail length and a greater orbit diameter than greeleyi.

### I. unicuspis

At the feeding stage, there are no significant differences between the body proportions of the males and the females (Appendix 2, Table 3). Specimens at the spawning stage were not available.

When both sexes are combined, adults of unicuspis at the feeding stage have a smaller trunk length but a greater tail length and branchial length than castaneus and bdellium. Unicuspis also has a greater head length, orbit diameter, disc length as a proportion of the total length and the branchial length than bdellium.

I. gagei

At the prespawning stage, there are no significant differences in body proportions between the males and the females (Appendix 2, Table 4). When the sexes are combined, adults of gagei at this stage have a smaller total length and tail length than fossor at the same stage.

At the spawning stage, the females have a greater trunk length but a smaller tail length and orbit diameter than males (Appendix 2, Table 5). The spawning females have a smaller orbit diameter but a greater disc length as a proportion of the total length than prespawning females; spawning males have a greater disc length as a proportion of the total length than prespawning males.

When the sexes are combined, spawning gagei have a smaller total length and disc length as a proportion of the branchial length than fossor and greeleyi. Gagei has a longer head length and disc length as a proportion of the total length than fossor, but a smaller trunk length than greeleyi.

I. castaneus

At the feeding stage, there are no significant differences in body proportions between the males and the females (Appendix 2, Table 6). Adults of castaneus at this stage have a smaller trunk length, but greater

head length, branchial length, tail length, orbit diameter and disc length as a proportion of the total length and the branchial length than bdellium at the same stage. Castaneus also has a smaller tail length and branchial length, but a greater trunk length than unicuspis at the same stage.

#### I. greeleyi

Specimens at the prespawning stage were not available. At the spawning stage, the females have a smaller head length, tail length, orbit diameter and disc length as a proportion of the total length, but a greater trunk length than males (Appendix 2, Table 7).

When the sexes are combined, adults of greeleyi at the spawning stage have a greater total length, trunk length and disc length as a proportion of the branchial length than gagei at the same stage. Greeleyi also has a greater head length, disc length as a proportion of the total length and the branchial length, but a smaller tail length and orbit diameter than fossor at the same stage.

#### I. bdellium

At the feeding stage, there are no significant differences between the proportionate body measurements of the males and the females (Appendix 2, Table 8). Adults of bdellium at this stage have a smaller head length, branchial length, tail length, orbit diameter, disc length as a proportion of the total length and the branchial length, but a longer trunk length than unicuspis and castaneus at the same stage.

At the spawning stage, females have a longer trunk length than males (Appendix 2, Table 9). The low number of females in the sample does

not permit search for significant variations in body proportions.

Males at the spawning stage have a smaller trunk length and disc length as a proportion of the branchial length, but a longer tail length and branchial length than males at the feeding stage. Females at the spawning stage have a smaller disc length as a proportion of the branchial length than females at the feeding stage.

When the sexes are combined, adults at the feeding stage have a smaller branchial length and tail length, but a greater trunk length and disc length as a proportion of the branchial length than adults at the spawning stage.

Adults of unicuspis and castaneus at the spawning stage were not available, so there is no comparison possible of this stage within the parasitic species.

In summary, the following overall trends stand out:

- a- at the prespawning stage, there are no significant differences between the males and the females of each of the nonparasitic species (this statement assumes that greeleyi follows the same pattern as fossor and gagei);
- b- at the feeding stage, there are no significant differences between the males and the females of each of the parasitic species;
- c- at the spawning stage, the females of the nonparasitic species have a greater trunk length than the males;
- d- at the spawning stage, the males of the nonparasitic species have a longer tail length and a greater orbit diameter than the females;
- e- at the spawning stage, the males and the females of the nonparasitic species have a greater disc length as a proportion of the total length than the males and the females at the prespawning stage (this statement

assumes that greeleyi follows the same pattern as fossor and gagei).

Table 9 is a summary of the body proportions of the combined sexes and stages of adult Ichthyomyzon. There are no significant differences in branchial length, trunk length and orbit diameter between the non-parasitic species fossor, gagei and greeleyi. Fossor has a longer tail length but smaller head length and disc length as a proportion of the branchial length than gagei and greeleyi. Greeleyi has a greater disc length as a proportion of the total length than fossor and gagei; the latter has smaller head length and disc length as a proportion of the branchial length than greeleyi. Within the parasitic species, bdellium has a smaller head length than unicuspis and castaneus; unicuspis has a greater branchial length and a longer tail length than castaneus and bdellium; unicuspis has a smaller trunk length than castaneus and bdellium, whereas castaneus is smaller than bdellium. Unicuspis and castaneus have a greater orbit diameter and disc length as a proportion of the branchial length than bdellium. The latter also has a smaller disc length as a proportion of the total length than unicuspis and castaneus.

The following differences between the nonparasitic and parasitic species stand out (Table 9):

- a- fossor, greeleyi and gagei have a smaller head length than unicuspis, castaneus and bdellium;
- b- fossor, gagei and greeleyi have a longer trunk length than unicuspis and castaneus;
- c- fossor, gagei and greeleyi have a greater tail length than bdellium; fossor is also longer than castaneus whereas greeleyi is smaller than unicuspis in this same body proportion;
- d- gagei has a greater orbit diameter than bdellium, whereas greeleyi

Table 9. Morphometric characters (as percentages) of the six species of adult Ichthyomyzon. Number of specimens, range, and mean  $\pm$  95% confidence interval are included.

Species	N	TL (mm)	$\frac{d-B_1}{TL}$	$\frac{B_1-B_7}{TL}$	$\frac{B_7-a}{TL}$	$\frac{a-C}{TL}$	$\frac{O}{TL}$	$\frac{d}{TL}$	$\frac{d}{B_1-B_7}$
<u>I. fossor</u>	59	98-158	7.4-9.9 8.64 $\pm$ 0.13	8.7-11.3 9.89 $\pm$ 0.15	46.7-54.6 50.54 $\pm$ 0.48	27.7-33.7 31.15 $\pm$ 0.38	1.1-2.0 1.22 $\pm$ 0.53	4.0-6.4 4.88 $\pm$ 0.78	40.0-62.5 50.37 $\pm$ 1.18
<u>I. unicuspis</u>	43	85-270	11.4-15.9 13.50 $\pm$ 0.36	8.7-10.8 9.62 $\pm$ 0.18	42.4-49.2 46.62 $\pm$ 0.54	26.8-32.6 30.20 $\pm$ 0.42	1.1-2.5 1.76 $\pm$ 0.10	7.9-12.4 10.10 $\pm$ 0.37	78.7-122.7 105.49 $\pm$ 2.67
<u>I. Regel</u>	35	86-129	8.3-11.2 9.61 $\pm$ 0.24	8.3-11.1 9.64 $\pm$ 0.22	47.0-56.0 51.26 $\pm$ 0.78	25.6-33.3 29.40 $\pm$ 0.55	1.3-2.1 1.59 $\pm$ 0.07	3.9-6.5 5.31 $\pm$ 0.28	40.0-63.6 54.44 $\pm$ 2.44
<u>I. castaneus</u>	36	89-261	11.5-15.5 13.80 $\pm$ 0.36	8.4-10.3 9.28 $\pm$ 0.15	44.4-52.9 48.64 $\pm$ 0.65	23.9-34.4 28.26 $\pm$ 0.67	0.8-2.4 1.66 $\pm$ 0.09	8.5-11.6 10.06 $\pm$ 0.27	86.4-123.8 108.72 $\pm$ 2.99
<u>I. Greeleyi</u>	48	110-165	8.1-11.5 10.25 $\pm$ 0.24	8.9-10.6 9.74 $\pm$ 0.13	46.6-55.0 51.02 $\pm$ 0.54	25.7-33.9 29.33 $\pm$ 0.43	0.9-1.8 1.44 $\pm$ 0.07	4.0-7.9 6.39 $\pm$ 0.23	53.6-78.6 66.65 $\pm$ 1.81
<u>I. bdeellium</u>	51	125-259	10.4-14.0 11.68 $\pm$ 0.35	7.6-10.6 9.14 $\pm$ 0.20	47.3-54.3 51.28 $\pm$ 0.30	25.1-31.2 27.69 $\pm$ 0.40	1.1-1.8 1.43 $\pm$ 0.05	6.9-9.5 8.17 $\pm$ 0.13	72.1-107.7 89.97 $\pm$ 1.98



is smaller than unicuspis and castaneus;  
e- fossor, gagei and greeleyi have a smaller disc length as a proportion of the total length and the branchial length than unicuspis, castaneus and bdellium.

#### Regression analysis

The branchial length does not vary much in the six species of adult Ichthyomyzon (Table 9). This character is therefore not of great systematic value within the genus. It was used along with the disc length in a regression analysis for each species. From the low values of the coefficients of allometry, it can be seen that the nonparasitic species tend to show negative allometric growth of the disc in relation to the branchial length; the parasitic species tend to show positive allometric growth for the same measurements, as demonstrated by the high value of their coefficients of allometry. The fact that nonparasitic species do not feed after transformation to the adult stage, while the parasitic species do, explains this difference. Figures 15 to 17 show the relationship between the nonparasitic and the parasitic members of each sympatric stem-satellite pairs.

#### Principal components analyses

The following twenty-three adult characters were used in principal components analyses: total length, number of myomeres, head length, branchial length, trunk length, tail length, post-orbital length, inter-branchial length, orbit diameter, disc length, dorsal fin height, supraorals, infraorals, endolaterals, posteriors and the presence or absence of pigmented lateral line organs, which were coded as (9) or (-9).

Fig. 15. Relationship of disc length to branchial length for I. fossor  
and I. unicuspis. Lengths in millimeters.

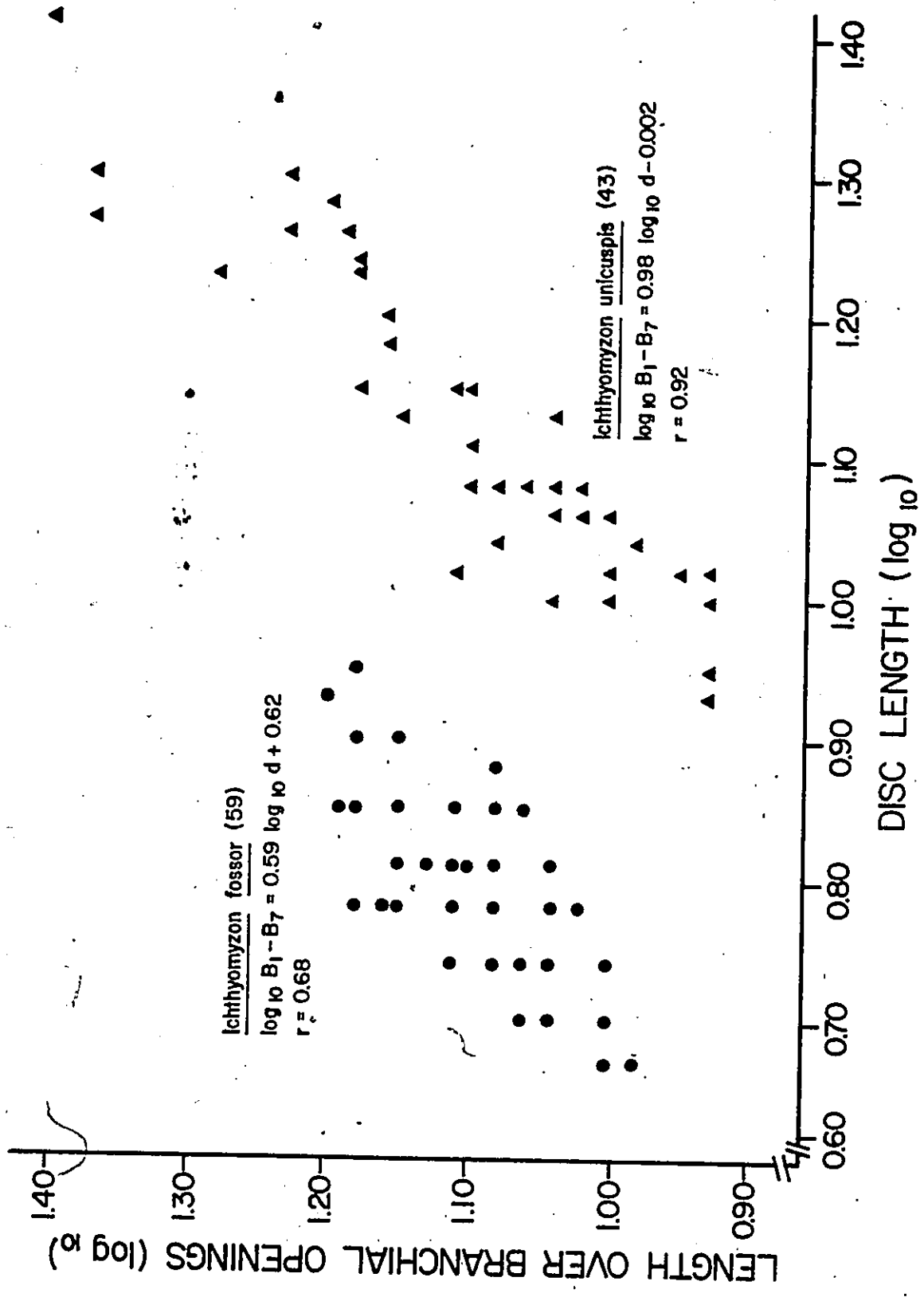


Fig. 16. Relationship of disc length to branchial length for I. gagei  
and I. castaneus. Lengths in millimeters.

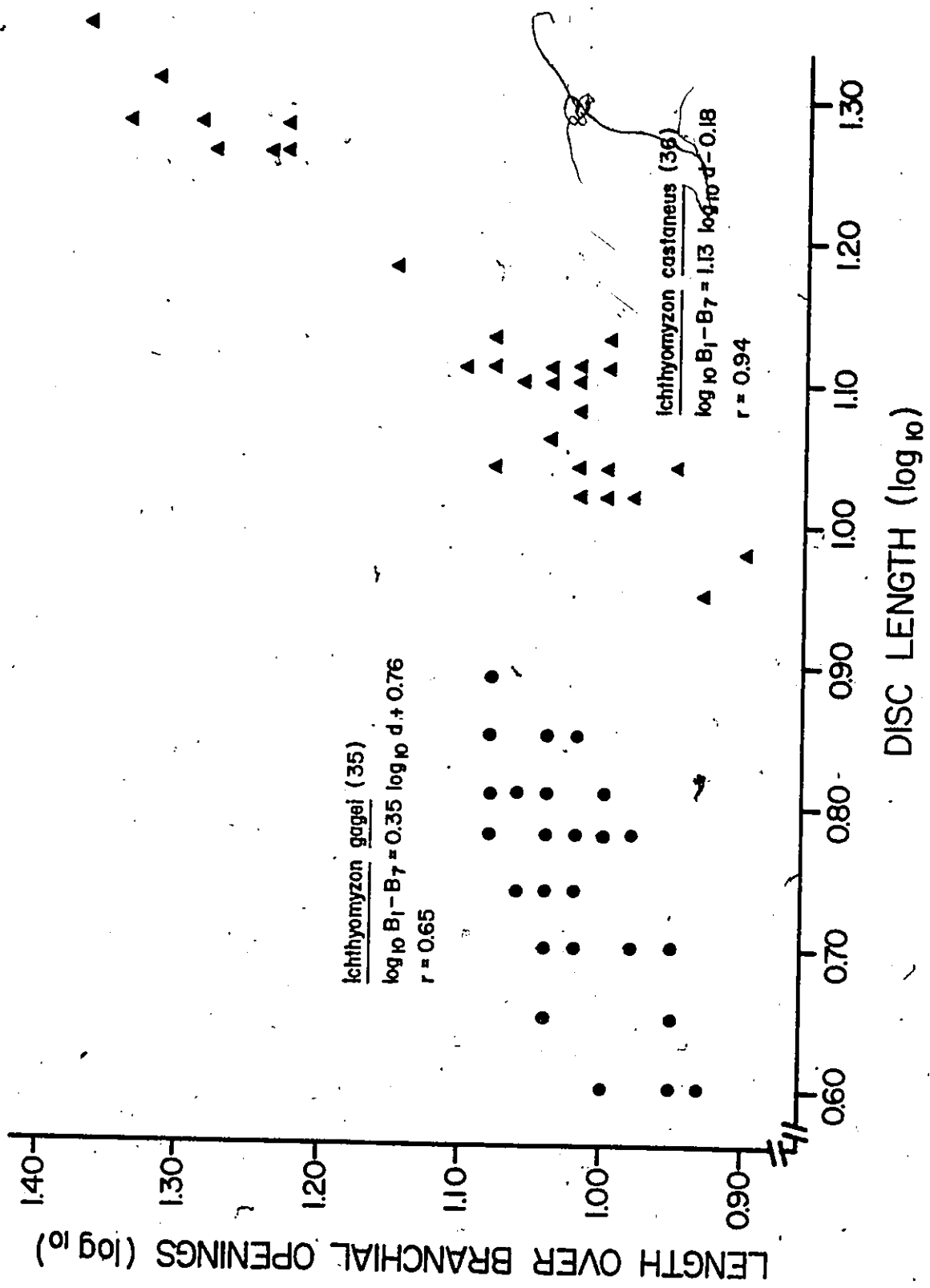
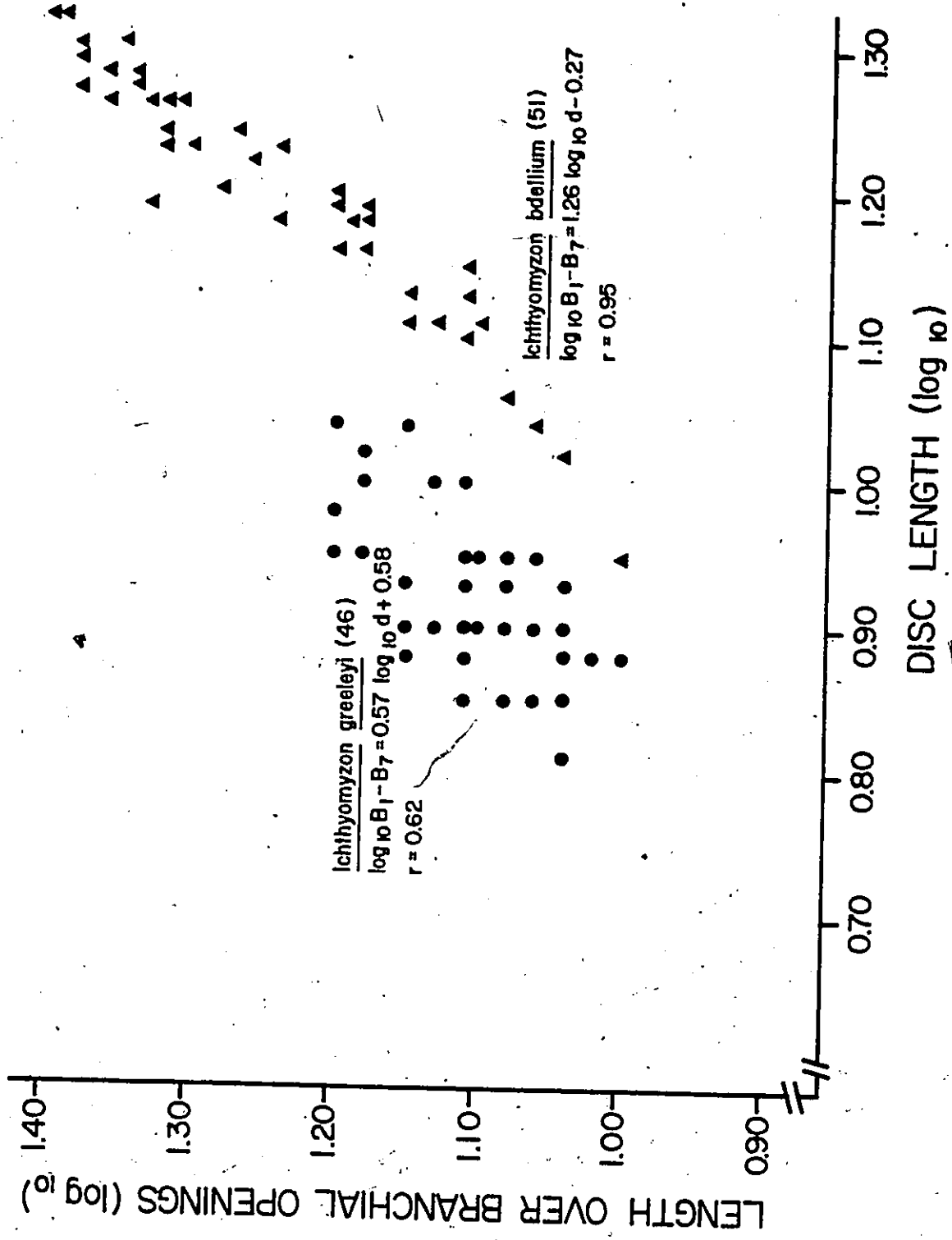


Fig. 17. Relationship of disc length to branchial length for I. greeleyi  
and I. bdeillum. Lengths in millimeters.



For the sympatric stem-satellite pair unicuspis-fossor, the main latent vectors of the first principal component (PC) are total length and trunk length (Table 10); this first PC accounts for 91.26% of the variance. The main latent vectors of the second PC are the presence or absence of pigmented lateral line organs and the disc length. This second PC accounts for 6.29% of the variance. Figure 18 is a scatter diagram showing the relationship between PC 1 and PC 2 for these two species. The specimens of unicuspis which lie outside the main cluster have the longest total lengths of the sample. Since the main latent vector of PC 1 is total length, it explains why these specimens are outside the main cluster. The same applies to the specimen of fossor lying outside the main cluster; it has the smallest total length of the sample. A 100% separation of the two species is obtained when using these two principal components.

The main latent vectors of the first principal component of the sympatric stem-satellite pair castaneus-gagei are total length and trunk length (Table 11). This first PC accounts for 95.91% of the variance. The main latent vector of the second PC is the number of trunk myomeres; it accounts for 1.92% of the variance. Figure 19 is a scatter diagram of the relationship between PC 1 and PC 2; there is wide overlap between the two species, and only 30% of castaneus can be separated from gagei. Only the longest specimens of castaneus are separated from the cluster of gagei. The third PC, whose main latent vectors are disc length and head length, accounts for 1.08% of the variance. In relationship to PC 1, it gives a 100% separation of the two species, as seen in Figure 20. The specimens of castaneus which lie outside the main cluster are the longest of the sample, and show the magnitude of the main latent vector of the

Table 10. Values of the latent vectors, latent roots and percent variance of the principal components analysis of twenty-three characters of the sympatric pair unicuspis-fossor.

