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THE UNIVERSITY OF ALBERTA

SYSTEMATICS, VARIATION, AND ZOOGEOGRAPHY OF TWO NORTH AMERICAN CYPRINID FISHES

by

ALAN W. WELLS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Systematics, variation, and zoogeography of two North American cyprinid fishes submitted by Alan W. Wells in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Zoology.

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DATE 4 October 1978

ABSTRACT

Systematics, geographic variation, and postglacial dispersal patterns are examined in Hybognathus hankinsoni (brassy minnow) and Couesius plumbeus (lake chub).

Morphological differences between Missouri River basin and Great Lakes basin H. hankinsoni were discovered. Northern Alberta and British Columbia populations most closely resemble those from the Great Lakes region. It is postulated that the Missouri form originated in the "Preglacial Plains Stream" and survived glaciation in the Missouri basin. The form presently found in the Great Lakes region most likely originated in the pre-Pleistocene Laurentian River system and/or Missouri River system and survived glaciation in the upper Mississippi basin. Dispersal into northern Alberta and British Columbia was probably via Campbell phase Lake Agassiz and glacial Lake Peace. Taxonomic recognition of the two forms does not seem warranted.

Existence of three morphological forms of C. plumbeus is confirmed - an upper Columbia River basin "greeni", a Missouri basin "dissimilis", and an eastern and Great Lakes "plumbeus". All three forms intergrade extensively throughout the northwest portion of the geographic range, while in the Lake Superior region "dissimilis" and "plumbeus" seem to be good biological species.

Morphological differences between the "dissimilis" and "plumbeus" forms appear related to ecological differences. The "greeni" form most likely originated in the Columbia River basin, while the "dissimilis" form probably originated in the Missouri River basin. The "plumbeus" form may have originated in the pre-Pleistocene Laurentian River system and survived glaciation in an eastern lower Great Lakes refugium.

Phenetic and cladistic analyses suggest that the genus Couesius is most closely related to the nominal genus Margariscus and it is suggested that they be combined into a single genus, Couesius. Proposals to unite Couesius with Hybopsis or Semotilus are not supported. Evidence indicating possible hybridization between Couesius plumbeus and Semotilus (Margariscus) margarita is presented.

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INTRODUCTION

Investigation into postglacial dispersal of northern North American fishes, beginning with Greene (1935) and Radforth (1944), continues to be an active area of scientific study (McAllister and Lindsey, 1961; McPhail, 1961, 1963; Olund and Cross, 1961; Nelson, 1969; Lindsey, Clayton, and Franzin, 1970; McPhail and Lindsey, 1970; Lindsey and Franzin, 1972; Bodaly and Lindsey, 1977; Franzin and Clayton, 1977; and many others). The primary method of reconstructing past dispersal routes in groups with a poor fossil record, such as the North American minnows, is to: 1) assess similarities between populations from different localities, under the assumption that morphologically similar groups have had similar evolutionary and dispersal histories, 2) examine present distribution patterns and 3) consider evidence of past geologic and climatic events. Recent advances in assessing geographic similarities (see Sneath and Sokal, 1973; Thorpe, 1976), improved computer technology, and additional distribution information have made the reexamination of some of the more problematical species practical and worthwhile.

Hybognathus hankinsoni, thought to be restricted to northeastern North America, has generally been considered to be derived from a Missouri - Mississippi Wisconsin refugium, but discoveries of this species in the lower and upper Fraser valley, and more recently in Musreau Lake and the

Athabasca River system, have led to speculations on additional refugia. However, virtually no information on geographic variation was available to lend credence to these speculations.

Zoogeographic theories on Couesius plumbeus, a common and widepspread North American minnow, have been contradictory (Underhill, 1957; McPhail, 1963; Brown, 1969). Although multiple glacial refugia have been postulated, again there has been little information on geographic variation to support these theories.

Investigations of these two species are reported in a series of four articles:

1. Variation and zoogeography of the brassy minnow, Hybognathus hankinsoni.
2. Variation and zoogeography of the lake chub, Couesius plumbeus.
3. Relationship of Couesius to certain other North American cyprinid genera.
4. Notes on possible hybridization between Couesius plumbeus and Semotilus margarita.

The first two articles deal with morphological variation and speculate on postglacial dispersal routes. The third and fourth articles arise from a possible nomenclatural problem in Couesius which necessitates defining the taxonomic relationship of the genus Couesius to Hybopsis and Semotilus.

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Article 1. VARIATION AND ZOOGEOGRAPHY OF THE BRASSY MINNOW, *HYBOGNATHUS HANKINSONI*

ABSTRACT

Hybognathus hankinsoni from 27 localities are compared using univariate and multivariate methods. Two forms, one from the Missouri River drainage characterized by a deep caudal peduncle, deep head, and long dorsal fin, and a second from the Great Lakes region with large eye and increased anal fin origin, pelvic fin origin, and pectoral fin origin to terminal caudal vertebra distances, were found. Specimens from northern Alberta and British Columbia most closely resemble the Great Lakes region specimens. It is postulated that the Missouri form originated in the "Preglacial Plains Stream" and survived late Pleistocene glacial episodes in the Missouri basin. The Great Lakes form may have originated in the pre-Pleistocene Laurentian River system and survived in the upper Mississippi basin. Dispersal into northern Alberta and British Columbia was probably via glacial Lake Agassiz and glacial Lake Peace approximately 9,500 years before present. The patchy distribution in northern areas may be the result of ecological factors and sampling bias. Taxonomic recognition of the two forms does not seem warranted.

INTRODUCTION

Recent discoveries of Hybognathus hankinsoni Hubbs (Figure 1) populations in northern Alberta (Bishop, 1975; Berry, 1977) have renewed interest in possible Wisconsin refugia and postglacial dispersal routes of this species. Often, when a species is suspected of having survived in more than one glacial refugium, morphological differences between populations derived from each refugium can be demonstrated (see McPhail, 1963). To date, no such differences have been reported in H. hankinsoni. Copes (1975), in the only published morphological comparison of populations of this species, compared four characters on specimens from four localities but found no significant differences. This paper investigates geographic variation within H. hankinsoni over a broad portion of its range and examines implications of patterns of variation with regard to the zoogeography of this species.

MATERIALS AND METHODS

A total of 1013 specimens (31-75 mm standard length) from 27 localities (Table 1; Figure 2) were obtained from the following institutions: University of Alberta Museum of Zoology (UAMZ); National Museum of Natural Sciences (NMC); American Museum of Natural History (AMNH); Cornell University (CU); National Museum of Natural History, Smithsonian Institution (USNM); University of British Columbia (BC); Montana State University (MSU); University of Kansas (KU); University of Michigan Museum of Zoology (UMMZ); Alberta Fish and Wildlife (AFW); and Royal Ontario Museum (ROM).

Counts or measurements (Table 2) on 30 characters were made as described by Hubbs and Lagler (1958), with the exceptions: 1) caudal peduncle scales were counted around a diagonal row starting at a point adjacent to the end of the depressed anal fin, and 2) diagonal scale row counts represent the sum of counts forward along a diagonal row from the base of dorsal and anal fins, but not including the lateral line scale. All measurements were made to the nearest 0.1 mm with needle point dial calipers and all counts were made with the aid of a dissecting microscope.

Sexes were treated separately since sexual dimorphism occurs in dorsal, anal, and pectoral fin lengths and overall body size. By assuming that sexual differences occur in all characters and analyzing each sex separately, the two groups serve as replicates. Patterns of variation in one sex may be expected to be repeated in the other.

Effects of size and allometry were minimized by adjusting each mensural character ($Y'ij$) by its average allometric coefficient to an overall average size such that: $Y'ij = ((\log 10\ Yij - (vj(\log 10\ Xi - \log 10\ \bar{X})))\ 100.00)$, where Yij = length in mm of character j of fish i; Xi = standard length (mm) of fish i; $\bar{X}$ = average standard length over all individuals; $\bar{v}j$ = average allometric coefficient for character j (slope of reduced major axis, $vj = (\Sigma\ yj^2/\Sigma\ x^2)^{0.5}$ averaged over n groups; $\Sigma\ yj^2$ = sum of squared deviations from character j (log10 transformed); and $\Sigma\ x^2$ = sum of squared deviations from standard length (log10 transformed). In general, average allometric coefficients ($\bar{v}j$) were calculated using only locality samples with 10 or more individuals which spanned a moderate to broad size range. The entire procedure is analogous to using a pooled within-slope for _a priori_ removal of size influence as suggested by Thorpe (1976) but uses a Model II regression (independent variable error assumed) for fitting allometric coefficients (Kidwell and Chase, 1967; Ricker, 1973). Multiplication of the score by 100.0 minimizes loss of significant decimals due to rounding errors.

Average allometric coefficients ($\bar{v}j$) were calculated based on localities 2-4, 6-18, 20, 21, and 23-27 for females and localities 2, 4-19, 21, 22, 24, and 25 for males (Table 2). There was no apparent difference among locality slopes.

Significance of deviation from isometry was not tested. These values were then used to adjust all mensural characters to correspond to an average size (X) of 51.9 mm standard length (log10 = 1.715302) for females and 47.7 mm standard length (log10 = 1.678684) for males. After transformation, sexes are not directly comparable unless readjusted to a common average size or converted to a standardized score (Z) as in the generalized distance (D^2) measure.

Most computations were done using programs written by myself, except the canonical variate analysis (BMD:07M; Dixon, 1973) and the unweighted pair-group method with arithmetic means (UPGMA) cluster analysis (CLUSTAN 1C: Wishart, 1975) routines. Descriptions of these methods are presented by Blackith and Reyment (1971) and Sneath and Sokal (1973). Generalized distances (D^2) (Mahalanobis, 1936) were calculated from the F-matrix generated by BMD:07M.

RESULTS AND ANALYSIS

Univariate descriptive statistics were calculated for all characters and localities for each sex (Appendix A). Although an analysis of variance (ANOVA) (Table 3) indicated significant ($p < 0.01$) differences among locality means for all characters of both sexes, no distinct geographic pattern of variation was evident.

Since large scale geographic patterns of variation in single character traits can be partially obscured by recent genetic drift, local selection, and founder effect, a combination of characters is often a better indicator of these patterns. Therefore, canonical variate analysis was performed using thirty characters on all localities with a sample size of 10 or greater. Group centroids for the remaining localities were calculated from canonical coefficients of the original solution for all canonical axes. Inspection of the canonical scores plotted on the first two canonical axes (Figure 3) indicates consistent differences between the Missouri River drainage populations (localities 1-12) and the Mississippi River - Great Lakes populations (localities 13, 20-27). The northern Alberta and British Columbia populations (localities 14-19), while widely scattered, tend to more closely resemble the Great Lakes region samples. Separation of these groups appeared to be due primarily to high scores on characters CPD, HDP, and SNA for the Missouri populations and high scores on characters AOTCV and DOTCV for the remaining samples. Although the first two canonical axes account for only approximately 40 percent of the total variance between centroids for each sex, variation on the remaining axes appeared to be unrelated to racial differences. UPGMA clustering on the averaged female and male D^2 (Figure 4), representing the distance between centroids in the full hyperspace, reveals a structure similar to the canonical variate plots. Again the Missouri samples seem closely related while the remaining forms are widely scattered.

Correlations of canonical scores (Table 4) and means for each character with latitude, longitude, elevation, average air temperature near spawning time, and water type (lentic versus lotic) were calculated to estimate the influence of geographic and environmental effects on meristics and morphometrics. When all localities were pooled many significantly non-zero correlations were found, however these generally explained less than 30 percent of the variance (r^2). Additionally, if several distinct races are involved, significant correlations may result solely from their geographic distribution. If environmental or geographic factors are influencing structure, then the effect may be expected to act similarly within these races. Such consistency was not apparent when the samples were analyzed by region, therefore suggesting these effects were negligible.

The relationship of the northern Alberta - British

Columbia material was further assessed by repeating the canonical variate analysis but with three groups. The first group consisted of the pooled Missouri samples (localities 1-12), the second group pooled northern Alberta - British Columbia samples (localities 14-19), and the third group pooled Mississippi - St. Lawrence - Hudson River samples (localities 12, 20-27). The analysis was performed in a stepwise manner, one character added at a time in order of discriminating power, and D^2 between centroids for the three groups was calculated for each step. Although significant differences occurred between all three groups for both sexes, the northern Alberta - British Columbia material was consistently more similar to the Mississippi - Great Lakes material (Figure 5). This similarity was especially evident when considering only 10 (accounting for approximately 70 percent of the total D^2) or fewer of the most discriminating characters.

If the northern Alberta - British Columbia populations can be considered as part of, or at least derived from, the Mississippi - Great Lakes region, can the Missouri form still be differentiated from the combined northern Alberta - British Columbia - Mississippi - Great Lakes form? This was tested by repeating the analysis with two groups, the first group containing the pooled Missouri samples (localities 1-12) while the second group contained all the remaining material (localities 13-27). Significant differences occurred in both univariate (Table 5) and multivariate analyses. A stepwise procedure was again used in the canonical variate analysis and D^2 between the two centroids was calculated. Approximately 90 percent of the individuals from the two groups could be correctly assigned with 30 characters, however as few as six characters can achieve approximately 85 percent correct assignment (Figure 6). Individual locality centroids calculated from canonical coefficients derived from the two-group thirty-character solution are presented in Figure 7. Characters which best discriminate the two groups are high scores for the Missouri group on CPD, HDO, and DFH, and for the Great Lakes group, high scores on AOTCV, OBD, PELTCV, and PECTCV.

Discriminant coefficients derived from the six most discriminating characters (Table 6) can be used to assign unknown specimens to one of the two groups by summing the product of the discriminant coefficient and the adjusted character measure over the six characters and adding the constant. The unknown is then classified into the group with the highest score.

DISCUSSION

Bailey (1954) documented the range of _H. hankinsoni_ as from northern New York and southern Ontario southwestward in a narrow latitudinal belt to eastern Colorado, Wyoming, and Montana. He stated that the distribution, as known then, indicated survival in the Missouri and upper Mississippi drainages during Wisconsin glaciation. Bailey supported Greene's (1935:121) theory that, following retreat of the Wisconsin ice, _H. hankinsoni_ made its way into the Red River drainage system through the outlet of glacial Lake Agassiz and into the Great Lakes region via the St. Croix outlet and Fox River connectives. Once in the Great Lakes, this species could expand eastward through the Trent outlet from glacial Lake Algonquin or the more recent Nipissing - Ottawa channel from the Nipissing Great Lakes, or both, into the upper Hudson River system via the St. Lawrence River and Lake Champlain. Bailey supported Radforth (1944) in stating that _H. hankinsoni_ did not reinvade the extreme eastern portion of its range from the Susquehanna River system. Although _H. hankinsoni_ does not presently occur in the Susquehanna system, Greene (1935) stated that an early dispersal from this region better explained the abundance of this species in the upland streams of the north and west slopes of the Adirondacks.

Bailey also noted the discovery of _H. hankinsoni_ in the Stave River (lower Fraser River drainage) of British

Columbia (Carl and Clemens, 1953; Keenleyside, 1954) and believed that this was the result of introduction. However, additional discoveries of this species in the Prince George region (upper Fraser River and upper Peace River drainages) of British Columbia (Lindsey, 1956) lend support to the theory that these are natural populations. McPhail and Lindsey (1970) accepted a Missouri or upper Mississippi postglacial origin for this species and hypothesized dispersal into the Fraser system of British Columbia through northward draining lakes in the Prince George and Nechako (into the upper Peace River system) regions formed by an ice-blocked Fraser River. Populations in the lower Fraser valley were probably derived from the upper Fraser system. They stated that H. hankinsoni may have reached the upper Peace from the Missouri system via a series of temporary lakes and outlets and its apparent absence from the supposed dispersal route may be explained by the warm postglacial Hypsithermal or subsequent invasion of predators and/or competitors.

The occurrence of at least two morphological groups appears to substantiate Bailey's (1954) hypothesis of two glacial refugia. The Missouri group undoubtedly represents the form isolated in the Missouri River system while the Great Lakes group probably represents upper Mississippi refugium derivatives. The greater similarity of the northern Alberta - British Columbia populations to those of the Great Lakes region indicates that they were probably derived from the upper Mississippi, rather than the Missouri refugium. However, an upper Missouri and upper Mississippi refugium does not necessarily imply that the two forms originated during isolation in these refugia. These Pleistocene refugia may have served to maintain or reinforce differentiation begun much earlier. Typical Missouri specimens (Figure 1:Top) are deep bodied, have a strongly arched dorsal profile, a relatively short head length, and small eye. The snout appears blunt and the mouth is inferior. Typical Mississippi derivatives (Figure 1:Bottom), on the other hand, are more fusiform, possess a less decurved dorsal outline, a relatively long head, and large eye. The snout region is less blunt and the mouth is terminal. These differences are identical to those noted by Metcalf (1966:81-89) for a wide variety of fishes with both northeastern and southwestern counterparts. He suggested that these differences arose in pre-Pleistocene times as common adaptations to supposed environmental differences between major preglacial drainage systems. Metcalf (1966:134) suggested a possible origin for H. hankinsoni in the north-flowing preglacial Hudson Bay system (ancestral Missouri) and/or the preglacial south-flowing "Preglacial Plains Stream" while Pflieger (1971:364) suggested a preglacial Hudson Bay or Laurentian River system origin (Figure 8).

Possible origin in the "Preglacial Plains Stream" system seems likely. Late Pliocene ancestral Plains streams were probably shallow, periodically sediment-laden, and of little gradient (Metcalf, 1966:64). Adaptations observed in the Missouri form of H. hankinsoni are those which Metcalf associated with this type of environment. The presence of this species in Illinoian beds in southwestern Kansas (Smith, 1963), far south of its present range, is also compatible with its presence in the pre-Pleistocene Plains Stream system. Its extinction from this region may be the result of changing climates and/or habitat (Cross, 1970).

The presence of H. hankinsoni in the north-flowing preglacial Hudson Bay drainage system is possible but not necessary to explain the observed differentation between the two forms. As Pleistocene ice advanced the ancestral Missouri system was deflected southward where it joined the ancient Plains Stream system (Metcalf, 1966:72-75). Dispersal from the south into the Missouri basin may have taken place during this time. Its limited distribution in the upper Missouri River and the lower Yellowstone River systems (Gould and Brown, 1966) tends to support this theory.

The Mississippi - Great Lakes form may have originated in the east-flowing preglacial Laurentian system and/or possibly the preglacial Hudson Bay system. The advancing Pleistocene ice may have brought it into the Mississippi valley (Pflieger, 1971:296).

Existence of additional Wisconsin refugia for the northern Alberta - British Columbia populations, such as the upper Columbia system or the "Ice Free Corridor" along the eastern slope of the Rocky Mountains, seems unlikely for several reasons. First, although significant differences between these populations and the Missouri - Mississippi - Great Lakes populations occur, this would be reasonable to expect since even a minimum estimate of separation time, approximately 9,000 years, would probably be long enough for differences to accumulate. Second, known geologic events can explain the distribution pattern without invoking additional refugia. Furthermore, a Columbia or "corridor" refugium seems inconsistent with the known distributional pattern of this species.

A Wisconsin upper Mississippi refugium can be postulated with a modification of the dispersal route proposed by McPhail and Lindsey (1970). H. hankinsoni may have entered northern Alberta and British Columbia by gaining access to glacial Lake Agassiz. Although access to Lake Agassiz may have been through the Warren River outlet, its limited distribution in the Red River system (see Underhill, 1957) suggests the use of alternate routes. The eastern outlets of Lake Agassiz to Lake Superior (Zoltai, 1967) may have been used. A northwestern reach of Lake Agassiz (Campbell phase), formed about 9,500 years before present (YBP) (Elson, 1967; Eddy, Tasker, and Underhill, 1972), discharged northward to the Clearwater system (Athabasca River drainage) and may have brought the species into the glacial Lake Peace - Lake Tyrrell complex. From there it probably crossed the Rocky Mountains through the Peace River valley.

The last major glaciation in the Peace River valley - Rocky Mountain Trench region was the late Portage Mountain advance (Rutter, 1976). At its maximum, about 11,600 ± 1,000 YBP, Cordilleran ice filled the valley to an area between Bull and Portage mountains, British Columbia. Just east of this region the initial stages of glacial Lake Peace (Bessborough and Hudson Hope stages) were formed by a Laurentide ice dam. By 9,289 ± 200 YBP the Cordilleran ice, followed by a series of glacial lakes, had retreated up the Peace valley and well into the Parsnip and Finlay valleys. During this period, or possibly somewhat later with the subsequent establishment of the Peace River, H. hankinsoni may have gained access to central British Columbia from glacial Lake Peace. Once into central British Columbia it probably followed the path outlined by McPhail and Lindsey (1970). Recent discoveries of this species in Musreau Lake, Alberta (upper Peace system), as well as House River, Horse River, and Athabasca River near Fort McMurray, Alberta (Athabasca drainage basin), seem to support this hypothesis as these localities appear to lie within the boundaries of the glacial Lake Peace - Lake Tyrrell complex (see Taylor, 1960). This explanation would also be more consistent with the apparent absence of H. hankinsoni north of the Milk River (Missouri drainage system) in southern Alberta. If this species had dispersed from the Missouri system, it might be expected to occur in the Saskatchewan River system in Alberta but to date has not been collected there. The Hypsithermal explanation for its absence from this region does not seem plausible as a generalized warming trend would probably have caused widespread extinction of southern latitude populations rather than localized extinction of northern latitude populations.

Alternately, the patchy distribution in northern Alberta and British Columbia may be explained by a combination of factors. Sampling bias may be a primary factor. Much of the region along the dispersal route through northern Saskatchewan and Alberta has been inadequately sampled, especially during spring to midsummer when this species is most likely to be collected. Ableson (1973) found spawning individuals to congregate along inshore areas starting in mid May and by the end of July to have largely left the shoreline. Therefore, collections taken in late summer may not detect this species. Ecological and physiological factors may also be important. H. hankinsoni appears to be restricted to lakes or slow moving rivers and streams with current velocities less than approximately 15 cm/sec (personal observation). In at least eastern and northern regions it is associated with bog streams and lakes (Bailey, 1954:291; personal observation). It also has a great sensitivity to elevated carbon dioxide levels (Black, Fry, and Black, 1954). This preference for slow moving, acidic waters combined with its carbon dioxide sensitivity may restrict its habitation of regions with prolonged ice cover. Thus, with a restricted habitat, inadequate sampling, and limiting physiological constraints, it would not be unusual to find isolated, or apparently isolated, populations in these northern regions.

Recognition of the Missouri and Mississippi derivatives of *H. hankinsoni* as distinct subspecies does not seem warranted at present. The morphological similarity (approximately 90 percent separation with 30 characters) is below the desired level of subspecific recognition (Mayr, 1969:190). This, combined with the mathematical inconvenience of calculating a classification score, makes the distinction unjustifiable from a practical viewpoint. Lack of knowledge about interactions between the two forms in contact zones, if such zones exist, makes it unwarranted from a biological viewpoint. Perhaps future work will reveal additional morphological or biochemical characters that would justify the distinction.

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I thank J.S. Nelson, M.V.H. Wilson, and G.E. Ball for their constructive criticisms and suggestions throughout this study, C.C. Lindsey for his helpful suggestions and kindly allowing me to use unpublished distribution information, and D.K. Berry for generously allowing me to examine specimens collected from the Athabasca River by Alberta Fish and Wildlife. I also thank W.E. Roberts (UAMZ), D.E. McAllister (NMC), C.L. Smith (AMNH), E.B. Brothers (CU), E.A. Lachner (USNM), N.J. Wilimovsky (BC), R.A. Hays (MSU), J.T. Collins (KU), E.J. Crossman (ROM), and E. Baker Koon (UMMZ) for the loan of specimens in their care.

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Table 1. Localities, collections, and sample sizes for *Hybognathus hankinsoni*.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
	Platte River Drainage					
1	Cache la Poudre R., CO	40°30'	104°58'	KU 4782	8	4
2	Lodgepole Ck., NE	41°14'	103°46'	KU 2013	30	48
3	No. Loup R., NE	41°45'	99°10'	UMMZ 135709	11	7
	Missouri River Drainage					
4	Snake R., NE	42°40'	101°15'	KU 8516	23	12
5	Van Tassel Ck., WY	42°42'	104°06'	UMMZ 182467	8	16
6	Antelope Ck., SD	43°16'	100°35'	UMMZ 127462	23	17
7	Slick Ck., SD	45°42'	103°58'	KU 14601, 14630	17	10
8	Beaver Ck., MT	46°40'	104°12'	MSU 5280	15	10
9	Redwater R., MT	47°26'	105°35'	MSU 1986	12	10
10	Gartside Res., MT	47°30'	104°30'	MSU 4041	39	37

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
Milk River Drainage						
11	Bare Ck., AB	49°15'	110°15'	UAMZ 3231, 3340, 3568, 3836	41	45
12	Lodge Ck., AB	49°19'	110°07'	UAMZ 3237, 3567, 3835, 3837	16	19
Mississippi River Drainage						
13	Ivanhoe L., WI	42°30'	88°25'	UMMZ 78452	15	16
Athabasca River Drainage						
14	Athabasca R., AB	56°44'	111°24'	UAMZ 3460, 3776; AFW	11	10
Peace River Drainage						
15	Summit L., BC	54°16'	122°38'	UAMZ 3228, 3897, 3944	26	24
16	Musreau L., AB	54°33'	118°36'	UAMZ 3536, 3941	42	30

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Male
Fraser River Drainage						
17	Sumas R., BC	49°07'	122°07'	BC 56-598	22	16
18	Stave R., BC	49°30'	122°17'	BC 56-109	13	13
19	Fish L., BC	54°16'	122°38'	UAMZ 3945	1	24
St. Lawrence River Drainage						
20	So. Otter Ck., ON	42°40'	80°41'	ROM 30575	10	10
21	Pigeon R. Trib., ON	44°08'	78°36'	ROM 20360	37	37
22	Rideau R., ON	45°03'	75°41'	NMC 60-420	9	11
23	Pigeon R. Trib., MI	45°11'	84°26'	UMMZ 112261	13	11
24	Popple R., WI	45°40'	88°15'	USNM uncatalogued	12	13
25	Manganese L., MI	47°29'	87°55'	KU 2014; UMMZ 133314	21	33
27	Ragged L., NY	44°44'	74°05'	CU 6442	12	13

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size	
					Female	Male
	Hudson River Drainage					
26	Voorheesville, NY	42°39'	73°56'	AMNH S77-74	17	13

Table 2. Character list and average allometric coefficient of mensural characters (vj) for female and male <u>Hybognathus hankinsoni</u>.

Character		Female (n=23)	Male (n=21)
LLS	Lateral line scales	******	******
DSR	Diagonal scale rows	******	******
CPS	Scales around caudal peduncle	******	******
TAGR	Total accessory gill rakers	******	******
DFR	Dorsal fin rays	******	******
AFR	Anal fin rays	******	******
HL	Head length	0.8934	0.9100
SNL	Snout length	1.3273	1.3390
ORBD	Orbit diameter	0.8288	0.8943
EMGS	Eye margin to top of gill slit	1.2054	1.1349
INW	Interorbital width	1.0338	1.0574
HDN	Head depth at nostril	1.1241	1.2412

TCV = terminal caudal vertebra

Table 2. Continued.

Character		Female (n=23)	Male (n=21)
HDP	Head depth at pupil	1.0513	1.0890
HDO	Head depth at occiput	1.0208	1.0805
CPD	Caudal peduncle depth	1.2540	1.2958
DOTCV	Dorsal fin origin to TCV	1.1209	1.1156
DOPEC	Dorsal fin origin to pectoral fin origin	1.1051	1.0818
AOTCV	Anal fin origin to TCV	1.1609	1.1852
PELTCV	Pelvic fin origin to TCV	1.0880	1.0941
PECTCV	Pectoral fin origin to TCV	1.0746	1.0576
SNA	Snout to anus distance	1.0080	0.9715
DFBL	Dorsal fin base length	1.5534	1.7484
DFH	Dorsal fin height (depressed)	1.0791	1.1450
AFBL	Anal fin base length	1.6674	1.6225
AFH	Anal fin height (depressed)	1.1089	1.3049

TCV = terminal caudal vertebra

Table 2. Continued.

Character		Female (n=23)	Male (n=21)
PELL	Pelvic fin length	1.1234	1.2478
PECL	Pectoral fin length	1.0922	1.2362
CFKD	Caudal fin fork depth	1.1207	1.1917
CFL	Caudal fin length	1.0502	1.0970
PELW	Width between pelvic fin origins	1.4548	1.5208
SL	Mean standard length (log10)	1.715302	1.678684
--	Mean standard length (mm)	51.9	47.7

TCV = terminal caudal vertebra

Table 3. Univariate ANOVA F-test value among character means for female and male *Hybognathus hankinsoni* from all localities with n > 9.

Character	Female F(22,455)	Male F(24,473)
DFBL	22.82**	17.56**
AOTCV	22.37**	20.69**
PELW	20.94**	12.75**
AFBL	19.93**	17.14**
HL	19.66**	22.56**
CPD	16.84**	18.10**
ORBD	16.73**	20.17**
DFH	16.62**	13.44**
PECTCV	14.98**	8.28**
AFH	14.01**	12.14**
HDO	13.04**	13.34**
PELTCV	13.02**	16.18**
CFKD	12.73**	10.32**
SNA	12.56**	12.61**
TAGR	12.52**	15.05**
DOTCV	9.44**	10.34**
INW	9.39**	9.18**
CFL	9.04**	10.64**
HDP	8.62**	10.63**
HDN	7.77**	8.26**
EMGS	7.14**	5.69**

** = $p<0.01$

Table 3. Continued.

Character	Female F(22,455)	Male F(24,473)
PECL	7.10**	11.25**
DOPEC	6.88**	6.78**
DSR	6.77**	5.66**
CPS	6.03**	6.42**
PELL	5.96**	9.56**
LLS	3.95**	4.32**
AFR	3.81**	3.50**
SNL	3.80**	7.13**
DFR	2.37**	2.25**

** = $p<0.01$

Table 4. Environmental correlations with canonical variate score (CVS) of first and second canonical axes for female and male _Hybognathus hankinsoni_.

	Missouri (n=12)		Alberta & British Columbia (n=6)		Great Lakes (n=9)		Combined (n=27)	
	Female	Male	Female	Male	Female	Male	Female	Male
Latitude								
CVS-1	-0.15	-0.01	0.66	0.54	0.13	0.02	0.09	-0.03
CVS-2	-0.48	0.55*	0.51	0.74*	-0.49	-0.42	-0.30	0.02
Longitude								
CVS-1	-0.63*	-0.56*	-0.54	-0.19	0.19	0.08	-0.50**	-0.48**
CVS-2	-0.75**	0.19	-0.45	-0.71	-0.08	-0.34	0.24	0.19
Temperature (average June air temperature)								
CVS-1	0.34	0.24	-0.43	-0.34	-0.47	-0.42	0.07	0.03
CVS-2	0.67**	-0.40	-0.72	-0.61	0.46	0.54	0.41*	0.19
Elevation								
CVS-1	-0.33	-0.53*	0.57	0.75*	-0.25	0.08	-0.22	-0.32
CVS-2	-0.16	-0.38	0.42	0.47	-0.59*	-0.84*	0.66**	0.53**
Water Type (lentic versus lotic)								
CVS-1	-0.16	-0.35	0.22	-0.01	0.50	0.43	0.03	-0.18
CVS-2	0.15	0.01	0.14	0.25	0.55	0.69*	0.46**	0.47**

* = p<0.05
** = p<0.01

Table 5. Mean, (standard deviation), and univariate ANOVA F-test value between group means for female and male *Hybognathus hankinsoni*. Missouri includes localities 1-12; Great Lakes includes localities 13-27.

	Female			Male		
Character	Missouri (n=243)	Great Lakes (n=261)	F (df=1,502)	Missouri (n=235)	Great Lakes (n=274)	F (df=1,507)
CPD	71.02 (2.54)	68.30 (2.86)	125.81**	68.11 (2.49)	66.07 (2.81)	74.04**
AOTCV	118.78 (1.84)	120.13 (1.99)	62.20**	115.87 (1.59)	117.65 (1.82)	136.53**
ORBD	46.74 (2.87)	48.84 (2.54)	74.31**	44.50 (2.75)	46.73 (2.59)	88.95**
PELTCV	139.98 (1.10)	140.69 (1.16)	49.10**	136.19 (0.98)	137.15 (1.08)	108.78**
HDO	93.31 (1.82)	92.12 (1.68)	58.23**	90.97 (2.03)	89.68 (1.96)	53.24**
DFH	102.37 (2.16)	100.79 (2.87)	47.90**	101.29 (2.18)	100.04 (2.56)	34.39**
SNA	155.54 (0.85)	155.10 (0.88)	33.04**	151.24 (0.87)	150.71 (0.90)	44.98**
PECTCV	159.02 (0.76)	159.42 (0.64)	40.44**	154.55 (0.80)	154.91 (1.23)	14.87**
DSR	11.16 (0.64)	10.85 (0.73)	25.46**	11.09 (0.65)	10.85 (0.62)	18.63**
CFKD	90.97 (2.71)	89.75 (3.61)	18.22**	109.71 (2.77)	109.67 (3.32)	13.81**

* = $p<0.05$
** = $p<0.01$

Table 5. Continued.

	Female			Male		
Character	Missouri (n=243)	Great Lakes (n=261)	F (df=1,502)	Missouri (n=235)	Great Lakes (n=274)	F (df=1,507)
HDP	83.97 (2.23)	83.42 (2.13)	8.07**	81.75 (2.08)	81.09 (2.21)	11.69**
SNL	54.05 (3.09)	54.30 (3.08)	0.75	50.04 (3.30)	51.25 (3.13)	17.94**
DFBL	68.63 (4.16)	66.99 (5.55)	13.94**	66.06 (3.90)	65.38 (5.88)	2.32
INW	67.15 (2.22)	67.69 (2.26)	7.13**	63.95 (2.15)	64.55 (2.42)	8.63**
DFR	7.90 (0.35)	7.98 (0.30)	7.31**	7.90 (0.33)	7.97 (0.26)	5.79*
DOTCV	142.93 (0.93)	143.08 (1.04)	2.86	139.22 (0.98)	139.49 (1.09)	8.52**
HDN	69.39 (2.91)	68.62 (2.49)	10.16**	66.73 (2.96)	66.46 (3.08)	0.98
DOPEC	118.61 (1.63)	118.13 (1.68)	10.34**	113.55 (1.71)	113.65 (1.70)	0.45
AFR	7.75 (0.46)	7.83 (0.47)	3.76	7.69 (0.47)	7.78 (0.43)	5.51*
HL	112.38 (1.46)	112.01 (1.47)	8.21**	109.56 (1.42)	109.46 (1.49)	0.64
PELW	52.27 (4.33)	51.31 (3.64)	7.29**	49.22 (3.66)	49.03 (3.55)	0.37
TAGR	14.14 (1.23)	13.85 (1.29)	6.79**	13.85 (1.37)	13.83 (1.11)	0.02

* = $p<0.05$
** = $p<0.01$

Table 5. Continued.

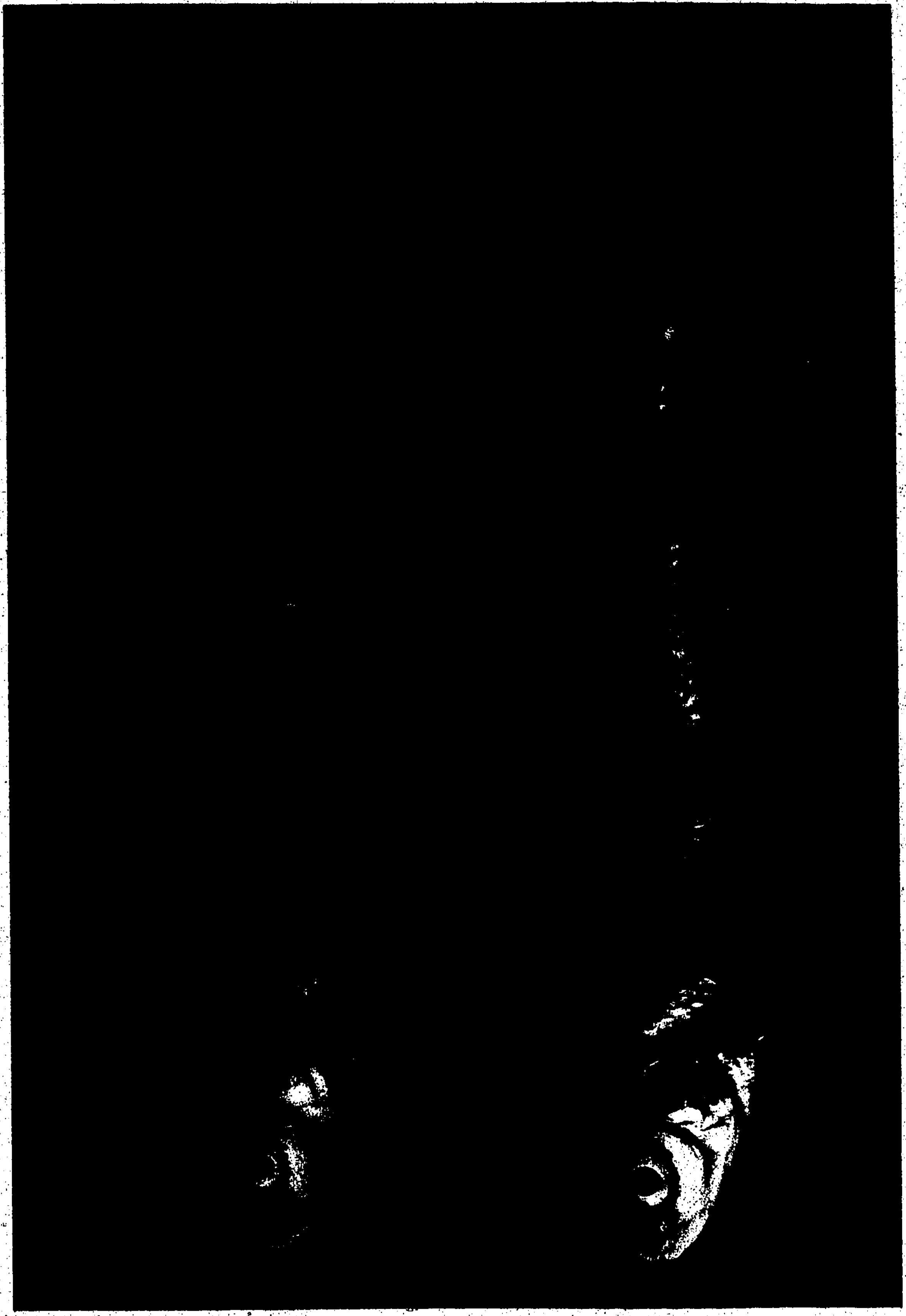
Character	Female Missouri (n=243)	Female Great Lakes (n=261)	Female F (df=1,502)	Male Missouri (n=235)	Male Great Lakes (n=274)	Male F (df=1,507)
CPS	16.44 (0.94)	16.28 (0.93)	3.71	16.45 (0.98)	16.45 (0.97)	0.00
PELL	84.51 (2.44)	84.17 (2.15)	2.69	83.73 (2.48)	83.51 (2.79)	0.85
AFH	89.48 (2.60)	89.14 (2.85)	2.04	88.67 (2.55)	88.82 (2.99)	0.38
EMGS	64.81 (3.13)	64.62 (3.39)	0.39	61.58 (2.78)	61.90 (2.83)	1.65
LLS	36.75 (1.10)	36.87 (1.32)	1.32	36.57 (1.17)	36.65 (1.38)	0.52
AFBL	60.26 (5.36)	60.36 (6.52)	0.03	58.66 (4.17)	59.22 (6.21)	1.41
PECL	94.44 (2.41)	94.44 (2.10)	0.00	97.36 (2.66)	97.26 (2.43)	0.18
CFL	112.65 (2.62)	112.59 (2.52)	0.06	109.71 (2.64)	109.67 (2.53)	0.03

* = p<0.05
** = p<0.01

Table 6. Two-group discriminant coefficients, based on six characters, for female and male *Hybognathus hankinsoni*.

	Female		Male	
	Missouri	Great Lakes	Missouri	Great Lakes
ORD	8.38373	8.90398	4.38383	5.02219
HDO	37.87941	37.47899	36.98149	36.63457
CPD	-10.67929	-11.12475	-3.64466	-4.13065
AOTCV	-3.96175	-3.45118	-8.97255	-8.32321
PELTCV	124.74876	125.30061	150.15070	150.74854
DFH	8.51487	8.29406	4.94877	4.66912
CONSTANT	-10519.21484	-10591.92578	-11614.00000	-11708.54688

Figure 1. *Hybognathus hankinsoni*. Top: 58 mm SL female, Lodge Ck, Alberta (UAMZ 3835). Bottom: 58 mm SL female, Musreau L, Alberta (UAMZ 3941).



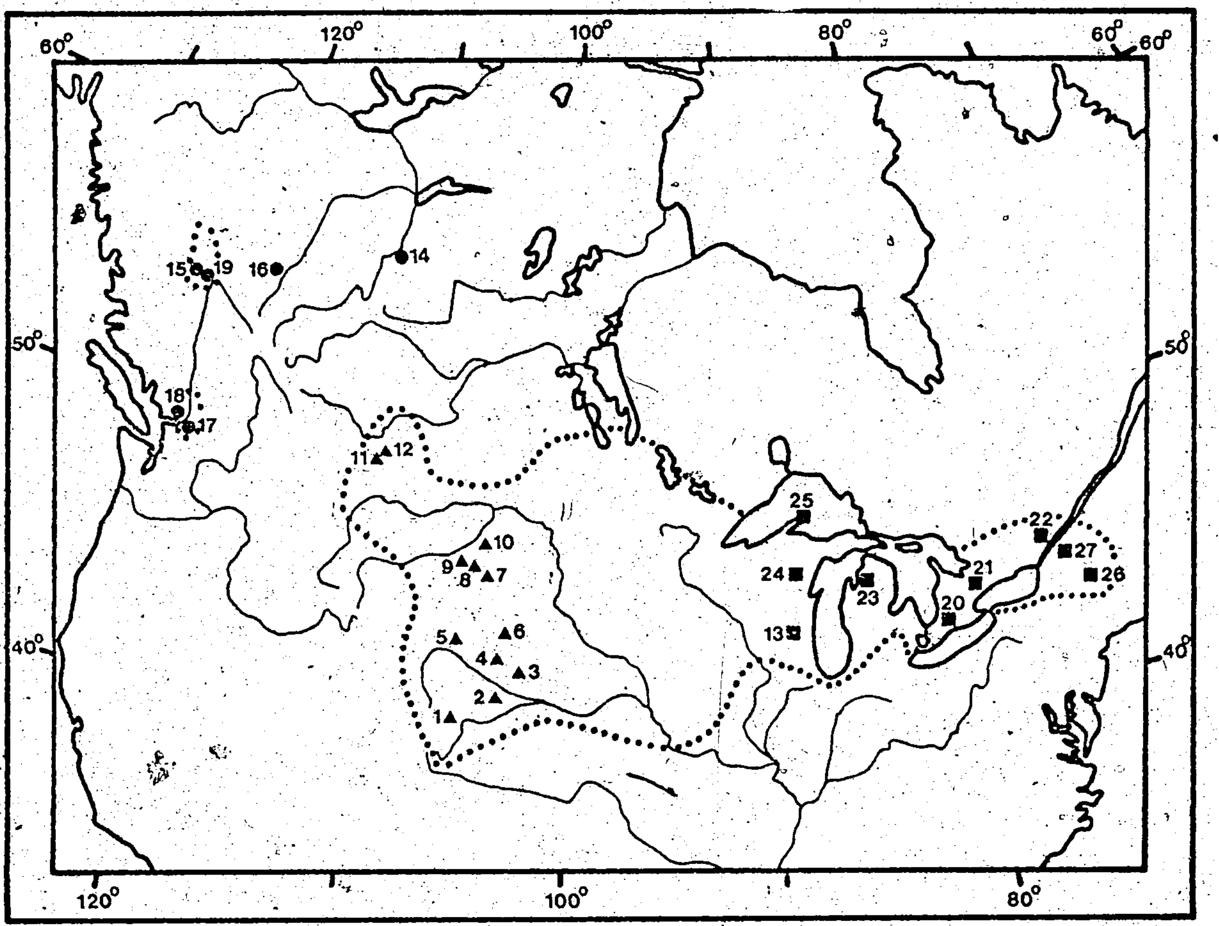
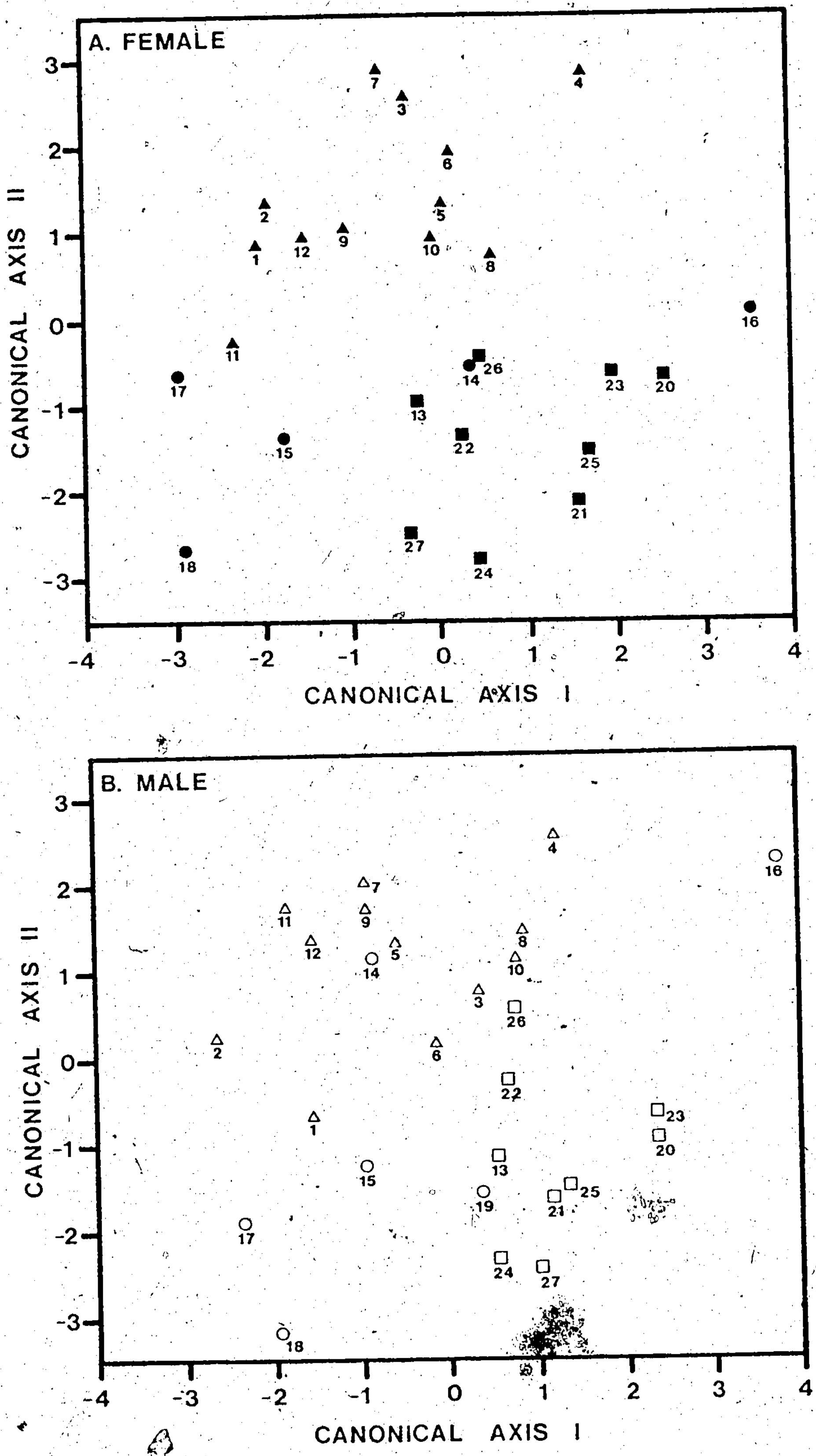


Figure 2. *Hybognathus hankinsoni* sample localities (triangle = Missouri drainage; circle = northern Alberta and British Columbia; square = Mississippi drainage and Great Lakes region) and approximate range (dotted line). Locality labels as in Table 1.

Figure 3. Canonical variate scores along canonical axes I and II for A) female (24.2% and 17.1% of variance, respectively; 23 groups, 30 characters) and B) male (20.6% and 17.4% of variance, respectively; 25 groups, 30 characters) *Hybognathus hankinsoni*. Locality labels as in Table 1; symbols as in Figure 2.


A. FEMALE
CANONICAL AXIS II
CANONICAL AXIS I
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4
7
3
4
6
2
5
12
9
10
1
8
16
11
17
14
26
23
20
13
15
22
25
21
27
18
24
B. MALE
CANONICAL AXIS II
CANONICAL AXIS I
3
2
1
0
-1
-2
-3
-4
-3
-2
-1
0
1
2
3
4
4
16
7
11
9
12
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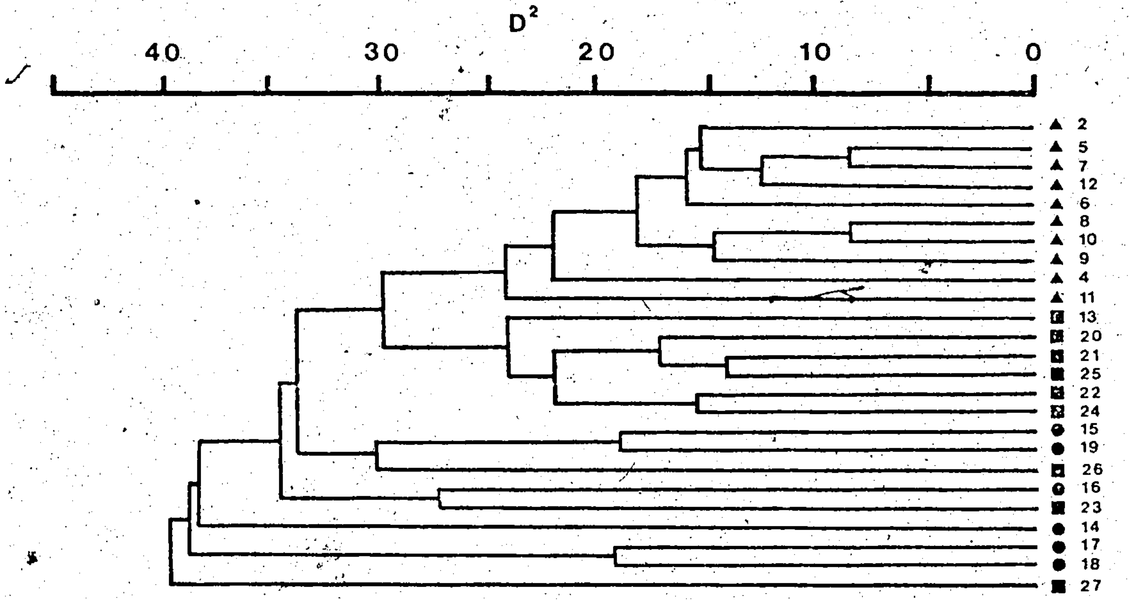

Figure 4. UPGMA clustering of averaged female and male *Hybognathus hankinsoni* generalized distances (D^2). Locality labels as in Table 1; symbols as in Figure 2. Localities 1 and 3 omitted because of small sample sizes.

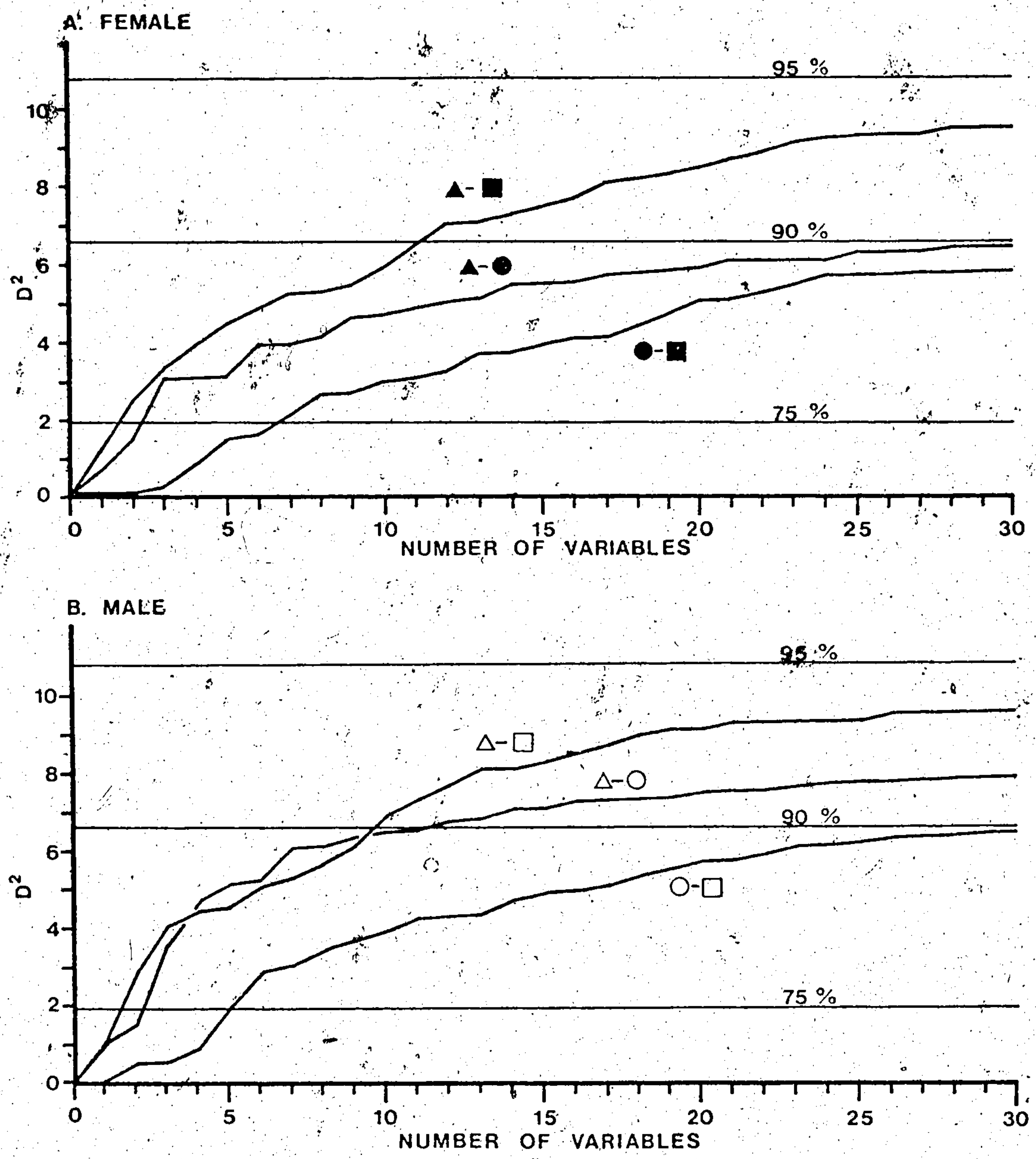

Figure 5. Generalized distance (D^2) between pooled Missouri (triangle), pooled northern Alberta and British Columbia (circle), and pooled Mississippi and Great Lakes (square) forms of A) female and B) male Hybognathus hankinsoni with number of variables (characters) entered into the analysis. Horizontal lines indicate theoretical percentage separation between groups based on D^2 values.