Character	PC 1	PC 2	PC 3
Total length	0.854	0.037	-0.037
Number of myomeres	0.054	-0.076	0.982
Head length	0.098	0.296	0.047
Branchial length	0.084	-0.011	-0.016
Trunk length	0.423	-0.251	-0.070
Tail length	0.252	-0.017	-0.008
Post-orbital length	0.019	0.015	0.011
Inter-branchial length	0.013	0.005	0.011
Orbit diameter	0.009	0.014	0.018
Disc length	0.073	0.297	0.037
Dorsal fin height	0.026	-0.007	-0.005
Supraorals	0.002	0.004	0.039
Infraorals	0.010	-0.014	0.132
Endolaterals	0.001	0.001	0.016
	0.002	0.001	0.015
	0.002	0.000	0.015
	0.001	0.001	0.017
	0.001	0.000	0.017
	0.001	0.000	0.016
	0.002	0.000	0.016
	0.001	0.003	0.018
Posteriorals	0.004	0.039	0.054
Lateral line organs	0.038	0.867	0.037
Latent roots	1452.053	100.037	23.000
% variance	91.263	6.287	1.446

Fig. 18. Scatter diagram showing the relationship between PC 1 and PC 2 for the sympatric stem-satellite pair unicuspis-fossor.

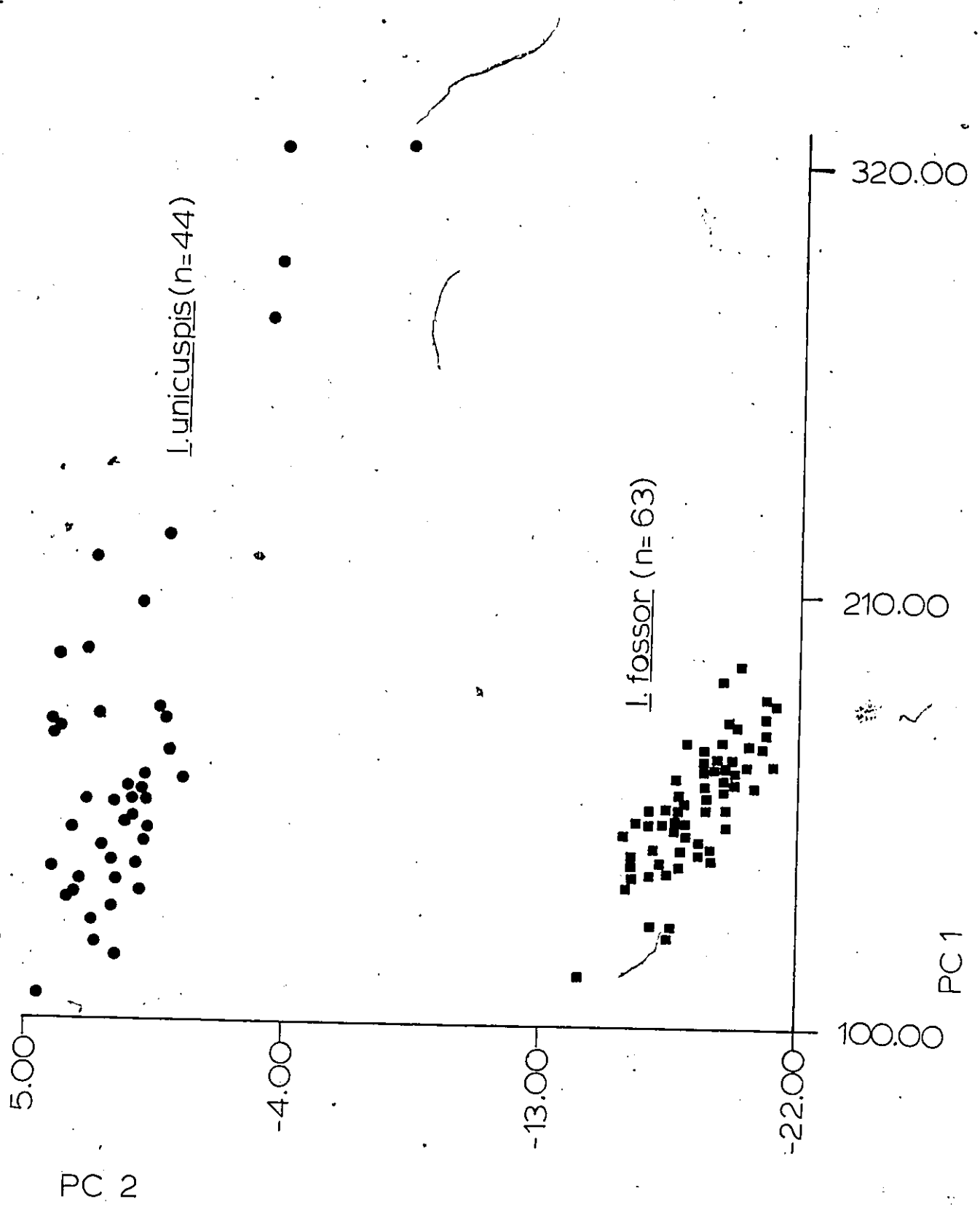


Table 11. Values of the latent vectors, latent roots and percent variance of the principal components analysis of twenty-three characters of the sympatric pair castaneus-gagei.

Character	PC 1	PC 2	PC 3
Total length	0.852	-0.074	0.063
Number of myomeres	0.082	0.973	-0.006
Head length	0.112	-0.035	0.517
Branchial length	0.079	-0.008	-0.000
Trunk length	0.427	-0.018	-0.397
Tail length	0.236	-0.020	-0.036
Post-orbital length	0.027	-0.009	0.037
Inter-branchial length	0.011	0.008	-0.001
Orbit diameter	0.010	0.011	0.025
Disc length	0.090	-0.067	0.548
Dorsal fin height	0.019	0.025	-0.011
Supraorals	0.007	0.024	0.092
Infraorals	0.026	0.095	0.440
Endolaterals	0.004	0.016	0.055
	0.006	0.020	0.063
	0.006	0.018	0.074
	0.003	0.028	0.080
	0.002	0.023	0.071
	0.004	0.027	0.077
	0.007	0.018	0.088
	0.006	0.019	0.083
Posterials	0.014	0.017	0.145
Lateral line organs	0.012	0.164	-0.005
Latent roots	1954.758	39.210	22.032
% variance	95.907	1.924	1.081

Fig. 19. Scatter diagram showing the relationship between PC 1 and PC 2 for the sympatric stem-satellite pair castaneus-gagei.

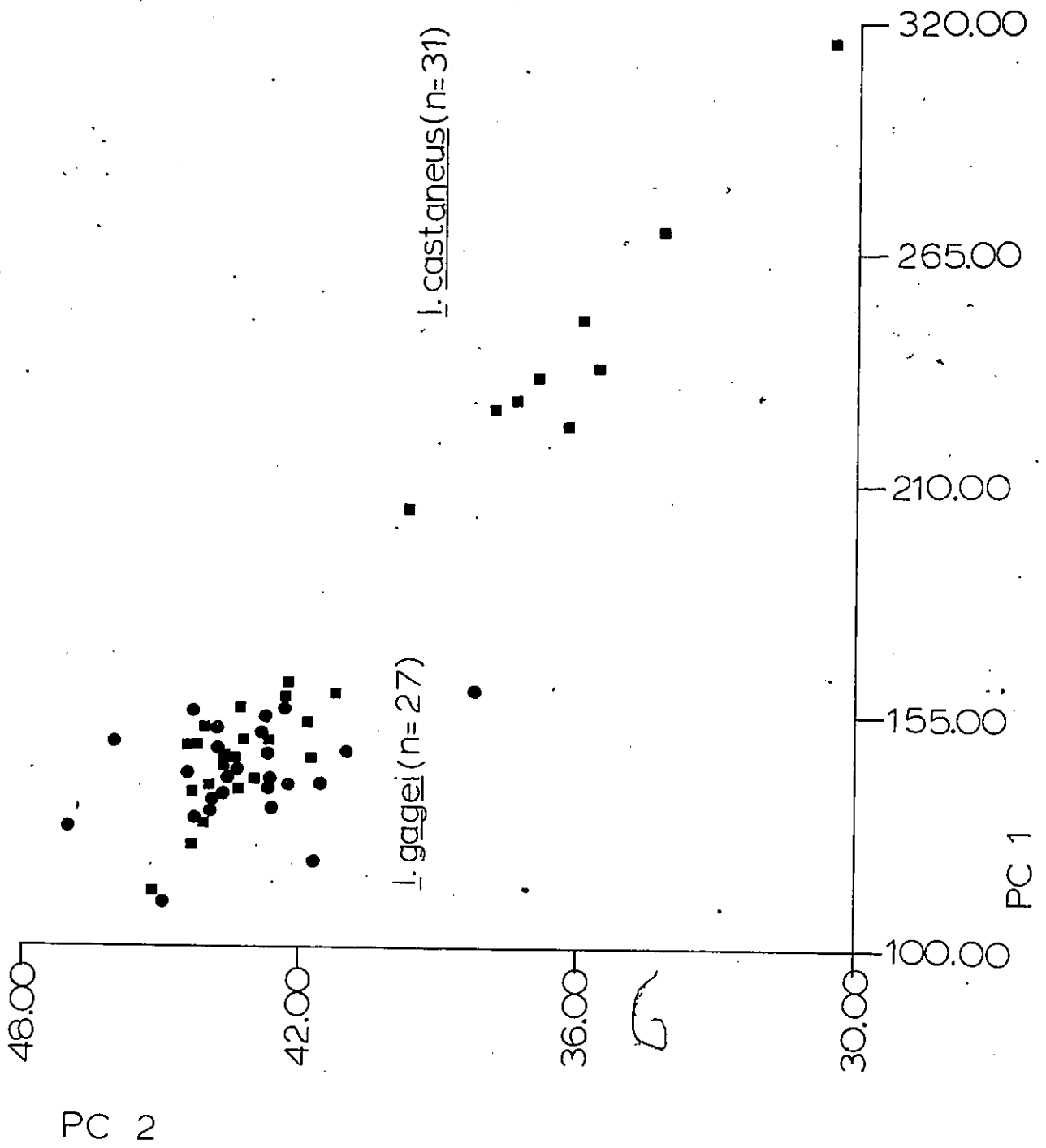
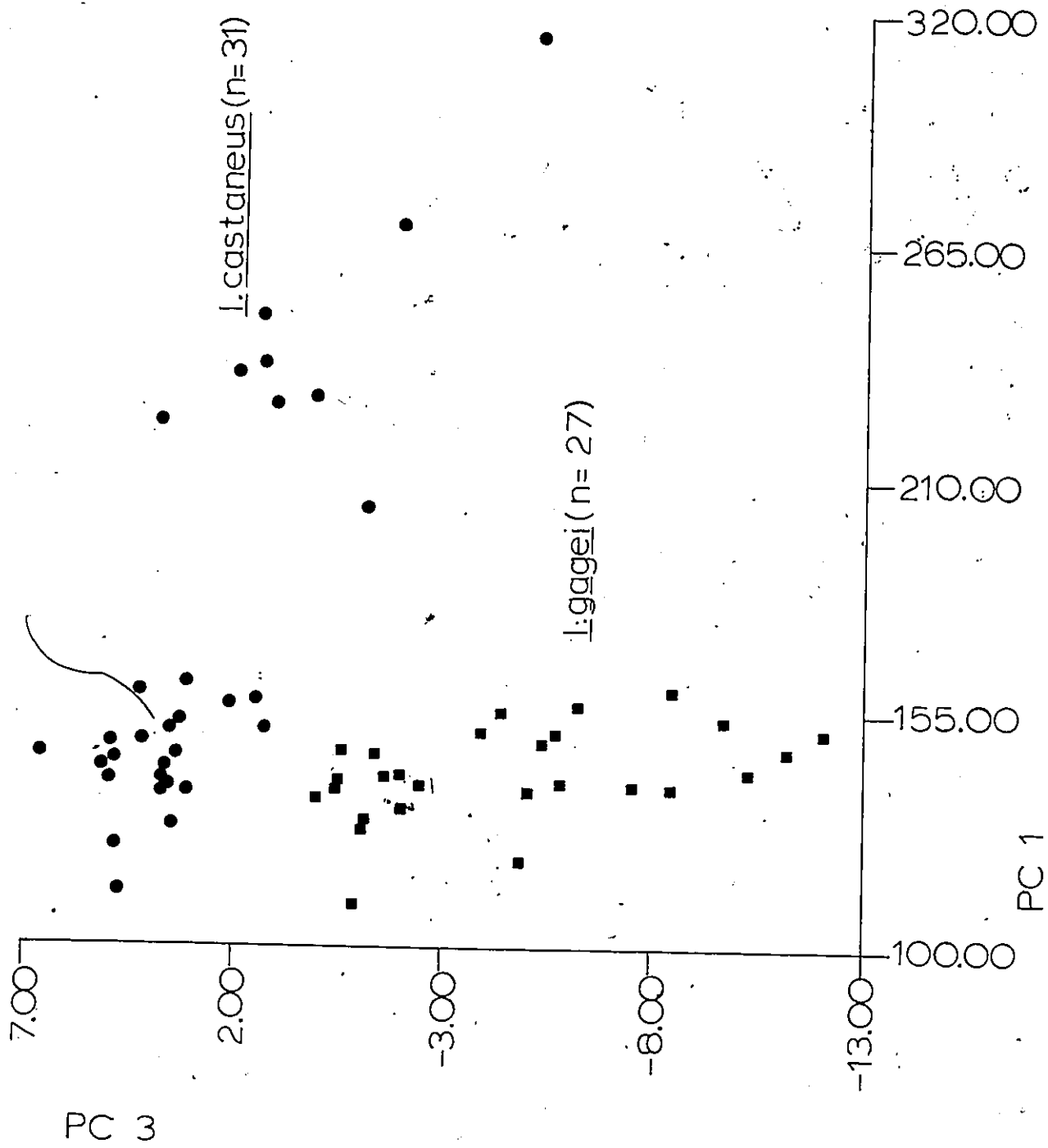


Fig. 20. Scatter diagram showing the relationship between PC 1 and PC 3 for the sympatric stem-satellite pair castaneus-gagei.



first PC.

The main latent vectors of the first principal component of the sympatric stem-satellite pair bdellium-greeleyi are total length and trunk length (Table 12). This first PC accounts for 97.12% of the variance. The main latent vectors of the second PC are the number of myomeres and the number of cusps on the infraoral lamina. This second PC accounts for 1.48% of the variance. The specimens of bdellium which are found within the greeleyi cluster have the shortest total length of the sample, and therefore overlap the longest greeleyi, as shown in Figure 21. PC 1 in relationship to PC 2 gives a 79% correct identification. The third PC, whose main latent vectors are the trunk length and the number of cusps on the infraoral lamina, has a variance of 0.54%. Here again, there is an overlap between the longest greeleyi and the shortest bdellium (Figure 22). A 75% separation of the two species is obtained when using these two principal components, 1 and 3.

The next procedure was a principal components analysis including the data of the holotype of hubbsi from Raney (1952) and the specimens of greeleyi examined in this study. Sixteen characters were used: total length, branchial length, tail length, disc length, orbit diameter, number of myomeres, supraorals, infraorals and bicuspid endolaterals (8). These were logged, standardized and analyzed using a dispersion matrix (Table 13). As shown in Figure 23, hubbsi readily falls within the greeleyi cluster. Therefore, hubbsi is considered synonymous to greeleyi. Vladykov and Kott (1979) synonymized them, but gave no proof of their statement.

In order to show the relationship between Ichthyomyzon and Petromyzon marinus, principal components analyses were performed using

Table 12. Values of the latent vectors, latent roots and percent variance of the principal components analysis of twenty-three characters of the sympatric pair bdellium-greeleyi.

Character	PC 1	PC 2	PC 3
Total length	0.852	-0.049	0.119
Number of myomeres	0.056	0.961	-0.156
Head length	0.105	-0.039	0.106
Branchial length	0.075	0.013	0.072
Trunk length	0.441	-0.038	-0.550
Tail length	0.229	0.033	0.488
Post-orbital length	0.022	0.007	0.005
Inter-branchial length	0.012	0.005	0.018
Orbit diameter	0.011	0.004	0.012
Disc length	0.078	-0.056	0.110
Dorsal fin height	0.030	0.013	0.114
Supraorals	0.003	0.049	0.077
Infraorals	0.008	0.192	0.551
Endolaterals	0.004	0.029	0.064
	0.005	0.028	0.067
	0.005	0.028	0.098
	0.006	0.024	0.094
	0.004	0.026	0.066
	0.005	0.023	0.063
	0.006	0.022	0.083
	0.005	0.023	0.089
Posteriors	0.008	0.036	0.136
Lateral line organs	0.008	0.145	-0.020
Latent roots	2593.040	39.502	14.471
% variance	97.123	1.480	0.542

Fig. 21. Scatter diagram showing the relationship between PC 1 and PC 2 for the sympatric stem-satellite pair bdellium-greeleyi.

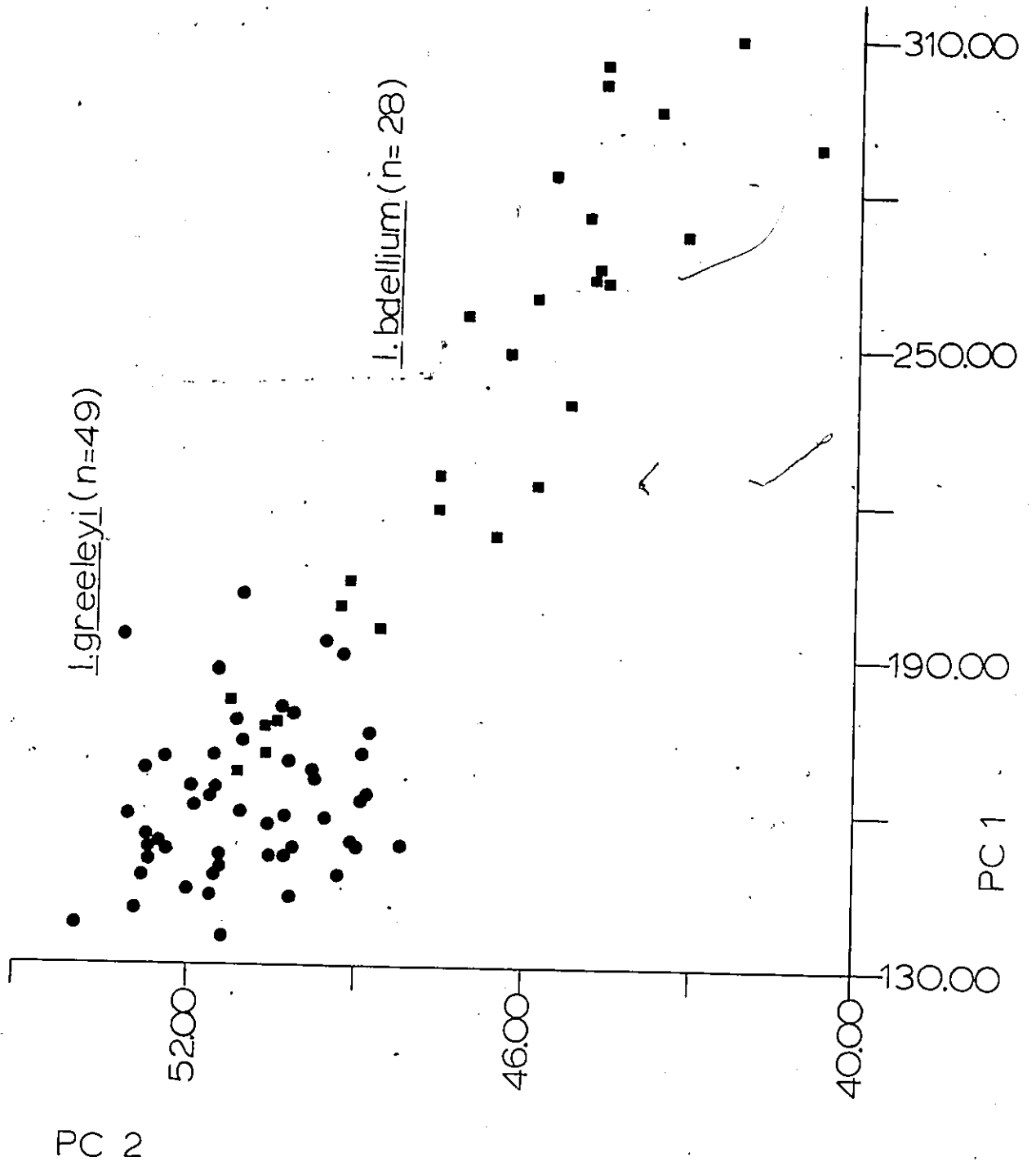


Fig. 22. Scatter diagram showing the relationship between PC 1 and PC 3 for the sympatric stem-satellite pair bdellium-greeleyi.