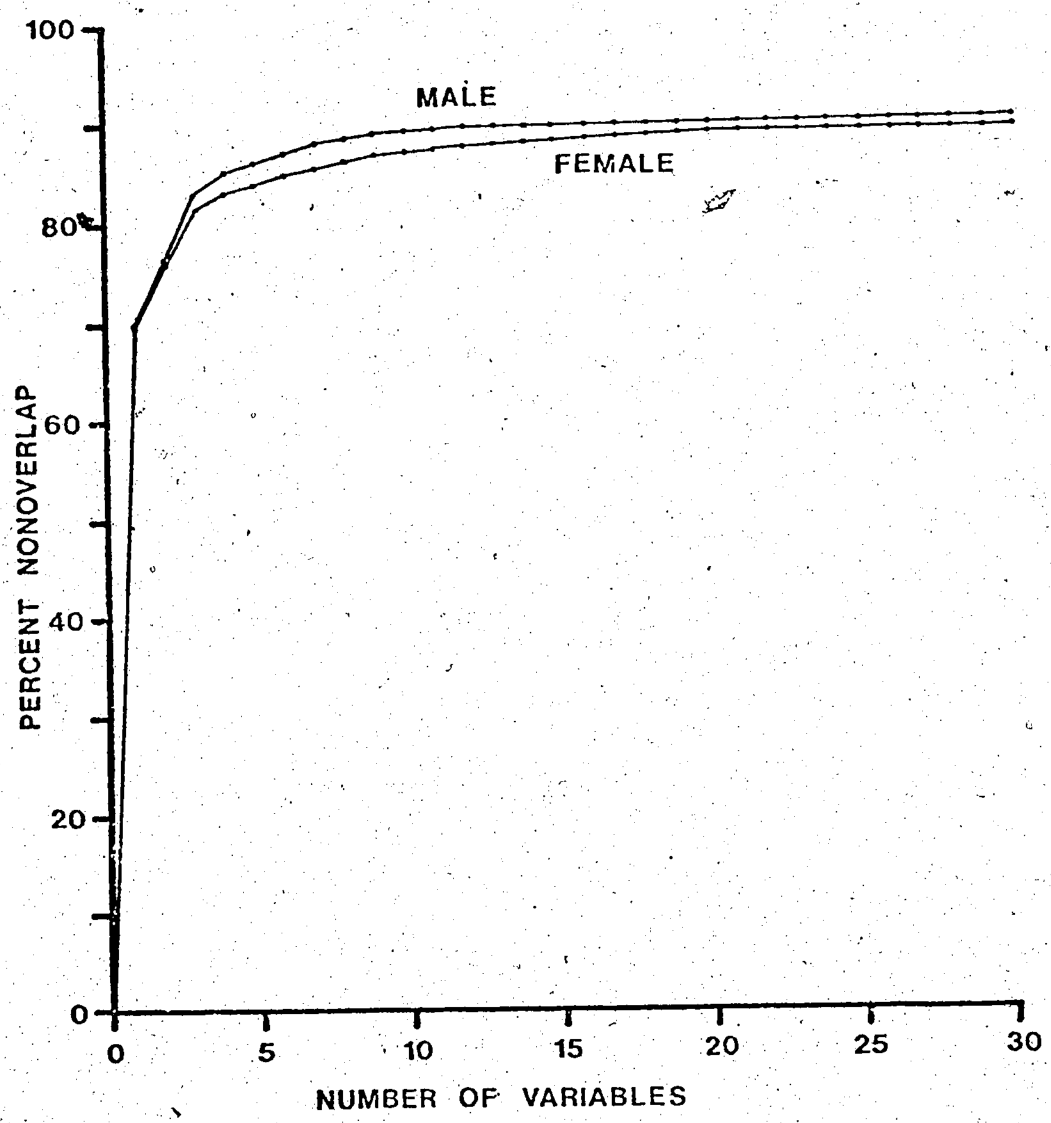

Figure 6. Theoretical percentage of nonoverlap between pooled Missouri localities and pooled northern Alberta, British Columbia, Mississippi, and Great Lakes localities (two-group solution) of female and male <u>Hybognathus</u> <u>hankinsoni</u> with number of variables (characters) entered into the analysis.

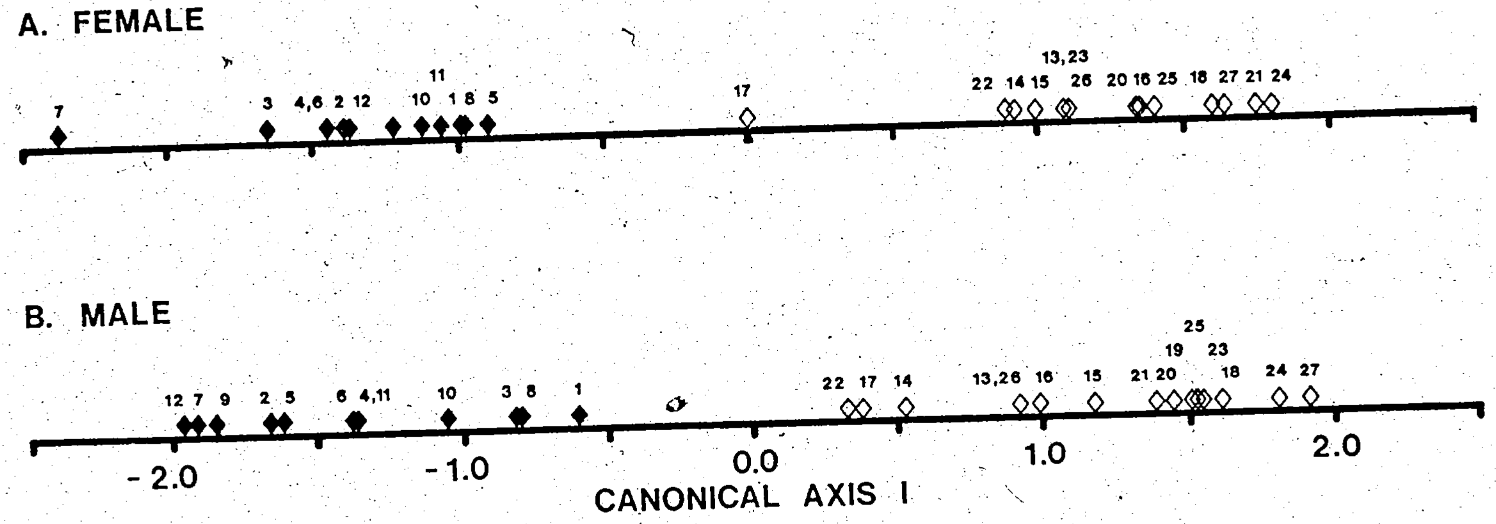

Figure 7. Two-group 30-character solution canonical variate scores along canonical axis I for A) female and B) male Hybognathus hankinsoni. Locality labels as in Table 1. Open = pooled northern Alberta, British Columbia, Mississippi, and Great Lakes localities; solid = pooled Missouri localities.

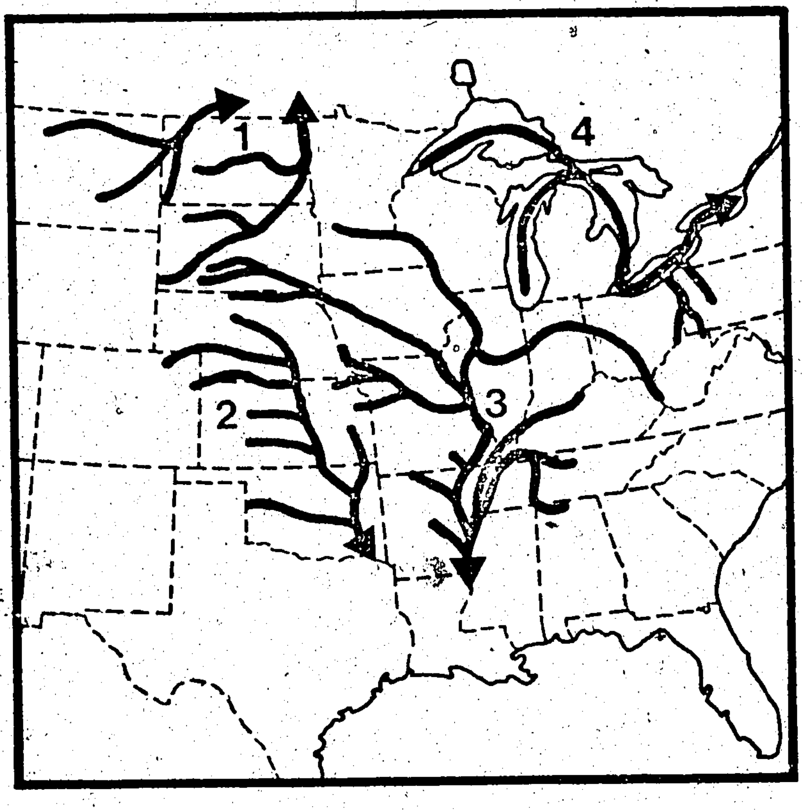

Figure 8. Hypothetical pre-Pleistocene drainage patterns of central United States. 1 = Hudson Bay; 2 = Plains; 3 = Teays - Mississippi; 4 = Laurentian. (After Pfliger, 1971).

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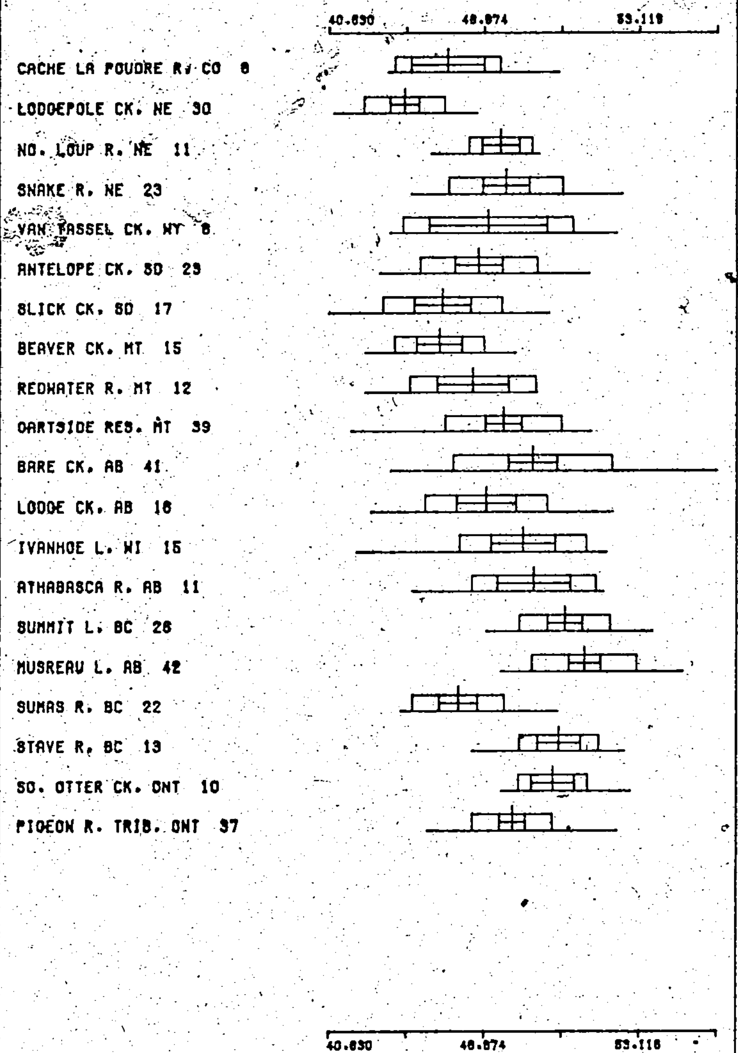
APPENDIX A

Univariate descriptive statistics (range, one standard deviation, two standard errors of mean, and mean) of selected characters (orbit diameter, head depth at occiput, caudal peduncle depth, anal fin origin to TCV, pelvic fin origin to TCV, and dorsal fin height) for female and male _Hybognathus hankinsoni_.



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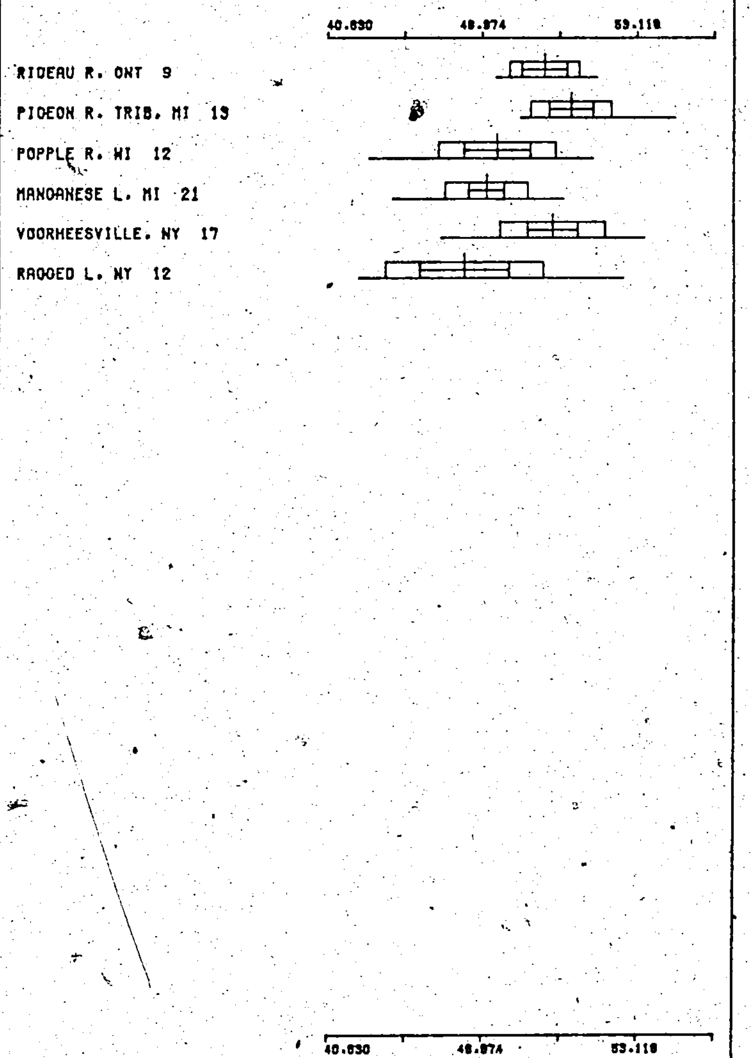

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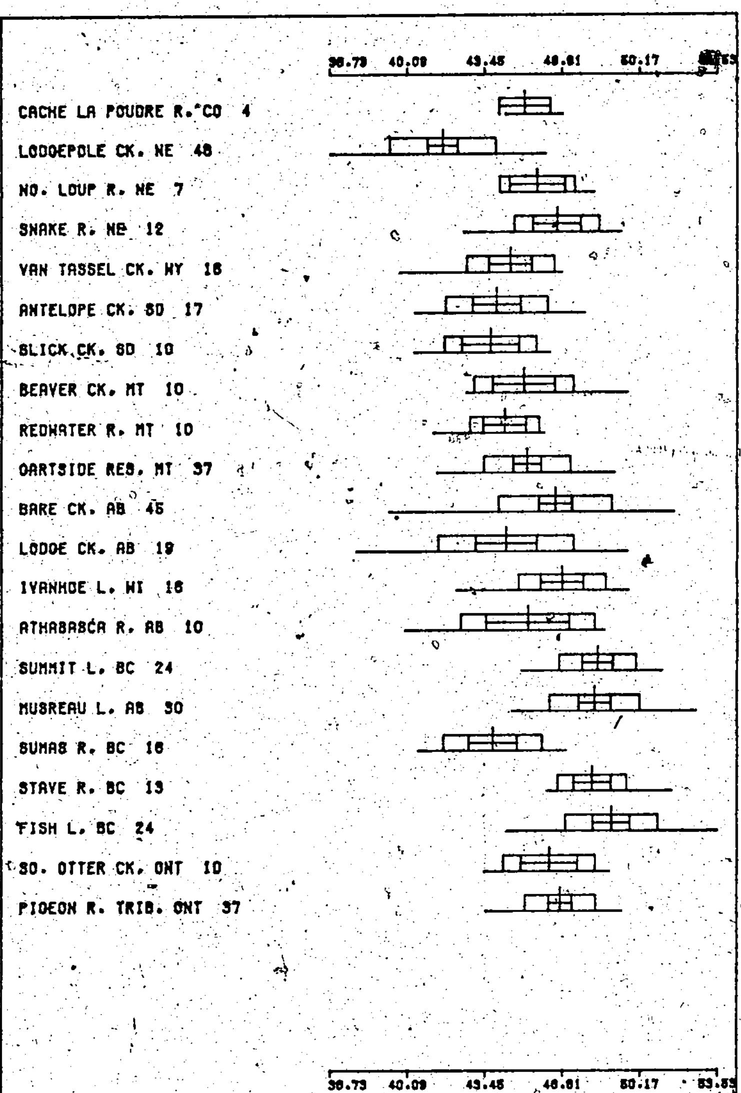

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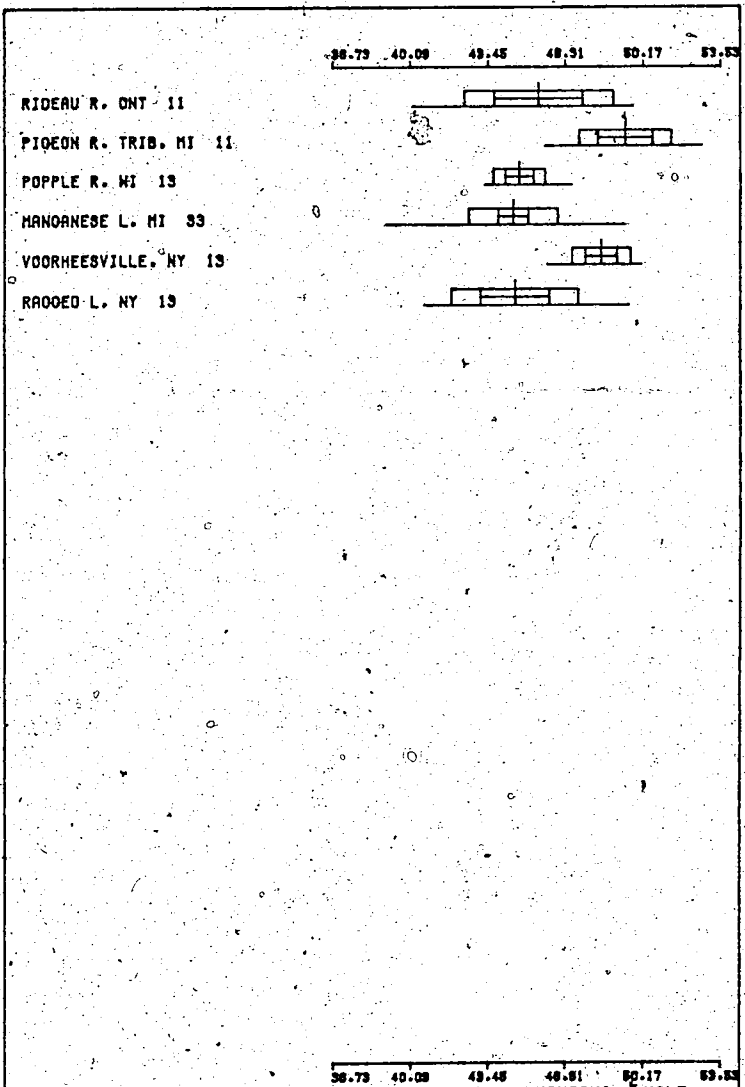

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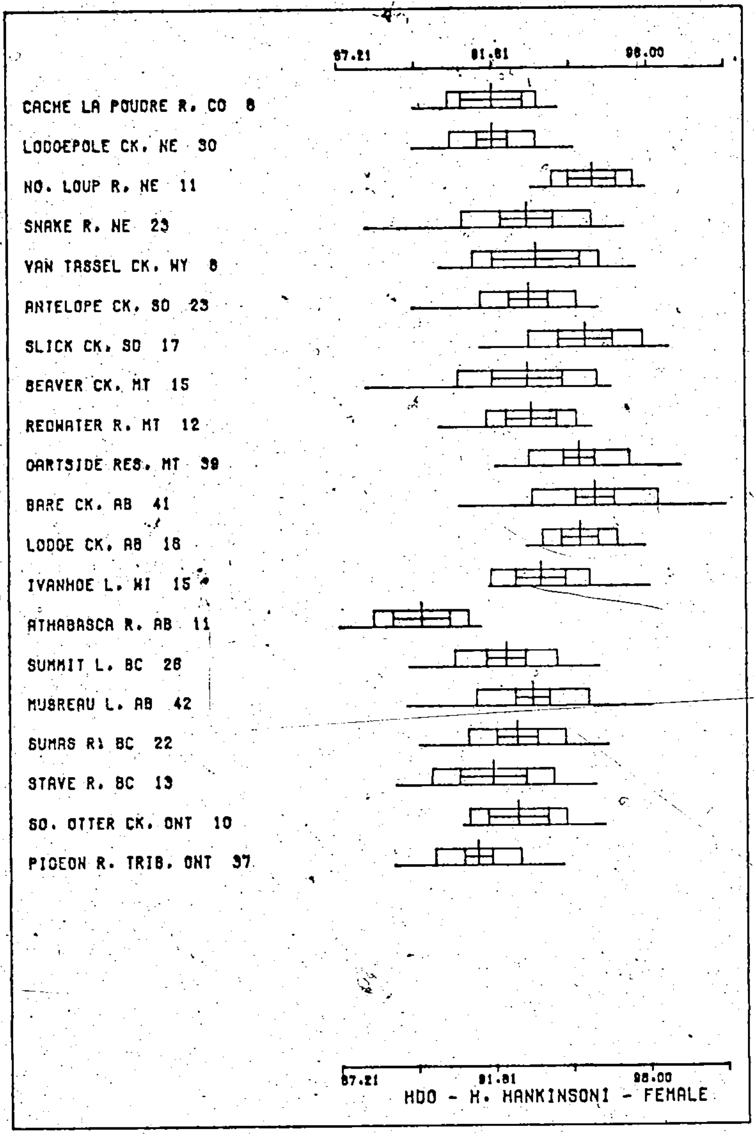
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91.61
96.00
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LODGEPOLE CK. NE 30
NO. LOUP R. NE 11
SNAKE R. NE 23
VAN TASSEL CK. WY 8
ANTELOPE CK. SD 23
SLICK CK. SD 17
BEAVER CK. MT 15
REDWATER R. MT 12
OARTSIDE RES. MT 39
BARE CK. AB 41
LODGE CK. AB 18
IVANHOE L. WI 15
ATHABASCA R. AB 11
SUMMIT L. BC 28
MUSREAU L. AB 42
SUMAS R. BC 22
STAVE R. BC 13
SO. OTTER CK. ONT 10
PIGEON R. TRIB. ONT 37
87.21
91.61
96.00
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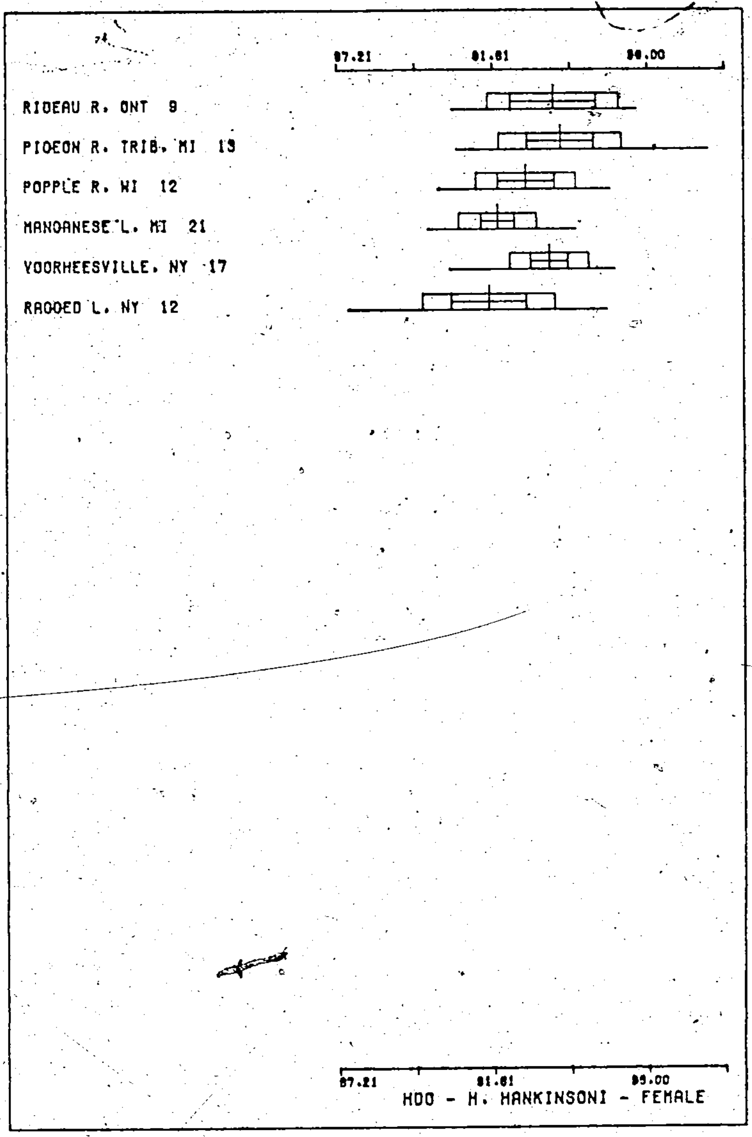
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91.61
96.00
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POPPLE R. WI 12
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RAGGED L. NY 12
87.21
91.61
96.00
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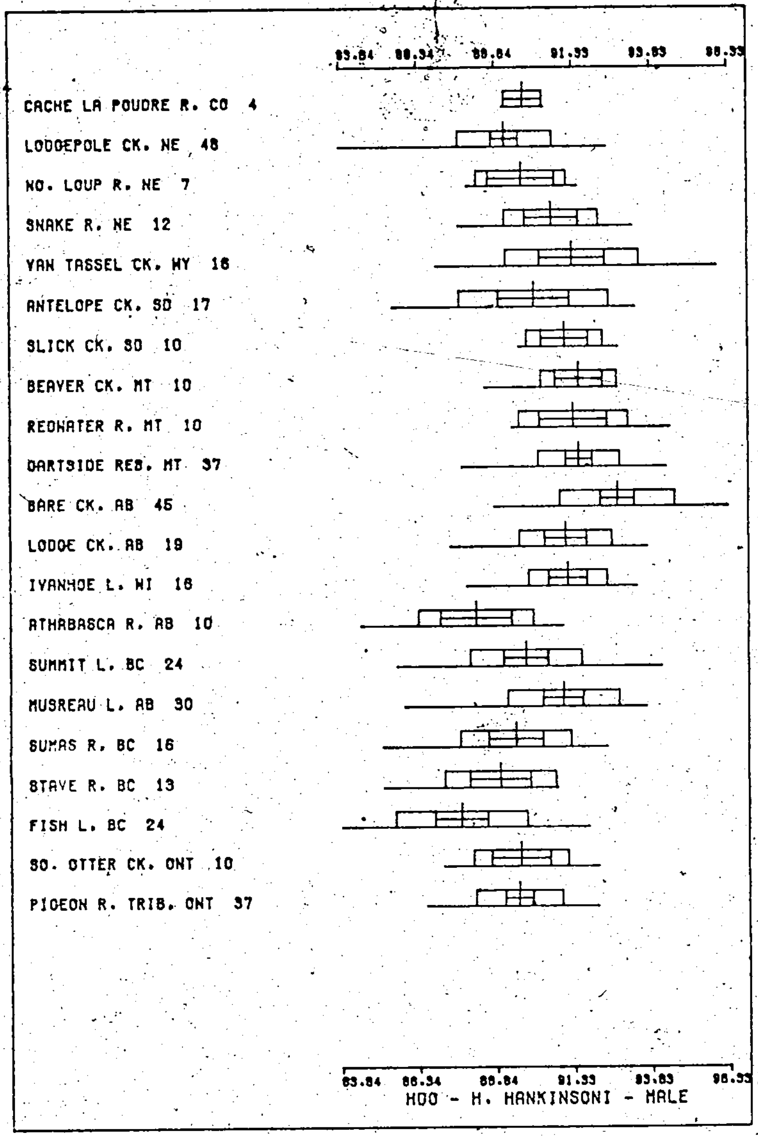
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SNAKE R. NE 12
VAN TASSEL CK. WY 16
ANTELOPE CK. SD 17
SLICK CK. SD 10
BEAVER CK. MT 10
REDWATER R. MT 10
DARTSIDE RES. MT 37
BARE CK. AB 45
LODGE CK. AB 19
IVANHOE L. WI 16
ATHABASCA R. AB 10
SUMMIT L. BC 24
MUSREAU L. AB 30
SUMAS R. BC 16
STAVE R. BC 13
FISH L. BC 24
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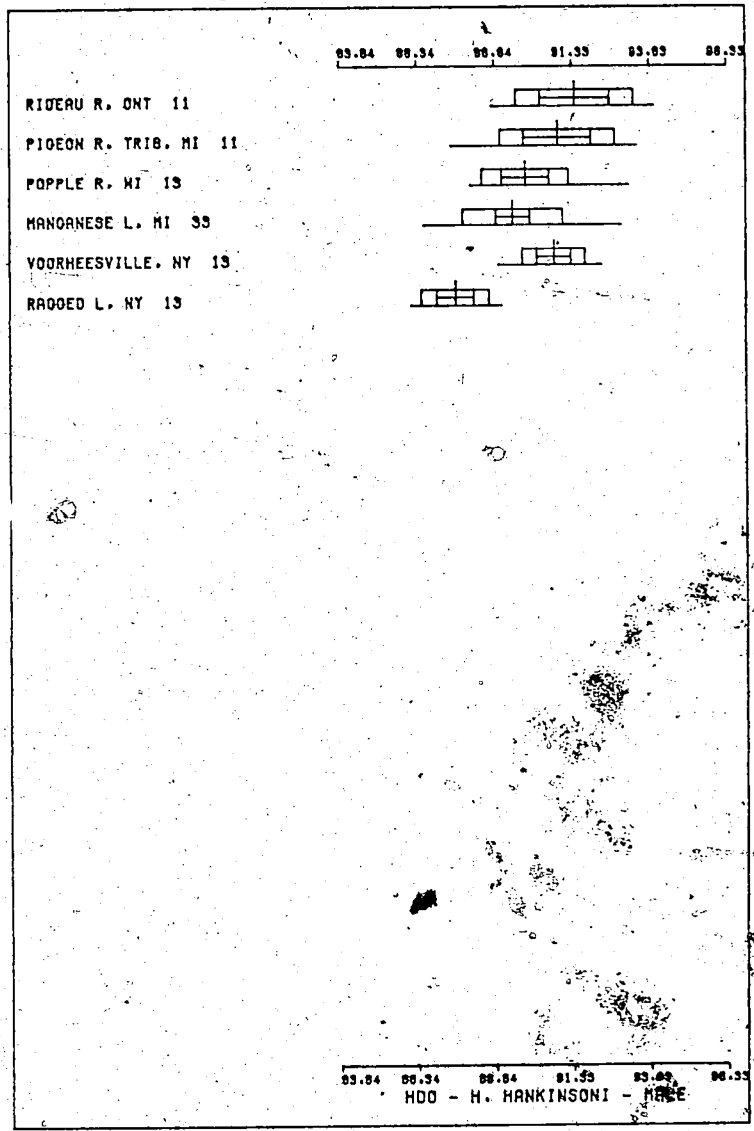
PIGEON R. TRIB. ONT 37
HDO - H. HANKINSONI - MALE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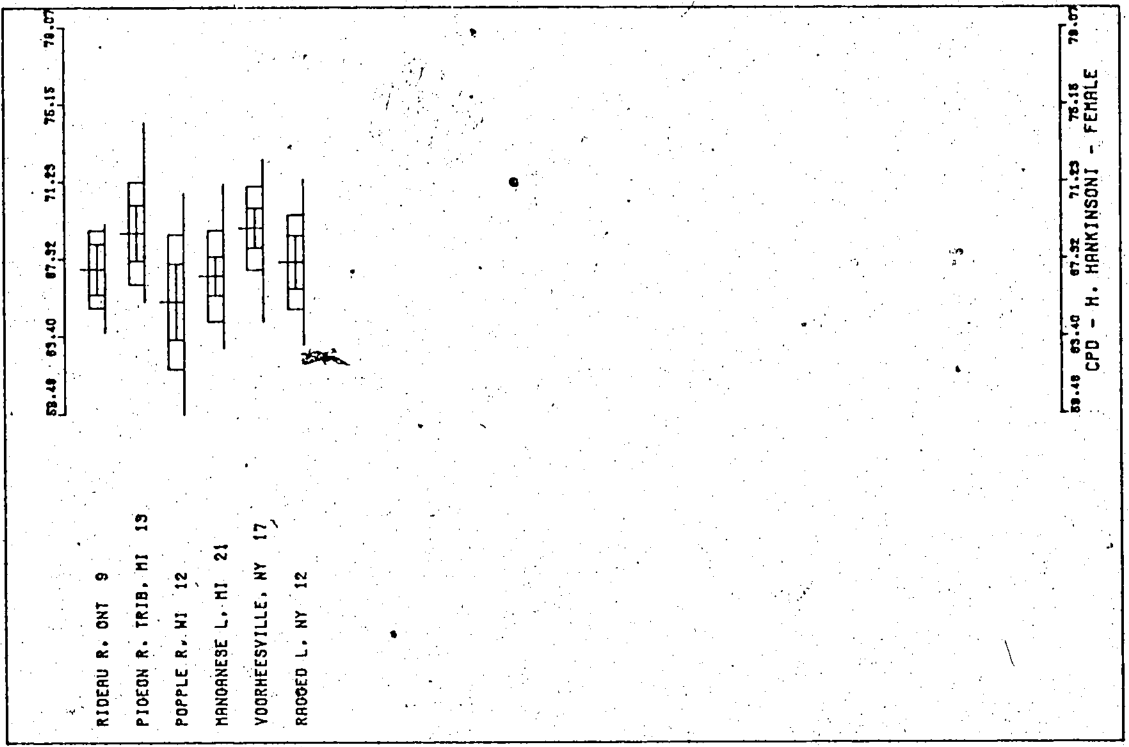
RAGGED L. NY 13
HDO - H. HANKINSONI - MALE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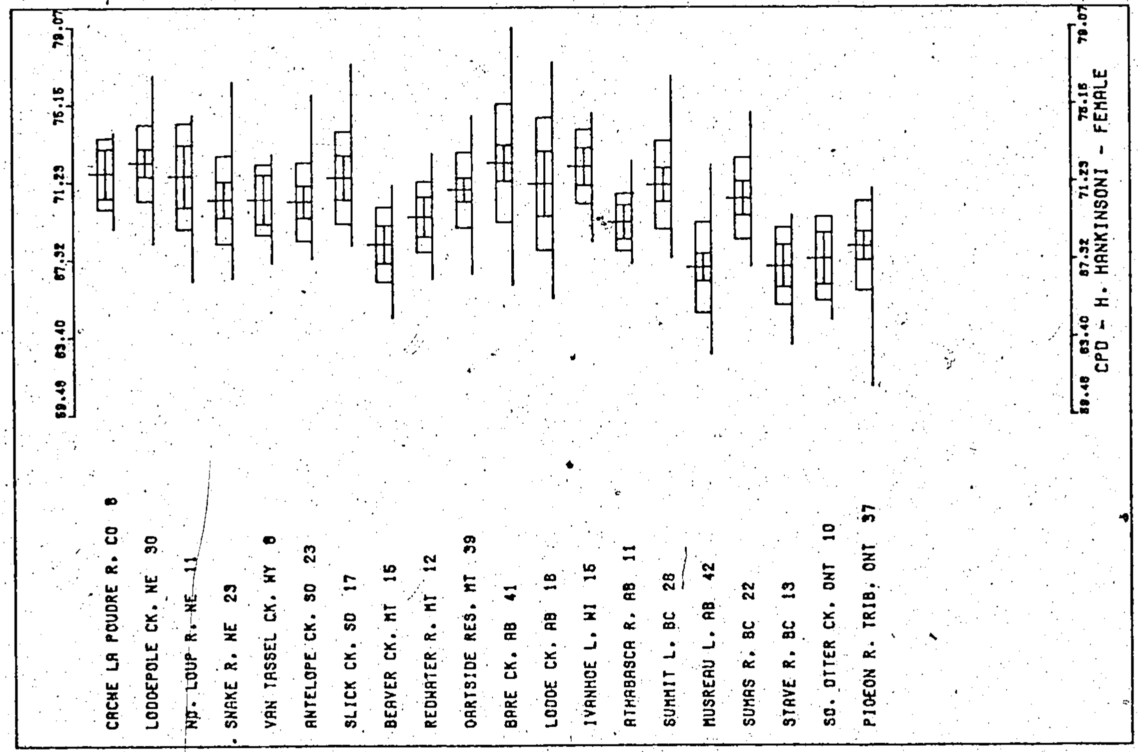
CPD - H. HANKINSONI - FEMALE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SLICK CK. SD 17
BEAVER CK. MT 15
REDWATER R. MT 12
OARTSIDE RES. MT 39
BARE CK. AB 41
LODGE CK. AB 18
IVANHOE L. WI 15
ATHABASCA R. AB 11
SUMMIT L. BC 28
MUSREAU L. AB 42
SUMAS R. BC 22
STAVE R. BC 13
SO. OTTER CK. ONT 10
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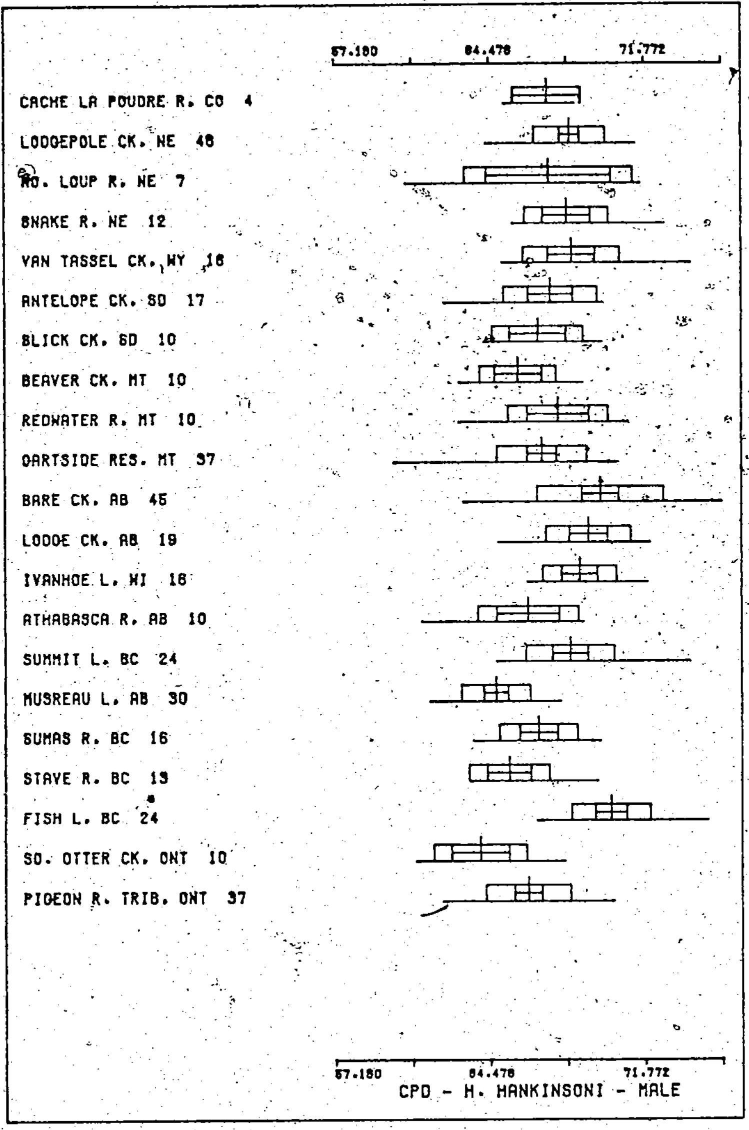
CPD - H. HANKINSONI - FEMALE



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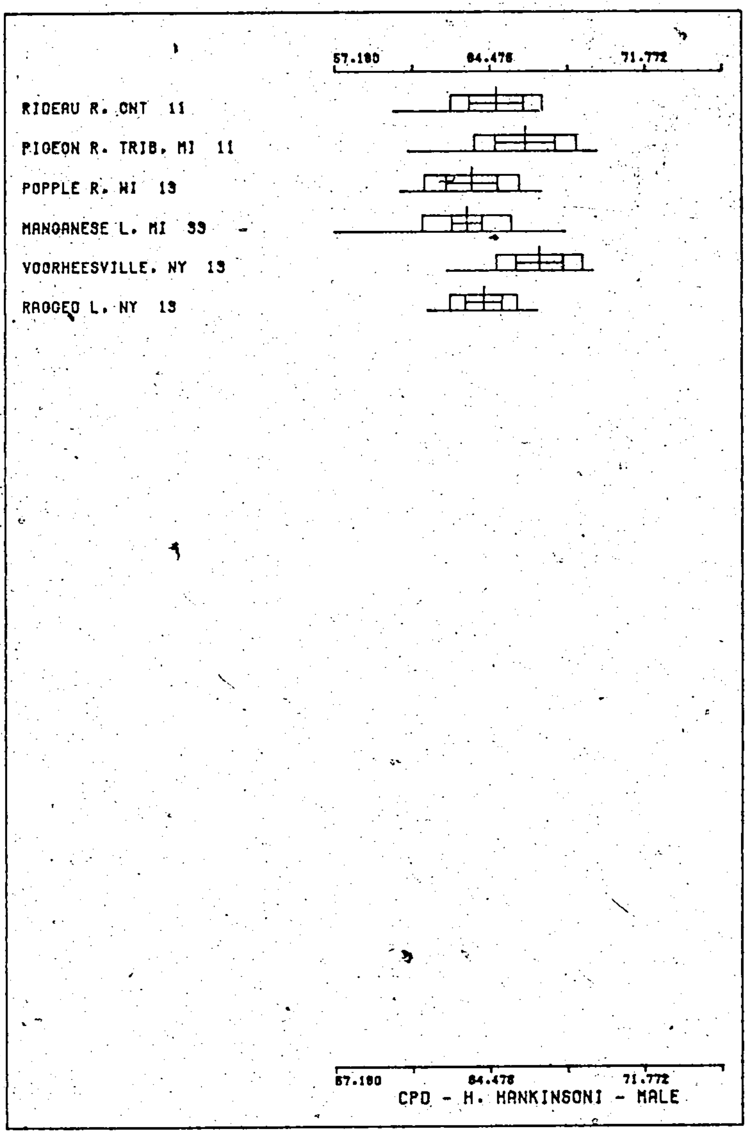

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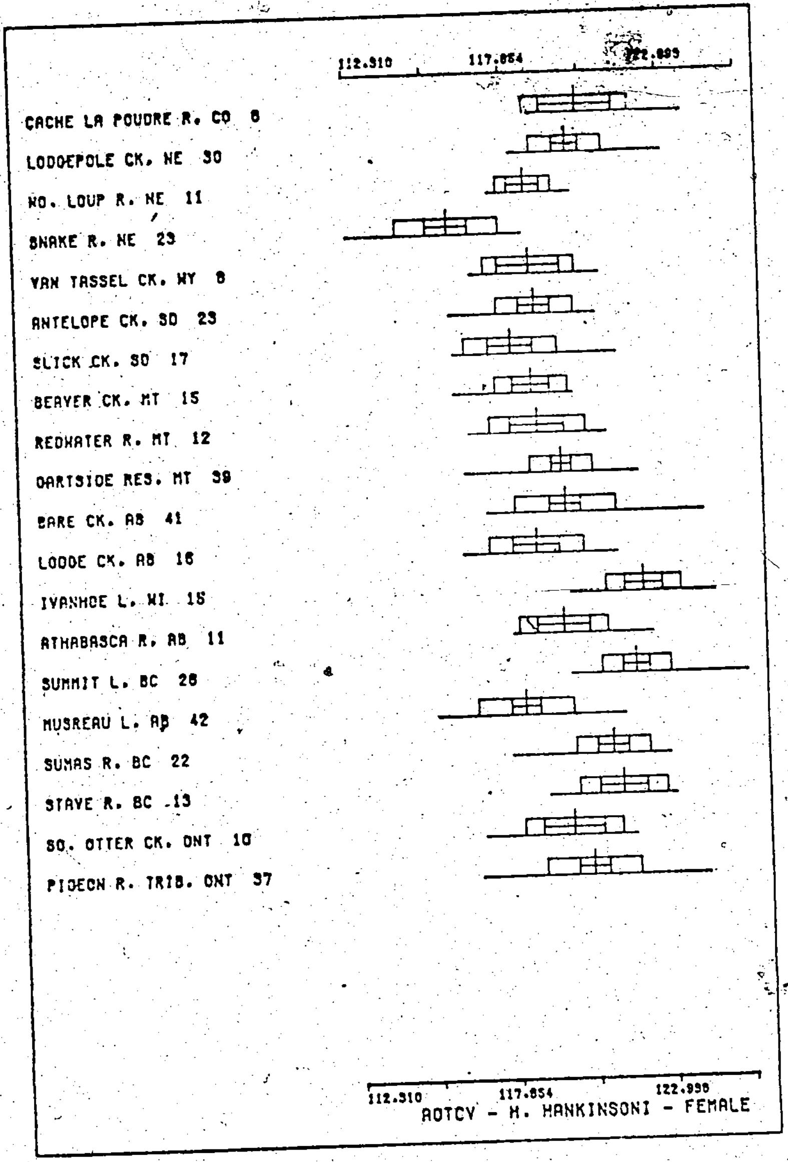

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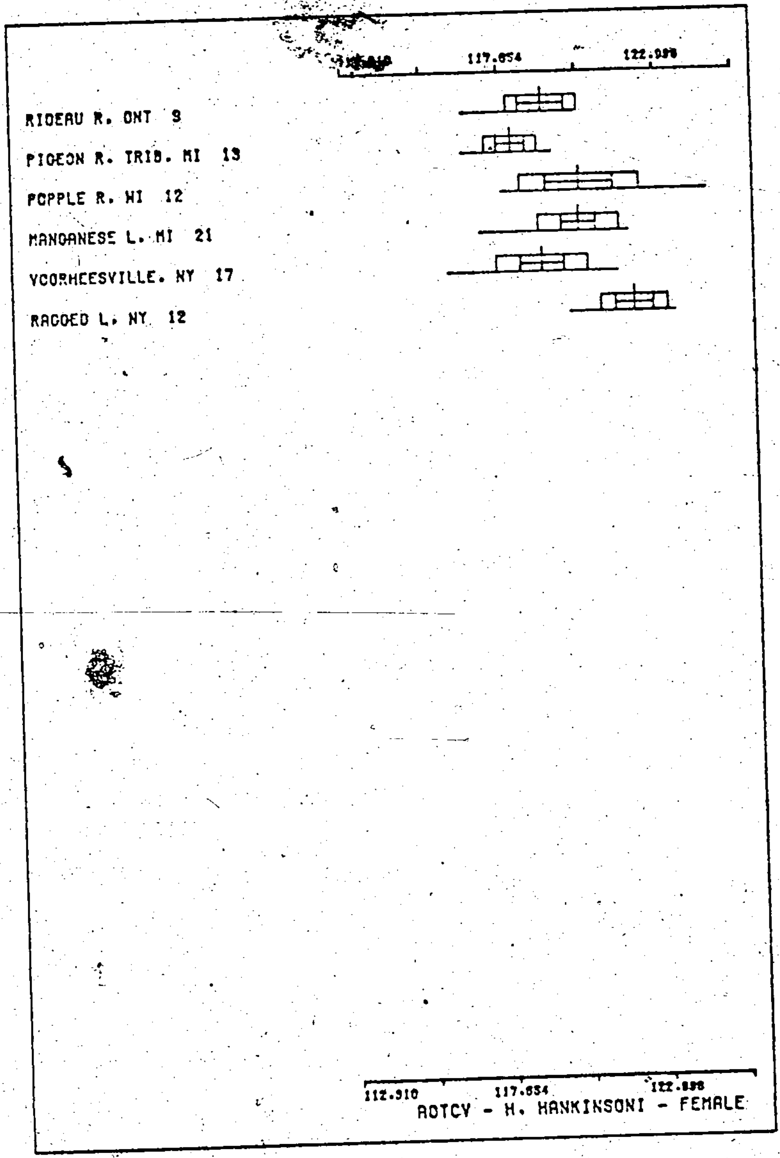

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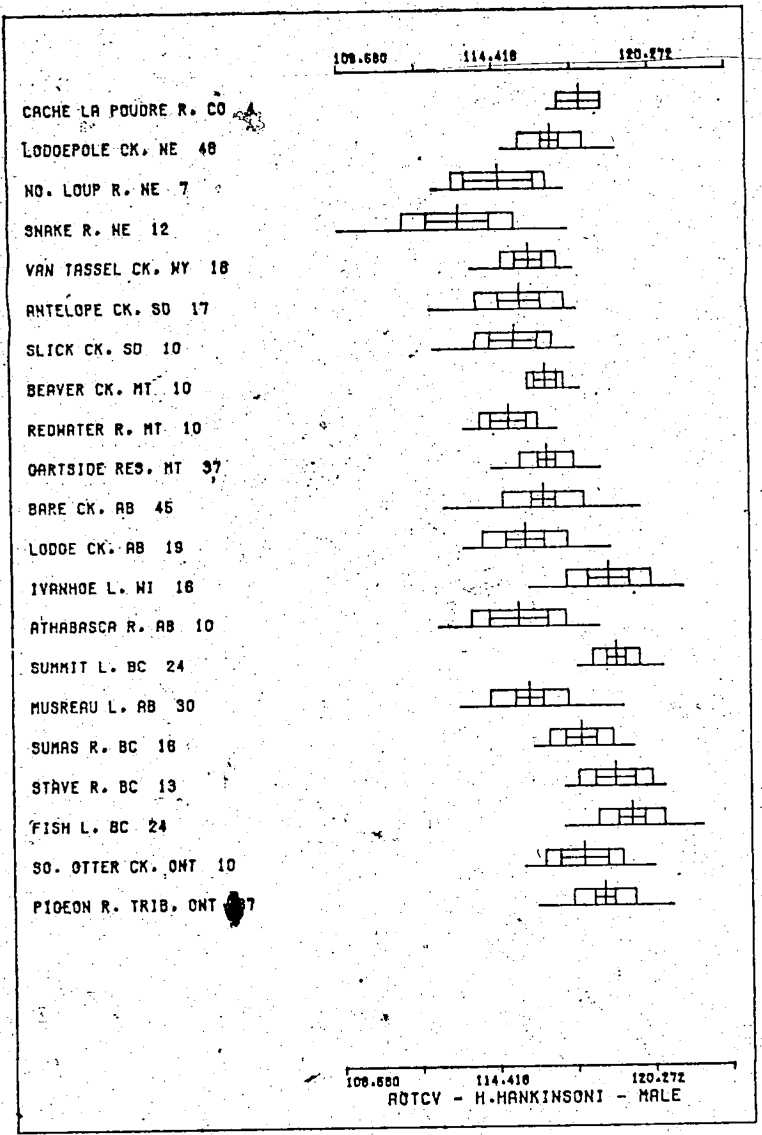

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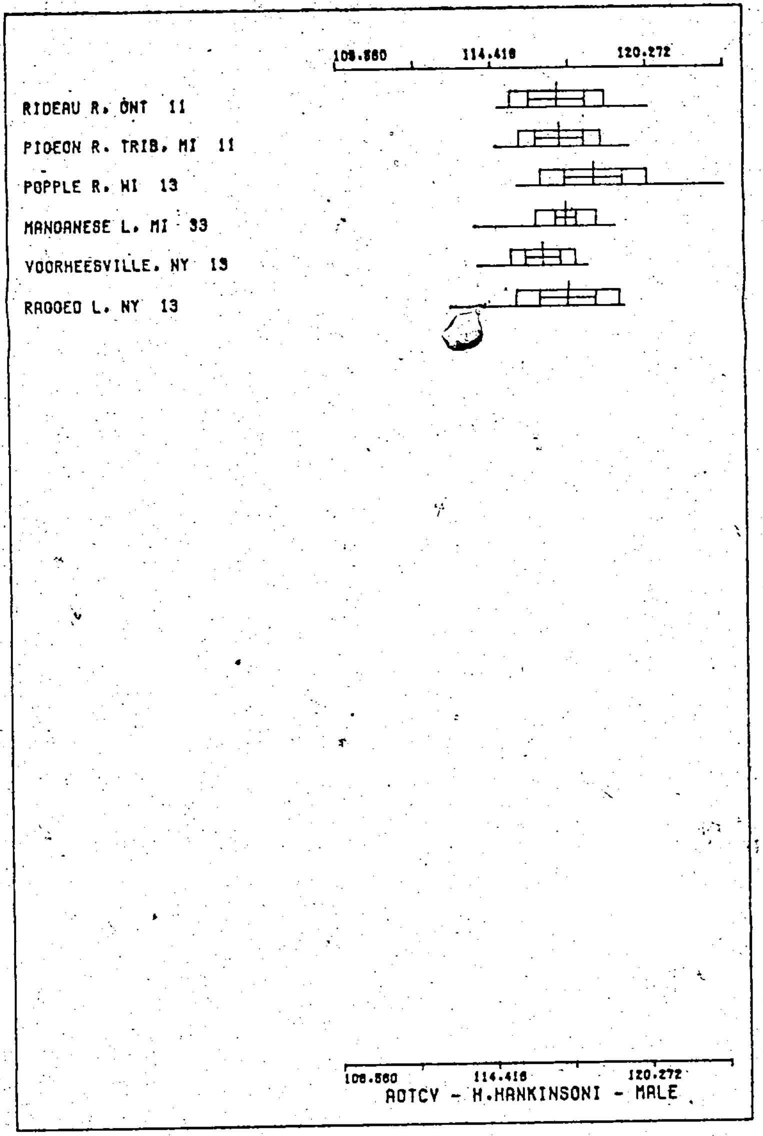