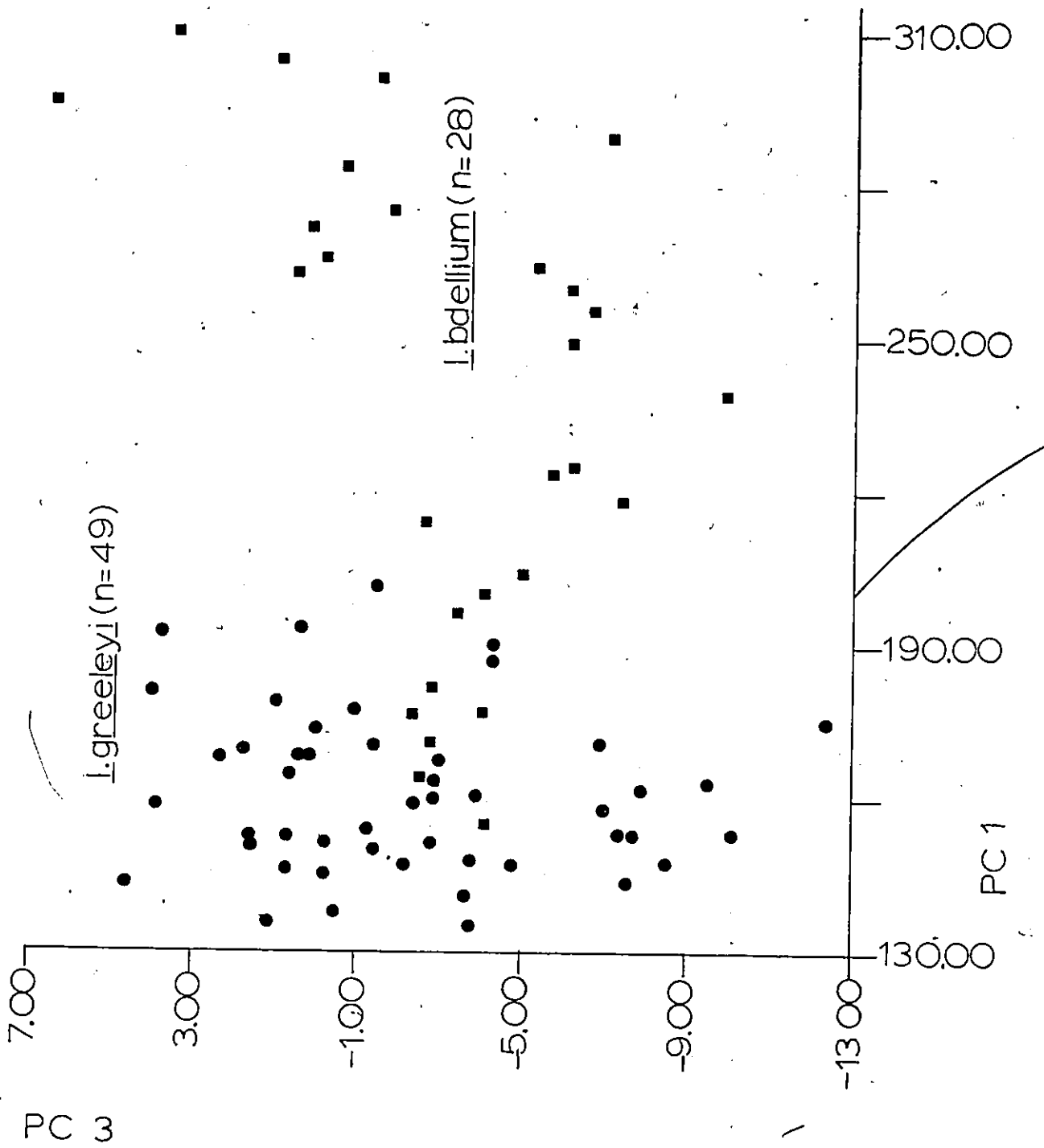


Table 13. Values of the latent vectors, latent roots and percent variance of the principal components analysis of sixteen characters of greeleyi and hubbsi.

Character	PC 1	PC 2	PC 3
Total length	0.035	-0.005	-0.002
Number of myomeres	0.969	-0.189	-0.008
Branchial length	0.018	-0.002	-0.003
Tail length	0.026	-0.003	-0.001
Orbit diameter	0.004	-0.000	0.002
Disc length	0.016	0.007	0.010
Supraorals	0.167	0.877	-0.422
Infraorals	0.035	0.138	0.311
Endolaterals	0.035	0.137	0.344
	0.034	0.180	0.213
	0.034	0.174	0.173
	0.032	0.131	0.410
	0.032	0.133	0.459
	0.032	0.174	0.296
	0.031	0.168	0.256
	0.146	-0.028	-0.023
Latent roots	73.491	15.299	1.511
% variance	80.224	16.701	1.650

Fig. 23. Scatter diagram showing the relationship between PC 1 and PC 2 for greeleyi and hubbsi.



the following characters: total length, head length, branchial length, trunk length, tail length, orbit diameter, disc length, number of myomeres, supraorals, infraorals, endolaterals, number of dorsal fins and parasitism or nonparasitism, which were coded as (1) and (0), respectively. This coding could alternately be regarded as coding whether the intestine is functional or not.

The first principal components analysis performed took into account the first twelve characters (Table 14). The first principal component, which accounts for 57.427% of the variance, has the size factor as the most important main latent vectors; total length is the most important one. The meristic characters, especially the number of cusps on the infraoral lamina, make up the main latent vectors of the second principal component, which accounts for 26.135% of the variance. The third and fourth principal components, accounting for 8.427% and 6.041% of the variance, respectively, have the number of dorsal fins as their main latent vector. The relationship between the species of Ichthyomyzon and Petromyzon marinus using the three main axes is shown in Figure 24.

Distances were computed between principal components calculated using a correlation matrix of the mean values of the characters. The mensural characters were logged, and all characters were standardized. The distances are presented in Table 15 and the resulting phenogram shown in Figure 25. Within the genus Ichthyomyzon, the non-parasitic species cluster together; unicuspis is also linked to that group, being most similar to fossor. I. bdellium and I. castaneus form the other cluster, along with Petromyzon marinus, which is most similar to bdellium.

Table 14. Values of the latent vectors, latent roots and percent variance of the principal components analysis of twelve characters of the six species of adult Ichthyomyzon and Petromyzon marinus.

Character	PC 1	PC 2	PC 3	PC 4	PC 5
Total length	0.355	-0.012	0.131	-0.224	-0.078
Head length	0.302	-0.261	-0.187	0.224	-0.132
Branchial length	0.346	-0.011	0.209	-0.268	0.079
Trunk length	0.341	0.063	0.171	-0.302	-0.269
Tail length	0.337	-0.056	0.226	-0.320	0.143
Orbit diameter	0.336	-0.112	-0.173	0.239	-0.026
Disc length	0.320	-0.154	-0.321	0.174	0.302
Number of myomeres	0.241	0.397	0.157	0.004	0.064
Endolaterals	0.185	0.418	-0.213	0.170	-0.035
Supraorals	0.068	0.509	-0.222	0.151	0.028
Infraorals	0.031	0.522	0.001	0.009	0.567
Dorsal fins	0.124	-0.033	0.684	0.686	0.018
Latent roots	7.466	3.398	1.095	0.785	0.194
% variance	57.427	26.135	8.427	6.041	1.489

9

Fig. 24. Scatter diagram showing the relationship between PC 1, PC 2 and PC 3 for the six species of Ichthyomyzon and Petromyzon marinus.

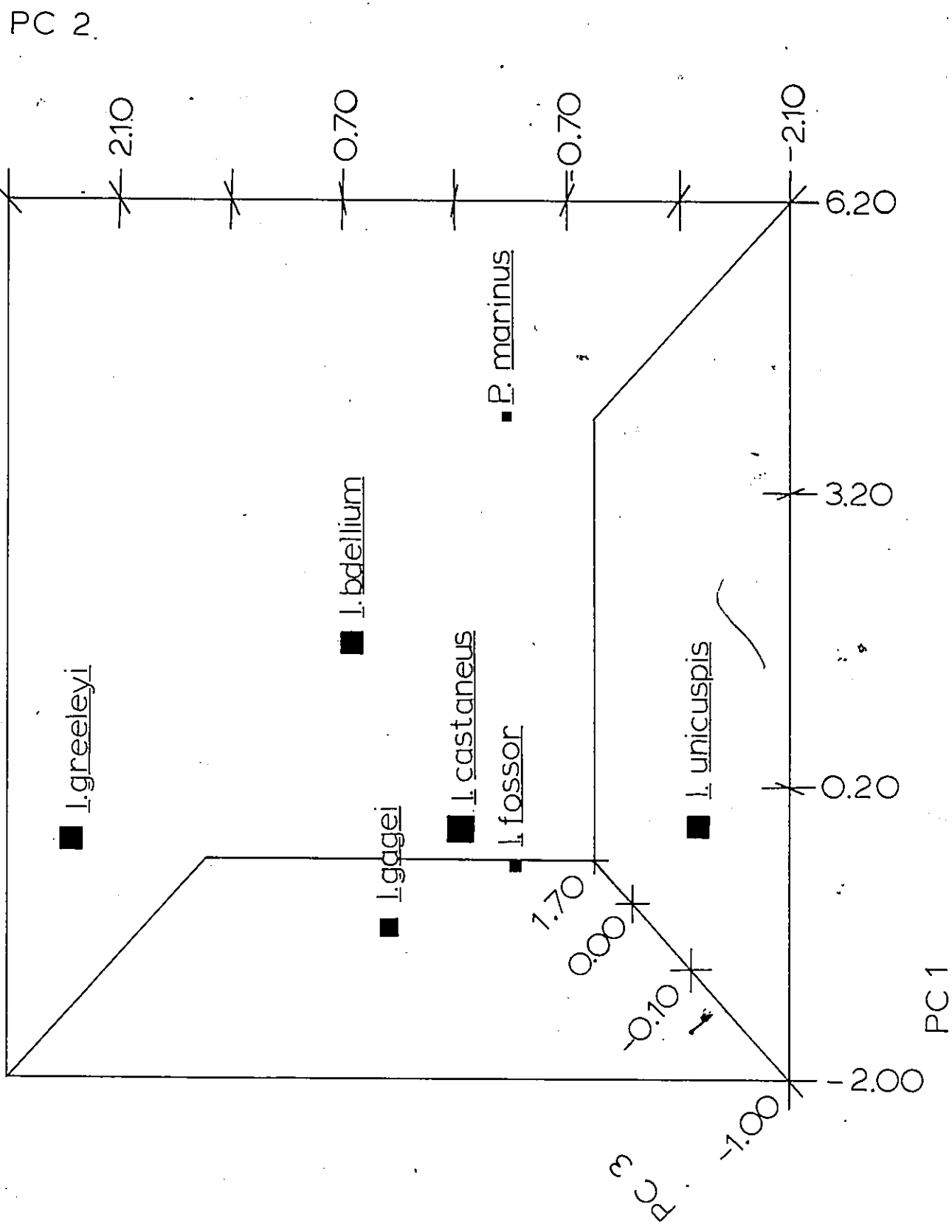


Table 15. Principal components distances computed from a correlation matrix of a principal components analysis of twelve adult characters.

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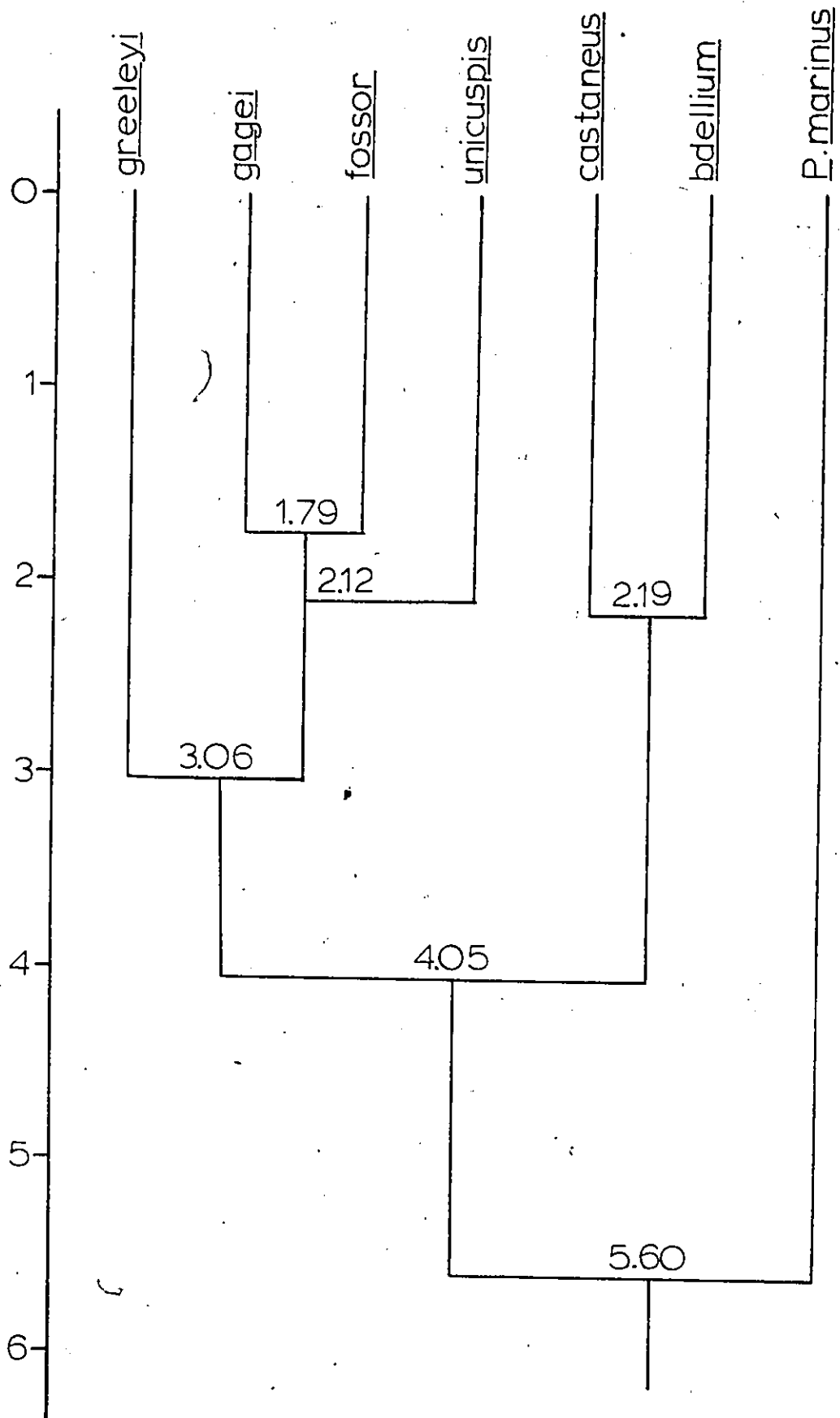
Taxon x taxon	Principal components distances
<u>fossor</u> x <u>unicuspis</u>	2.1268
<u>fossor</u> x <u>gagei</u>	1.7963
<u>fossor</u> x <u>castaneus</u>	2.8122
<u>fossor</u> x <u>greeleyi</u>	4.1608
<u>fossor</u> x <u>bdellium</u>	4.2244
<u>fossor</u> x <u>Petromyzon</u>	8.6110
<u>unicuspis</u> x <u>fossor</u>	2.1268
<u>unicuspis</u> x <u>gagei</u>	3.0818
<u>unicuspis</u> x <u>castaneus</u>	2.2956
<u>unicuspis</u> x <u>greeleyi</u>	4.8498
<u>unicuspis</u> x <u>bdellium</u>	3.6924
<u>unicuspis</u> x <u>Petromyzon</u>	7.5358
<u>gagei</u> x <u>fossor</u>	1.7963
<u>gagei</u> x <u>unicuspis</u>	3.0818
<u>gagei</u> x <u>castaneus</u>	2.3583
<u>gagei</u> x <u>greeleyi</u>	3.0574
<u>gagei</u> x <u>bdellium</u>	4.0458
<u>gagei</u> x <u>Petromyzon</u>	9.0361

Table 15. (cont.)

Principal components distances

<u>castaneus</u> x <u>fossor</u>	2.8121
<u>castaneus</u> x <u>unicuspis</u>	2.2956
<u>castaneus</u> x <u>gagei</u>	2.3583
<u>castaneus</u> x <u>greeleyi</u>	3.0589
<u>castaneus</u> x <u>bdellium</u>	2.1933
<u>castaneus</u> x <u>Petromyzon</u>	7.2315
<u>greeleyi</u> x <u>fossor</u>	4.1608
<u>greeleyi</u> x <u>unicuspis</u>	4.8498
<u>greeleyi</u> x <u>gagei</u>	3.0574
<u>greeleyi</u> x <u>castaneus</u>	3.0589
<u>greeleyi</u> x <u>bdellium</u>	3.3568
<u>greeleyi</u> x <u>Petromyzon</u>	8.4378
<u>bdellium</u> x <u>fossor</u>	4.2244
<u>bdellium</u> x <u>unicuspis</u>	3.6924
<u>bdellium</u> x <u>gagei</u>	4.0458
<u>bdellium</u> x <u>castaneus</u>	2.1933
<u>bdellium</u> x <u>greeleyi</u>	3.3568
<u>bdellium</u> x <u>Petromyzon</u>	5.6083
<u>Petromyzon</u> x <u>fossor</u>	8.6110
<u>Petromyzon</u> x <u>unicuspis</u>	7.5358
<u>Petromyzon</u> x <u>gagei</u>	9.0361
<u>Petromyzon</u> x <u>castaneus</u>	7.2315
<u>Petromyzon</u> x <u>greeleyi</u>	8.4378
<u>Petromyzon</u> x <u>bdellium</u>	5.6083

Fig. 25. Phenogram computed from a correlation matrix of a principal components analysis of twelve logged standardized characters. Scale is values of principal components distances.



The second principal components analysis performed used parasitism or nonparasitism as a thirteenth character (Table 16). The morphometric characters, especially total length, comprise the main latent vectors of the first principal component, which accounts for 57.405% of the variance. The meristic characters, dentition and myomeres, on the other hand, comprise the main latent vectors of the second principal component, which accounts for 26.063% of the variance. The number of dorsal fins is the main latent vector of the third and fourth principal components, which account for 8.998% and 5.696% of the variance, respectively. The relationship between the species of Ichthyomyzon and Petromyzon marinus using the three main axes is shown in Figure 26.

The principal components distances computed from a correlation matrix of the principal components analysis are summarized in Table 17 and presented as a phenogram (Figure 27). Within the genus Ichthyomyzon, the nonparasitic species cluster together. The second cluster, made up of the parasitic species of Ichthyomyzon, also includes Petromyzon marinus, which is most similar to bdellium.

Table 16. Values of the latent vectors, latent roots and percent variance of the principal components analysis of thirteen characters of the six species of adult Ichthyomyzon and Petromyzon marinus.

Character	PC 1	PC 2	PC 3	PC 4	PC 5
Parasitism or non-	0.278	-0.254	0.331	0.091	-0.033
Total length	0.337	0.043	-0.180	-0.212	-0.079
Head length	0.309	-0.222	0.124	0.178	-0.122
Branchial length	0.327	0.048	-0.255	-0.244	0.077
Trunk length	0.319	0.116	-0.211	-0.280	-0.271
Tail length	0.321	0.005	-0.282	-0.295	0.140
Orbit diameter	0.333	-0.073	0.127	0.198	-0.016
Disc length	0.322	-0.122	0.255	0.113	0.313
Number of myomeres	0.206	0.419	-0.111	0.033	0.059
Endolaterals	0.159	0.412	0.255	0.147	-0.632
Supraorals	0.041	0.484	0.287	0.134	0.027
Infraorals	-0.000	0.504	0.071	0.024	0.562
Dorsal fins	0.111	0.008	-0.585	0.766	0.012
Latent roots	8.037	3.649	1.260	0.797	0.194
% variance	57.405	26.063	8.998	5.696	1.385

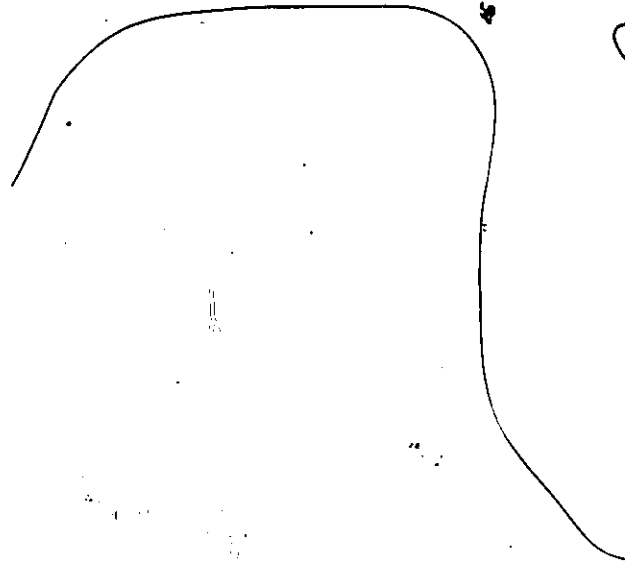


Fig. 26. Scatter diagram showing the relationship between PC 1, PC 2 and PC 3 for the six species of Ichthyomyzon and Petromyzon marinus.

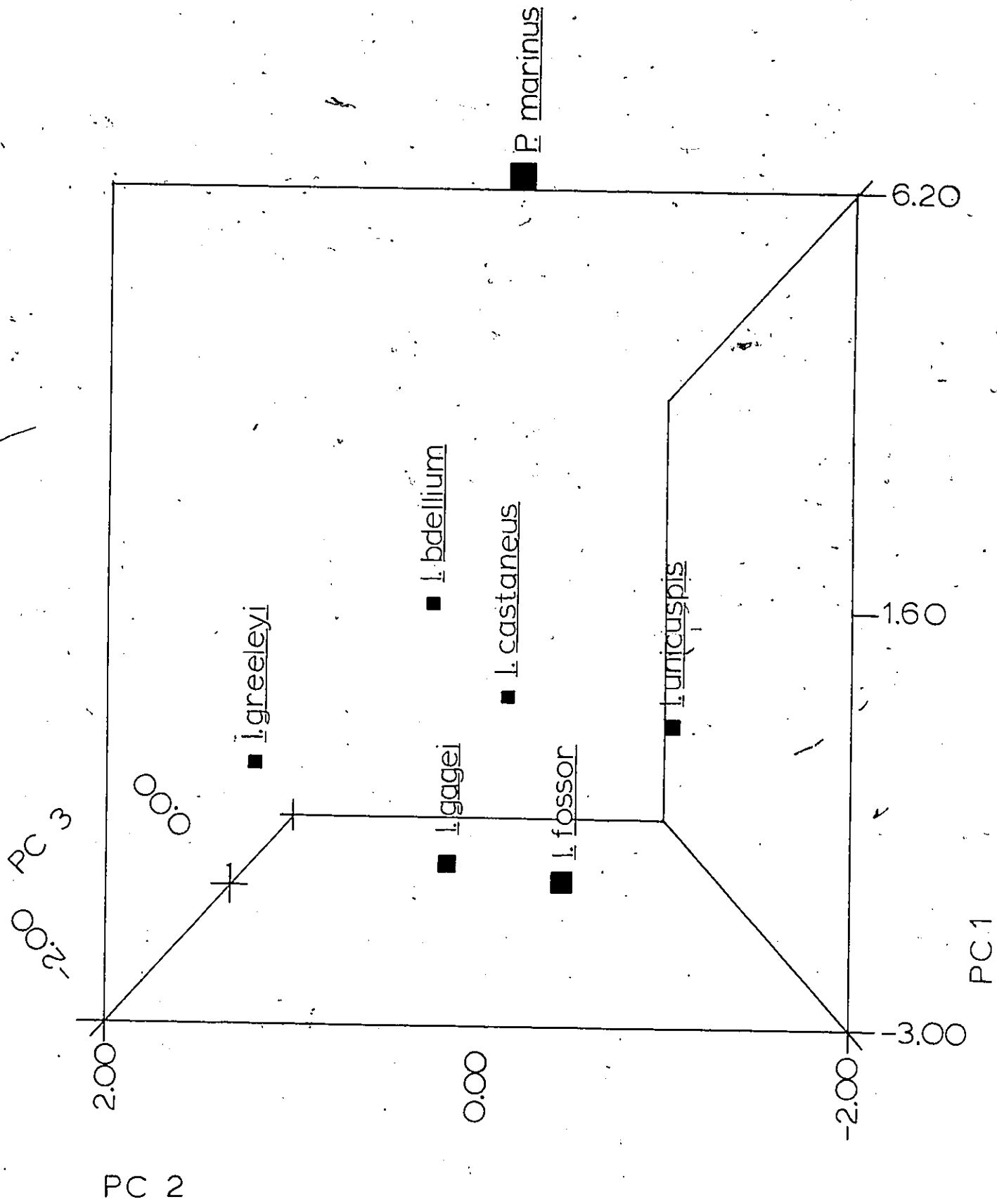


Table 17. Principal components distances computed from a correlation matrix of a principal components analysis of thirteen adult characters.