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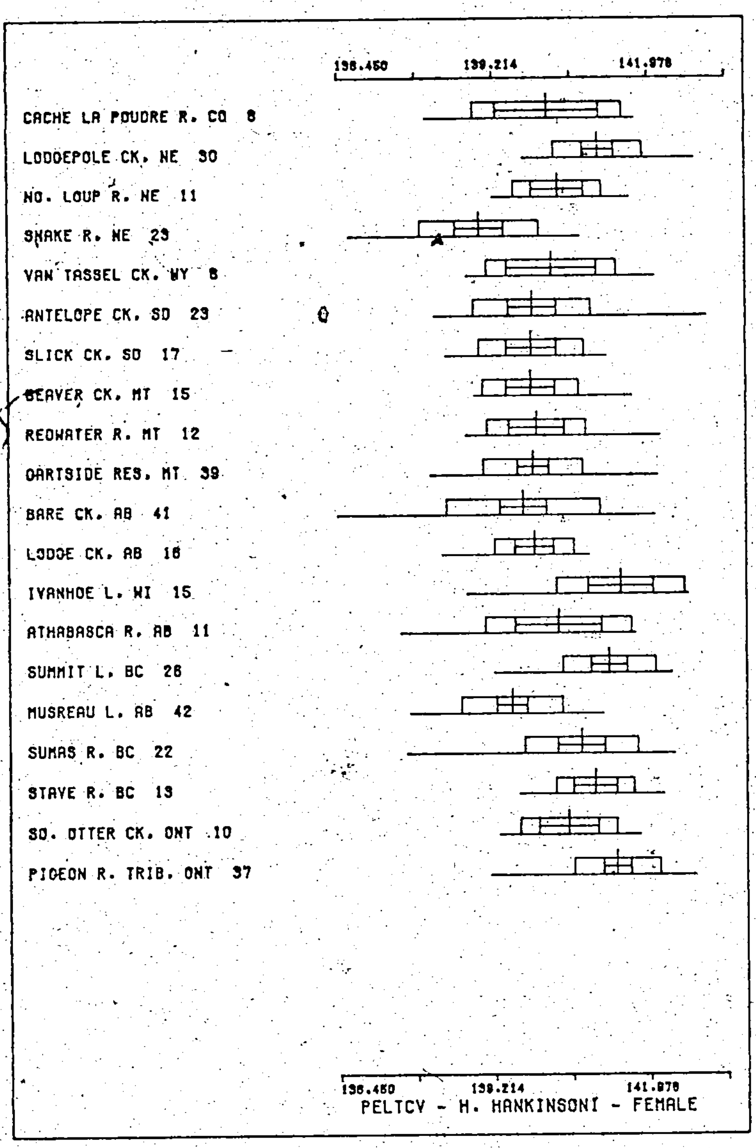

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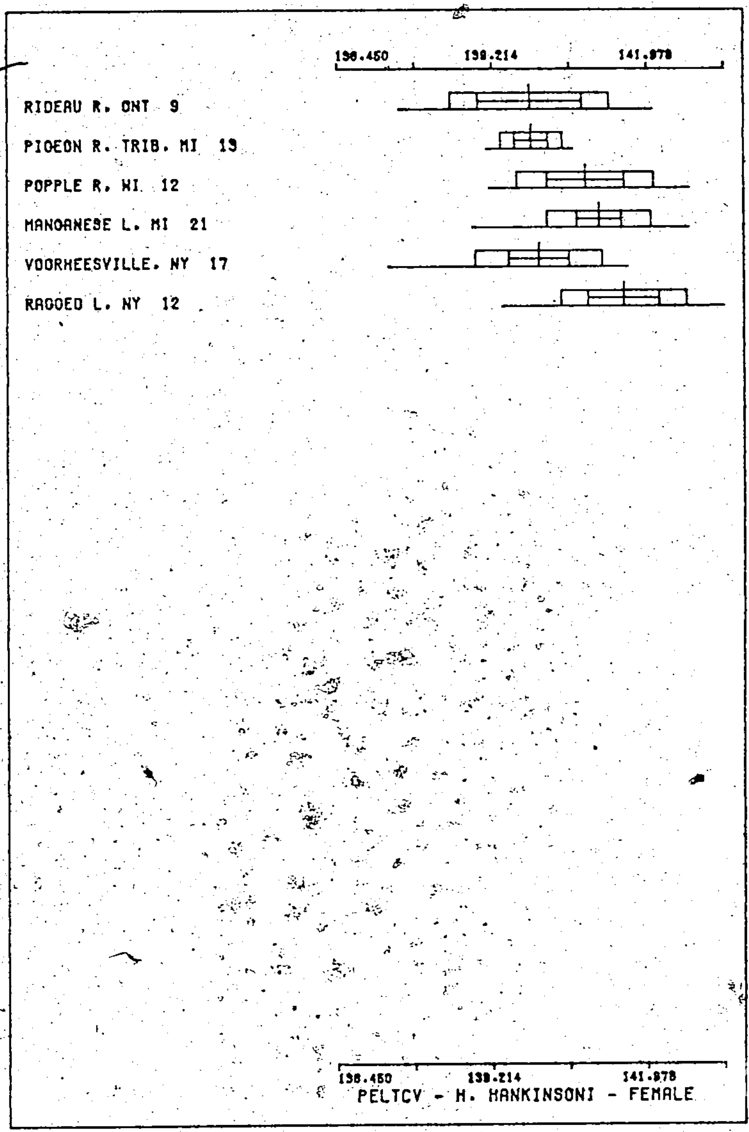

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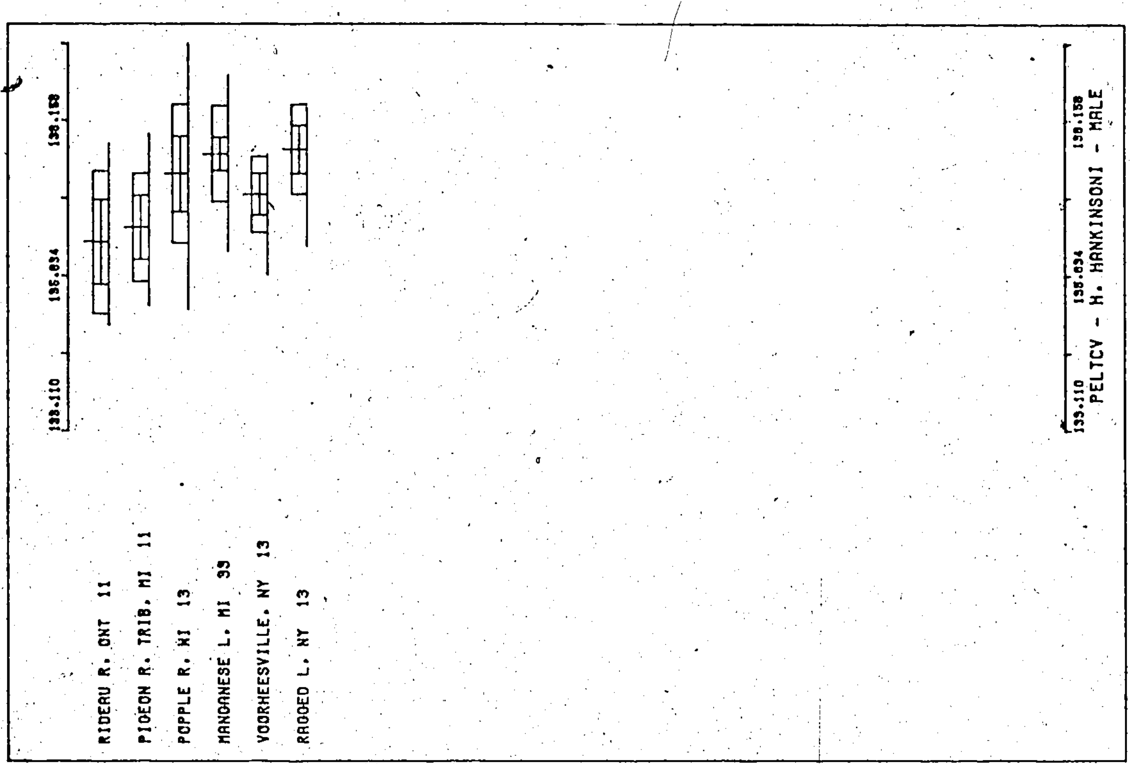
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RAGGED L. NY 13
193.110
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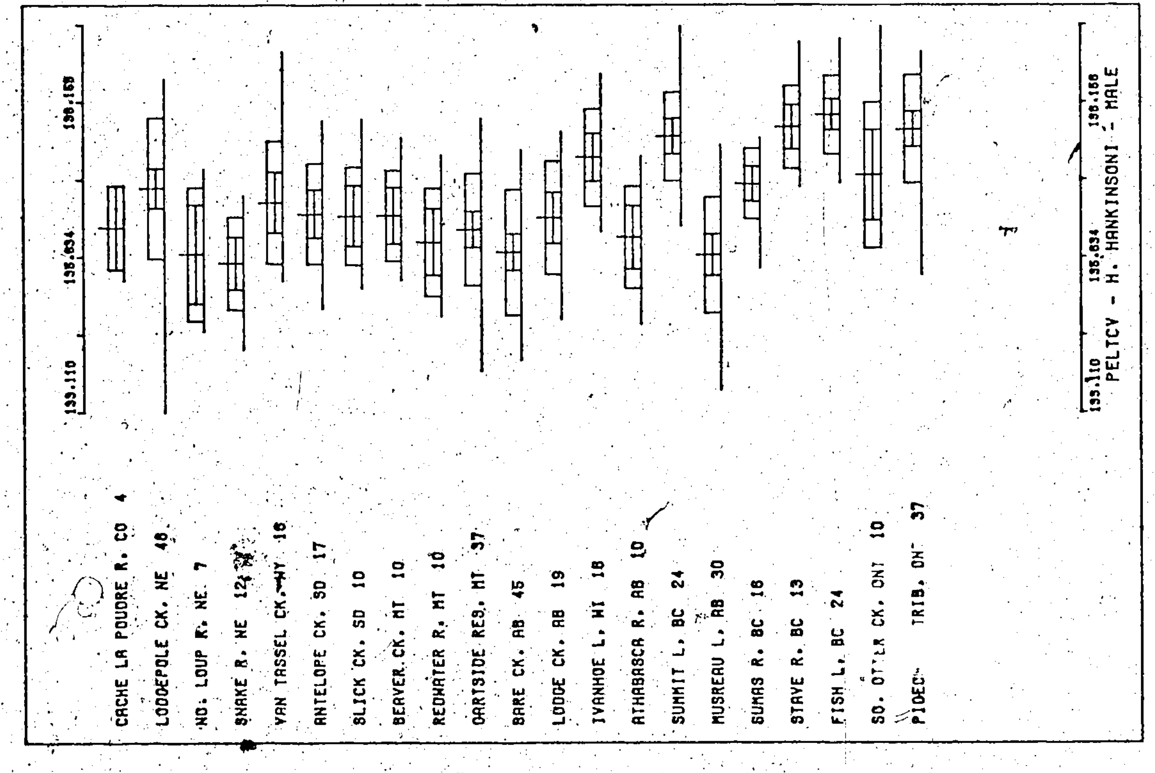
PELTCV - H. HANKINSONI - MALE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SNAKE R. NE 12
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ANTELOPE CK. SD 17
SLICK CK. SD 10
BEAVER CK. MT 10
REDWATER R. MT 10
GARTSIDE RES. MT 37
BARE CK. AB 45
LODGE CK. AB 19
IVANHOE L. WI 18
ATHABASCA R. AB 10
SUMMIT L. BC 24
MUSREAU L. AB 30
SUMAS R. BC 18
STAVE R. BC 13
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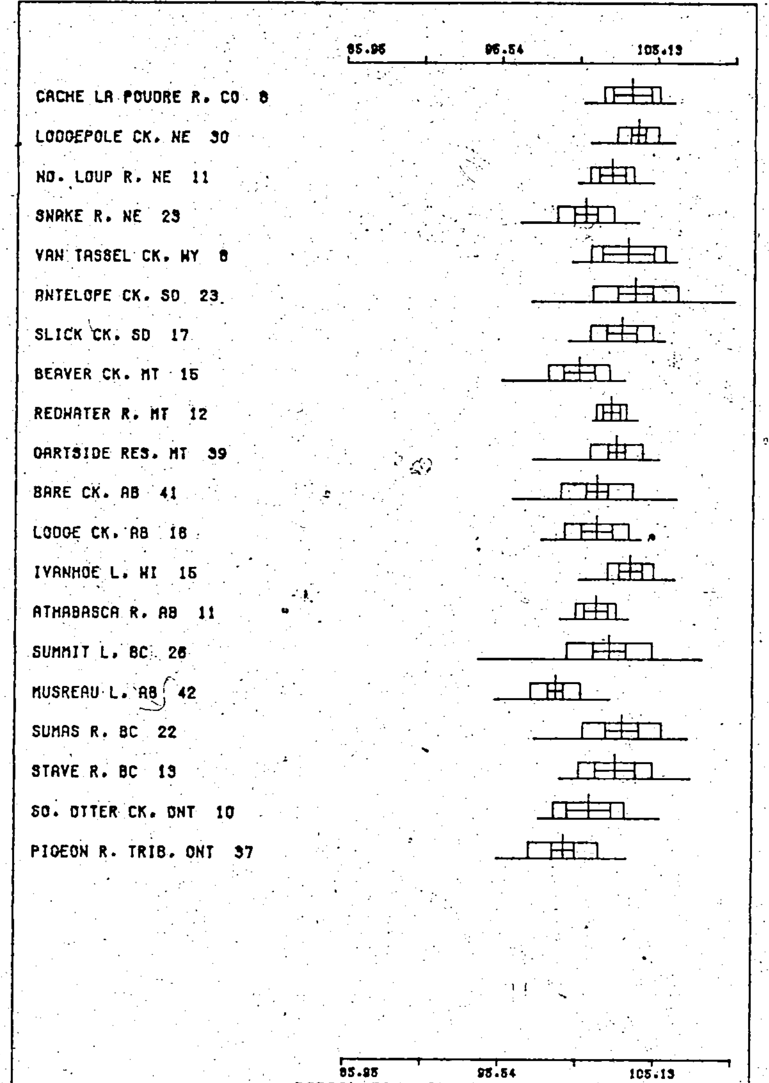
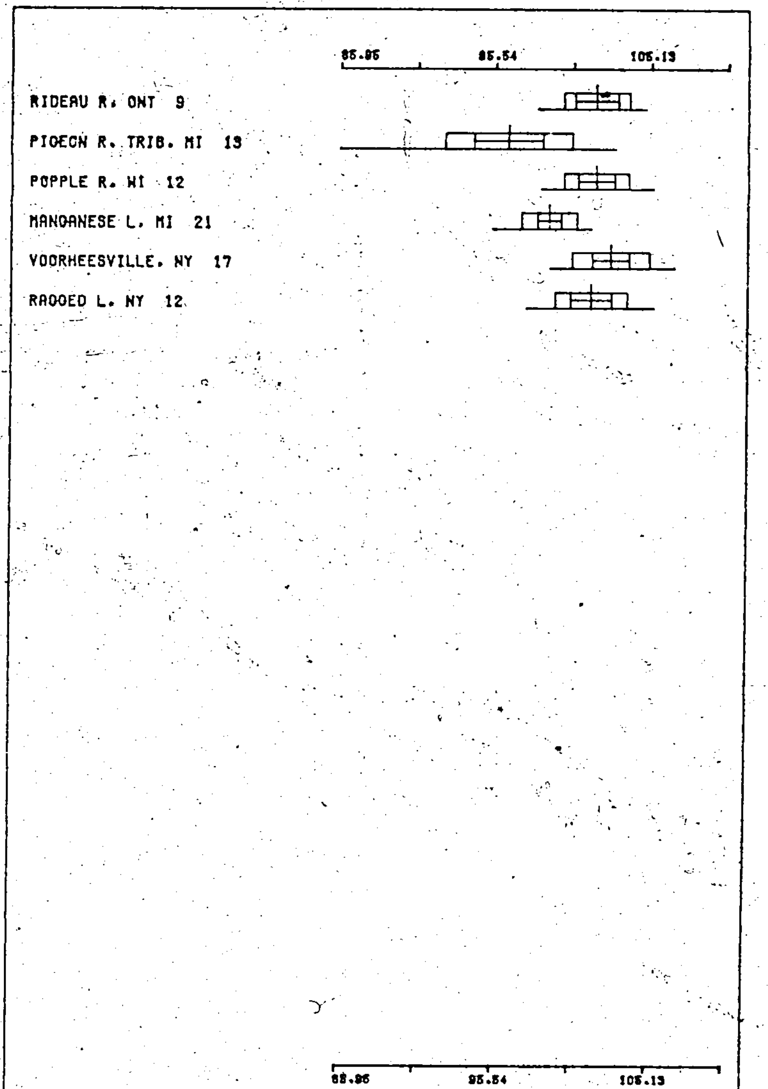


DORSAL FIN HEIGHT - H. HANKINSONI - FEMALE



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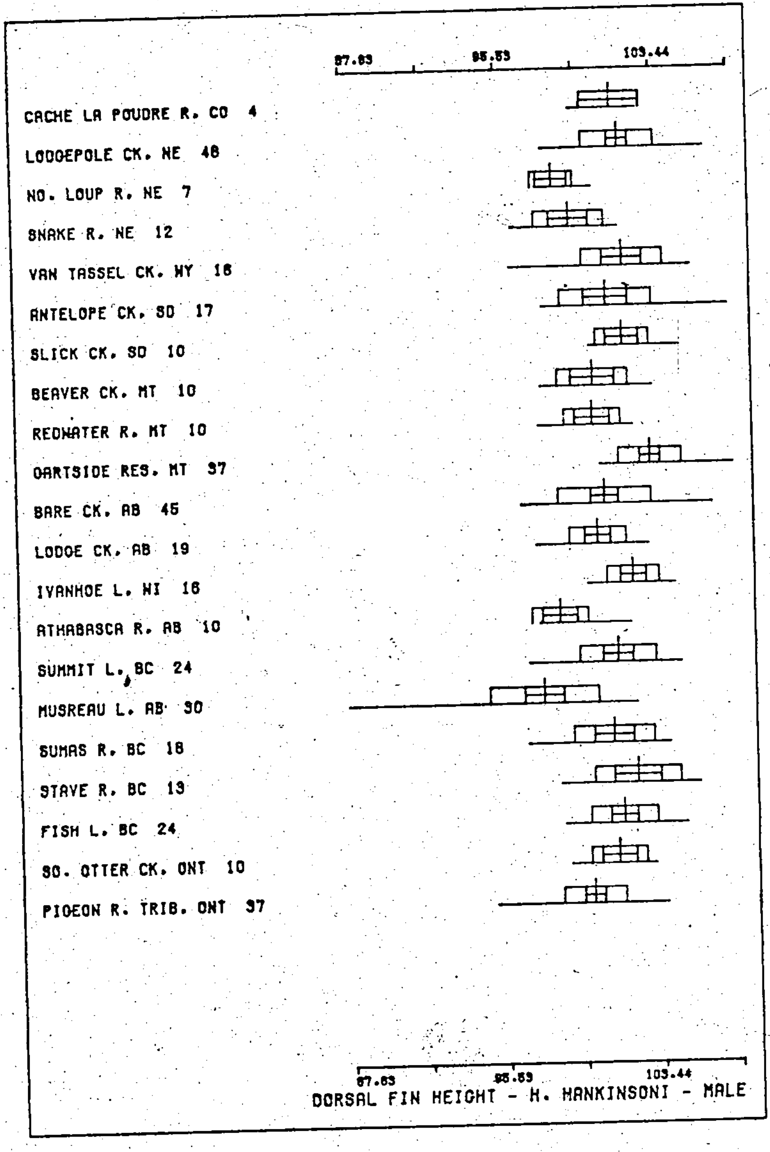

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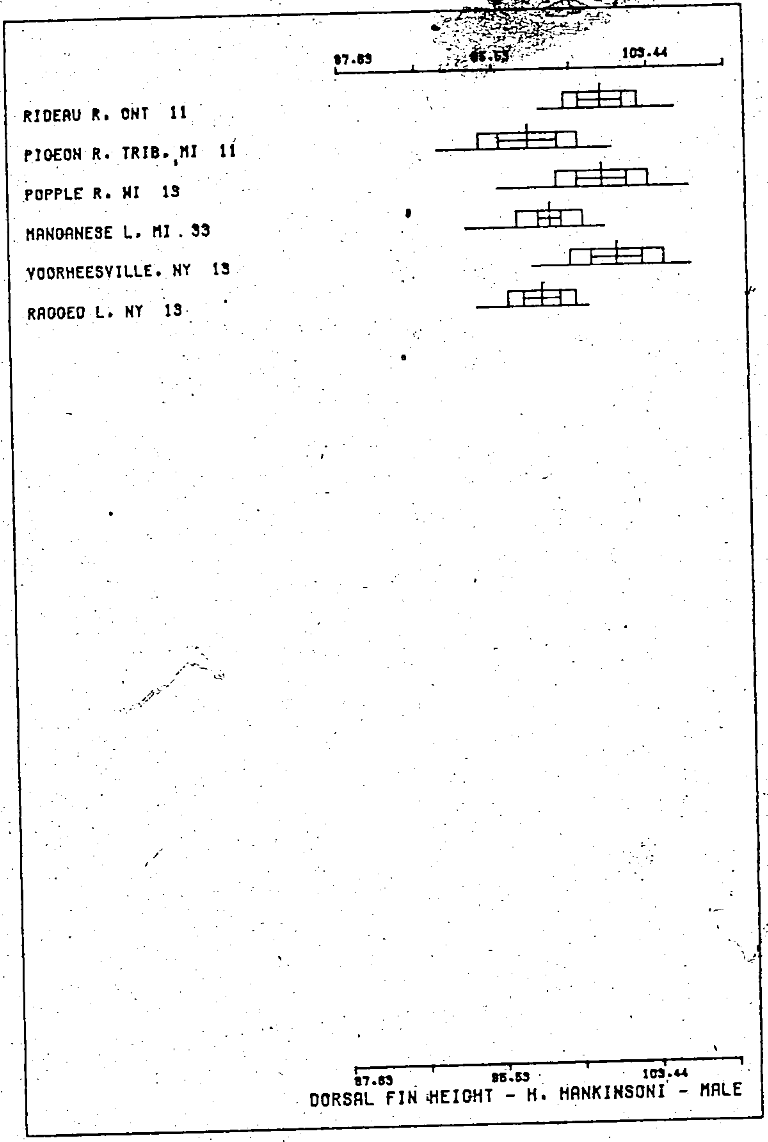

DORSAL FIN HEIGHT - H. HANKINSONI - MALE

Article 2. VARIATION AND ZOOGEOGRAPHY OF THE LAKE CHUB, COUESIUS PLUMBEUS

ABSTRACT

Over 3,300 Couesius plumbeus from 104 localities are compared using univariate and multivariate methods. Existence of three forms is confirmed. An upper Columbia River basin form, termed "greeni", possesses low scale counts and short dorsal, anal, pectoral, and caudal fins. The Missouri River basin "dissimilis" form possesses high scale counts, relatively blunt snout, long head, and small orbit diameter. The Atlantic - Great Lakes "plumbeus" form possesses relatively pointed snout, long dorsal, anal, pectoral, and caudal fins, long pelvic fin origin to terminal caudal vertebra distance, and large orbit diameter. All three forms intergrade extensively throughout the northwestern portion of the geographic range, while in the Lake Superior region "dissimilis" and "plumbeus" appear to be good biological species. Morphological differences between the "dissimilis" and "plumbeus" forms appear related to ecological differences.

The "greeni" form is postulated to have originated in the pre-Pleistocene Columbia River basin. During Pleistocene glacial periods it survived south of the Cordilleran ice sheet and then dispersed northward after the withdrawal of Sumas Stade ice from the Fraser valley. The

"dissimilis" form may have originated in the north-flowing pre-Pleistocene Missouri drainage system. Advancing Laurentide ice probably isolated it in the upper Missouri basin during the Wisconsin glacial period. Northward dispersal from this refugium may have begun as early as the Early Wisconsin. The "plumbeus" form may be of pre-Pleistocene Laurentian River system origin. During the Wisconsin it most likely survived in the upper Genesee River and lower Hudson River valleys. Dispersal was northwestward through the Great Lakes and glacial Lake Agassiz.

INTRODUCTION

Couesius plumbeus is a common and widespread North American cyprinid. Although as many as three forms have long been recognized, considerable controversy exists over their characteristics, taxonomic status, evolutionary origins, and postglacial dispersal routes. Recent studies of geographic variation attempting to resolve some of these questions (Lindsey, 1956; McPhail, 1963; Brown, 1969) were based on a few character trends derived from limited portions of the range. This study reexamines variation in this species using numerous characters sampled over the entire geographic range.

MATERIALS AND METHODS

Specimens from 104 localities (Table 1 and Figure 1) were obtained from the following institutions: University of Alberta Museum of Zoology (UAMZ); National Museum of Natural Sciences (NMC); Cornell University (CU); University of British Columbia (BC); University of Michigan Museum of Zoology (UMMZ); Royal Ontario Museum (ROM); Museum of Comparative Zoology, Harvard University (MCZ); University of Saskatchewan (US); Tulane University (TU); and University of Washington, College of Fisheries (UW).

Twenty-four characters (Table 2) were scored for 3,371 Co[illegible]beus. Counts and measurements were made as de[illegible] Hubbs and Lagler (1958) except as noted under "Uni[illegible]te Analysis". All measurements were made to the nearest 0.1 mm with needle point dial calipers and all counts were made with the aid of a dissecting microscope. Specimens under 35 mm standard length were not used.

When analyzing geographic variation one or more of the following confounding sources of variation must also be contended with: 1) sexual dimorphism, 2) growth , 3) individual variation, 4) measurement error, 5) environmentally induced variation, and 6) nonconcordance of characters resulting from recent genetic drift, founder effect, and selection. The methods used must be as such to identify and minimize these additional sources of variation.

Sexual dimorphism

Sexual dimorphism in pectoral fin length is obvious in C. plumbeus. In males this fin is larger, more rounded at the distal end, and at a somewhat different angle and position in relation to the body. Lesser degrees of dimorphism are associated with longer dorsal, anal, and pelvic fins in males and increased abdominal distances in females. Since dimorphism can occur in growth rates (slopes) as well as in average size (elevations), each character should be tested by analysis of covariance. By assuming sexual differences occur in all characters and analyzing each sex separately, not only are these tests eliminated but the two groups serve as replicates.

Growth

The general desirability of removing the growth factor can be questioned since size itself is often a useful taxonomic character. However, fishes are plastic in growth responses to environmental and populational parameters. Additionally, different collection techniques, each with its own inherent size bias, as well as various collection seasons, make the de-emphasis of size necessary.