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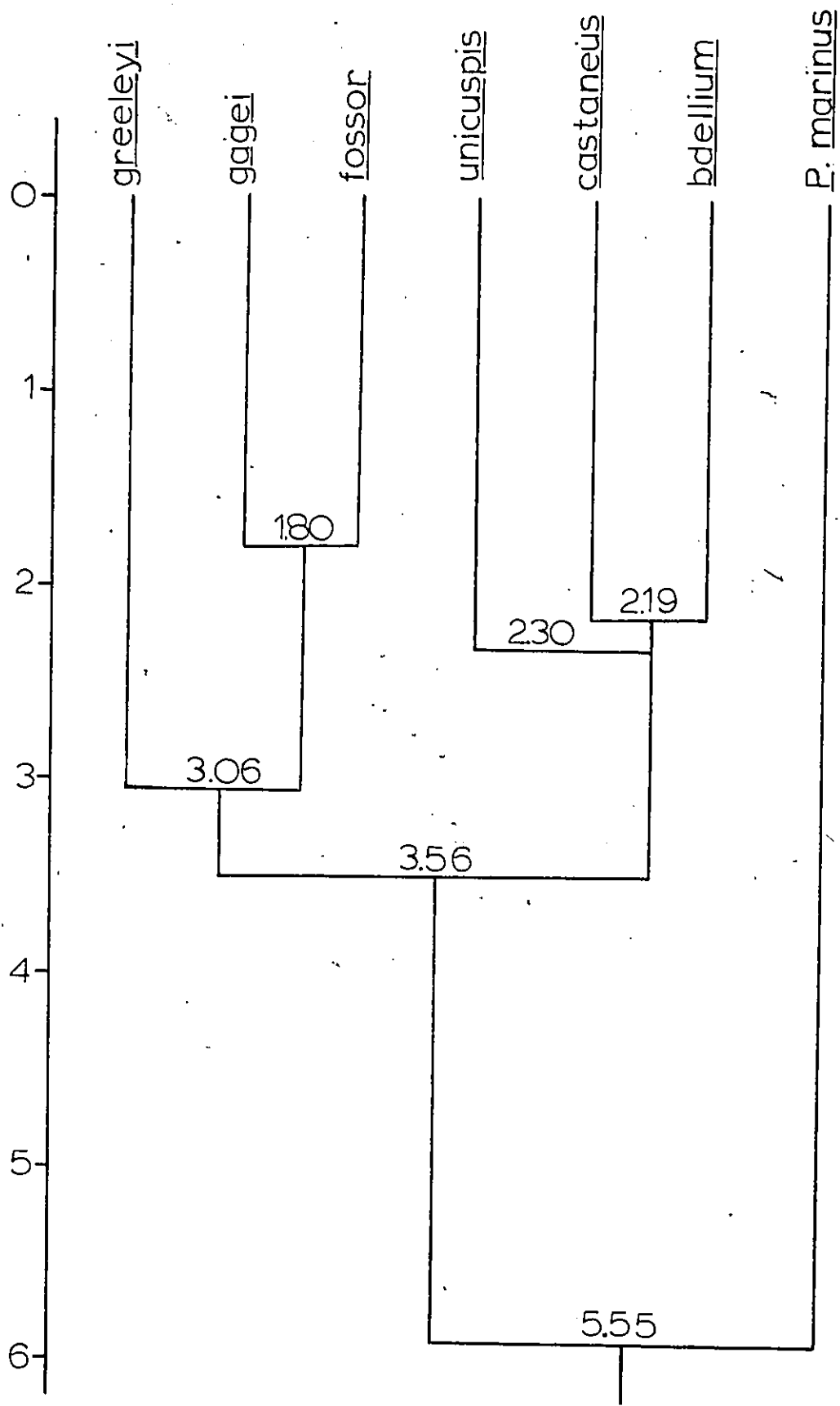
Taxon x taxon	Principal components distances
<u>fossor</u> x <u>unicuspis</u>	2.7691
<u>fossor</u> x <u>gagei</u>	1.7964
<u>fossor</u> x <u>castaneus</u>	3.3200
<u>fossor</u> x <u>greeleyi</u>	4.1604
<u>fossor</u> x <u>bdellium</u>	4.5833
<u>fossor</u> x <u>Petromyzon</u>	8.8077
<u>unicuspis</u> x <u>fossor</u>	2.7691
<u>unicuspis</u> x <u>gagei</u>	3.5550
<u>unicuspis</u> x <u>castaneus</u>	2.2959
<u>unicuspis</u> x <u>greeleyi</u>	5.1690
<u>unicuspis</u> x <u>bdellium</u>	3.6920
<u>unicuspis</u> x <u>Petromyzon</u>	7.4876
<u>gagei</u> x <u>fossor</u>	1.7964
<u>gagei</u> x <u>unicuspis</u>	3.5550
<u>gagei</u> x <u>castaneus</u>	2.9437
<u>gagei</u> x <u>greeleyi</u>	3.0554
<u>gagei</u> x <u>bdellium</u>	4.4184
<u>gagei</u> x <u>Petromyzon</u>	9.2247

Table 17. (cont.)

Principal components distances

<u>castaneus</u> x <u>fossor</u>	3.3200
<u>castaneus</u> x <u>unicuspis</u>	2.2959
<u>castaneus</u> x <u>gagei</u>	2.9437
<u>castaneus</u> x <u>greeleyi</u>	3.5396
<u>castaneus</u> x <u>bdellium</u>	2.1936
<u>castaneus</u> x <u>Petromyzon</u>	7.1792
<u>greeleyi</u> x <u>fossor</u>	4.1604
<u>greeleyi</u> x <u>unicuspis</u>	5.1690
<u>greeleyi</u> x <u>gagei</u>	3.0554
<u>greeleyi</u> x <u>castaneus</u>	3.5396
<u>greeleyi</u> x <u>bdellium</u>	3.8066
<u>greeleyi</u> x <u>Petromyzon</u>	8.6375
<u>bdellium</u> x <u>fossor</u>	4.5833
<u>bdellium</u> x <u>unicuspis</u>	3.6920
<u>bdellium</u> x <u>gagei</u>	4.4184
<u>bdellium</u> x <u>castaneus</u>	2.1936
<u>bdellium</u> x <u>greeleyi</u>	3.8066
<u>bdellium</u> x <u>Petromyzon</u>	5.5469
<u>Petromyzon</u> x <u>fossor</u>	8.8077
<u>Petromyzon</u> x <u>unicuspis</u>	7.4876
<u>Petromyzon</u> x <u>gagei</u>	9.2247
<u>Petromyzon</u> x <u>castaneus</u>	7.1792
<u>Petromyzon</u> x <u>greeleyi</u>	8.6375
<u>Petromyzon</u> x <u>bdellium</u>	5.5469

Fig. 27. Phenogram computed from a correlation matrix of a principal components analysis of thirteen logged standardized characters. Scale is values of principal components distances.



## Discussion

The analysis of the meristic and morphometric characters of adult Ichthyomyzon offers a confirmation and extension of previous findings (Hubbs and Trautman, 1937) regarding the range and average values of these characters in each species. The upper limit of the range of values of fossor has been extended for the following characters: total length, tail length, orbit diameter, disc length and the number of cusps on the supraoral lamina. The lower limit has been extended for tail length and branchial length. The mean number of cusps on the infraoral lamina was lower in this study. In unicuspis, the upper limit has been extended for the following characters: orbit diameter, disc length and branchial length. The lower limit has been extended for disc length and total length. In gagei, the upper limit has been extended for trunk myomeres, total length, tail length, orbit diameter, disc length, branchial length and number of cusps on the supraoral lamina. The lower limit has been extended for trunk myomeres, number of cusps on the infraoral lamina, number of bicuspid endolaterals, total length, tail length and branchial length. The mean number of bicuspid endolaterals was lower in this study. In castaneus, the upper limit has been extended for the number of cusps on the supraoral lamina, tail length, orbit diameter and disc length. The lower limit has been extended for the number of cusps on the supraoral lamina, total length and tail length. The mean number of bicuspid endolaterals was lower in this study. In greeleyi, the upper limit has been extended for trunk myomeres, total length, tail length, orbit diameter and disc length. The lower limit has been extended for the number of bicuspid endolaterals, orbit diameter and disc length. The mean number of bicuspid endolaterals was lower in this study. In bdellium,

the upper limit has been extended for orbit diameter and disc length. The lower limit has been extended for the number of cusps on the infraoral lamina and branchial length. The mean number of bicuspid endolaterals was higher in this study, as also found by McBath (1968).

Though the ranges of some of the meristic and morphometric characters have been extended in all species of adult Ichthyomyzon, it is still possible to separate them. Most of these ranges already overlapped in the revision of the genus by Hubbs and Trautman (1937).

The head length, trunk length and disc length as a proportion of the branchial length were not evaluated by these authors.

On the average, the myomere counts in this study exceed Hubbs and Trautman's (1937) by one. This could be due to a difference in counting methodology. Bdellium has two myomeres over the average value found by these authors, but McBath (1968) found the same value as this study. The discrepancy can be explained by the low number of specimens of this species studied by Hubbs and Trautman (1937).

Key to species of adult Ichthyomyzon

The key to the species by Hubbs and Trautman (1937) used parasitism or nonparasitism as the main couplet. In this study, each sympatric stem-satellite pair is united in a couplet. The key is accompanied by a series of illustrations of the discs to show the different teeth patterns.

1	Endolaterals unicuspid (Fig. 28b).....	2
	Endolaterals in part (1-10) bicuspid (Fig. 29b).....	3

Lateral line organs non-pigmented; teeth blunt and degenerate (Fig. 28a); disc 4.0-6.4% TL (mean: 4.9) and 40.0-62.5% B<sub>1</sub>-B<sub>7</sub> (mean: 50.4); intestine non-functional.

2

.....fossor

Lateral line organs pigmented; teeth sharp (Fig. 28b); disc 7.9-12.4% TL (mean: 10.1) and 78.7-122.7% B<sub>1</sub>-B<sub>7</sub> (mean: 105.5); intestine functional in feeding stage.

.....unicuspis

Myomeres 50-55, mean: 54; bicuspid endolaterals 1-8, most frequently 5.

3

.....4

Myomeres 56-62, mean: 58; bicuspid endolaterals 6-10, most frequently 8.

.....5

Disc 3.9-6.5% TL (mean: 5.3) and 40.0-63.6% B<sub>1</sub>-B<sub>7</sub> (mean: 54.4); anterials and marginals degenerate (Fig. 29a); intestine non-functional.

4

.....gagei

Disc 8.5-11.6% TL (mean: 10.1) and 86.4-;23.8% B<sub>1</sub>-B<sub>7</sub> (mean: 108.7); anterials and marginals sharp (Fig. 29b); intestine functional in feeding stage.

.....castaneus



Disc 4.0-7.8% TL (mean: 6.4) and 38.5-78.6% B<sub>1</sub>-B<sub>7</sub> (mean: 65.6) (Fig. 30a); intestine non-functional.

5

.....greeleyi  
Disc 6.9-9.5% TL (mean: 8.2) and 72.1-107.7% B<sub>1</sub>-B<sub>7</sub> (mean: 90.0) (Fig. 30b); intestine functional in feeding stage.

.....bdellium

### Principal components analyses

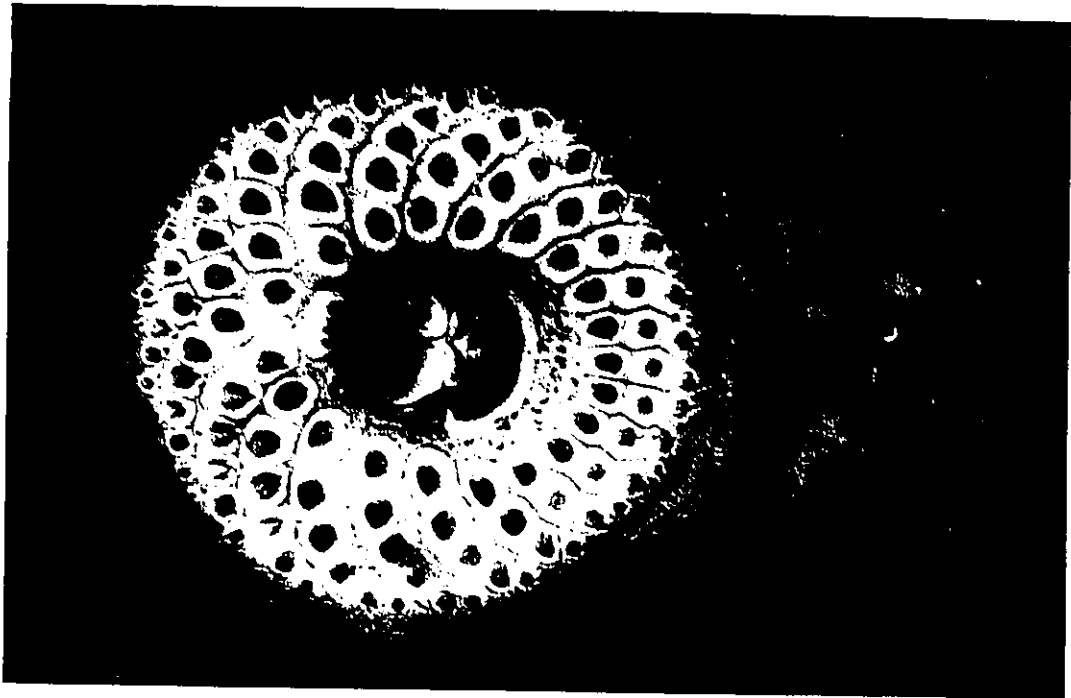
Since taxonomy is concerned with the classification of organisms based upon relationships inferred from characteristics of the whole organism, statistical analysis in this field must take into consideration the simultaneous covariation of as many characters of the organism as possible. Simultaneous consideration of several characters may better evaluate the overall relationships or may permit the distinction of taxa inseparable using any single character. For these reasons, the techniques of multivariate analysis are of particular importance in taxonomy (Sokal, 1965).

A multivariate scaling analysis such as principal components analysis enables one to reduce the dimensionality of the system which needs to be considered. This involves the construction of a few axes which contain most of the information about the covariation among the observations found in the original characters. The coordinates of the principal axes are therefore linear weighted combinations of the original variables and summarize the major dimensions of variation (Sneath and Sokal, 1973).

An eigenvalue is equal to the variance along its corresponding axis. Thus, the first or principal axis corresponding to the largest

Fig. 28. Discs of:

- a- Ichthyomyzon fossor: ♀, 150 mm TL; Birch River, upstream of  
Prawda, Manitoba; May 13, 1977; J. Jyrkkanen; ROM 34264.
- b- Ichthyomyzon unicuspis: ♂, 146 mm TL; Lower Duck Island, Ottawa  
River, at Ottawa, Ontario; July 1977; J.M. Hanson.



b

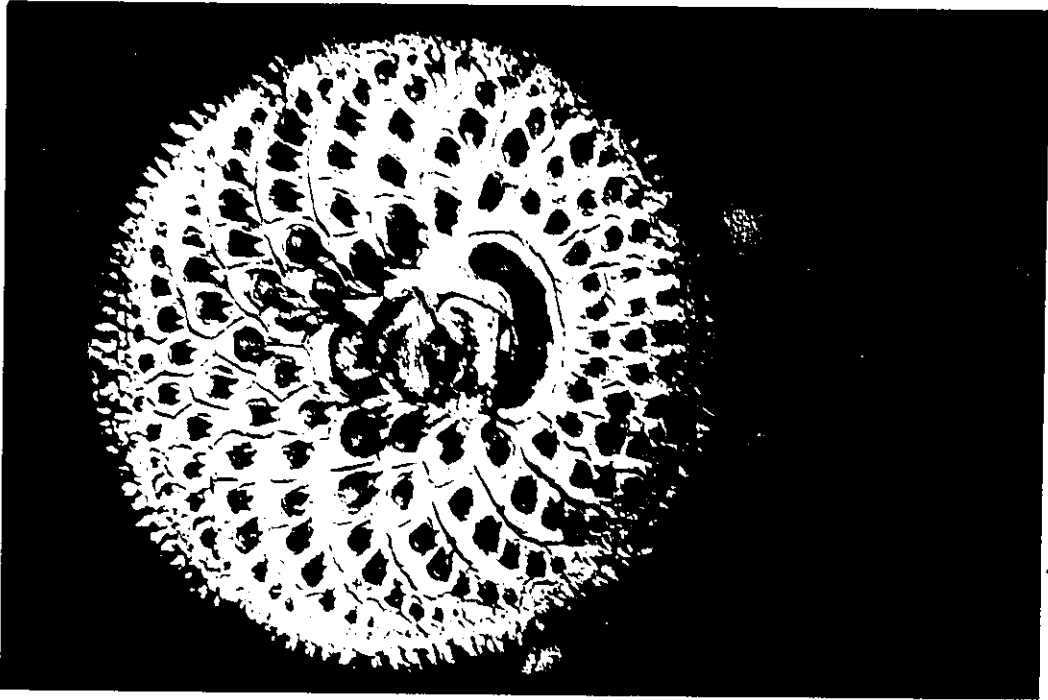


d

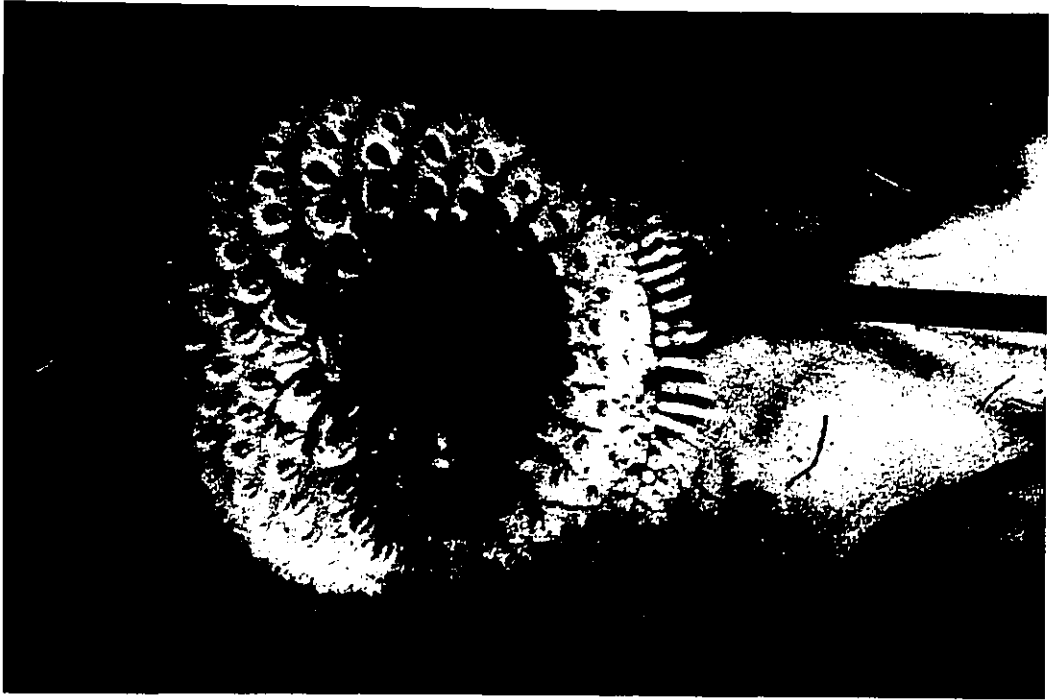
Fig. 29. Discs of:

Ichthyomyzon gagei: ♀, 107 mm TL; Wircher Creek, 3.2 km SW  
Yorkville, Paulding Co., Georgia; April 18, 1964; J.C. Hall,  
J.D. Williams. UA 1249.

Ichthyomyzon castaneus: ♀, 224 mm TL; Black Lake, Ottawa Co.,  
Michigan; March 1, 1929; J. Metzelaar.



b.

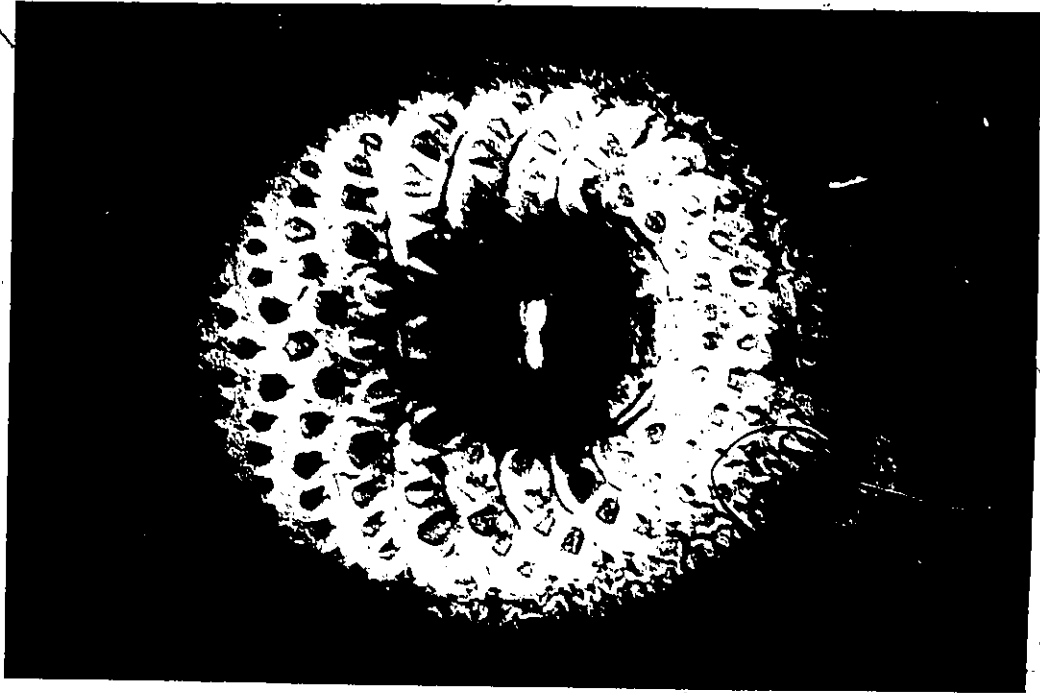


d.

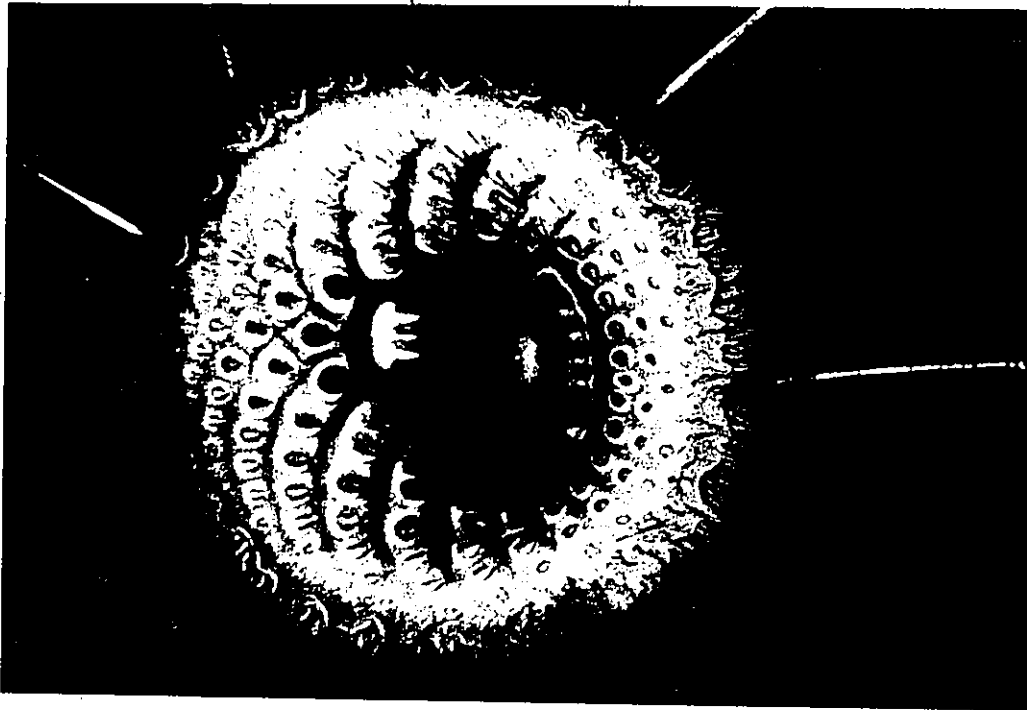
Fig. 30. Discs of:

a- Ichthyomyzon greeleyi: ♂, 143 mm TL; French Creek, 3.2 km  
W Mill Village, Erie Co., Pennsylvania; May 14, 1977;  
E.L. Cooper, J. Lanteigne, E. Kott.

b- Ichthyomyzon bdellium: ♀, 250 mm TL; same collection data as  
greeleyi.



b



d

eigenvalue is the dimension that accounts for the greatest amount of variance from the sample. In data that are very highly correlated, most of the variance can be accounted for by the major axis (Sokal and Rohlf, 1973). The first eigenvalue often, but not necessarily, corresponds to variation in overall size of the specimens, as shown in this study. The main latent vectors (whose size indicates the importance of that particular character) of the first principal component of the three pair-complexes were total length and trunk length. This variation can be accounted for by the fact that the range of total length is wide, especially in the parasitic species where growth occurs after metamorphosis. The maximum total length attained by the parasitic species is always higher than the nonparasitic species. On the other hand, nonparasitic species have a proportionately longer trunk length than their parasitic counterparts, except for the sympatric pair bdellium-greeleyi.

The second principal axis accounts for the second largest amount of variance from the sample, and so on. These other principal components often corresponds to various shape differences between specimens (Jolicoeur and Mosimann, 1960). These differences are usually expressed as contrasts (high positive coefficients for some characters and high negative coefficients for other characters). In the sympatric pair unicuspis-fossor, the main latent vectors of the second principal component were the presence or absence of pigmented lateral line organs and the disc length. The latter is directly correlated to parasitism or nonparasitism, and is an adaptation to a mode of life. Fossor has the most degenerate disc and dentition; therefore, it does not show as much variation as unicuspis, whose disc grows in proportion to the body. In the sympatric pair castaneus-gagei, this adaptation is only

shown in the third principal component. The second principal component for this pair has the number of trunk myomeres as its main latent vector. As also shown by Hubbs and Trautman (1937), gagei shows a wide variation in the number of trunk myomeres. In the sympatric pair bdellium-greeleyi, the variations in the number of trunk myomeres and the number of cusps on the infraoral lamina are shown in the second principal component. Even though the trunk length is not significantly different between the two species, it accounts for most of the variation of the third principal component, along with the number of cusps on the infraoral lamina, which has a wide range in bdellium.

The particular contrasts which result from the analysis are a consequence of the structure of the correlation between the characters (Rohlf, 1971). It is customary to extract only enough eigenvectors to remove the majority (75%) of the variance of the data matrix. In this study, most of the variance was accounted for in the first principal component.

In both principal components analyses of the adult characters of the six species of Ichthyomyzon and Petromyzon marinus, the main latent vectors of the first five principal components are the same. Their values are similar, except in the third principal component, where the value of the main latent vector, the number of dorsal fins, changes from positive to negative. The second main latent vector of the third principal component also changes from the disc length to parasitism or nonparasitism. But these two characters are correlated, as a longer disc length, found in the parasitic species, is an adaptation to a mode of life. The only effect of using correlated characters, according to Rohlf (1967), appears to be that it causes the generic clusters to appear very elongated in the

n dimensional space. But even though disc length and parasitism are correlated, the phenograms representing the phenetic relationships between the species of Ichthyomyzon and Petromyzon marinus differ. In the analysis where parasitism or nonparasitism is used as a character, unicuspis is closer to castaneus, but when that character is excluded, unicuspis becomes closer to fossor. This can be accounted for by the fact that unicuspis has a similar number of cusps on the supraoral and infraoral laminae and a similar tooth formula of the endolaterals as fossor. Moreover, the range of total length of unicuspis does not include the longer length classes usually found in this species. When parasitism or nonparasitism is introduced as a thirteenth character, this species naturally moves to the parasitic cluster, where it is most similar to castaneus. The other phenetic relationships remain the same at similar principal components distances.

Hubbs and Trautman (1937) hypothesized that each nonparasitic species was derived from the sympatric parasitic species, using geographical distribution as a support of this hypothesis. They thus suggest independent parallel evolution of each nonparasitic species. Vladykov and Kott (1979) espoused this theory and extended it to other genera. They coined the term "satellite" for the one or more nonparasitic derivatives of the parasitic form.

An alternate hypothesis is that there is a parasitic and nonparasitic branch in the genus. Thus the nonparasitic species would have given rise to other nonparasitic species, and the parasitic species would have given rise to other parasitic species. The similarities of the nonparasitic species are thus due as much to genealogy as to parallelism (Mayr, 1965). A third hypothesis, that phylogeny resulted from both types

of evolution, is admitted possible, but will be ignored for purposes of simplicity.

The results of the principal components analyses favour the second hypothesis, i.e. two separate lines, one parasitic and the other nonparasitic. The problem is that characters, such as dentition, head length and orbit diameter are adaptive. The similarity of the nonparasitic species thus could be explained by parallel adaptations to nonparasitic life or through inheritance from a common ancestor. Thus this principal components analysis cannot provide an adequate test of the hypothesis shaped by Hubbs and Trautman (1937). This is not regarded as a failure of the multivariate approach. Using the same data, numerical taxonomy would come to the same conclusions. Interpreting the loss of teeth and their lack of development, small disc and eyes as advanced character states, the cladistic approach would also draw the same conclusions. In the face of character sets largely reflecting adaptation to two life styles, none of the taxonomic schools are able to extract themselves from the quagmire of parallelism.

The solution of the problem is discovering a sufficient number of characters which are not adaptive to the life styles. The pigmentation patterns of the larvae and the presence or absence of pigment in the neuromasts discovered in this study are contributions toward an eventual resolution of the problem. Perhaps protein or chromosome characters may add sufficient data to test Hubbs and Trautman's (1937) hypothesis.

## GEOGRAPHICAL DISTRIBUTION

### Results

The genus Ichthyomyzon is restricted to the inland waters of eastern North America. It is present in the following drainage basins: Hudson Bay, Western Great Lakes, Eastern Great Lakes-St. Lawrence, Upper and Lower Mississippi, Upper and Lower Missouri, Eastern and Western Gulf of Mexico, Lower Arkansas-Red-White, Tennessee-Cumberland and Ohio (Fig. 31).

Ichthyomyzon unicuspis is found in the following drainage basins and provinces/states: Hudson Bay: Ontario and Manitoba; Western Great Lakes: Ontario, Michigan, Wisconsin; Eastern Great Lakes-St. Lawrence: Ontario (rare in Lake Ontario), Michigan, Ohio, Pennsylvania, Quebec; Ohio: Indiana, Ohio, Kentucky, West Virginia; Upper Missouri: South Dakota; Lower Missouri: Nebraska, Missouri; Upper Mississippi: Minnesota, Wisconsin, Iowa, Illinois (Figs. 32, 33). The nonparasitic sympatric satellite species, fossor, is found in the following drainage basins and provinces/states: Hudson Bay: Manitoba; Western Great Lakes: Ontario, Wisconsin, Michigan; Eastern Great Lakes- St. Lawrence: Ontario, Quebec, Michigan, Ohio, Pennsylvania (not present in Lake Ontario); Ohio: Illinois, Indiana, Ohio, Kentucky; Lower Missouri: Missouri (Figs. 34, 35).

I. castaneus is present in the following drainages and provinces/states: Hudson Bay: Saskatchewan, Manitoba, North Dakota, Minnesota; Western Great Lakes: Wisconsin, Michigan, Indiana (restricted to Lakes Michigan and Huron); Upper Missouri: Nebraska, Kansas; Lower Missouri: Missouri; Upper Mississippi: Wisconsin, Iowa, Illinois, Missouri; Lower Mississippi: Illinois, Missouri, Mississippi; Eastern Gulf: Mississippi,

Alabama; Western Gulf: Texas; Lower Arkansas-Red-White: Kansas, Missouri, Oklahoma, Texas, Arkansas, Louisiana; Tennessee-Cumberland: Kentucky, Tennessee, Alabama; Ohio: Illinois, Indiana (Figs. 36, 37). The nonparasitic satellite species, gagei, is found in the following drainages and states: Lower Missouri: Missouri; Lower Mississippi: Mississippi; Eastern Gulf: Mississippi, Alabama, Georgia, Florida; Western Gulf: Texas, Louisiana; Lower Arkansas-Red-White: Missouri, Oklahoma, Arkansas, Louisiana; Tennessee-Cumberland: Kentucky, Tennessee, Alabama (Fig. 38).

I. bdellium is confined to the Ohio drainage basin of Indiana, Illinois, Kentucky, Pennsylvania, Ohio, West Virginia and the Tennessee-Cumberland drainage basin of Alabama, Kentucky, North Carolina, Tennessee and Virginia (Fig. 39). Its nonparasitic satellite species, greeleyi, is restricted to the Ohio drainage basin of Kentucky, Ohio, Pennsylvania and West Virginia, and the Tennessee-Cumberland drainage basin of Alabama, Kentucky, Tennessee and Virginia (Fig. 40).

Fig. 31. Principal drainage basins of Eastern United States where the genus Ichthyomyzon is distributed.

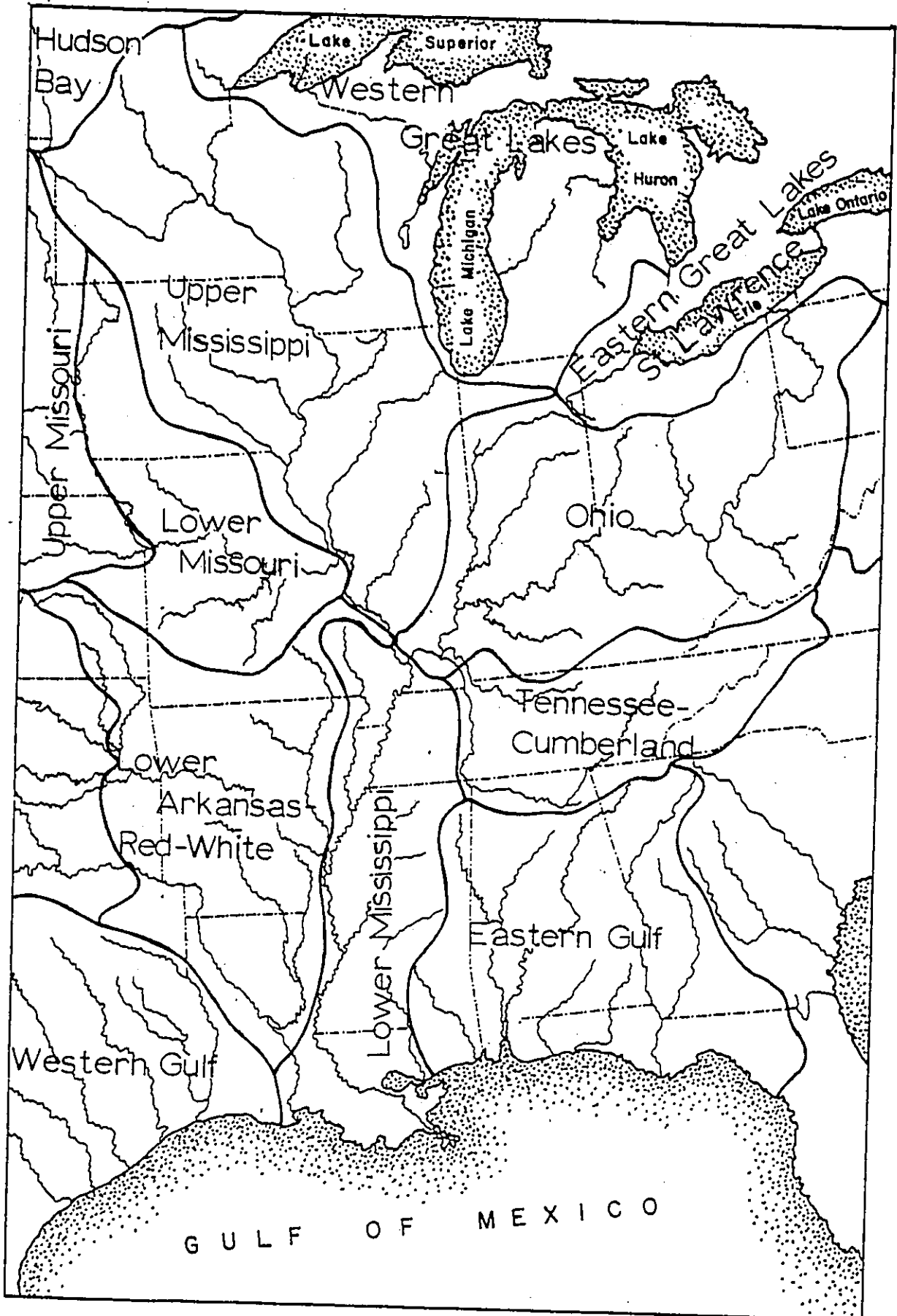


Fig. 32. Distributional records of Ichthyomyzon unicuspis in Canada.

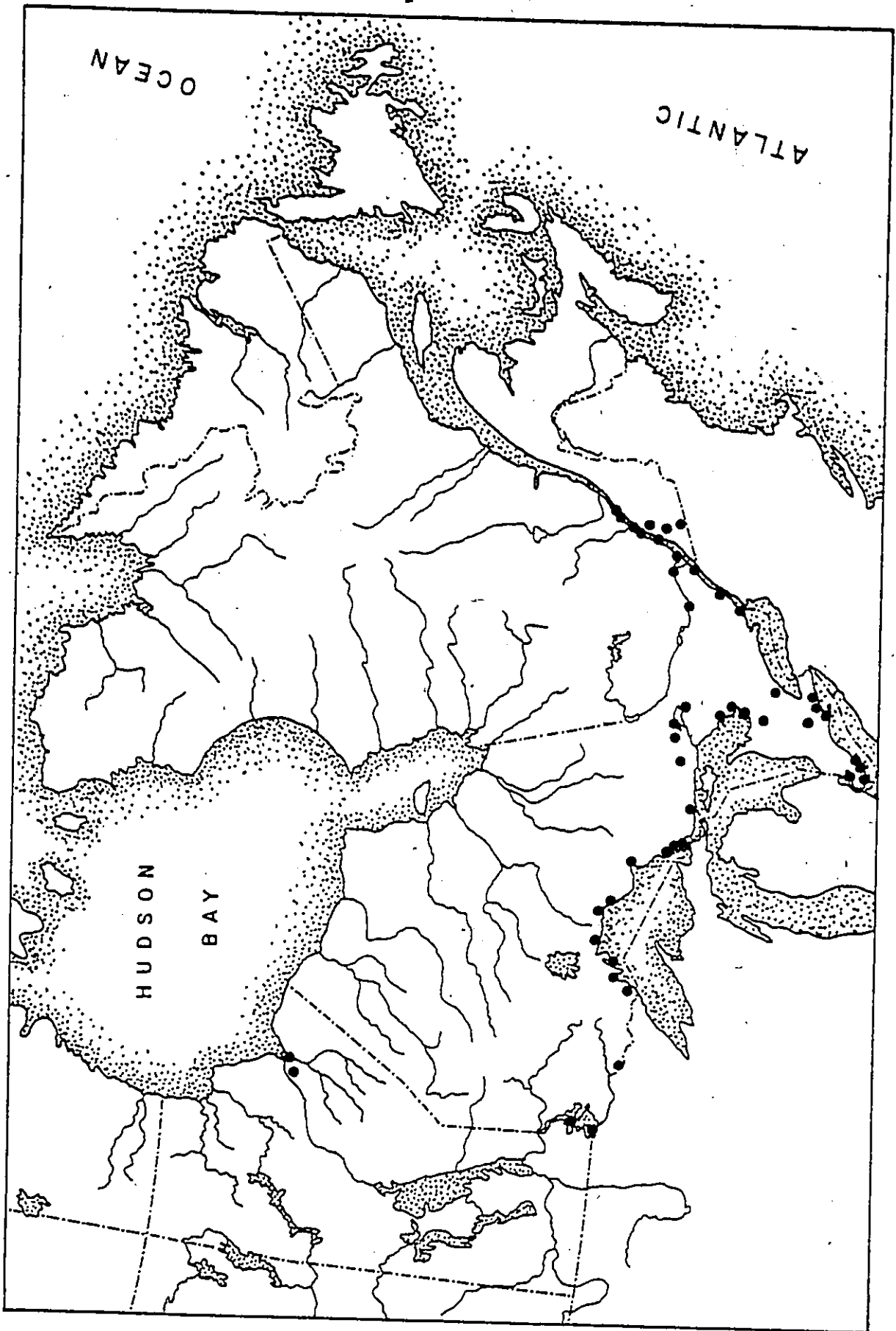


Fig. 33. Distributional records of Ichthyomyzon unicuspis in Eastern United States.