Problems associated with growth have traditionally been solved by the use of morphometric ratios despite severe criticisms (Marr, 1956; Atchley, Gaskins, and Anderson, 1976; Atchley 1978). The primary function of ratios, elimination of the size factor, is accomplished only when certain precautions are taken (see Corruccini, 1977).

Additionally, ratios increase the complexity of interpretation by compounding each variable. Several statistical methods, such as regression analysis or principal component analysis, provide a much sounder basis for elimination of bias caused by the size factor. Although Model I linear regression techniques (no error in the independent variable) have been used for fitting allometric equations, Model II regression (independent variable error assumed), such as a reduced major axis on log transformed data, appears more applicable on theoretical grounds (Ricker, 1973) and gives a better fit in trials by computer simulation (Kidwell and Chase, 1967). A principal component solution can also be used to identify and remove size influence but, as demonstrated by Thorpe (1976), is generally less effective than a <u>priori</u> elimination of size by regression.

The effect of growth on mensural characters was minimized by first calculating the slope of the reduced major axis, allometric coefficient (v), for each character (j) such that $vj = (\Sigma\ vj^2 / \Sigma\ x^2)^{0.5}$ where $\Sigma\ yj^2$ = sum of squared deviations from mean character j (log10 transformed), and $\Sigma\ x^2$ = sum of squared deviations from mean standard length (log10 transformed). In general, allometric coefficients were calculated only for groups with 15 or more individuals which spanned a moderate to broad size range. Next, an average allometric coefficient for each character ($\bar{v}j$) was calculated from the following 58 localities: 1, 4, 5, 7-11, 13-20, 22, 24, 25, 27, 31-36, 39-42, 44-46, 50, 51, 54-56, 60, 63, 65-67, 69, 73, 74, 83-85, 91, 92, 94-97, 100-102 (Table 2). There was no apparent difference among locality slopes. Significance of deviation from isometry was not tested. Finally, each mensural character for each individual (Y'_{ij}) was adjusted by the average allometric coefficient to correspond to an average size ($\bar{X}$) of 58.2 mm standard length (log10 = 1.764612) for females and 55.4 mm standard length (log10 = 1.743650) for males, such that: $Y'_{ij} = (\log_{10} Y_{ij} - (\bar{v}_j (\log_{10} X_i - \log_{10} \bar{X}))100.0)$ where Y_{ij} = length in mm of character j of fish i, and X_i = standard length (mm) of fish i. Multiplication of the score by 100.0 minimizes loss of significant decimals due to rounding errors. After transformation sexes are no longer comparable unless readjusted to a common average size or converted to a standardized score (Z) as in the generalized distance (D^2) measure.

Individual variation

Individual variation is easily summarized for each locality and each character with univariate descriptive statistics once the effects of size have been minimized. Pooling of samples was generally restricted to samples collected at various times from the same locality. Only rarely, when few specimens were available, were samples from several geographically near collections pooled. Occasionally a single collection was suspected of non-homogeneity, e.g. two sympatric forms from Eagle River, Michigan. In these collections, homogeneity of the sample was analyzed with principal component analysis and the resulting two- or three-dimensional plots were inspected for obvious clusters. Discriminant analysis was then used to check the significance of the clusters and help reclassify any outliers. Descriptive statistics for the new groups were then recalculated.

Measurement error

Errors resulting from the inability to count or measure each character exactly are often ignored in hopes that they are equal between groups and characters. However, magnitude of the error component is relatively greater in small measurements thereby exaggerating the variance of these characters. This can have undesirable effects in several multivariate techniques but can be minimized by a priori elimination of those characters with unduly high within group variances. Characters with no variance over several groups generally must also be eliminated since matrix inversion cannot be performed if the matrix is singular.

Several characters were eliminated from further analysis on the basis of: 1) a nonsignificant analysis of variance (ANOVA) F-test, indicating no significant difference between localities in that character, or 2) an exceptionally high within group coefficient of variation (CV = (standard deviation * 100)/mean). A character with locality CV values commonly over 5-6% was suspected to have a relatively large error component. Number of dorsal fin rays showed little variance, being almost always eight, and was therefore eliminated. The two gill raker counts, interorbital width, and distance between pelvic fin origins were eliminated because of excessively high (over 5%) CV values. Gill raker counts were affected by the severity of damage by gill parasites, whereas the two mensural characters were too small to be measured accurately.

Environmentally induced variation

Environmental factors, such as temperature, oxygen, and productivity during early stages of development, are known to induce profound phenotypic changes (Martin, 1949; Taning, 1952; Lindsey, 1953; Barlow, 1961). The simplest method of estimating the effects of various environmental factors on wild caught specimens is a correlation analysis. Pearson product moment correlation coefficients between character means for each locality, as well as the first several canonical variate scores for each locality, with latitude, longitude, elevation, mean air temperature during spawning time, and water body type (lentic versus lotic), were calculated. Although these environmental parameters may not in themselves directly influence development, it is hoped that they will be correlated in some manner to factors, such as local water temperature and oxygen levels during early development, which may exert a direct influence and therefore indicate possible environmental induction.

Character nonconcordance

Nonconcordance of geographic variation between different characters demonstrates an obvious shortcoming in the use of univariate statistical measures of racial similarity. This can be overcome by combining many charaters into some overall measure. But, by combining characters information redundancy can occur due to such effects as pleiotropy and gene linkage. This difficulty can be overcome by using a measure of similarity that takes into consideration the variance - covariance structure of the data matrix, such as the generalized distance (D^2) of Mahalanobis (1936) or the closely related technique of canonical va[illegible] analysis. By these methods only the nonredundant information contributed by each character is used.

Display of the relationship among group centroids in a reduced dimensionality was accomplished with the canonical variate procedure BMD:07M (Dixon, 1973). Although this program does not give the generalized distance between any pair of centroids directly, it is easily calculated from the F-matrix. Unweighted pair-group method with arithmetic means (UPGMA) cluster analysis (CLUSTAN 1C: Wishart, 1975) using D^2 as a similarity measure was used if more than two or three axes were needed to account for a large percentage of the variance between centroids.

Sometimes local selective factors can obscure large scale geographic trends even with multivariate estimates of affinities. Use of polynomial trend surfaces can determine the degree of local influence and define regional trends

(Marcus and Vandermeer, 1966; Vandermeer, 1966). Polynomial trend surfaces of various degrees were fitted to the canonical scores for the first several canonical axes as well as to each character using SURFACE II (Sampson, 1975).

TAXONOMIC HISTORY

Agassiz (1850) described Gobio plumbeus from specimens taken during his 1848 exploration of Lake Superior. The exact location of this collection is unknown but was presumably along the northern shore of Lake Superior between Sault Ste. Marie and Thunder Bay. Girard (1856) moved Gobio plumbeus Agassiz to the genus Leucosomus and described a new species, Leucosomus dissimilis, from the Milk and Little Muddy rivers of the upper Missouri drainage. This new species was described as having smaller scales on the back as compared to those of the flanks, a large head and eye, and being "uniform greyish brown above, silvery along the middle of the flank and yellowish beneath." Jordan (1878) removed a species which he previously recognized as Nocomis milneri from Nocomis and placed it into a new genus, Couesius, honoring the ornithologist Dr. Elliott Coues. Four years later Jordan and Gilbert (1883) described the genus with four species: Couesius squamilentus (Cope), currently regarded as conspecific with Rhinichthys osculus (Baxter and Simon, 1970); Couesius dissimilis (Girard), with Gobio plumbeus Agassiz, Leucosomus dissimilis Girard, and Nocomis milneri Jordan placed in synonomy; Couesius prosthemius (Cope) from Montreal River, Keweenaw Point, Michigan (Cope, 1869); and Couesius physignathus (Cope), currently recognized as Hybopsis gracilis. Jordan (1893) added a new species, Couesius greeni, based on two specimens obtained from Stuart Lake, near Fort St. James, British Columbia, and stated that the new species differed "in the larger size of the scales and in some details of form." The head was noted as being especially large and heavy. Jordan and Evermann (1896) recognized five species in the genus. *Couesius prosthemius* was recognized as conspecific with the resurrected *Couesius plumbeus* Agassiz. *Couesius dissimilis* consisted of only Girard's *Leucosomus dissimilis*, with *Gobio plumbeus* Agassiz and *Nocomis milneri* being referred to *C. plumbeus* Agassiz. *Couesius greeni* Jordan, *C. squamilentus* Cope (= *Rhinichthys osculus*), and *C. adustus* Woolman were also recognized as distinct species. The latter species, from Rio de los Conchos, Chihuahua, Mexico (Woolman, 1895), now appears to be an error resulting from a labelling mix-up and/or confusion with *Algansea* and at least one other genus (Miller, 1976, and personal communication).

Doubt concerning the specific distinction of the three apparently valid forms, *C. plumbeus*, *C. dissimilis*, and *C. greeni*, seems to stem from Hubbs' (1926) statement in his "Check-list" regarding *C. plumbeus* from the Great Lakes. He states that "on comparison I am wholly unable to distinguish *C. dissimilis* from this species." In 1941, Hubbs and Lagler relegated at least the "plumbeus" and "dissimlis" forms to subspecific status and in subsequent editions of *Fishes of the Great Lakes Region* gave a refined list of key characters separating the two Great Lakes forms (see Table 3). In later editions, Hubbs and Lagler also pointed out that the subspecific designation of the "plumbeus" and "dissimilis" forms is in doubt since the two occur sympatrically in the Keweenaw Peninsula region of Michigan (see Taylor, 1954). This would seem to indicate full specific distinction, but they state that intermediate types have been reported to occur elsewhere. Unfortunately, no further details were given.

Bailey (1951) combined *Couesius* with *Hybopsis* with little discussion. From 1951 to 1970, when he reversed his decision, various authors accepted the change while others did not. Taylor (1954) noted that if *Couesius* were to be recognized as *Hybopsis*, then the name *Couesius plumbeus dissimilis* Girard was a junior homonym of *Luxilus dissimilis* Kirtland under the expanded *Hybopsis* and therefore must be abandoned. Taylor thought the name *Couesius greeni* Jordan was applicable and renamed *C. p. dissimilis* as *C. p. greeni*. Lindsey (1956), after examining specimens from 16 localities in the Mackenzie, Fraser, and Columbia systems as well as both eastern subspecies from Eagle River, Michigan, stated that equating the name *C. p. dissimilis* with *C. p. greeni* was erroneous. He also recommended that *C. plumbeus* be left without trinomial designation until a more thorough investigation was completed. McPhail (1963), in his study of dispersal patterns of fishes in northern North America, found evidence based on caudal peduncle scale cou[illegible] and vertebra numbers for two forms of *Couesius*; a Pacific form, in the Columbia, Fraser, and upper Peace drainage systems, and a widespread Missouri - Mississippi form (see Table 3). Brown (1969), in a study of variation in *Couesius plumbeus* from northern Saskatchewan, noted that although the eye diameter/snout ratio indicated *C. p. plumbeus*, the dorsal fin/predorsal ratio was intermediate between *C. p. plumbeus* and *C. p. dissimilis*. Both mean number of vertebrae (41.4) and mean number of caudal peduncle scales (20.9) were intermediate to McPhail's (1963) Missouri - Mississippi and Pacific forms. Brown therefore thought the Saskatchewan populations bridged the Missouri - Mississippi and Pacific forms and stated that there was probably no distinction between the eastern and western forms. Coad (1975) presented data on geographic variation in number of scale radii for *C. plumbeus* which tend to support McPhail (1963). He found mean total radii counts of 12.18, 12.62, and 12.06 for Nova Scotia, Saskatchewan, and Alberta, respectively, while counts from British Columbia averaged somewhat lower at 10.62.

DISTRIBUTION

Couesius plumbeus is one of the most wide ranging cyprinids in North America, occurring from the Atlantic to Pacific coasts and from Colorado northward to the Mackenzie Delta, Northwest Territories (Figure 1). In Alaska it occurs in the Yukon River as far downstream as Nulato (single specimen), but appears to be uncommon and restricted to the Yukon River proper and a few major tributaries (Wynne-Edwards, 1952; Walters, 1955; McPhail and Lindsey, 1970; Netsch, 1975). It is widespread throughout the Peace, Athabasca, and Mackenzie systems as well as throughout the Barren Grounds (McPhail and Lindsey, 1970; Paetz and Nelson, 1970; Scott and Crossman, 1973; Stein, Jessop, Porter, and Chang-Kue, 1973; Elson, 1974; Bishop, 1975; Bodaly and Lindsey, 1977). In British Columbia it is found in the upper Columbia system, portions of the Fraser system, and in the Skeena, Stikine, and Liard drainage systems, but appears to be absent from most of the coastal rivers south of the Skeena River (Jordan, 1893; Gilbert and Evermann, 1895; Godfrey, 1955; Lindsey, 1956, 1957, 1975; McPhail, 1963; Carl, Clemens, and Lindsey, 1967). Records from the upper Columbia River system extend as far south as Lake Pend d'Oreille, Idaho, while it appears absent from the lower Columbia system of Washington (Reimers and Bond, 1967). It has not been reported from the Clearwater system (Maughan, 1976), the next major drainage south of Lake Pend d'Oreille.

It also occurs in Twin Lakes, Washington, of the Stillaguamish River basin. This species has been recorded from most of the rest of Canada and the Great Lakes area and into the New England region of the United States (Kendall and Smith, 1895; Dymond, 1926; Bajkov, 1928; Greeley, 1935, 1936; Greene, 1935; Bailey, 1938; Hubbs and Lagler, 1941; Hinks, 1943; Radforth, 1944; Legendre and Rousseau, 1949; Dunbar and Hildebrand, 1952; Taylor, 1954; Backus, 1957; Keleher and Kooyman, 1957; Raney, 1969; Scott and Crossman, 1973; McAllister, 1975; Crossman, 1976). A report by Hankinson (1923) from Cattaraugus Creek in western New York appears to be in error as the predorsal scale counts given indicate possible confusion with *Semotilus*. Hubbs and Lagler (1949) reported *C. plumbeus plumbeus* from Desor Lake, a small isolated lake on Isle Royale, Lake Superior. The occurrence of *C. plumbeus* in the Mississippi River system appears to be based upon a single collection record from Iowa (Gerking, 1945; Bailey, 1956; Trautman, 1957). A previous report by Meek (1892) was apparently based on a hybrid of other species (Bailey, 1951). There appears to be only a single record from the Rainy River system and none from the Red River system of Minnesota (Underhill, 1957; Eddy, Tasker, and Underhill, 1972; Crossman, 1976). Absence of literature reports and collection records indicates that it is also absent or rare in the Qu'Appelle River, Souris River, Lake Manitoba, and Lake Winnipeg vicinities of southern Saskatchewan and Manitoba. *C. plumbeus* occurs in widely scattered regions of the Missouri and Platte river systems but is becoming increasingly rare in some areas while being artificially introduced into other areas (e.g. Yellowstone Lake) (Girard, 1856; Evermann, 1893; Eigenmann, 1895; Evermann and Cox, 1896; Schultz, 1941; Personius and Eddy, 1955; Bailey and Allum, 1962; Henderson and Peter, 1969; Willock, 1969; Baxter and Simon, 1970; Brown, 1971; Morris, Morris, and Witt, 1972). It appears to be no longer present in Colorado (Boulder and St. Vrain creeks) or the Great Divide Basin (Picket Lake), Wyoming (Ellis, 1914; Baxter and Simon, 1970).

RESULTS

Several collections from the Great Lakes region, especially the Eagle River material, were suspected of non-homogeneity on the basis of Hubbs and Lagler (1958). Principal component analysis on these localities failed in most cases to show distinct clusters, possibly due to insufficient sample sizes. However, the Eagle River material did show two clusters (Figure 2), which were significantly different above 95% confidence level. Although these collections were labled Couesius plumbeus plumbeus and Couesius plumbeus dissimilis by UMMZ, this designation was temporarily ignored. After the analysis, several individuals were found to be most likely misidentified. Characters with high positive loadings on the first principal component, i.e. those contributing substantially to the separation of the two groups, were dorsal fin height, anal fin height, caudal fin length, and orbit diameter. These characters closely correspond to those indicated by Hubbs and Lagler (1958) as separating the two forms.

Univariate Analysis

Univariate descriptive statistics were calculated for all characters and all localities for both sexes (Appendix A). Analysis of variance (ANOVA) was also conducted on both sexes for 37 localities with large sample sizes (Table 4). All characters for both sexes from these 37 localities displayed significant differences between locality means ($p < 0.01$). Coefficient of determination (r^2) and its significance for third degree polynomial trend surface on each character (Appendix A) are given in Table 5.

DIAGONAL SCALE ROWS - Diagonal scale row counts represent the sum of the count forward along a diagonal row from the base of the dorsal and anal fins, excluding the lateral line scale. Counts are highly variable both within localities (CV ≈ 6.0%) and between localities (both ANOVA F-tests are highly significant). Trend surface analyses indicate highest mean diagonal scale row counts, 20.0 to 18.5, occur throughout Ontario, Manitoba, Saskatchewan, Alberta, and the Missouri River basin. Counts gradually decrease to the north and east of this region and abruptly decrease west of the Continental Divide. Only approximately 30% of the total variance is explained by the third degree polynomial trend surfaces, indicating a great deal of local influence on this character. Both male and female trend surfaces are highly congruent.

CAUDAL PEDUNCLE SCALE ROWS - Caudal peduncle scales were counted around a diagonal row starting at a point adjacent to the end of the depressed anal fin. Counts obtained by this method are not directly comparable to those of McPhail (1963). This character is significantly correlated with number of diagonal scale rows ($r \approx 0.35$) and therefore contains some of the same information as the previous character. Again, within locality variation is high (CV ≈ 6.0%) as well as between locality variation. Although the coefficient of determination for each sex indicates that the third degree surface does not explain a significant amount of variance, higher order surfaces are highly significant and indicate a trend similiar to that of diagonal scale rows. East of the Continental Divide caudal peduncle scale counts averaged 25 - 27 while west of the divide they were generally 23 - 24.

HEAD LENGTH - Head length displays a high degree of between locality variation but little within locality variation (CV ≈ 1.0%). Both male and female trend surfaces are highly congruent and indicate longest head lengths in the Missouri basin. Shortest head lengths occur in eastern Ontario, Quebec, and New England region. Intermediate lengths are found throughout Alberta and Saskatchewan radiating northward into the Northwest Territories. The trend surfaces explain only 32% and 37% of the variance, indicating a great deal of local deviation from the regional trend.

ORBIT DIAMETER - This character shows a moderate degree of both within locality variation (CV ≈ 4.0%) and between locality variation. Male and female third degree trend surfaces show a relatively low degree of congruence with neither surface explaining a significant amount of variance. Higher order trend surfaces indicate a slight trend toward larger orbit diameters in the eastern portion of the range.

HEAD DEPTH AT NOSTRIL - Head depth at nostril tends to measure the bluntness of the snout. This character shows a moderate degree of within locality variation (CV ≈ 3.0%) while showing a high degree of between locality variation. Both male and female trend surfaces appear highly congruent and, respectively, explain 46% and 45% of the variance. Although the explained variance of this character is greater than almost any other character, the amount explained remains low and suggests that local factors are the major influence on overall variation. The trend surfaces indicate lowest scores (more pointed snout) occur in the east and highest scores (more rounded snout) occur in the Missouri basin. However, all regions show a rather steep gradient in character change. The only plateau region occurs throughout Alberta.

DORSAL FIN ORIGIN TO TERMINAL CAUDAL VERTEBRA - Distance from the origin of the dorsal fin to the terminal caudal vertebra displays very little within locality variation (CV ≈ 0.7%) but also little between locality variation. Both male and female trend surfaces show a north-south trend with a northward deflection in the west. Highest scores occur in the south and decrease northward. A plateau occurs throughout northern Quebec, northern Ontario, Manitoba through northern Saskatchewan and Alberta and into the Northwest Territories. Both trend surfaces are moderately congruent and account for 32% and 38% of the variance.

DORSAL FIN ORIGIN TO PECTORAL FIN ORIGIN - Distance from the origin of the dorsal fin to the anterodorsal origin of the pectoral fin shows, as might be expected, a significant negative correlation (r ≈ -0.50) to the previous character. This character displays a slightly higher within locality variation (CV ≈ 1.0%) and a slightly greater degree of between locality variation. Highest scores occur in the southwest portion of the range and decrease towards the northeast. There is relatively poor congruence between the male and female trend surfaces and only 28% and 26% of the variance is explained.

ANAL FIN ORIGIN TO TERMINAL CAUDAL VERTEBRA - This character shows little within locality variation (CV ≈ 1.0%) and a low degree of between locality variation. Both trend surfaces display a north-south trend with a northward deflection in the western portion of the distribution. Lowest scores are found within the Missouri River basin. There is moderate congruence between male and female trend surfaces with 24% and 32% of the variance explained.

PELVIC FIN ORIGIN TO TERMINAL CAUDAL VERTEBRA - Distance from pelvic fin origin to terminal caudal vertebra shows little within locality variation (CV ≈ 0.7%) and a low degree of between locality variation. Both trend surfaces are highly congruent and account for 31% and 42% of the variance. Highest scores occur in the extreme eastern portion of the range while lowest scores are found in the Missouri River basin. A steep gradient in character change occurs along a zone from the Great Lakes region northwestward to Alaska.

PECTORAL FIN ORIGIN TO TERMINAL CAUDAL VERTEBRA - This character displays the lowest within locality variation (CV ≈ 0.4%), but also shows a low amount of between locality variation. Both trend surfaces are only moderately congruent and indicate low scores in the south. High scores predominate in the west. There is relatively little change throughout Alberta northward into the Northwest Territories. Trend surfaces account for 34% of the variance in males and 57% in females.

PECTORAL FIN LENGTH - Pectoral fin length is moderately variable both within localities (CV ≈ 1.5%) and between localities. There is poor congruence between male and female trend surfaces. The female trend surface is highly significant and accounts for 27% of the variance while the male trend surface is just significant at the 95% level and accounts for only 21% of the variance. The difference in trend surfaces may reflect the extreme dimorphism of this character and the importance of the pectoral fin in male reproductive behavior. Both trend surfaces indicate lowest scores in the southwest and highest scores in the east.

CAUDAL FIN FORK DEPTH - Depth of the caudal fin fork, measured from the terminal caudal vertebra to the edge of the deepest indentation of the caudal fin, is moderately variable (CV ≈ 3.0%). This character shows a low degree of between locality variation. Both male and female trend surfaces indicate a general north-south trend with a slight northward deflection in the west. Lowest scores occur in the southwest portion of the range. A region of increased character change occurs through northern Alberta and northern British Columbia northwestward into Alaska. There is only moderate congruence between the male and female trend surfaces. The female trend surface accounts for 22% of the variance while a third degree trend surface for males does not explain a significant proportion of the variance.

CAUDAL FIN LENGTH - Caudal fin length is moderately variable both within localities (CV ≈ 2.0%) and between localities. Trend surfaces of both sexes are highly congruent and explain 34% and 28% of the variance. Highest scores occur in the east while lowest scores occur in the west. A region of rapid character change occurs over a broad belt extending from the Great Lakes northwestward to Alaska.

SNOUT TO ANUS DISTANCE - This character displays the next to lowest within locality variation (CV ≈ 0.6%) but also shows little between locality variation. Both trend surfaces are highly congruent and explain 45% and 44% of the variance. Highest scores occur in the Missouri River basin but rapidly decrease northward into central Alberta. Low scores form a plateau from Ontario northwestward into the Northwest Territories. Low scores also occur in the southwest portion of the distribution.

DORSAL FIN HEIGHT - Depressed dorsal fin lengths are moderately variable (CV ≈ 2.0%) within localities but show a high degree of interlocality differentiation. Both trend surfaces are highly congruent and explain 31% and 37% of the variance. High scores occur in the extreme eastern portion of the range while low scores occur in the southwest. A region of transition occurs over a broad area from the Great Lakes northwestward to Alaska.

ANAL FIN HEIGHT - This character is highly correlated with dorsal fin height ($r \approx 0.65$). Anal fin height is only moderately variable within localities (CV ≈ 2.0%) but shows a high degree of between locality differentiation. Both trend surfaces are highly congruent. The male trend surface explains 25% of the variance while that of the female explains 31%. Trends are very similar to those of dorsal fin height.

BREAST TUBERCLES - McPhail and Lindsey (1970) stated that male C. plumbeus in western populations develop an extremely rough patch of tubercles just anterior to the pectoral fins, and also indicated that it was not known whether this condition was present in the "Mississippi" form. This roughened patch of tubercles was observed in males from nearly all samples, including the Missouri and Atlantic (= "Mississippi") populations. Development of these tubercles is size dependent, rarely being present in males under approximately 50 mm standard length and is undoubtedly associated with sexual maturity. They also appear to be more pronounced during reproductive periods.

NUPTIAL COLORATION - The occurrence of reddish orange markings in the pectoral axil and around the corners of the mouth has been widely reported in the literature (Brown, 1969; Scott and Crossman, 1973) from populations east of the Continental Divide. McPhail and Lindsey (1970) state that breeding males of the "Pacific" form (= "greeni") do not develop this coloration. Personal observation of live, mature, reproductive specimens from throughout southern and central Alberta indicate that both sexes develop this color pattern. Mature specimens of both sexes collected from Gantahaz Lake (locality 39, upper Peace River system, British Columbia) collected by myself also possessed reddish orange pectoral axil markings. However, this area may represent a region of intergradation between the "greeni" and eastern Missouri "dissimilis" forms.

Multivariate Analysis

The following 37 localities, chosen on the basis of sample size and geographic location, were considered as "knowns" for canonical variate analysis: 8, 10, 11, 13-16, 18-20, 22, 24, 27, 31, 34, 39-42, 44, 46, 50, 51, 59, 65, 67, 69, 73, 74, 83, 85, 91, 94, 97, and 100-102. Centroids for the remaining 67 localities (Appendix A) were calculated for the first, second, and third canonical axes from the 37-group solution canonical coefficients. Characters providing the most separation between locality centroids for males were both scale counts, head length, dorsal fin height, pectoral fin length, and dorsal fin origin to pectoral fin origin (Appendix A). Characters contributing to the separation of the female groups were similar with both scale counts, head length, dorsal fin height, pelvic fin origin to terminal caudal vertebra, dorsal fin origin to pectoral fin origin, and pectoral fin origin to terminal caudal vertebra contributing most heavily (Appendix A).

However, by choosing 37 separate localities, characters which emphasize interlocality differences will be selected by the analysis. These character combinations may or may not be the optimal character set for revealing any racial structure. Absence of distinct clusters in the 37-group canonical plots, as well as in the UPGMA cluster analysis (Figure 3), indicates several possibilities: 1) no racial structure occurs, 2) the choice of many individual localities has obscured any racial structure by emphasizing interlocality differences rather than interracial differences, or 3) extensive intergradation has occurred. To examine these possibilities, the scores of only those localities within possible refugia (Columbia, Missouri, and Atlantic coastal drainages) were plotted (Figure 4) (see ZOOGEOGRAPHY for reasons on excluding Bering and Mississippi refugia). At least some geographical consistency, with a minimum of three groups, is present but the clusters are poorly defined.