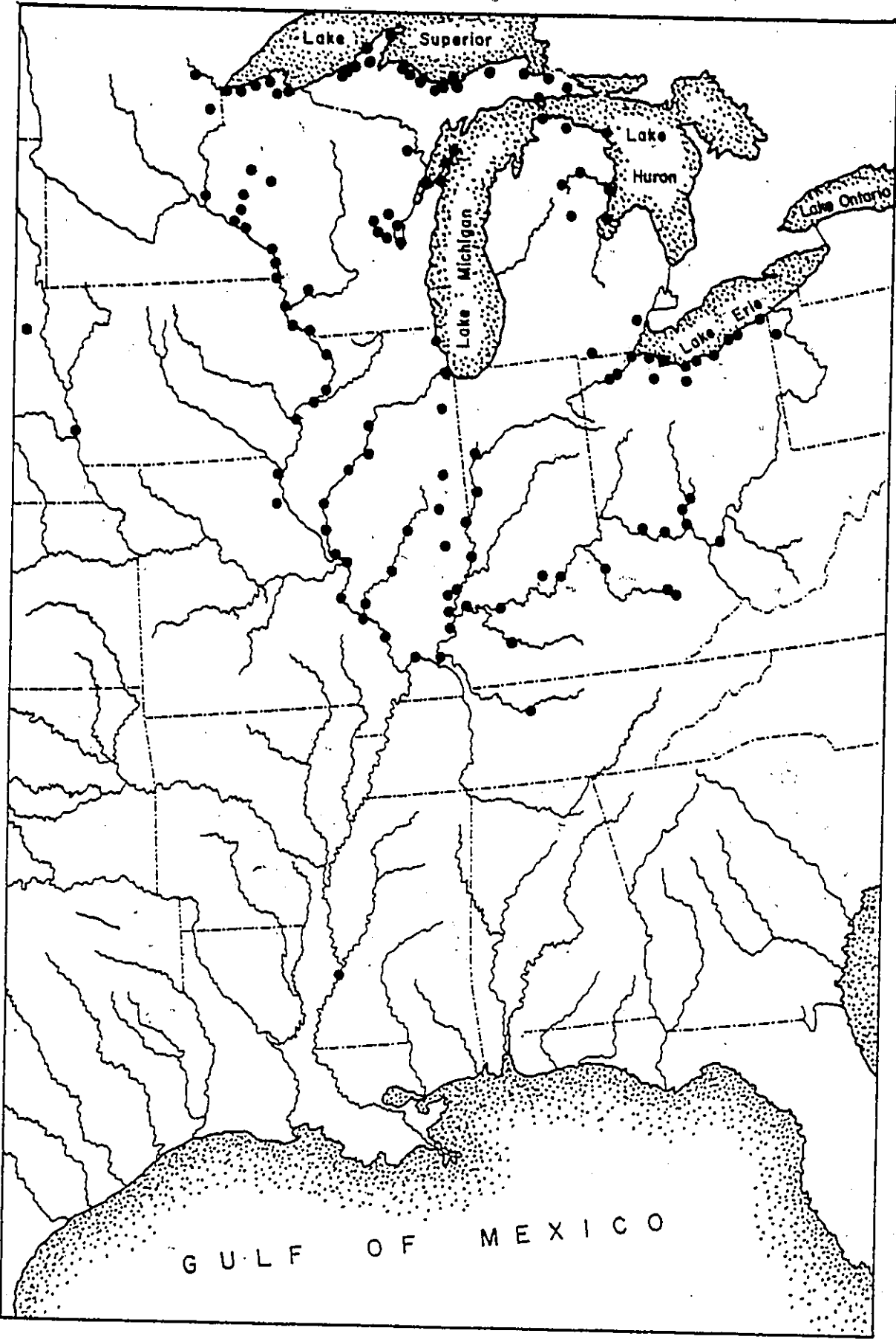
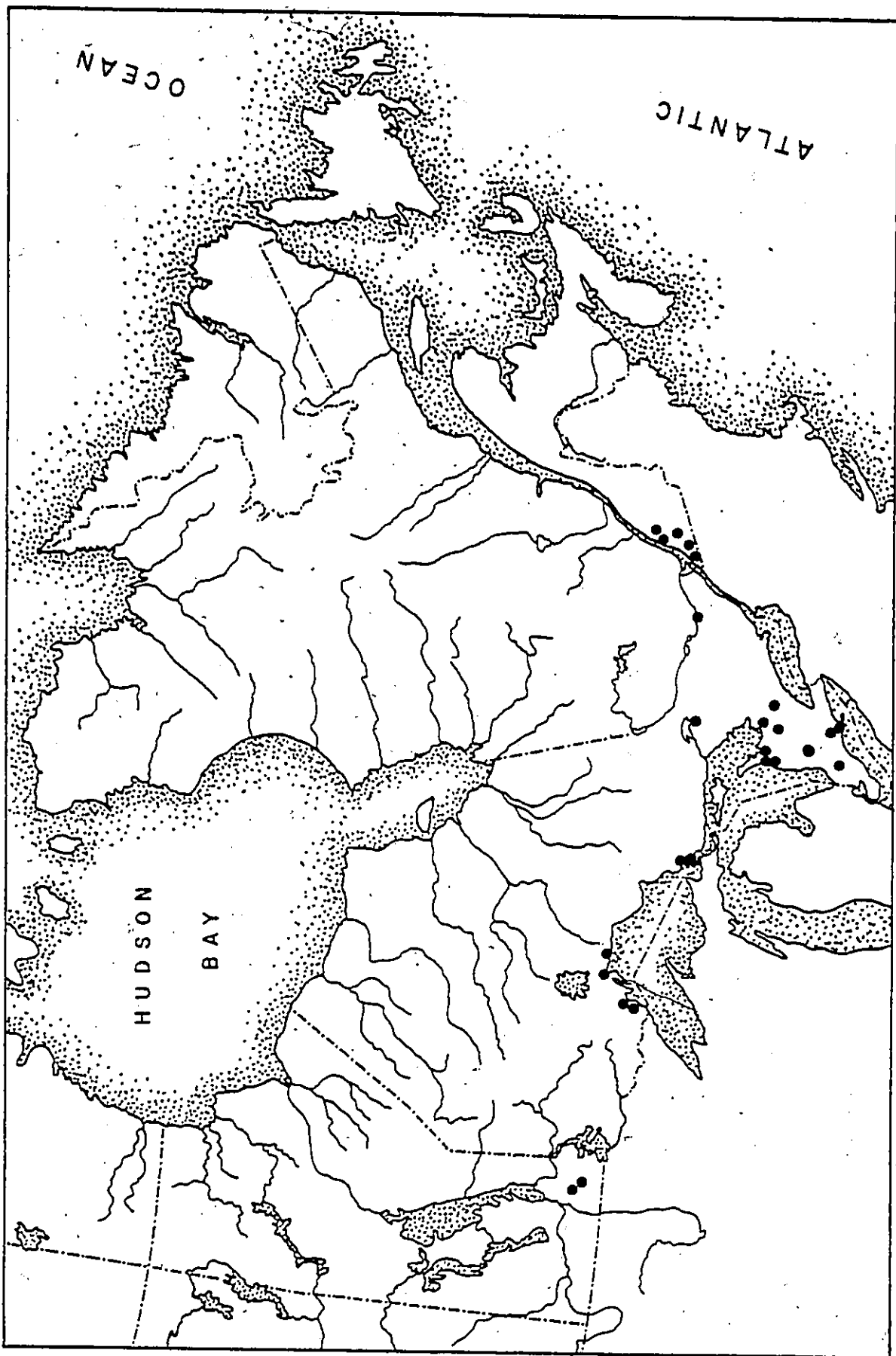
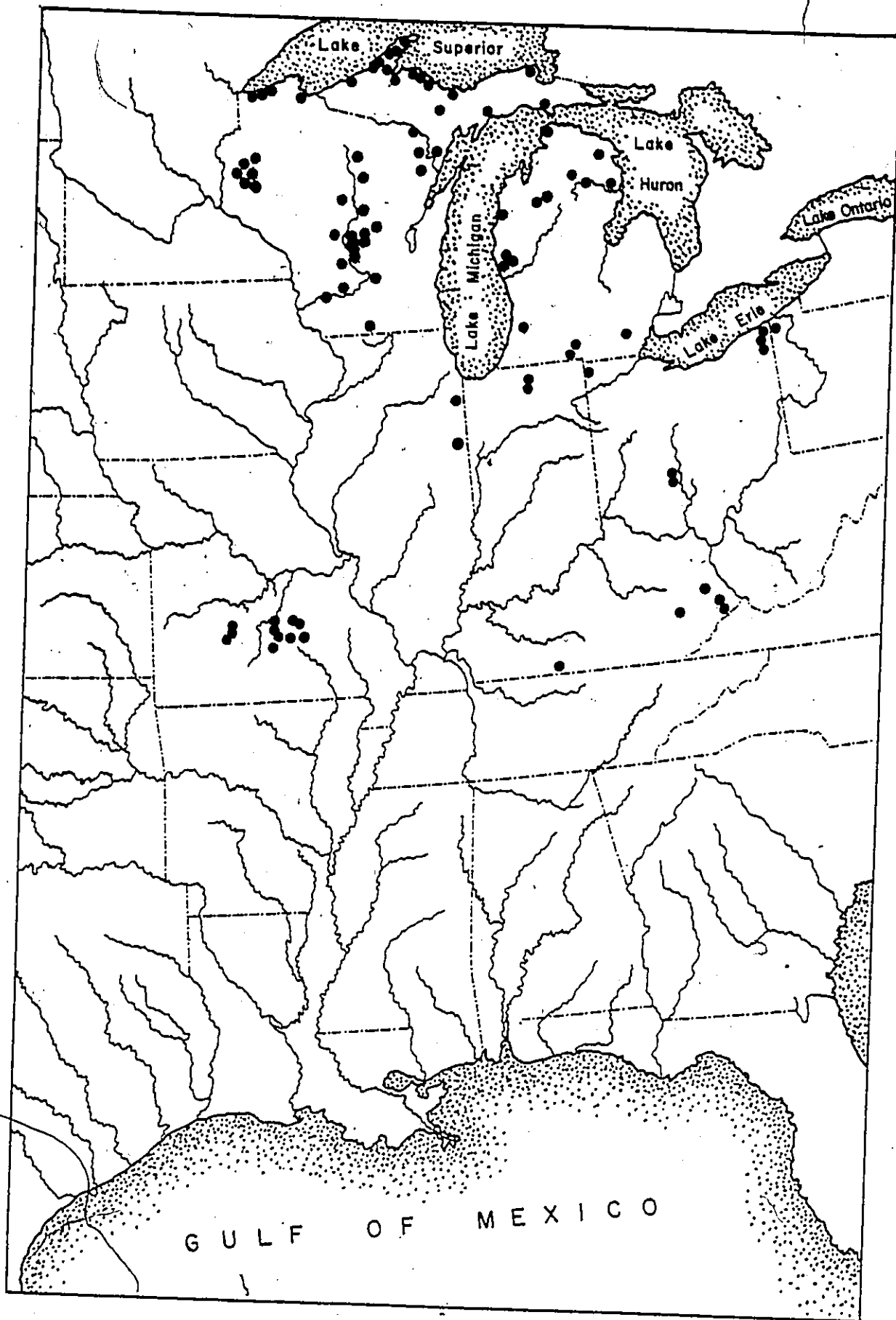


Fig. 34. Distributional records of Ichthyomyzon fossor in Canada.



3

Fig. 35. Distributional records of Ichthyomyzon fossor in Eastern United States.



*Handwritten mark*

Fig. 36. Distributional records of Ichthyomyzon castaneus in Canada.

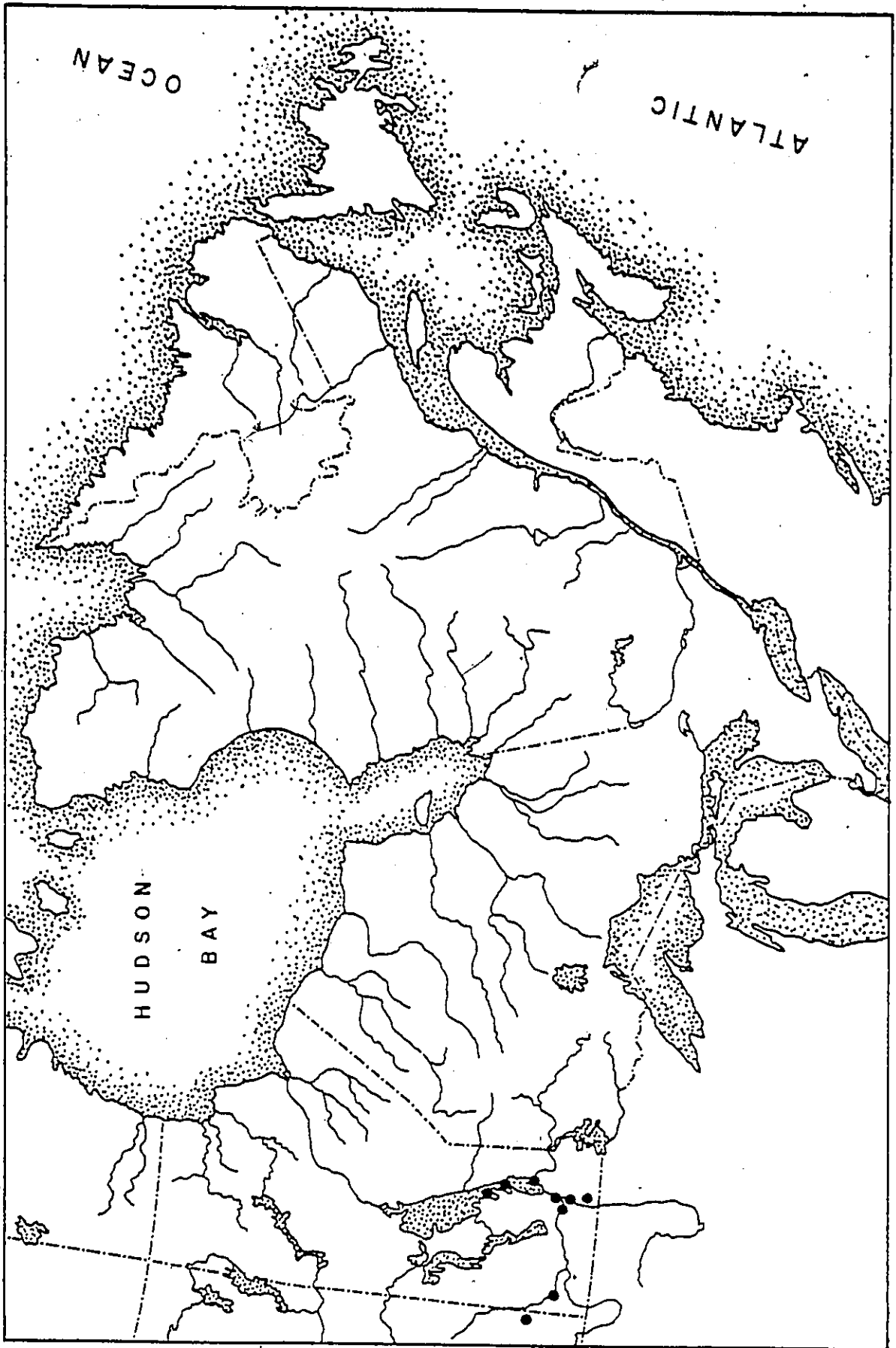


Fig. 37. Distributional records of Ichthyomyzon castaneus in Eastern United States.

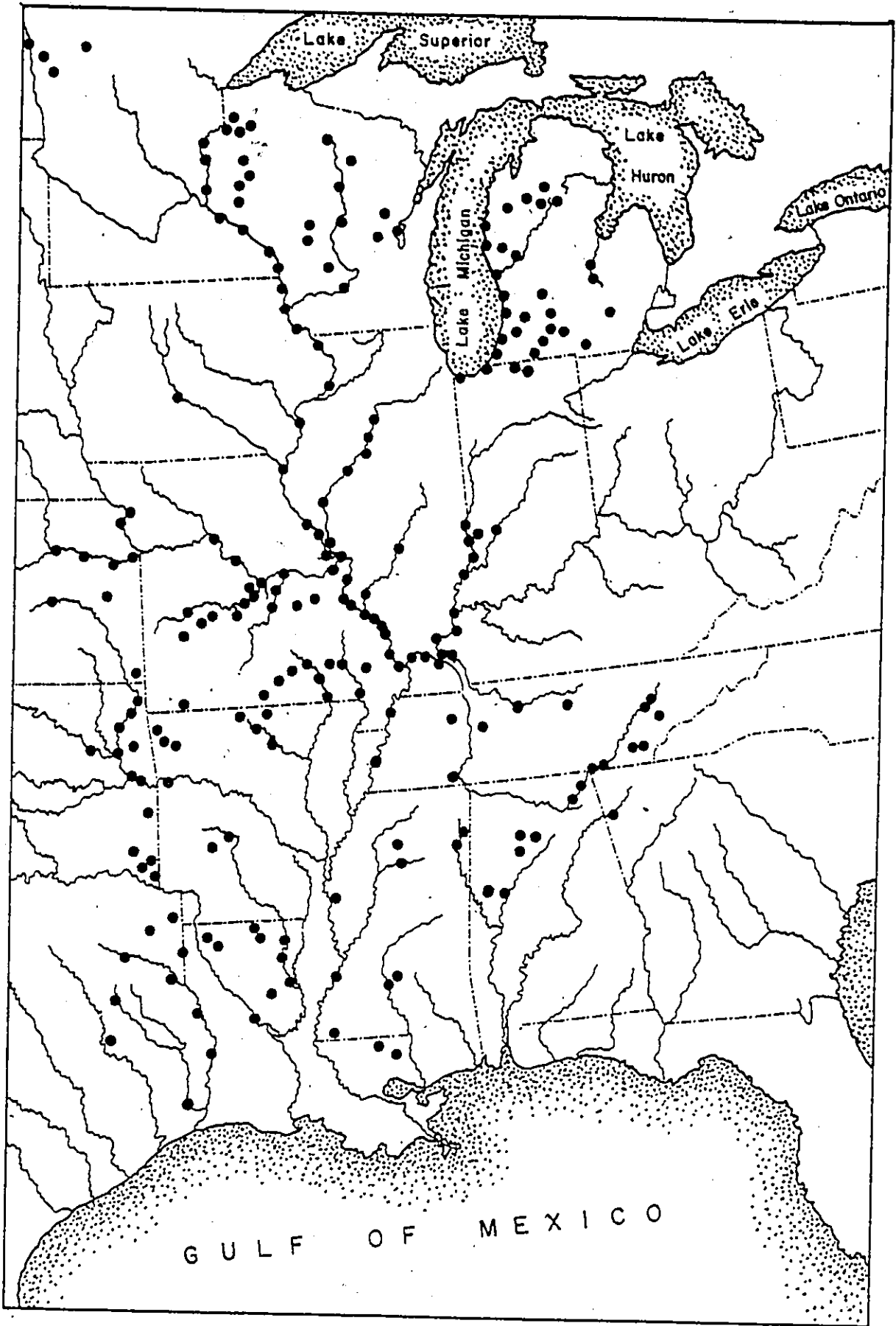


Fig. 38. Distributional records of Ichthyomyzon gagei in Eastern United States (absent from Canada).

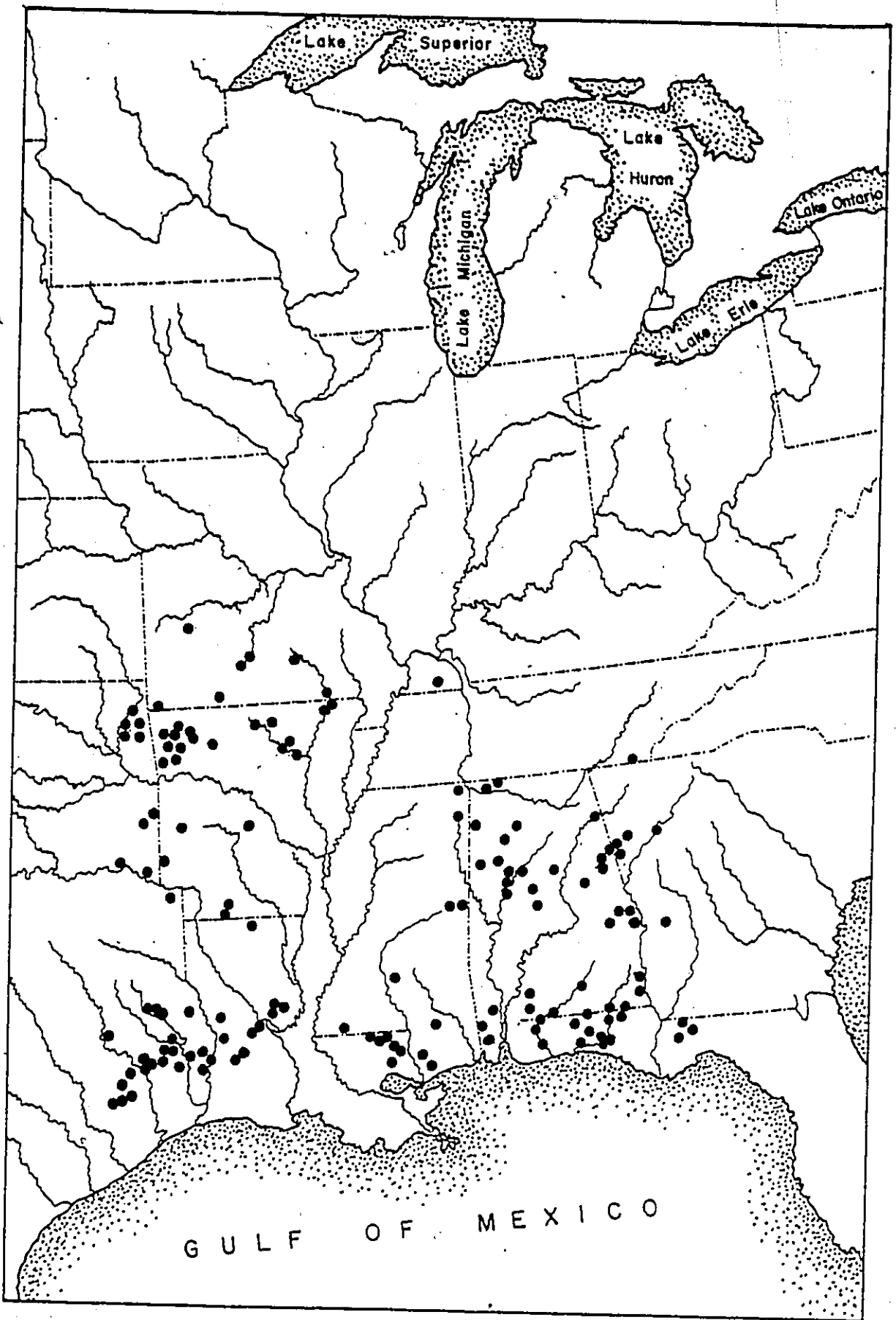


Fig. 39. Distributional records of Ichthyomyzon bdellium in Eastern United States (absent from Canada).

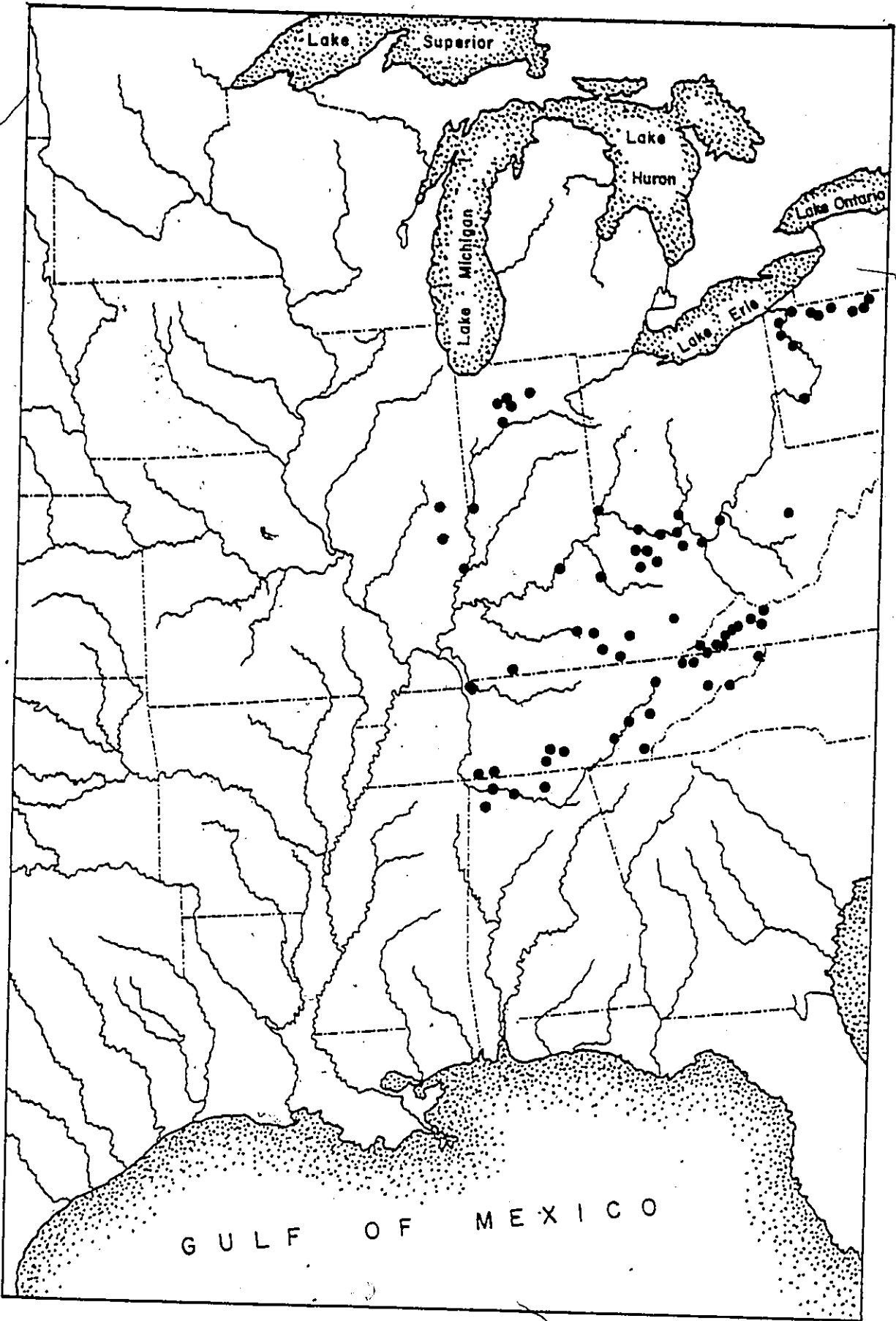
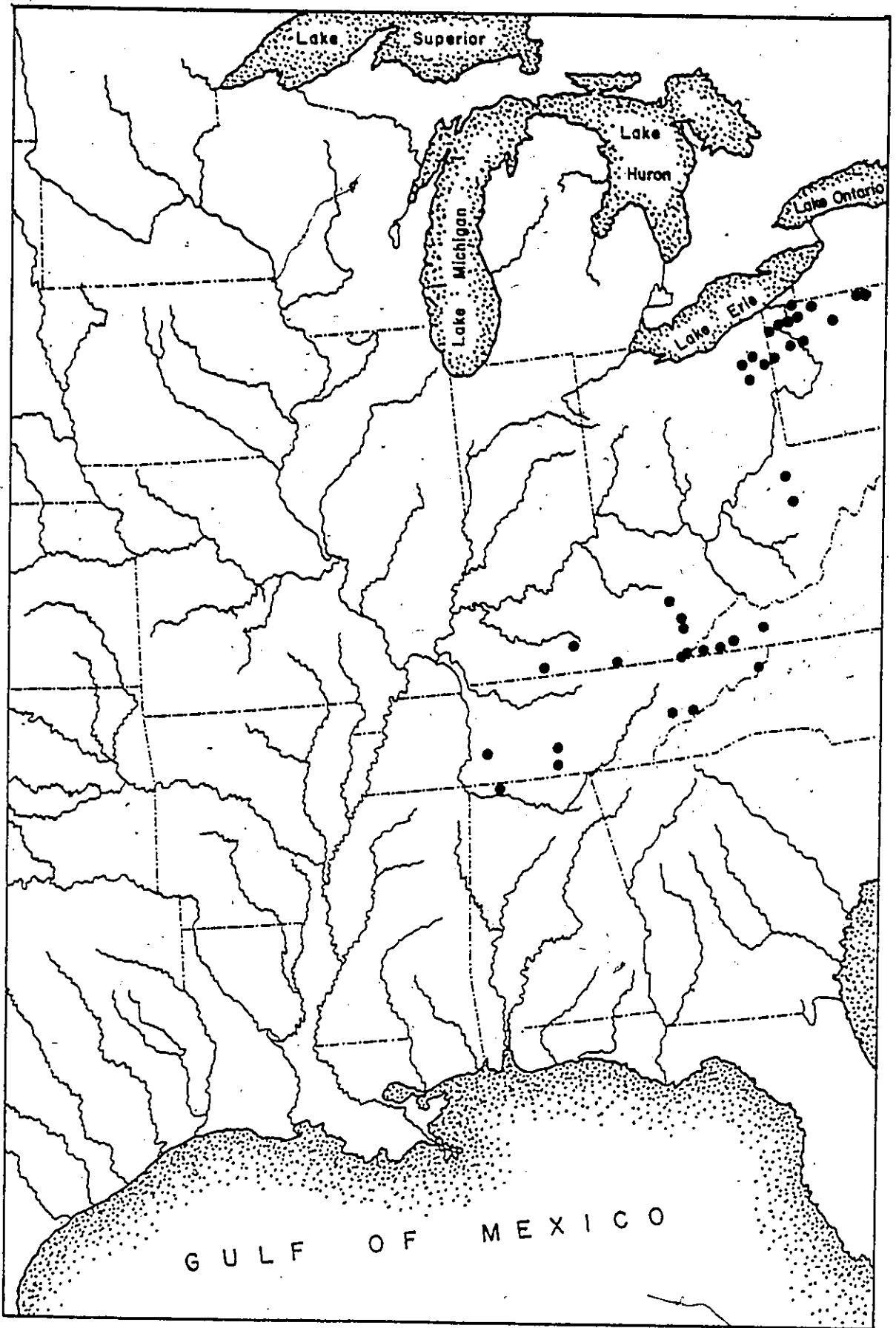


Fig. 40. Distributional records of Ichthyomyzon greeleyi in Eastern United States (absent from Canada).





## Discussion

The geographical distribution of the three parasitic species is largely complementary. However, the range of castaneus does overlap the range of unicuspis in the Hudson Bay, Upper Mississippi and Ohio drainage basins and the range of bdellium in the Ohio and Tennessee-Cumberland drainage basins. The range of unicuspis also overlaps the range of bdellium in the Ohio drainage basin. In sympatry, the species tend to avoid each other by living in different sections of a river or a lake. Thus, in their ecological distribution, they also show mutual avoidance.

The distribution of each of the nonparasitic species is closely related with that of its parasitic stem species, but it is always less extensive in area. The nonparasitic species tend to inhabit small rivers and brooks tributaries to large rivers and lakes where their parasitic counterparts are found. None of the nonparasitic species are found in lotic environments. Fossor and greeleyi both occur in the Ohio drainage basin, but they have never been collected in the same stream system. Greeleyi and gagei are both found in the Tennessee-Cumberland drainage system, but they show a similar mutual avoidance.

The distribution of unicuspis is extended to include the Upper and Lower Missouri drainage basins. In the Upper Mississippi and Ohio drainage basins, the species is now known to reach into Iowa, and West Virginia and Kentucky, respectively. It is still rare and local in Lake Ontario. A lone specimen caught near Vicksburg, Mississippi, was probably washed down the Mississippi River during the spring floods (specimen caught on March 29, 1937).

From the known range of the Eastern Great Lakes-St. Lawrence and Western Great Lakes drainage basins (Hubbs and Trautman, 1937), the

distribution of fossor is now extended to include the Hudson Bay, Ohio and Lower Missouri drainage basins. Hubbs and Trautman (1937) correctly speculated that future collections might extend the range eastward and northward, as fossor has since been reported from tributaries of the St. Lawrence River in Quebec and from Whitemouth River in Manitoba. The range has also been extended southward to Missouri River tributaries, in Missouri. In the other two drainage basins, the range has been extended to the following provinces/states: Western Great Lakes: Wisconsin; Eastern Great Lakes-St. Lawrence: Ontario, Quebec, Ohio, Pennsylvania. The species is absent from Lake Ontario and its tributaries and rare and local in tributaries of Lake Erie.

In the Hudson Bay drainage basin, the range of castaneus has been extended as far west as the Qu'Appelle River, in Saskatchewan. It is still restricted to Lake Michigan in Michigan and Indiana in the Western Great Lake drainage basin. Following the revision of the genus by Hubbs and Trautman (1937), extensive collections have extended the known distribution of the species to the following drainages: Upper and Lower Missouri, Western Gulf of Mexico, Tennessee-Cumberland and Ohio. In three other drainages, the distribution has been extended to the following states: in the Lower-Arkansas-Red-White: Kansas, Missouri, Texas; in the Lower Mississippi: Illinois, Mississippi; in Eastern Gulf of Mexico: Mississippi. It is now known in the Ohio and Tennessee-Cumberland drainage basins; Hubbs and Trautman (1937) had thought that castaneus was represented in the entire Ohio drainage basin by bdellium. It is also found sympatrically with unicuspis in the Upper Mississippi and Ohio drainage basins.

The known distribution of gagei was extended to the following drainage basins: Lower Missouri, Lower Mississippi, Western Gulf of Mexico,

and Tennessee-Cumberland. In the Lower Arkansas-Red-White and Eastern Gulf of Mexico drainage basins, the range has been extended to Missouri and Arkansas, and Mississippi, Georgia and Florida, respectively. It does not occur as far north as northwestern Oklahoma, as speculated by Hubbs and Trautman (1937).

As in the other sympatric stem-satellite pairs, the ranges of bdellium and greeleyi overlap, even though greeleyi is not as widely distributed as its parasitic stem species. Following Hubbs and Trautman (1937) revision of the genus, the range of bdellium was extended in the Ohio drainage basin to Pennsylvania and West Virginia. Hubbs and Trautman (1937) speculated that the species probably ranged to Pennsylvania, but they had no satisfactory records. The distribution of greeleyi, which was thought to be restricted in the Ohio drainage basin to northwestern Pennsylvania, has been extended to Kentucky, Ohio and West Virginia. It is also now known from the Tennessee-Cumberland drainage basin of Alabama, Kentucky, Tennessee and Virginia.

CONCLUSIONS

The main conclusions which can be drawn from this study are the following:

- a- characters were discovered which enabled the separation of the larvae of the six species of Ichthyomyzon for the first time; the pigmentation patterns on the caudal fin and the different sections of the head were the most important;
- b- the study of the morphometric characters showed them to be of no taxonomic value in the separation of the ammocoetes of each sympatric stem-satellite pair;
- c- the trunk length ( $B_7-a$ ) was found to be an important character in separating the adults of the sympatric pairs unicuspis-fossor and castaneus-gagei.
- d- the disc length as a proportion of the branchial length is a good index of parasitism or nonparasitism, and as such was used in the revised key to the adults;
- e- hubbsi was confirmed to be synonymous with greeleyi;
- f- the phenetic analysis showed that there are two branches in the genus, one nonparasitic and the other, parasitic; thus the nonparasitic species gave rise to other nonparasitic species, and the parasitic species gave rise to other parasitic species; Petromyzon marinus was found to be most similar to bdellium;
- g- the geographical distribution of each species has been extended since the study by Hubbs and Trautman (1937); the range of the nonparasitic species has been extended the most as new methods of collecting have been devised, and interest in the biology of lampreys has increased over the years.

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APPENDIX 1

The material examined is listed on the following pages in alphabetical order. Under the heading of the province or state where the specimens were captured, the collection data are given in the following order: alphanumeric tag (for easier reference), number of specimens, stage of development (a- ammocoetes, t- transformed), sex (if applicable), range in total length (mm), collection data, repository museum or institution and catalogue number (if applicable).

Uncatalogued material has been deposited in the collections of the University of Ottawa or at the National Museum of Canada, Ichthyology Section, Ottawa, Ontario. Abbreviations for catalogued material are as follows:

\*: E.L. Cooper's personal collection, Pennsylvania State University

AU: Auburn University, Auburn, Alabama

NMC: National Museums of Canada, Ottawa, Ontario

OSU: Ohio State University, Columbus, Ohio

PSU: Pennsylvania State University, University Park, Pennsylvania

ROM: Royal Ontario Museum, Toronto, Ontario

TAM: Texas Agricultural and Mechanical University, College Station, Texas

TU: Tulane University, New Orleans, Louisiana

UA: University of Alabama, Tuscaloosa, Alabama

UMMZ: University of Michigan, Museum of Zoology, Ann Arbor, Michigan

UWSP: University of Wisconsin, Stevens Point, Wisconsin

Ichthyomyzon bdellium

Pennsylvania

G(VDV) 3356 (1♀, 254 mm): Woodcock Creek, 0.8 km SE Saergerstown, Crawford Co.; May 14, 1977; E.L. Cooper, J. Lanteigne, E. Kott.

G(VDV) 3360, 3364-70 (3♂, 139-148 mm; 5♀, 133-250 mm); Q(B) 3419-21, 3431, 3433, 3435-38, 3440, 3443-44, 3448-50, 3452, 3457-58, 3460-62, 3467 (22a, 110-169 mm): French Creek, at jct. of 6 and 6-19, 3.2 km W Mill Village, Erie Co.; May 14, 1977; E.L. Cooper, J. Lanteigne, E. Kott.

W(Can) 1575-82 (4♂, 167-214 mm; 4♀, 176-210 mm): French Creek, Erie Co.; June 26, 1976; E.L. Cooper. PSU 1549.

\*G(VDV) 3357-59 (3♀, 197-236 mm): Potato Creek, just off rte 46, 4.8 km S East Smethport, McKean Co.; May 26, 1977; E.L. Cooper.

\*G(VDV) 3361-63 (2♂, 125-220 mm; 1♀, 240 mm): Oswayo Creek, at Millport, Potter Co.; May 26, 1977; E.L. Cooper.

\*W(Can) 1589-92 (4♂, 218-247 mm): Allegheny River, at Hemlock Eddy, Warren Co.; June 19, 1973; J. Marancik.

\*W(Can) 1713, 1715-22 (4♂, 130-181 mm; 5♀, 172-187 mm); W(Can) 1703, 1705 (2a, 115-129 mm): Allegheny River, at Kinzua, Warren Co.; August 9, 1960; E.L. Cooper.

W(Can) 1555, 1557-66 (11a, 111-159 mm): Brokenstraw Creek, at mouth of Little Brokenstraw Creek, Warren Co.; July 27, 1965; T. Wohnsiedler, J. Nist.

\*W(VDV) 5176-90 (15♂, 200-259 mm): Brokenstraw Creek, Warren Co.; May 24, 1965; E.L. Cooper, J.A. Bocardy, C.C. Wagner.

Ichthyomyzon castaneus

Manitoba

G 670, 672-73 (1♂, 124 mm; 2♀, 128-261 mm): exact locality unknown;  
October 30, 1951.

W(Can) 1774 (1a, 152 mm): Rat River, 9.6 km upstream from St. Malo dam;  
no collection date; V. Gyselman. NMC 77-1768.

Michigan

G 700, 702-04, 708-27, 730 (16♂, 91-127 mm; 9♀, 89-130 mm): Manistee  
River, Kalkaska Co.; June 17 and 22, 1960; J.D. Hall.

B(Can) 1197 (1♀, 224 mm): Black Lake, Ottawa Co.; March 1, 1929;  
J. Metzelaar.

Missouri

W(Can) 1173 (1a, 140 mm): White River, between Shell Knob and Viola,  
Barry Co.; September 2-10, 1948; E.M. Lowry.

W(Can) 1170 (1a, 125 mm): Black River, 4.8 km N Poplar Bluff, Butler Co.;  
July 25, 1950; C. Purkett.

G 677, Q (J) 728-29 (2♂, 166-184 mm; 1♀, 195 mm): Sac River, Cedar Co.;  
May 20-23, 1951; P.E. Robinson.

W(Can) 1174 (1a, 135 mm): Upper Black River, near Lesterville, Reynolds  
Co.; October 12-15, 1948; E.M. Lowry.

W(Can) 1180 (1a, 123 mm): Current River, 2.4 km SW Doniphan, Ripley Co.;  
April 24-26, 1950; M.H. Patriarche.

Q(S) 1741 (1a, 128 mm): Current River, at Powdermill Ferry, Shannon Co.;  
July 1-4, 1949; M.H. Patriarche.

W(Can) 1165 (1a, 117 mm): Gasconade River, 0.6 km E Hartville, Wright Co.; September 10-13, 1950; E.M. Lowry.

Wisconsin

W(Can) 1723 (1♀, 185 mm): Prairie River, Lincoln Co.; June 22, 1976; M. Ebbers. UWSP 5373.

W(Can) 1506-15 (10a, 119-165 mm): Prairie River, below Dudley, Lincoln Co.; September 3, 1976; G. and K. Becker. UWSP collection.

W(Can) 1724-26 (3♂, 188-205 mm): Namekagon River, 3.2 km S Hayward (T-Bass Lake), Sawyer Co.; September 19, 1971; M. Kruger. UWSP 3783.

Ichthyomyzon fossor

Manitoba

W(Can) 2210-16 (6♂, 98-134 mm; 1♀, 150 mm): Birch River, tributary of Whitemouth River, at Hadashville; May 13, 1977; J. Jyrkkanen. ROM 34264.

W(Can) 1783-84 (1♂, 100 mm; 1♀, 117 mm): Whitemouth River, 105 km E Winnipeg, 1 km S Prov. Hy. 408; July 14, 1977; H. Smart. NMC 78-0104.

Michigan

G 72-79 (8a, 68-96 mm): Manistee River, Kalkaska Co.; August 6, 1959; J.D. Hall.

Missouri

Q(S) 1716 (1♂, 155 mm): Middle Big Piney River, Pulaski Co.; April 18-19, 1951; P.E. Robinson.

Q(S) 1717-19 (3Q, 130-149 mm): Upper Big Piney River, Texas Co.; April 20-22, 1951; P.E. Robinson.

Q(S) 1710-15 (4Q, 117-135 mm; 2Q, 142 mm): Upper Niangua River, Webster Co.; May 10-16, 1950; P.E. Robinson.

#### Ontario

Q(V) 1800-13, (R) 1498 (7Q, 124-140 mm; 8Q, 122-144 mm): McIntyre River, near Port Arthur and Fort Williams, Thunder Bay District; June 8, 1960; FRB London. NMC 65-125.

Q(V) 1859 (1Q, 118 mm): Nottawasaga River, S of dam near Ypres, Simcoe Co.; May 28, 1958; R. Tiede.

Q(V) 1835 (1Q, 142 mm): July 21, 1958; G(VDV) 2271-73 (2Q, 129-135 mm; 1Q, 142 mm): September 10, 1958; Q(V) 1848, G(VDV) 2270 (2Q, 115-132 mm): September 13, 1958; Nottawasaga River, Simcoe Co.; D. Mason.

W(Can) 5085 (1Q, 158 mm): Pine River, Simcoe Co.; May 26, 1958; D. Mason  
G 103 (1Q, 135 mm), G 91, 93-98, 100-02, 104-05, 131-39, 141-45 (26a, 88-151 mm): Willow Creek, Simcoe Co.; October 27, 1958; R. Tiede.

Q(V) 1822 (1Q, 132 mm), (V) 1816-21, 1838-41 (10a, 79-167 mm): Willow Creek, Simcoe Co.; October 27-28, 1958; R. Tiede, T. Gibbons.

Q(V) 1836-37 (2a, 86-162 mm): outlet of Willow Creek, Simcoe Co.; August 28, 1958; D. Mason.

Q(S) 1934-55 (22a, 76-159 mm): Sauble River; July 3, 1958; D. Mason.

#### Quebec

Q(S) 1725-29, #30 (2Q, 112-126 mm; 4Q, 115-135 mm): Yamaska River, at St. Césaire; May 22, 1948; V.D. Vladykov, R. Lafrance.

Q(S) 1731-32, (R) 4967, DPQ 809 (4Q, 109-126 mm): Yamaska River, at

St. Césaire; May 1949; R. Lafrance.

Wisconsin

W(Can) 1739-42, 1744 (4♂, 136-145 mm; 1♀, 129 mm), 1735-38, 1743 (5a, 136-164 mm): Blake Creek, Waupaca Co.; June 7, 1960; G. Becker. UWSP 1318.

Ichthyomyzon gagei

Alabama

W(Can) 510 (1♀, 90 mm): Beck Creek, 7.2 km N Bradley, Conecuh Co.; January 21, 1968; J.C. Williams, J.C. Wolfe. AU 2811.

W(Can) 905-08 (4♀, 96-101 mm); 904, 909 (2a, 79-111 mm): Escambia River, NE Atmore, Escambia Co.; March 17, 1968; J.C. Williams, F.A. Pagan, C.W. Wade. AU 1082.

Q(S) 1902-06, #6 (6a, 70-84 mm): Crossways Creek, Escambia Co.; May 1, 1949; J.S. Dendy.

W(Can) 1727-28 (2♀, 110-118 mm): Clear Creek, 10.7 air km NNW Berry, Fayette Co.; February 1, 1964; J.C. Hall, J.D. Williams. UWSP 2602.

Q(V) 3379, (J) 726-727, W(Can) 891, 911-13 (4♂, 94-118 mm; 3♀, 108-113 mm): Choctawhatchee Creek, 16 km SW Auburn, Macon Co.; May 1, 1948; Ichthyology class. AU 2841, 2842.

Q(S) 1907-27, (J) 2700-10, 2791-92, 2800-09, W(Can) 1761-64 (48a, 60-147 mm): Choctawhatchee Creek, Macon Co.; June 13-15, 1951; J.S. Dendy, D.C. Scott.

W(Can) 534 (1♂, 112 mm): Unnamed Creek, 4.8 km W Vance, Tuscaloosa Co.; March 29, 1966; W.M. Howell, J.D. Williams. UA 1902.

Florida

W(Can) 1171-72 (2Q, 91-102 mm): Pond Creek, 4.3 km W Milton, Santa Rosa Co.; January 22, 1968; J.D. Williams, J.C. Wolfe. AU 2814.

Georgia

W(Can) 1222 (10, 107 mm): Wircher Creek, 3.2 SW Yorkville, Paulding Co.; April 18, 1964; J.C. Hall, J.D. Williams. AU 1249.

Louisiana

Q(S) 1769 (10, 86 mm), 1783-84 (2a, 111-118 mm): Atchafalaya River, tributary to Bayou Cocodrie, 13.4 km W Bringham, Rapides Co.; April 4, 1952; R.D. Suttus, B. Anderson. TU 3464.

Q(S) 1761 (1a, 94 mm): Big Creek, Grant Co.; January 14, 1950; R.D. Suttus.

Q(S) 1793-99 (7a, 56-102 mm): Big Creek, tributary to Little River, at Fishville, Grant Co.; June 14, 1950; F.R. Cagle. TU 1261.

Missouri

W(Can) 1168-69 (2a, 103-120 mm): Current River, 2.4 km SW Doniphan, Ripley Co.; July 6-12, 1948; E.M. Lowry.

W(Can) 1181 (1a, 122 mm): Current River, E of Eminence, Shannon Co.; September 25-28, 1948; E.M. Lowry.