A second canonical variate analysis was performed with the localities from the Columbia (localities 49-51), Missouri (localities 1-5, 7-11), and Atlantic coastal (localities 82-85, 91, 102) regions pooled to form three "known" groups. ANOVA on the characters from the pooled samples again revealed a significant difference between the univariate character means of the three groups (Table 6). Characters emphasized by this analysis are only slightly different in terms of relative discriminating power from those in the 37-group solution, but direction of influence of some characters (Figure 5) was radically changed. The clusters are compact and well defined with average generalized distances (D^2) of 20.4, 14.6, and 13.4 between the Missouri and Columbia centroids, Missouri and Atlantic centroids, and Columbia and Atlantic centroids, respectively, giving a theoretical separation of 98.8%, 97.2%, and 96.6%, respectively (Figure 6). This corresponds closely to the number of individuals actually correctly assigned by the classification phase of the program (Table 7).

Based on the canonical coefficients from the three-group solution, the centroids for each of the 104 localities on the first two axes were computed. The results still show no distinct clusters, indicating extensive intergradation has probably taken place (Figure 7).

Third degree trend surfaces for canonical scores along the first three axes of the 37-group solution and the first two axes of the three-group solution are significantly related to geography (Table 5).

CANONICAL AXIS I - Trend surfaces for 37-group male (Appendix A), three-group female (Figure 8a), and three-group male (Figure 8b) are highly congruent. The trend surface for 37-group female (Appendix A), while slightly different, reflects the same relationship. A small plateau of high scores in the Missouri basin gradually decreases in value as it radiates northwestward through Alberta to Alaska. Scores drop rapidly but smoothly west of the Rocky Mountains. Low scores occur from the upper Columbia system northward into the Fraser, upper Peace, and Liard River systems. Low scores also cccur throughout New England, the Atlantic provinces, Quebec, and eastern Ontario, rising gradually to the west. There is no abrupt break between the eastern region and the ridge of high scores just east of the Rocky Mountains, only a smooth, gradual transition. The relatively low amount of explained variance (39%, 38%, 37%, 43%) indicates a high degree of local influence.

CANONICAL AXIS II - Trend surfaces for both sexes and both 37- (Appendix A) and three-group (Figure 9) analyses are highly congruent. High scores occur west of the Rocky Mountains from the upper Columbia basin northward to the Yukon system. Scores drop sharply but smoothly east of the Continental Divide and form a plateau of low scores throughout Saskatchewan eastward. Again, low coefficients of determination (29%, 31%, 51%, 51%) indicate a high degree of local influence.

CANONICAL AXIS III - The 37-group solution appears to represent much the same trend as canonical axis I. Low coefficients of determination (37%, 43%) again indicate a high degree of local influence. This third axis is not calculated for the three-group solution.

Trend surfaces appear to represent radiations from three centers: upper Columbia, upper Missouri, and Atlantic coast. The upper Columbia center radiates northward as far as Alaska and is primarily restricted to west of the Rockies. The upper Missouri center radiates northward to Alaska along the eastern slope of the Rockies and through the prairie regions while the Atlantic coast center radiates in a northwestward direction.

Environmental Induction

Although many significant non-zero correlations between structure and environment were found, most were of the order of 0.20 to 0.40, or explaining less that 16% of the variance (r^2) of that character. Additionally, if several different races are involved, spurious correlations may occur based solely on the geographic distribution of these races. If environmental factors are influencing structure, then the effects might be expected to be similar within the sexes and races. However, when considered in this manner (Appendix B), no characters or canonical axes appeared to be strongly and consistently correlated to any environmental parameter. Therefore, environmental factors appeared to have negligible effects on structural features of Couesius plumbeus.

It should be noted that in pooled samples (all localities), significant correlations between water type (sample from lentic or lotic habitat) and length of the anal, dorsal, and caudal fins, head length, head depth at nostril, and caudal fin fork depth occurred. These characters are among the most discriminating between the "plumbeus" and "dissimilis" forms. The significant correlations probably reflect an association between the "plumbeus" form and lacustrine environments and between the "dissimilis" form and fluviatile environments.

Summary

Three distinct but intergrading forms of C. plumbeus can be recognized. An Atlantic form occurs along the Atlantic coast and into the Great Lakes. This form may be termed the "plumbeus" form as Agassiz's syntypes (locality 103, Figure 7) appear to correspond to this group. The Mississippi drainage specimens (locality 12, Figure 7) do not appear significantly different from this type. This form intergrades extensively to the northwest but remains distinct throughout most of the Great Lakes. The "plumbeus" form typically possesses intermediate scale counts, large orbit diameter, long dorsal, anal, pectoral, and caudal fins, intermediate caudal fork depth, short head length, pointed snout, dorsal fin position similar to "dissimilis", anus in an intermediate position, and long pectoral fin origin, pelvic fin origin, and anal fin origin to terminal caudal vertebra distances (probably resulting from an elongation of the caudal peduncle region) (Table 6). Eagle River "plumbeus" (locality 74) while closely resembling typical Atlantic "plumbeus", differ by possessing longer fins and a larger orbit diameter. Suggestions by Greeley (1935, 1936) and Raney (1969) that specimens from the Delaware River (locality 102) differ from specimens from upper New York are not substantiated as upper New York specimens, based on zoogeographic reasons (see ZOOGEOGRAPHY), are most likely typical "plumbeus". The typical Missouri form corresponds to C. dissimilis Girard and occurs in the upper Missouri and Platte River systems. Specimens from Swiftcurrent Creek (locality 14) of the South Saskatchewan River system and Pothole Creek (locality 13) of the St. Mary River system do not appear to be significantly different from this form (Figure 7). "Dissimilis" from the Lake Superior region, while somewhat different from the typical Missouri form, appear closest to this form. In the Lake Superior region this form occurs in the rivers of the Keweenaw Peninsula region and possibly a few rivers along the northern lake shore. Specimens from Desor Lake, Isle Royale (locality 75), are not significantly different from the Eagle River (locality 73) "dissimilis" (Figure 7). The "dissimilis" form typically possesses high scale counts, intermediate orbit diameter, intermediate dorsal, anal, pectoral, and caudal fin lengths, shallow caudal fork depth, long head length, blunt snout, dorsal position similar to "plumbeus", anus situated more posteriorly, and short pectoral fin origin, pelvic fin origin, and anal fin origin to terminal caudal vertebra distances (probably resulting from a shortening of the caudal peduncle region). The upper

Columbia form occurs in the upper Columbia, lower Fraser, Kootenay, Okanagan, Pend d'Oreille, and Stillaguamish River systems. This form may only approximate C. greeni Jordan as Stuart Lake, the type locality, lies within a region of apparent intergradation with the "dissimilis" form. Typically the "greeni" form has low scale counts, small orbit diameter, short dorsal, anal, pectoral, and caudal fin lengths, deeply forked caudal fin, long head length, snout region intermediate to "plumbeus" and "dissimilis", dorsal fin position further posterior than "plumbeus" or "dissimilis", anus situated more anteriorly, and intermediate pectoral fin origin, pelvic fin origin, and anal fin origin to terminal caudal vertebra distances. The "greeni" form appears to intergrade with "dissimilis" in the upper Fraser and upper Peace systems. Yukon Territory and Alaska specimens appear intermediate to all three forms.

If evolutionary rates can be considered relatively constant, then the "plumbeus", "dissimilis", and "greeni" stocks are most likely of equivalant geologic age since the square root of the generalized distance (D), the distance between centroids expressed in standard deviation units, is nearly equal between each of the three groups.

ZOOGEOGRAPHY

The last major event to shape the distribution patterns of northern North American fishes was the Wisconsin glaciation, beginning approximately 50,000 years before present (YBP). During this period, freshwater fishes survived in ice free regions of the Yukon, Columbia, Missouri, Mississippi, and Atlantic basins (McPhail and Lindsey, 1970). The present range of C. plumbeus potentially includes all of these possible refugia but its limited distribution in the Yukon River system suggests recent arrival and therefore an unlikely refugium (Walters, 1955; McPhail, 1963; McPhail and Lindsey, 1970).

Genetic differences accumulated during long periods of isolation have been used to speculate possible Pleistocene refugia and postglacial dispersal routes (see McPhail, 1963; Nelson, 1969; Lindsey, Clayton, and Franzin, 1970; Franzin and Clayton, 1977; and many others). However, many of these differences may have been established in pre-Pleistocene times. Metcalf (1966:81) suggested that repeated Pleistocene glacial episodes in plain-like regions may have enhanced mixing of stocks rather than isolation. He attributed some specific and subspecific differences in several groups of fishes to extended periods of isolation in pre-Pleistocene drainage systems, as did Pflieger (1971). The fossil record also suggests longer periods of evolution. Nearly all post-Nebraskan North American fossil fishes are indistinguishable from living species (Miller, 1965:571). Even most Miocene remains are referable to extant genera. Therefore, any discussion of the zoogeography of C. plumbeus must consider pre-Pleistocene history as well.

The "greeni" populations may have originated in the pre-Pleistocene Columbia River basin. Its entrance into this system may have occurred as early as Early Pliocene to as late as Middle Pleistocene. Transfer of fishes from east to west of the Continental Divide during this time is evident from the fossil occurrence of the eastern catfish genus, Ictalurus, in Early Pliocene to Middle Pleistocene deposits of Washington, western Oregon, and southern Idaho (Miller, 1965:577). During Pleistocene glacial episodes, "greeni" probably remained in the Columbia basin (McPhail, 1963; McPhail and Lindsey, 1970) (Figures 9 and 10). Flooding of glacial lakes Missoula, Couer d'Alene, Spokane, and Columbia during the Bull Lake (Early Wisconsin) and Pinedale (Late Wisconsin) glacial periods (Richmond, et al., 1965) may have served to widen its distribution in this region.

The "greeni" stock could have dispersed northward soon after the retreat of the Sumas Stade ice (Figure 12). The lower Fraser River valley was probably ice free by at least 9,000 YBP (Armstrong, et al., 1965; Fulton, 1971) and as the ice retreated a series of glacial lakes formed in the Nicola, Thompson, North Okanagan, and Shuswap basins (Fulton, 1969) allowing access to the Fraser River system.

The thermal maximum at about 6,000 YBP (Fulton, 1969:19-24) may have eliminated many of the southern populations.

The isolated occurrence of "greeni" in Twin Lakes, Washington (locality 104, Stillaguamish River drainage), is somewhat puzzling. The "greeni" stock may have survived in glacial Lake Russell, which occupied the Puget Sound basin (McPhail, 1967), but extinction may have occurred with a post-Vashon rise in sea level (approximately 13,000 YBP). Crandell (1965:346) indicated that sea levels relative to land in northwestern Washington fluctuated through a vertical interval of 180 m, due to eustatic rise in sea level and isostatic rebound, before settling to its modern level. Twin Lakes lies at a present elevation of 227 m and therefore may have escaped marine encroachment.

Following the final major glaciation of north central British Columbia, glacial lakes formed in the Fort St. James, Vanderhoof, and Prince George basins (Armstrong and Tipper, 1948). The Prince George basin received water from the upper and lower Fraser River and drained northward to the Peace River system via the Crooked River (Tipper, 1971). Specimens from this region appear intermediate between the "greeni" and "dissimilis" stocks. Mixing could have occurred since "dissimilis" may have entered via the Peace River system and/or via the upper Fraser River. Glacial Lake Miette formed from below Brule Lake, Alberta, and crossed the Continental Divide nearly to Moose Lake (Fraser River drainage), British Columbia (Taylor, 1960), at approximately 14,000 YBP (estimate based on St-Onge, 1972). Specimens from Moose Lake (locality 56) show greatest similarity to the "dissimilis" form (Figure 7), indicating an early transfer of fishes from the Missouri basin (via Athabasca system) to the upper Fraser River system.

The "greeni" form may have also spread through the Peace system to the Liard, Skeena, Stikine, Tanana, and upper Yukon systems (McPhail, 1963; McPhail and Lindsey, 1970). The Liard Hot Springs specimens (locality 41), while most closely related to the "greeni" form, are highly unusual in that they possess an especially long, deep head and short fins. These differences may be the result of direct environmental induction on phenotypic expression resulting from the warm water temperature (25 C, D.E. McAllister, personal communication) or possibly have a genetic basis. Clarke (1976) mentioned an undescribed species of snail, Physa, which is only found in the cool water adjacent to the warm effluent from the hot springs. Although this may argue for endemism in the Laird Hot Springs area, again the question of direct environmental influence must be asked. Unfortunately, specimens of C. plumbeus from adjacent cool springs were unavailable for comparison.

The Missouri or "dissimilis" form most likely originated in the pre-Pleistocene north-flowing ancestral Missouri system. Its absence or scarcity in most of the lower Missouri, lower Platte, Kansas, and Arkansas drainages suggests that it did not occur in the pre-Pleistocene Plains Stream. Advancing Pleistocene ice may have isolated it in the upper Missouri basin (Figure 10). Postglacially it appears to have dispersed into the upper Saskatchewan River system. Horberg (1954) indicated several glacial lakes that could have been used. Willock (1969) hypothesized a connection between Frenchman River (locality 9, Missouri drainage) and Swiftcurrent Creek (locality 14, South Saskatchewan drainage) as well as between the Milk River (locality 8, Missouri drainage) and St. Mary River (locality 13, South Saskatchewan drainage). There is no significant difference between canonical scores for these four localities (Figure 7), further suggesting an intimate connection.

Much of southern Alberta and the eastern Rocky Mountain foothill region was ice free possibly as early as Early Wisconsin, more than 55,000 YBP (Reeves, 1973). The last Laurentide advance reached only as far south as the present Oldman River in the Medicine Hat to Lethbridge region (Stalker, 1977). Radiocarbon dates indicate that this advance corresponds to the Late or Classical Wisconsin, approximately 25,000 YBP (Stalker, 1977:2618-2619). Deposits in the Smoky River valley, near Watino, Alberta, also indicate early ice free areas. Radiocarbon dates from this locality range from 43,500±620 to 27,400±850 YBP (Westgate, et al., 1972). These fossiliferous sediments are overlain by proglacial lacustrine silts and clays. Alley and Harris (1974) also indicated a series of glacial lakes of probably similar age in the foothill region of southern Alberta. This "Ice Free Corridor" may have extended far northward and, with the exception of the relatively short-lived coalescence of the Marlboro and Edson glaciers in the Athabasca region, dispersal via its numerous proglacial lakes and channels may have been relatively unrestricted (Reeves, 1973:11). If so, the "dissimilis" form may have gained very early access to southern Alberta and the foothill regions and may have, as discussed previously, crossed the Continental Divide through the Athabasca and Peace River systems (Figure 11). Northward dispersal would be easily accomplished through the Mackenzie River system. In the southern portion of its range its presence in the Cheyenne system of South Dakota might be explained by headwater capture from the Little Missouri River (locality 4) by the Belle Fourche River, which in turn joins the Cheyenne River (Bailey and Allum, 1962). Bailey and Allum (1962) suspected that its occurrence in the Sweetwater River (locality 1, Platte drainage) was also due to stream capture between the upper Bighorn or Powder rivers and the North Platte River.

Occurrence of the "dissimilis"-like form in the Lake Superior region has several possible explanations. If the "dissimilis" stock had its origin in the north-flowing pre-Pleistocene Missouri system, then advancing Laurentide ice probably diverted fishes both west to the upper Missouri basin and east to the upper Mississippi basin (McPhail and Lindsey, 1970:9; Pflieger, 1971:288). A portion of the "dissimilis" stock may have become isolated in the upper Mississippi basin at this time. Its morphological differentation from the typical Missouri "dissimilis" and its presence in Desor Lake, Isle Royale, seem to indicate an extended period of isolation and early arrival into the area. However, the lakes of Isle Royale were formed by receding levels of the Great Lakes, probably during the Minong phase (Hubbs and Lagler, 1949), which Hough (1958) dated at between 6,000 and 8,000 YBP. This would not exclude the possibility of transfer from the Missouri system via the Saskatchewan River system to glacial Lake Agassiz and into the Great Lakes, as proposed by McPhail (1963) (Figure 12). The eastern outlets of glacial Lake Agassiz may have begun operating prior to this period (Elson, 1967; Zoltai, 1967). If this were the situation, then the morphological differentation between the Great Lakes "dissimilis" vis-a-vis the typical Missouri "dissimilis" as well as the Eagle River "plumbeus" vis-a-vis the typical Atlantic "plumbeus" might be explained in terms of character displacement.

Possible refugia and dispersal routes of the eastern populations of C. plumbeus have stirred considerable controversy. Greene (1935), in probably the first discussion of the zoogeography of C. plumbeus, stated that it must have closely followed the retreating ice margin and most likely used all main glacial dispersal routes (Lake Agassiz outlet, St. Croix outlet, Fox River connectives, Chicago outlet, and Fort Wayne outlet) in its dispersal into the Great Lakes from a supposed refugia in the upper Mississippi basin. However, Underhill (1957) noted that C. plumbeus is absent from the upper Mississippi and present-day St. Croix River systems. He considered it common only in the Lake Superior and Hudson Bay drainage systems of Minnesota and pointed out that if it had used all postglacial routes, as suggested by Greene, then its absence from suitable habitats in the headwaters of the St. Croix and upper Mississippi rivers must be explained. Underhill did not accept the notion of an upper Mississippi basin refugium and stated that it probably reached the Lake Superior region in post-Lake Duluth time. He postulated that dispersal from an eastern center via eastern outlets of glacial Lake Agassiz would explain the present distribution without the necessity of rationalizing its absence from its supposed source. McPhail (1963) argued against this theory, claiming that absence from a particular unglaciated region does not exclude it from being a possible refugium since postglacial ecological changes may have brought about localized extinction. McPhail postulated a single eastern form that was thought to have survived in widespread areas throughout the unglaciated portions of the upper Missouri, upper Mississippi, and possibly Ohio River valleys. The distribution pattern of this eastern form could be explained by dispersal from the upper Missouri into the Saskatchewan and Mackenzie River systems and then eastward through glacial Lake Agassiz II. Its absence from the upper Mississippi - St. Croix region could be explained by its reaching Agassiz II after the Warren River outlet ceased to function. Dispersal into the Great Lakes was probably eastward into glacial Lake Duluth after the St. Crcix outlet closed. He also suggested that the isolated Mississippi River drainage population in Iowa (locality 12) represented a relict population that failed to expand or possibly one that may have dispersed there postglacially through the Des Plaines River outlet.

The "plumbeus" form probably originated in the east-flowing pre-Pleistocene Laurentian River system. The advancing ice may have restricted it to the extreme eastern portion of North America during glacial episodes (Figure 10). Dadswell (1974:49) suggested that small proglacial lakes in eastern Ohio, upper Genesee River valley, and lower Hudson River valley may have served as refugia for some fishes and aquatic crustaceans. The "plumbeus" form may have survived in this region. Its occurrence in the Delaware River system (locality 102) and Finger Lakes of New York is best explained by refugia in the Genesee River valley (Salamanca re-entrant) and the lower Hudson River basin (glacial Lake Albany). Entrance from the Genesee basin to the Lake Arkona phase of the Great Lakes could have occurred via glacial Lake Hall, approximately 13,000 YBP

(Goldthwait, et al., 1965; Muller, 1965; Wayne and Zumberge, 1965) (Figure 11). For a detailed discussion of aquatic dispersal routes in this area see Dadswell (1974).

Eastward dispersal of "plumbeus" from the Great Lakes region could have been facilitated by the Mohawk - Hudson, Trent, and Ottawa outlets while northern and westward dispersal may have occurred through glacial lakes Agassiz and Barlow - Ojibway. Late Campbell phase Lake Agassiz (9,500 YBP) drained northwest to the Clearwater River system (Athabasca - Mackenzie system) and may have brought it into the glacial Lake Tyrrell region. Eastern outlets of Lake Superior in the Lake Nipigon region (Zoltai, 1967) most likely would have given access to glacial Lake Agassiz only after the Warren outlet ceased to function.

The Mississippi drainage population (locality 12) most likely represents a late postglacial dispersal rather than preglacial relict population. The similarity of this population to the typical "plumbeus" stock argues against the relict theory. Dispersal may have been through the Des Plaines outlet or more likely through the Fox River outlet.

As McPhail (1963) suggested, C. plumbeus from the Missouri basin (= "dissimilis") may have also entered glacial Lake Agassiz from the Saskatchewan system during this time. This may have resulted in an intergraded stock which dispersed northward through the Mackenzie system (Figure 12). McPhail envisaged northern dispersal as through the Mackenzie system into the Yukon via a Peel River

(Mackenzie) and Porcupine River (Yukon) connection. Its presence in the Anderson River could be explained by headwater capture while its occurrence in the Thelon, Dubawut, and Kazan rivers could result from flooding of lowland areas connecting these systems to the Mackenzie system. Bodaly and Lindsey (1977) disagree with a dispersal route to the Yukon through the Peel system (via the Davis outflow channel) since, if this were the route, C. plumbeus should now be present in the Peel River. They cite its distribution in the Peel system as only as far upstream as mile 62 of the Snake River and Dog Lake. This suggests that dispersal into the Yukon system was rather via Summit Lake at McDougall Pass in post-Wisconsin periods of high water.

The absence of C. plumbeus from much of the present day Ohio, New England, and Lake Erie regions may be explained by a combination of factors. The Hypsithermal period (6,000 YBP) may have eliminated it from much of this region. The present southern limit of the "plumbeus" form closely parallels the 21 C July - August surface water isotherm, indicating a possible strong temperature influence (Figure 13). Distribution of "plumbeus" in eastern North America may also have been influenced by late glacial intrusion of the Champlain Sea into Lake Ontario, and the St. Lawrence River and lower Ottawa River valleys approximately 11,900 to 10,500 YBP (Mott, 1968; Dadswell, 1974). For some reason, C. plumbeus has not been able to re-invade much of this area.

TAXONOMIC CONCLUSIONS

Formal taxonomic recognition of any or all of the three forms of Couesius plumbeus cannot be recommended as the differences between them do not lend themselves to taxonomic categorization. In most northern areas the three stocks have freely introgressed while in the Lake Superior basin, the "dissimilis" and "plumbeus" forms occur sympatrically and seem to be good biological species. The primary distinction between "dissimilis" and "plumbeus" appears to be ecological. The "plumbeus" form is lentic, only entering streams to spawn (Radforth, 1944; Hubbs and Lagler, 1958), and is generally associated with cold water species such as coregonids and salmonids (Greene, 1935). The "dissimilis" form, on the other hand, is lotic and appears to be associated with warmer water fauna. In southern and central Alberta it is rarely collected in lakes, and is associated with such species as Pimephales promelas, Catostomus catostomus, Catostomus commersoni, Etheostoma exile, Phoxinus eos, Rhinichthys cataractae, Culaea inconstans, Hybopsis gracilis, and Lota lota (personal collection records). Morphological adaptations between the "plumbeus" and "dissimilis" forms bear out this distinction. Hopkirk (1973), in listing fluviatile versus lacustrine adaptations, cites many of the major differences observed between the two forms. Taylor (1954) also indicated this ecological separation. He reported the sympatric occurrence of the two forms in the upper peninsula of Michigan from only the Eagle River. Whereas the "dissimilis" form was taken at all upstream localities, the "plumbeus" form was taken only at the mouth of the river where it outnumbered the "dissimilis" form 321 to nine.

Svardson (1957:269) described an analogous situation of morphological similarity and ecological diversity in Palearctic whitefishes. He suggested ecological traits of a species may be the last to disappear when introgression takes place and that introgression may be extensive in small lakes while slight in large lakes. This may be the explanation for the persistence of separate stocks in the Lake Superior region. Similar situations have also been described in Nearctic whitefishes (Lindsey, 1963; McPhail and Lindsey, 1970) as well as stickleback (Bell, 1976; Larson, 1976) and cyprinids (Hopkirk, 1973). As additional northern freshwater species are examined in greater detail, this phenomenon may be discovered to be even more widespread.