Texas

W(VDV) 6459-60 (20, 111-117 mm): Bracken Creek, Houston Co.; April 24, 1970; A. Peden, J. Velderman, S. Wehner. NMC 70-387.

Q(S) 1788-92 (30, 97-112 mm; 2Q, 109-129 mm), 1770-79, (R) 1890-99,

(V) 3378 (21a, 100-150 mm): Little Loco Bayou, tributary to Angelina

River, 7.5 km W Nacogdoches, Nacogdoches Co.; April 7, 1952; R.D. Suttkus, B. Anderson. TU 3381.

W(Can) 1001-09 (4♂, 103-119 mm; 5♀, 119-125 mm): Mill Creek, immediately below mouth Mitchill Creek, Newton Co.; March 11, 1974; B.J. Galloway. TAM 0541.

Unknown locality

Q(S) 1764-67, 1800 (5a, 82-148 mm).

Ichthyomyzon greeleyi

Ohio

W(Can) 1519-35 (11♂, 110-129 mm; 3♀, 113-129 mm): Mahoning River, Ravenna Twp., Portage Co.; May 10, 1941; M.B. and M.A. Trautman. OSU 3132.

• Pennsylvania

G(VDV) 3374 (1♂, 140 mm): Woodcock Creek, 0.8 km SE Saengerstown, Crawford Co.; May 14, 1977; E.L. Cooper, J. Lanteigne, E. Kott.

\*G(VDV) 3375 (1♂, 140 mm): Muddy Creek, tributary to French Creek, at Little Cooley, Crawford Co.; May 24, 1977; E.L. Cooper.

G(VDV) 3377-78 (2♂, 140-143 mm), Q(B) 3428-30, 3432, 3434, 3439, 3441-42, 3445-47, 3451, 3453-56, 3459, 3463-66 (21a, 110-160 mm): French Creek, at jct. of 6 and 6-19, 3.2 km W Mill Village, Erie Co.; May 14, 1977; E.L. Cooper, J. Lanteigne, E. Kott.

W(Can) 1593-1600 (3♂, 119-124 mm; 5♀, 127-138 mm): W branch French Creek, Erie Co.; May 22, 1975; E.L. Cooper. PSU 1529.

W(Can) 1583-88 (4♂, 135-158 mm; 2♀, 155-165 mm): Little Neshannock Creek,

Lawrence Co.; May 14, 1975; E.L. Cooper. PSU 1530.

Q(S) 1743-45 (2♂, 118-127 mm; 1♀, 124 mm): Little Neshannock Creek,  
Mercer Co.; May 26, 1935; E.C. Raney. UMMZ 108111 (paratypes).

\*G(VDV) 3372-73 (1♂, 137 mm; 1♀, 124 mm): Oswayo Creek, at Millport and  
Coneville, Potter Co.; May 26, 1977; E.L. Cooper.

W(Can) 1567-72 (2♂, 132-134 mm; 4♀, 118-132 mm): Oswayo Creek, Potter  
Co.; May 30, 1975; E.L. Cooper. - PSU 1521.

W(Can) 1702, 1704, 1706-07 (4a, 113-138 mm): Allegheny River, near Kinzua,  
Warren Co.; August 9, 1960; E.L. Cooper.

Q(S) 1898 (1a, 118 mm), 1899 (1♂, 131 mm): French Creek, at Wattsburg,  
Erie Co.; September 19, 1931; J.R. Greeley.

#### Tennessee

G 678-79, #5 (1♂, 137 mm; 3♀, 145-158 mm): Duck River, at Manchester,  
Coffee Co.; May 7, 1950; G.Gentry.

#### Ichthyomyzon unicuspis

#### Manitoba

G 671, W(Can) 2221-23, Q(B) 3837 (4♂, 112-233 mm; 1♀, 270 mm): no  
collection data.

#### Ontario

W(Can) 2218 (1♂, 117 mm): Ottawa River, at Ottawa, Ottawa-Carleton  
Reg. Mun.; 1927; G. White. NMC 58-251.

W(Can) 1775-78 (4♂, 85-146 mm): Lower Duck Island, Ottawa River, at  
Ottawa, Ottawa-Carleton Reg. Mun.; July 1977; J.M. Hanson.

Y(Can) 848-55, 857-60 (12a, 90-126 mm): Upper Duck Island, Ottawa River, at Ottawa, Ottawa-Carleton Reg. Mun.; June 4, 1979; J. Lanteigne, J.M. Hanson.

Y(Can) 861-900, 1001-20 (60a, 73-138 mm): Upper and Lower Duck Islands, Ottawa River, at Ottawa, Ottawa-Carleton Reg. Mun.; June 7, 1979; J. Lanteigne, J.M. Hanson.

W(Can) 1789-1800 (50, 112-172 mm; 70, 115-151 mm): Lake-of-the-Woods, 27.2 km N Rainy River; July 1970; C.G. Gruchy, T.A. Willock. NMC 70-222.

Q(S) 3477-78 (20, 127-160 mm): Nottawasaga River; June 20, 1961; FRB London. NMC 65-114.

G 140 (10, 131 mm): Willow Creek, Simcoe Co.; October 27, 1958; C. Tiede.

Q(B) 3469 (10, 185 mm): McIntyre River, Thunder Bay District; June 11, 1957; J.C. Hall. NMC 65-111.

#### Quebec

W(Can) 1073, 2219 (20, 100-144 mm): Kettle Island Bay, Ottawa River, at Hull, Hull Co.; June 19 and July 18, 1978; J.M. Hanson.

Q(S) 1901 (10, 159 mm): Kettle Island Bay, Ottawa River, at Hull, Hull Co.; August 10, 1973; P. Rubec.

Q(S) 1862, WA 12701 (10, 145 mm; 10, 106 mm): Ottawa River, at Hull, Hull Co.; June 24, 1976, and July 29, 1971; A. Armstrong.

W(Can) 1779 (10, 245 mm): Brewery Creek, tributary to Ottawa River, at Hull, Hull Co.; June 24, 1976; J.M. Hanson.

Q(B) 3479 (10, 142 mm): Ottawa River, at Papineauville, Papineau Co.; September 1963; R.L. Séguin. NMC 65-3

Q(S) 1751-60 (30, 92-112 mm; 70, 95-130 mm): St. Lawrence River, at St. Pierre-les-Becquets; June 15, 1961; F. Lefebvre.

Appendix 2. Tables 1-9 summarize the total length and body proportions for the males, the females and the total sample for each species of adult Ichthyomyzon.

Table 1. Morphometric characters (in percentages) of the males, the females and the total sample of prespawning I. fossor. Sample size, range and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	6	109-135	125.33 $\pm$ 8.78
	F	2	135-142	138.50 $\pm$ 44.61
	T	8	109-142	128.63 $\pm$ 9.23
*Head length	M	6	7.58-9.09	8.49 $\pm$ 0.49
	F	2	7.40-7.75	7.58 $\pm$ 2.23
	T	8	7.40-9.09	8.20 $\pm$ 0.54
*Branchial length	M	6	8.70-10.08	9.29 $\pm$ 0.40
	F	2	9.63-10.56	10.10 $\pm$ 5.93
	T	8	8.70-10.56	9.49 $\pm$ 0.51
*Trunk length	M	6	47.29-53.03	50.22 $\pm$ 1.57
	F	2	52.11-54.07	53.09 $\pm$ 12.49
	T	8	47.29-54.07	50.94 $\pm$ 1.80
*Tail length	M	6	29.92-33.33	31.69 $\pm$ 1.01
	F	2	28.89-29.58	29.24 $\pm$ 4.40
	T	8	28.89-33.33	31.08 $\pm$ 1.30

Table 1. (cont.)

*Orbit diameter	M	6	1.30-1.55	$1.46 \pm 0.08$
	F	2	1.11-1.41	$1.26 \pm 1.91$
	T	8	1.11-1.55	$1.42 \pm 0.12$
*Disc length	M	6	4.35-5.05	$4.79 \pm 0.23$
	F	2	4.23-4.44	$4.34 \pm 1.34$
	T	8	4.23-5.05	$4.67 \pm 0.27$
**Disc length	M	6	50.00-55.00	$51.53 \pm 1.96$
	F	2	40.00-46.15	$43.08 \pm 39.19$
	T	8	40.00-55.00	$49.42 \pm 3.93$

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 2. Morphometric characters (in percentages) of the males, the females and the total sample of spawning I. fossor. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	30	98-158	126.53 $\pm$ 5.59
	F	21	115-150	132.29 $\pm$ 4.28
	T	51	98-158	129.12 $\pm$ 3.72
*Head length	M	30	8.15-9.92	8.87 $\pm$ 1.47
	F	21	7.58-9.30	8.44 $\pm$ 0.25
	T	51	7.58-9.92	8.71 $\pm$ 0.16
*Branchial length	M	30	9.29-11.34	10.04 $\pm$ 0.20
	F	21	9.09-10.85	9.82 $\pm$ 0.25
	T	51	9.09-11.34	9.95 $\pm$ 0.16
*Trunk length	M	30	46.67-52.63	49.62 $\pm$ 0.56
	F	21	48.06-54.62	51.70 $\pm$ 0.67
	T	51	46.67-54.62	50.48 $\pm$ 0.51
*Tail length	M	30	29.66-33.63	31.65 $\pm$ 0.47
	F	21	27.69-33.71	30.46 $\pm$ 0.65
	T	51	27.69-33.71	31.16 $\pm$ 0.41

Table 2. (cont.)

*Orbit diameter	M	30	1.27-2.04	1.65 ± 0.08
	F	21	1.28-1.74	1.50 ± 0.04
	T	51	1.27-2.04	1.59 ± 0.05
*Disc length	M	30	4.48-6.38	5.31 ± 0.18
	F	21	4.03-5.22	4.64 ± 0.17
	T	51	4.03-6.38	5.03 ± 0.15
**Disc length	M	30	42.86-62.50	52.75 ± 1.97
	F	21	41.38-54.55	47.33 ± 1.94
	T	51	41.38-62.50	50.52 ± 1.56

\*denotes character as a percentage of total length

\*\*denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 3. Morphometric characters (as percentages) of the males, the females and the total sample of feeding I. unicuspis. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	27	85-245	138.37 $\pm$ 15.35
	F	16	95-270	132.25 $\pm$ 21.21
	T	43	85-270	136.09 $\pm$ 11.97
*Head length	M	27	11.45-15.88	13.75 $\pm$ 0.49
	F	16	11.36-14.63	13.06 $\pm$ 0.51
	T	43	11.36-15.88	13.50 $\pm$ 0.36
*Branchial length	M	27	8.80-10.76	9.74 $\pm$ 0.23
	F	16	8.70-10.63	9.41 $\pm$ 0.31
	T	43	8.70-10.76	9.62 $\pm$ 0.18
*Trunk length	M	27	42.35-48.98	46.10 $\pm$ 0.78
	F	16	44.81-49.21	47.25 $\pm$ 0.76
	T	43	42.35- 49.21	46.62 $\pm$ 0.54
*Tail length	M	27	27.68-32.48	30.23 $\pm$ 0.52
	F	16	26.77-32.58	30.16 $\pm$ 0.78
	T	43	26.77-32.58	30.20 $\pm$ 0.42

Table 3. (cont.)

*Orbit diameter	M	27	1.08-2.50	1.76 ± 0.15
	F	16	1.44-2.17	1.77 ± 0.14
	T	43	1.08-2.50	1.76 ± 0.10
*Disc length	M	27	7.94-12.35	10.34 ± 0.55
	F	16	8.73-11.38	9.73 ± 0.35
	T	43	7.94-12.35	10.10 ± 0.37
**Disc length	M	<del>27</del>	78.72-122.73	106.15 ± 4.65
	F	16	91.67-115.79	104.38 ± 4.15
	T	43	78.72-122.73	105.49 ± 3.20

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample




Table 4. Morphometric characters (as percentages) of the males, the females and the total sample of prespawning *I. gagei*. Sample size, range, mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	4	103-119	112.75 $\pm$ 11.35
	F	15	90-129	109.87 $\pm$ 7.41
	T	19	90-129	110.47 $\pm$ 5.88
*Head length	M	4	8.82-10.19	9.34 $\pm$ 0.99
	F	15	8.33-9.90	8.93 $\pm$ 0.27
	T	19	8.33-10.19	8.99 $\pm$ 0.25
*Branchial length	M	4	8.40-9.82	9.23 $\pm$ 1.06
	F	15	8.33-10.00	9.34 $\pm$ 0.27
	T	19	8.33-10.00	9.32 $\pm$ 0.25
*Trunk length	M	4	49.03-55.98	53.20 $\pm$ 4.71
	F	15	51.25-54.20	52.70 $\pm$ 0.54
	T	19	49.03-55.98	52.81 $\pm$ 0.72
*Tail length	M	4	25.64-30.10	28.22 $\pm$ 2.97
	F	15	27.47-31.01	28.92 $\pm$ 0.51
	T	19	25.64-31.01	28.77 $\pm$ 0.55

Table 4. (cont.)

*Orbit diameter	M	4	1.34-1.94	1.67 ± 0.40
	F	15	1.36-1.68	1.55 ± 0.07
	T	19	1.34-1.94	1.55 ± 0.06
*Disc length	M	4	4.91-5.83	5.21 ± 0.57
	F	15	3.92-5.24	4.56 ± 0.24
	T	19	3.92-5.83	4.70 ± 0.25
**Disc length	M	4	50.00-60.00	56.79 ± 7.51
	F	15	40.00-54.55	48.21 ± 2.73
	T	19	40.00-60.00	50.01 ± 2.87

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total length

Table 5. Morphometric characters (as percentages) of the males, the females and the total sample of spawning I. gagei. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	12	86-118	106.25 $\pm$ 6.13
	F	4	108-113	109.50 $\pm$ 3.79
	T	16	86-118	107.06 $\pm$ 4.50
*Head length	M	12	9.88-11.22	10.39 $\pm$ 0.23
	F	4	9.17-11.11	10.05 $\pm$ 1.30
	T	16	9.17-11.22	10.31 $\pm$ 0.27
*Branchial length	M	12	8.93-10.68	9.98 $\pm$ 0.33
	F	4	9.63-11.11	10.39 $\pm$ 1.08
	T	16	8.93-11.11	10.03 $\pm$ 0.29
*Trunk length	M	12	47.01-50.58	48.75 $\pm$ 0.71
	F	4	51.38-51.85	51.49 $\pm$ 0.39
	T	16	47.01-51.85	49.43 $\pm$ 0.83
*Tail length	M	12	29.07-33.33	30.89 $\pm$ 0.78
	F	4	26.85-29.82	28.08 $\pm$ 2.09
	T	16	26.85-33.33	30.18 $\pm$ 0.93

Table 5. (cont.)

*Orbit diameter	M	12	1.34-2.06	1.69 ± 0.16
	F	4	1.33-1.39	1.37 ± 0.05
	T	16	<del>1.33-2.06</del>	1.61 ± 0.14
*Disc length	M	12	5.80-6.54	6.19 ± 0.17
	F	4	5.05-6.02	5.60 ± 0.65
	T	16	5.05-6.54	6.04 ± 0.21
**Disc length	M	12	55.56-63.64	61.23 ± 1.88
	F	4	50.00-59.09	55.14 ± 7.42
	T	16	50.00-63.64	59.71 ± 2.27

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 6. Morphometric characters (as percentages) of the males, the females and the total sample of feeding I. castaneus. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	22	91-205	131.46 $\pm$ 14.41
	F	14	89-261	142.07 $\pm$ 29.70
	T	36	89-261	135.86 $\pm$ 13.85
*Head length	M	22	11.45-15.25	13.83 $\pm$ 0.37
	F	14	11.49-15.51	13.75 $\pm$ 0.78
	T	36	11.45-15.51	13.80 $\pm$ 0.36
*Branchial length	M	22	8.43-10.24	9.24 $\pm$ 0.17
	F	14	8.56-10.27	9.33 $\pm$ 0.30
	T	36	8.43-10.27	9.28 $\pm$ 0.15
*Trunk length	M	22	44.35-52.89	48.46 $\pm$ 0.87
	F	14	46.07-51.89	48.91 $\pm$ 1.08
	T	36	44.35-52.89	48.64 $\pm$ 0.65
*Tail length	M	22	23.89-32.26	28.22 $\pm$ 0.85
	F	14	25.23-34.38	28.33 $\pm$ 1.25
	T	36	23.89-34.38	28.26 $\pm$ 0.67

Table 6. (cont.)

*Orbit diameter	M	22	1.30-2.42	1.74 ± 0.10
	F	14	0.77-1.80	1.54 ± 0.15
	T	36	0.77-2.42	1.66 ± 0.09
*Disc length	M	22	9.04-11.02	10.03 ± 0.25
	F	14	8.48-11.64	10.11 ± 0.63
	T	36	8.48-11.64	10.06 ± 0.27
**Disc length	M	22	91.67-123.81	108.69 ± 3.33
	F	14	86.36-122.22	108.76 ± 8.45
	T	36	86.36-123.81	108.72 ± 3.60

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 7. Morphometric characters (as percentages) of the males, the females and the total sample of spawning *I. greeleyi*. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	28	110-158	128.93 $\pm$ 4.54
	F	20	113-165	133.45 $\pm$ 6.91
	T	48	110-165	131.06 $\pm$ 3.81
*Head length	M	28	9.48-11.45	10.68 $\pm$ 0.23
	F	20	8.07-10.77	9.65 $\pm$ 0.34
	T	48	8.07-11.45	10.25 $\pm$ 0.24
*Branchial length	M	28	8.87-10.48	9.74 $\pm$ 0.16
	F	20	8.90-10.61	9.75 $\pm$ 0.25
	T	48	8.87-10.61	9.74 $\pm$ 0.13
*Trunk length	M	28	46.61-52.27	49.80 $\pm$ 0.47
	F	20	50.63-55.00	52.74 $\pm$ 0.52
	T	48	46.61-55.00	51.02 $\pm$ 0.54
*Tail length	M	28	28.33-33.90	30.16 $\pm$ 0.41
	F	20	25.71-31.01	28.18 $\pm$ 0.57
	T	48	25.71-33.90	29.33 $\pm$ 0.43

Table 7. (cont.)

*Orbit diameter	M	28	1.10-1.82	1.55 ± 0.08
	F	20	0.85-1.64	1.30 ± 0.11
	T	48	0.85-1.82	1.44 ± 0.07
*Disc length	M	28	5.65-7.86	6.82 ± 0.23
	F	20	4.03-6.65	5.78 ± 0.27
	T	48	4.03-7.86	6.39 ± 0.23
**Disc length	M	28	58.33-78.57	69.93 ± 2.42
	F	20	38.46-71.43	59.61 ± 3.81
	T	48	38.46-78.57	65.63 ± 2.54

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 8. Morphometric characters (as percentages) of the males, the females and the total sample of feeding I. bdellium. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	12	125-214	162.00 $\pm$ 18.0
	F	13	133-210	172.77 $\pm$ 11.85
	T	25	125-214	167.60 $\pm$ 10.03
*Head length	M	12	10.38-13.51	12.01 $\pm$ 0.48
	F	13	10.48-13.97	12.40 $\pm$ 0.57
	T	25	10.38-13.97	12.15 $\pm$ 0.38
*Branchial length	M	12	8.29-9.23	8.65 $\pm$ 0.18
	F	13	7.62-9.46	8.60 $\pm$ 0.26
	T	25	7.62-9.46	8.62 $\pm$ 0.15
*Trunk length	M	12	51.33-53.91	52.53 $\pm$ 0.66
	F	13	50.83-54.29	52.59 $\pm$ 0.59
	T	25	50.83-54.29	52.56 $\pm$ 0.40
*Tail length	M	12	26.01-28.42	27.09 $\pm$ 0.64
	F	13	25.14-28.06	26.56 $\pm$ 0.15
	T	25	25.14-28.42	26.81 $\pm$ 0.41

Table 8. (cont.)

*Orbit diameter	M	12	1.20-1.80	$1.51 \pm 0.11$
	F	13	1.13-1.74	$1.42 \pm 0.13$
	T	25	1.13-1.80	$1.46 \pm 0.08$
*Disc length	M	12	6.92-9.46	$8.28 \pm 0.40$
	F	13	7.62-9.03	$8.35 \pm 0.22$
	T	25	6.92-9.46	$8.32 \pm 0.21$
**Disc length	M	12	75.00-107.69	$95.73 \pm 5.02$
	F	13	85.71-104.00	$97.21 \pm 3.18$
	T	25	75.00-107.69	$96.50 \pm 2.71$

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample

Table 9. Morphometric characters (as percentages) of the males, the females and the total sample of spawning I. bdellium. Sample size, range, and mean and its 95% confidence interval are included.

Character		N	Range	Mean $\pm$ 95% C.I.
Total length	M	20	200-259	224.80 $\pm$ 6.66
	F	6	197-254	232.58 $\pm$ 22.55
	T	26	197-259	226.58 $\pm$ 6.47
*Head length	M	20	10.93-13.59	11.97 $\pm$ 0.29
	F	6	10.63-11.81	11.36 $\pm$ 0.49
	T	26	10.63-13.59	11.83 $\pm$ 0.26
*Branchial length	M	20	8.77-10.62	9.67 $\pm$ 0.25
	F	6	8.33-10.17	9.48 $\pm$ 0.72
	T	26	8.33-10.62	9.63 $\pm$ 0.23
*Trunk length	M	20	47.33-51.09	49.51 $\pm$ 0.54
	F	6	50.39-53.05	51.82 $\pm$ 1.26
	T	26	47.33-53.05	50.04 $\pm$ 0.62
*Tail length	M	20	27.07-31.17	28.86 $\pm$ 0.54
	F	6	26.12-28.75	27.49 $\pm$ 1.16
	T	26	26.12-31.17	28.54 $\pm$ 0.51

Table 9. (cont.)

*Orbit diameter	M	20	> 1.13-1.77	1.42 ± 0.06
	F	6	1.18-1.52	1.37 ± 0.13
	T	26	1.13-1.77	1.41 ± 0.06
*Disc length	M	20	7.59-8.85	8.13 ± 0.17
	F	6	7.08-8.27	7.70 ± 0.54
	T	26	7.08-8.85	8.03 ± 0.17
**Disc length	M	20	78.26-94.60	84.32 ± 1.55
	F	6	72.09-86.67	81.51 ± 5.94
	T	26	72.09-94.60	83.67 ± 1.63

\* denotes character as a percentage of total length

\*\* denotes character as a percentage of branchial length

M: male; F: female; T: total sample