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Table 1. Localities, collections, and sample sizes for *Couesius plumbeus*.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size	
					Female	Male
Platte River Drainage						
1	Sweetwater R., WY	42°31'	108°12'	UMMZ 127543, 127552	14	20
Missouri River Drainage						
2	Wind R. Trib., WY	43°02'	108°23'	UMMZ 114646	8	7
3	Spring Ck., SD	43°58'	103°11'	UMMZ 87303	11	9
4	Little Missouri R., WY	44°35'	104°56'	UMMZ 161937	18	12
5	Pennel Ck., MT	46°34'	104°47'	UMMZ 94157	16	22
6	Powers L., ND	48°32'	102°40'	UMMZ 162338	0	1
7	Sage Ck., AB	49°07'	110°15'	NMC 66-390	17	29
8	Milk R., AB	49°07'	112°24'	UAMZ 170, 3840, 3841, uncatalogued; NMC 67-666	37	40
9	Frenchman R., SASK	49°10'	107°35'	NMC 67-642	12	21
10	Bare Ck., AB	49°15'	110°15'	UAMZ 3340, 3836	24	45

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size	
					Female	Male
11	Lodge Ck., AB	49°19'	110°07'	UAMZ 3566, 3835, 3837	30	43
	Mississippi River Drainage					
12	Twin Springs Ck., IOWA	42°30'	90°44'	UMMZ 171146; TU 10208	2	5
	South Saskatchewan River Drainage					
13	Pothole Ck., AB	49°25'	112°52'	UAMZ 3843, 4000	43	21
14	Swiftcurrent Ck., SASK	49°54'	108°16'	NMC 70-207	27	27
15	Upper Kananaskis Res., AB	50°38'	115°08'	UAMZ 3346	26	34
16	Lower Kananaskis Res., AB	50°40'	115°07'	UAMZ 2522, 2746, 2754, 3345	29	30
17	Red Deer R., AB	51°28'	112°42'	UAMZ 174, 3326, 3847, 3871	28	22
	North Saskatchewan River Drainage					
18	Abraham Res., AB	52°18'	116°20'	UAMZ 3350, 3354, 3369	39	32
19	Battle R., AB	52°35'	111°18'	BC 67-10	25	31

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size	
					Female	Male
20	North Saskatchewan R., AB	53°37'	113°34'	UAMZ 588, 589, 590, 592, 593, 1135, uncatalogued	30	34
Churchill River Drainage						
21	Cold L., AB	54°36'	110°12'	UAMZ 3602	2	0
22	Lac la Ronge, SASK	55°05'	105°19'	ROM 24646; US uncatalogued	30	44
Athabasca River Drainage						
23	House R. AB	55°37'	112°11'	UAMZ 3445, 3844, 3845	7	9
24	Hangingstone R., AB	56°25'	110°23'	UAMZ 3432	32	18
25	Dover R., AB	57°05'	112°06'	UAMZ 3417, 3436	24	23
26	Cree L., SASK	57°30'	106°30'	ROM 19078	13	8
Slave River Drainage						
27	Little Buffalo R., NWT	60°20'	112°50'	UAMZ 2152, 2153, 2561, 3905; NMC 68-180	34	39
28	Hay R., NWT	60°45'	115°50'	UAMZ 3038	8	1

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Male
29	Slave R., NWT	61°10'	113°15'	UAMZ 1581	5	1
Lower Peace River Drainage						
30	Cutbank R., AB	54°38'	118°41'	UAMZ 3903	5	7
31	Little Smoky R., AB	54°45'	117°10'	UAMZ 1654	35	27
32	Smoky R., AB	55°14'	118°15'	UAMZ 1657	24	25
33	Dunvegan Ck., AB	55°56'	118°36'	UAMZ 1663	20	24
34	Hotchkiss R., AB	57°04'	117°34'	UAMZ 3341	31	20
Upper Peace River Drainage						
36	Summit L., BC	54°16'	122°38'	UAMZ 3897, 3944; BC 56-363	16	23
37	Firth L., BC	54°50'	122°45'	NMC 76-329	9	9
38	McLeod L., BC	54°55'	122°57'	UAMZ 3226, 3943	12	6
39	Gantahaz L., BC	55°25'	123°12'	UAMZ 3220, 3942	47	55
40	Williston Res., BC	55°25'	123°20'	UAMZ 3223, 3224	32	27

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Male
Liard River Drainage						
41	Liard Hot Springs, BC	59°25'	126°03'	NMC 74-485	16	14
Mackenzie River Drainage						
42	Lac la Martre, NWT	63°07'	117°48'	BC 61-56	42	34
43	Fort Norman, NWT	64°56'	125°35'	ROM 21147	18	5
44	Norman Wells, NWT	65°20'	126°52'	ROM 21145, 21146; NMC 73-201, 73-202, 73-204	36	29
45	Fort Good Hope, NWT	66°16'	128°29'	ROM 21151, 21153	17	16
46	Peel R., YT	66°30'	134°11'	BC 60-349	25	33
47	Mackenzie Delta, NWT	68°32'	134°48'	NMC 60-455, 62-136, 62-139	6	4
Anderson River Drainage						
48	Anderson R., NWT	68°25'	128°51'	NMC 62-524	2	0

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size	
					Female	Male
Columbia River Drainage						
49	Deep Ck., ID	48°35'	116°20'	UMMZ 157026	7	8
50	Jewel L., BC	49°12'	118°37'	BC 59-342	35	23
51	Hiawatha L., BC	49°19'	115°50'	BC 56-496	17	18
52	Okanagan L., BC	49°36'	119°37'	BC 54-203	5	0
Fraser River Drainage						
53	Sumas R., BC	49°07'	122°07'	BC 56-598	1	0
54	Alkali L., BC	51°46'	122°16'	BC 55-437	11	21
55	Chimney Ck., BC	52°05'	122°15'	BC 56-370	13	17
56	Moose L., BC	52°58'	118°55'	UAMZ 2228	14	10
57	Ten Mile L., BC	53°05'	122°27'	BC 59-128	12	4
35	Eulatezella L., BC	53°42'	123°35'	BC 64-260	19	23
58	Purden L., BC	53°55'	121°55'	UAMZ 3230	5	6
59	Fish L., BC	54°16'	122°38'	UAMZ 3945	20	6

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
60	Middle R., BC	54°30'	124°15'	BC 54-258	12	19
Yukon River Drainage						
61	Takhini R., YT	60°50'	135°10'	ROM 33213	1	2
62	Donjek R., YT	61°41'	139°46'	BC 58-179; ROM 33202	5	11
63	Sandpete Ck., YT	62°03'	140°40'	BC 58-183	12	15
64	Niggerhead L., YT	62°15'	140°20'	BC 58-185	7	26
65	Enger L., YT	62°15'	140°40'	ROM 33219	29	15
66	Tanana R., AK	63°18'	142°38'	BC 58-187; ROM 33272	12	14
67	Stewart R., YT	63°35'	135°52'	BC 58-287	32	23
68	Yukon R., YT	64°04'	139°26'	BC 58-281	8	10
St. Lawrence River Drainage						
69	Sable R., ONT	46°28'	82°10'	NMC 64-738	23	25
70	Crogan L., ONT	46°31'	79°00'	ROM 32383	2	18
71	Emerald L., ONT	46°48'	79°18'	ROM 32384	6	6

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
72	Salmon Trout R., MI	46°50'	87°46'	UMMZ 193642	11	6
73	Eagle R., MI (D)	47°24'	88°17'	UMMZ 133274, 133280, 133303, 133383, 133391	44	39
74	Eagle R., MI (P)	47°24'	88°17'	UMMZ 133280, 133381, 133383, 133392	43	29
75	Isle Royale, MI	47°58'	88°59'	UMMZ 99984	7	4
76	Simons Harbour, ONT	48°16'	86°08'	NMC 73-448	0	3
77	Louie L., ONT	48°25'	85°51'	NMC 72-215	5	1
78	Current R., ONT	48°33'	89°16'	NMC 64-52; ROM 19891	4	5
79	MacIntosh L., ONT	48°45'	88°43'	NMC 64-53	2	0
80	Nishin L., ONT	48°55'	87°38'	NMC 64-55	1	1
81	Durie R., ONT	48°58'	91°15'	ROM 30254	2	8
Atlantic Coastal Drainages						
82	Latimer L., NB	45°19'	65°54'	NMC 60-73	3	2

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
83	Caribou R., NS	45°45'	62°47'	NMC 59-292	29	18
84	Miramichi R., NB	47°00'	65°34'	NMC 59-278	16	10
85	Escuminac R. Trib., NB	47°04'	64°53'	NMC 59-281	18	28
Hudson Bay Drainage						
86	Lac des Commisaires, QUE	48°10'	72°16'	NMC 71-725	2	6
87	Lac Chibougamau, QUE	49°50'	74°15'	NMC 70-463	1	1
88	Lac du Lagopede, QUE	52°29'	70°12'	NMC 71-227	1	2
89	Lac Vallard, QUE	52°52'	68°57'	NMC 71-223	5	4
90	La Grande R., QUE	53°50'	79°00'	NMC 74-206	2	0
91	Sandgirt L. Trib., NFLD	53°52'	65°17'	NMC 69-379	27	27
92	Knob L. Trib., QUE	54°46'	66°46'	NMC 58-350	8	10
93	Lake Canichico, QUE	56°47'	68°41'	NMC 58-355	0	1
94	Big Trout L., ONT	53°43'	90°06'	NMC 61-268; ROM 21318	28	32
95	Kanuchuan Rapids, MAN	54°22'	94°49'	ROM 19336	12	13

Table 1. Continued.

#	Locality	Latitude (N)	Longitude (W)	Collection(s)	Sample Size Female	Sample Size Male
96	Weir R., MAN	56°47'	94°14'	ROM 17517	17	10
97	Silcox Ck., MAN	57°09'	94°10'	ROM 17487	32	44
98	Caribou R., MAN	59°24'	95°18'	NMC 66-223	7	4
99	Thlewiaza R., NWT	60°23'	95°45'	NMC 66-224	1	1
100	Angikuni L., NWT	62°16'	99°36'	BC 60-40, 60-42	32	33
101	Whitefish L., NWT	62°36'	106°43'	BC 60-106	11	8
	Delaware River Drainage					
102	E. Br. Delaware R., NY	42°06'	74°37'	CU 50885, 55506, 55507, 55508, 55510	11	13
	Syntypes - Gobio plumbues					
103	"Lake Superior"	-----	-----	MCZ 1747+27505, 18716	16	3
	Stillaguamish River Drainage					
104	Twin Lakes, WA	48°11'	121°56'	UW 12531	6	3

Table 2. Character list and average allometric coefficient of mensural characters (vj) for female and male Couesius plumbeus.

	Character	Female (n=58)	Male (n=58)
DSR	Diagonal scale rows	******	******
CPS	Scales around caudal peduncle	******	******
TPGR	Total primary gill rakers	******	******
TAGR	Total accessory gill rakers	******	******
DFR	Dorsal fin rays	******	******
BT	Breast tubercles	******	******
RPAC	Red pectoral axil coloration	******	******
HL	Head length	0.9489	0.9232
ORBD	Orbit diameter	0.7803	0.7945
INW	Interorbital width	0.9868	1.0084
HDN	Head depth at nostril	1.0291	1.0063
DOTCV	Dorsal fin origin to TCV	1.0269	1.0733

TCV = terminal caudal vertebra

Table 2. Continued.

	Character	Female (n=58)	Male (n=58)
DOPEC	Dorsal fin origin to pectoral fin origin	1.1030	1.0663
AOTCV	Anal fin origin to TCV	1.0055	1.0497
PELTCV	Pelvic fin origin to TCV	1.0197	1.0448
PECTCV	Pectoral fin origin to TCV	1.0405	1.0370
SNA	Snout to anus distance	1.0382	0.9920
DFH	Dorsal fin height (depressed)	0.9593	1.0061
AFH	Anal fin height (depressed)	1.0060	1.0873
PECL	Pectoral fin length	1.0664	1.1903
CFKD	Caudal fin fork depth	0.9847	1.1092
CFL	Caudal fin length	0.9433	0.9783
PELW	Width between pelvic fin origins	1.2388	1.2952
SL	Mean standard length (log10)	1.764612	1.743650
--	Mean standard length (mm)	58.2	55.4

TCV = terminal caudal vertebra

Table 3. Summary of published differences among "plumbeus", "dissimilis", and "greeni" forms of Couesius. Compiled from Jordan and Evermann (1896), Lindsey (1956), Hubbs and Lagler (1958), and McPhail (1963).

	"plumbeus" Agassiz 1850	"dissimilis" Girard 1856	"greeni" Jordan 1893
Lateral line scales	60-70	64-72	54-65
Scales above lateral line	11	12	10
Shape of dorsal fin	falcate	rounded	med. falcate
Dorsal fin length	longer	shorter	variable
Dorsal / predorsal ratio	<1.7	>1.7	****
Eye diameter	>2/3 snout length	<2/3 snout length	variable, closer to "plumbeus"
Body shape	compressed	terete	****
Mouth position	terminal	subterminal	****
Mean caudal peduncle scales	21.5-23.6		18.8-20.8
Mean vertebra numbers	41.5-42.4		40.5-40.7

Table 4. Univariate ANOVA F-test value among character means for female and male <u>Couesius plumbeus</u> from thirty-seven localities.

Character	Female F(36,1064)	Male F(36,1020)
DFH	54.79**	42.12**
DSR	42.14**	40.24**
AFH	38.57**	33.69**
HL	32.00**	37.76**
HDN	35.45**	27.28**
CPS	30.11**	28.22**
CFL	25.03**	25.12**
ORBD	25.37**	24.37**
PECL	23.29**	18.47**
DOPEC	17.11**	14.74**
PELTCV	15.86**	14.08**
AOTCV	14.15**	13.65**
PECTCV	12.69**	15.05**
CFKD	13.15**	13.93**
SNA	14.15**	12.55**
DOTCV	13.77**	11.46**

** = $p<0.01$

Table 5. Third degree polynomial trend surface coefficient of determination for characters and canonical variate scores of female and male _Couesius plumbeus._

Character	Female	Male
DSR	0.326***	0.287***
CPS	0.123	0.081
HL	0.315***	0.367***
ORBD	0.128	0.098
HDN	0.447***	0.464***
DOTCV	0.323***	0.381***
DOPEC	0.275***	0.262**
AOTCV	0.320***	0.241**
PELTCV	0.310***	0.418***
PECTCV	0.341***	0.556***
SNA	0.451***	0.442***
DFH	0.313***	0.367***
AFH	0.311***	0.249**
PECL	0.274***	0.205*
CFKD	0.215**	0.155
CFL	0.336***	0.275***

* = $p<0.05$
** = $p<0.01$
*** = $p<0.001$

Table 5. Continued.

Character	Female	Male
CS37-1	0.393***	0.379***
CS37-2	0.287***	0.309***
CS37-3	0.275***	0.291***
CS3-1	0.368**	0.433***
CS3-2	0.505***	0.506***

* = $p<0.05$
** = $p<0.01$
*** = $p<0.01$

Table 6. Mean, (standard deviation), and univariate ANOVA F-test value among group means for female *Couesius plumbeus*. Missouri includes localities 1-5 and 7-11; Columbia includes localities 49-51; Atlantic includes localities 82-85, 91, and 102.

Character	Missouri (n=187)	Columbia (n=59)	Atlantic (n=104)	F (df=2,347)
DSR	20.30 (1.60)	15.71 (1.05)	18.05 (1.30)	254.86**
HDN	74.46 (3.25)	71.11 (2.35)	69.29 (2.44)	113.71**
HL	120.08 (1.43)	118.23 (1.12)	117.84 (1.30)	107.73**
DFH	106.46 (2.67)	103.04 (2.73)	108.96 (2.00)	106.42**
CPS	27.42 (2.42)	23.59 (1.26)	25.74 (1.22)	90.53**
PELTCV	146.26 (0.96)	146.68 (0.64)	147.43 (0.75)	63.23**
PECL	102.63 (2.68)	99.03 (1.99)	103.29 (2.30)	61.84**
AFH	98.02 (2.85)	96.46 (1.85)	100.55 (2.11)	58.01**
CFL	116.62 (2.67)	114.49 (2.30)	118.22 (2.08)	44.06**
CFKD	91.84 (3.60)	88.46 (3.63)	93.40 (3.61)	26.27**
PECTCV	164.27 (0.62)	164.81 (0.46)	164.59 (0.48)	24.45**

* = $p<0.05$
** = $p<0.01$

Table 6. Continued

Character	Missouri (n=187)	Columbia (n=59)	Atlantic (n=104)	F (df=2,347)
AOTCV	127.11 (1.48)	128.12 (1.39)	128.21 (1.49)	22.90**
DOPEC	127.92 (1.55)	129.37 (1.00)	128.39 (1.66)	20.75**
DOTCV	144.50 (0.98)	143.58 (0.99)	144.22 (0.99)	19.64**
SNA	158.79 (0.93)	158.07 (1.10)	158.26 (0.80)	19.21**
ORBD	58.37 (2.83)	56.78 (3.33)	59.64 (3.12)	17.42**

* = $p<0.05$
** = $p<0.01$

Table 7. Mean, (standard deviation), and univariate ANOVA F-test value among group means for male *Couesius plumbeus*. Missouri includes localities 1-5 and 7-11; Columbia includes localities 49-51; Atlantic includes localities 82-85, 91, and 102.

Character	Missouri (n=248)	Columbia (n=49)	Atlantic (n=98)	F (df=2,392)
DSR	20.14 (1.65)	15.96 (0.91)	17.75 (1.10)	220.01**
HL	118.15 (1.31)	116.19 (1.27)	115.90 (1.11)	135.87**
CPS	27.20 (2.29)	23.33 (1.33)	25.55 (1.11)	90.00**
HDN	72.10 (3.17)	69.06 (2.20)	67.76 (2.46)	87.23**
DFH	105.32 (2.65)	102.49 (3.35)	107.66 (2.34)	63.29**
PELTCV	144.46 (0.98)	144.77 (0.78)	145.67 (0.88)	59.46**
AFH	96.67 (2.86)	96.10 (3.04)	99.97 (2.30)	56.63**
CFL	115.05 (2.60)	113.03 (2.48)	116.96 (2.47)	41.38**
CFKD	93.60 (3.83)	90.35 (3.07)	94.64 (3.77)	30.72**
DOTCV	142.91 (0.96)	141.85 (1.20)	142.74 (1.04)	22.49**
AOTCV	125.94 (1.40)	127.07 (1.28)	126.74 (1.28)	21.92**

* = $p<0.05$
** = $p<0.01$

Table 7. Continued.

Character	Missouri (n=248)	Columbia (n=49)	Atlantic (n=98)	F (df=2,392)
ORBD	56.30 (2.89)	55.42 (3.25)	58.14 (2.74)	19.08**
SNA	155.97 (0.98)	155.21 (0.98)	155.72 (0.75)	16.55**
PECL	106.40 (3.20)	103.41 (5.17)	105.48 (2.80)	16.24**
DOPEC	124.55 (1.65)	125.77 (1.56)	125.01 (1.64)	12.32**
PECTCV	161.80 (1.13)	162.17 (0.52)	162.12 (0.51)	5.87**

* = $p<0.05$
** = $p<0.01$

Table 8. Number of individuals and percentage of *Couesius plumbeus* (both sexes) classified to Missouri (M), Columbia (C), and Atlantic coastal (A) drainages.

	M	C	A	TOTAL
M	413 (94.9%)	7 (1.6%)	15 (3.4%)	435
C	1 (0.9%)	105 (97.2%)	2 (1.9%)	108
A	3 (1.5%)	5 (2.5%)	194 (96.0%)	202

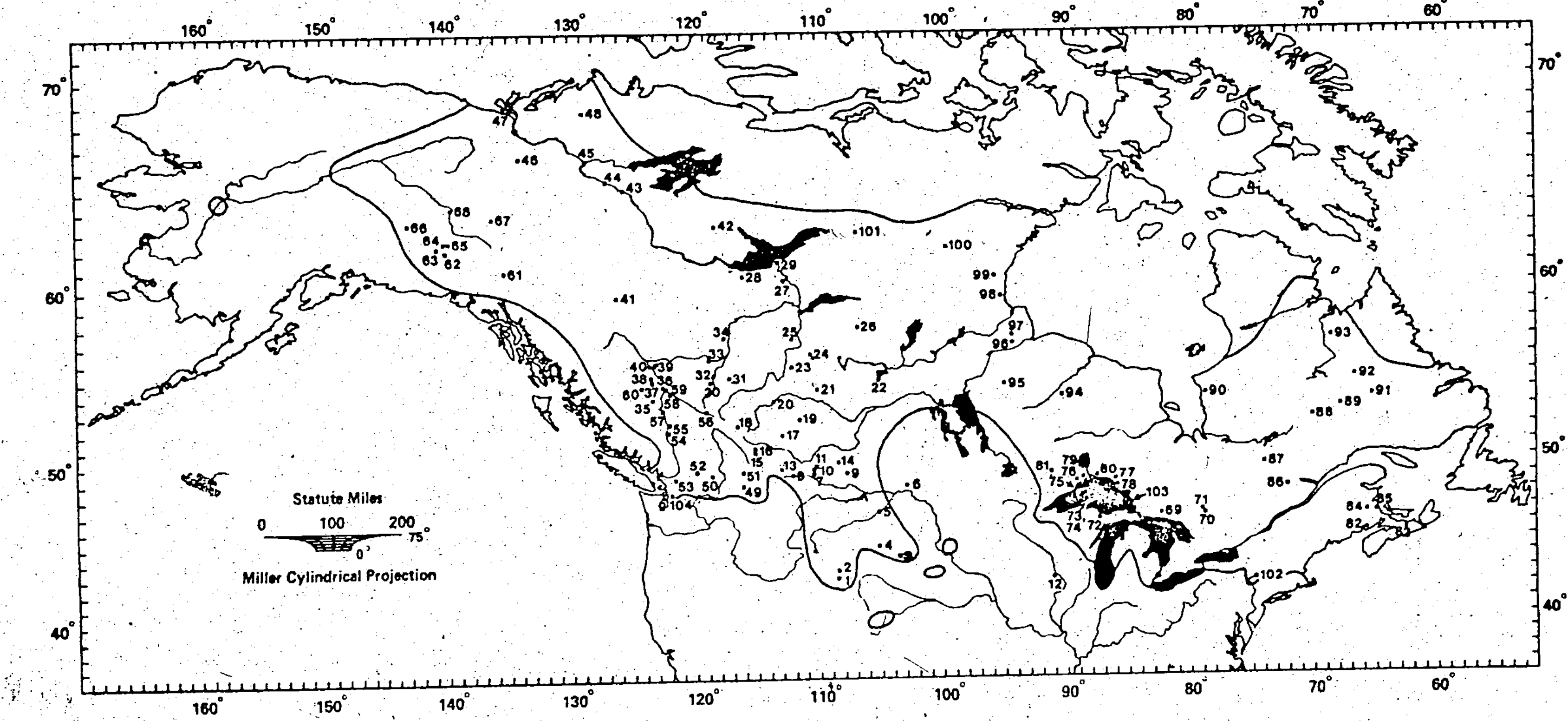
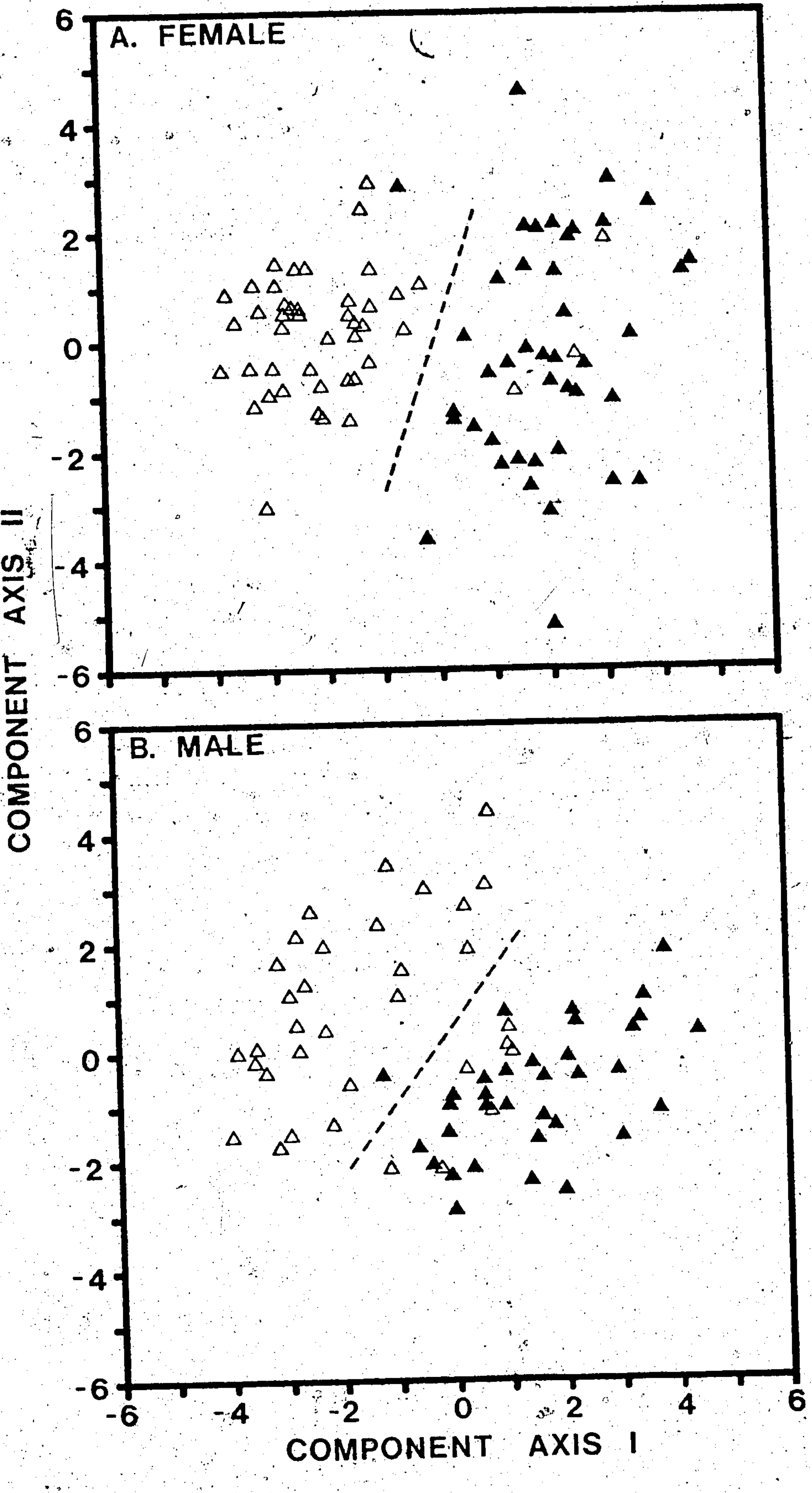


Figure 1. Couesius plumbeus sample localities and approximate range. Locality labels as in Table 1.

Figure 2. Principal component scores along component axes I and II for Eagle River, Michigan, A) female (30.3% and 15.8% of variance, respectively) and B) male (25.8% and 15.2% of variance, respectively) *Couesius plumbeus*. Size component reduced by *a priori* regression. Solid triangles = UMMZ designated *C. p. dissimilis* ; open triangles = UMMZ designated *C. p. plumbeus*.


A. FEMALE
B. MALE
COMPONENT AXIS II
COMPONENT AXIS I
6
4
2
0
-2
-4
-6
-6
-4
-2
0
2
4
6

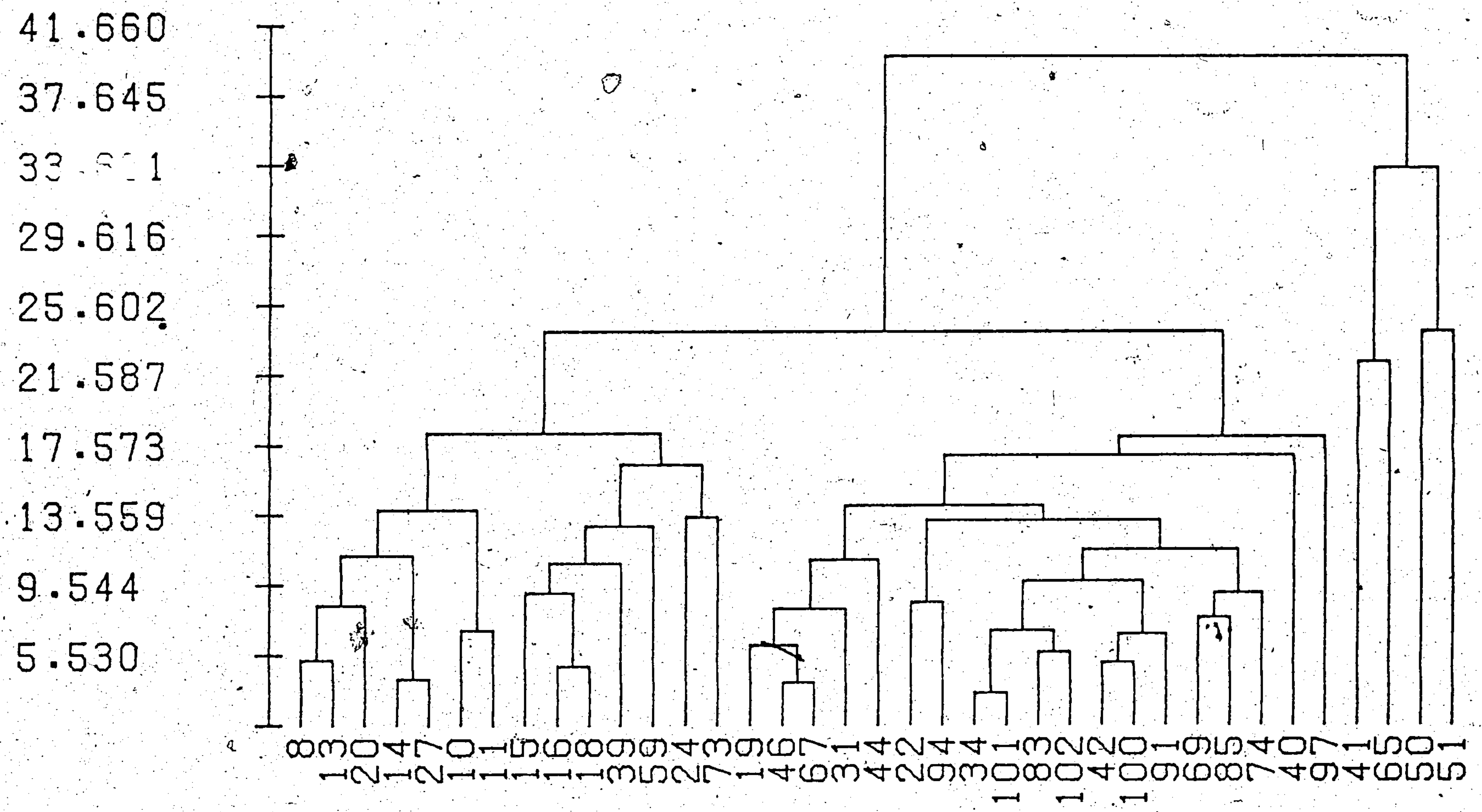


Figure 3A. UPGMA cluster analysis of female Couesius plumbeus generalized distances (D^2) (37 localities). Scale is generalized distance (D^2). Locality labels as in Table 1.

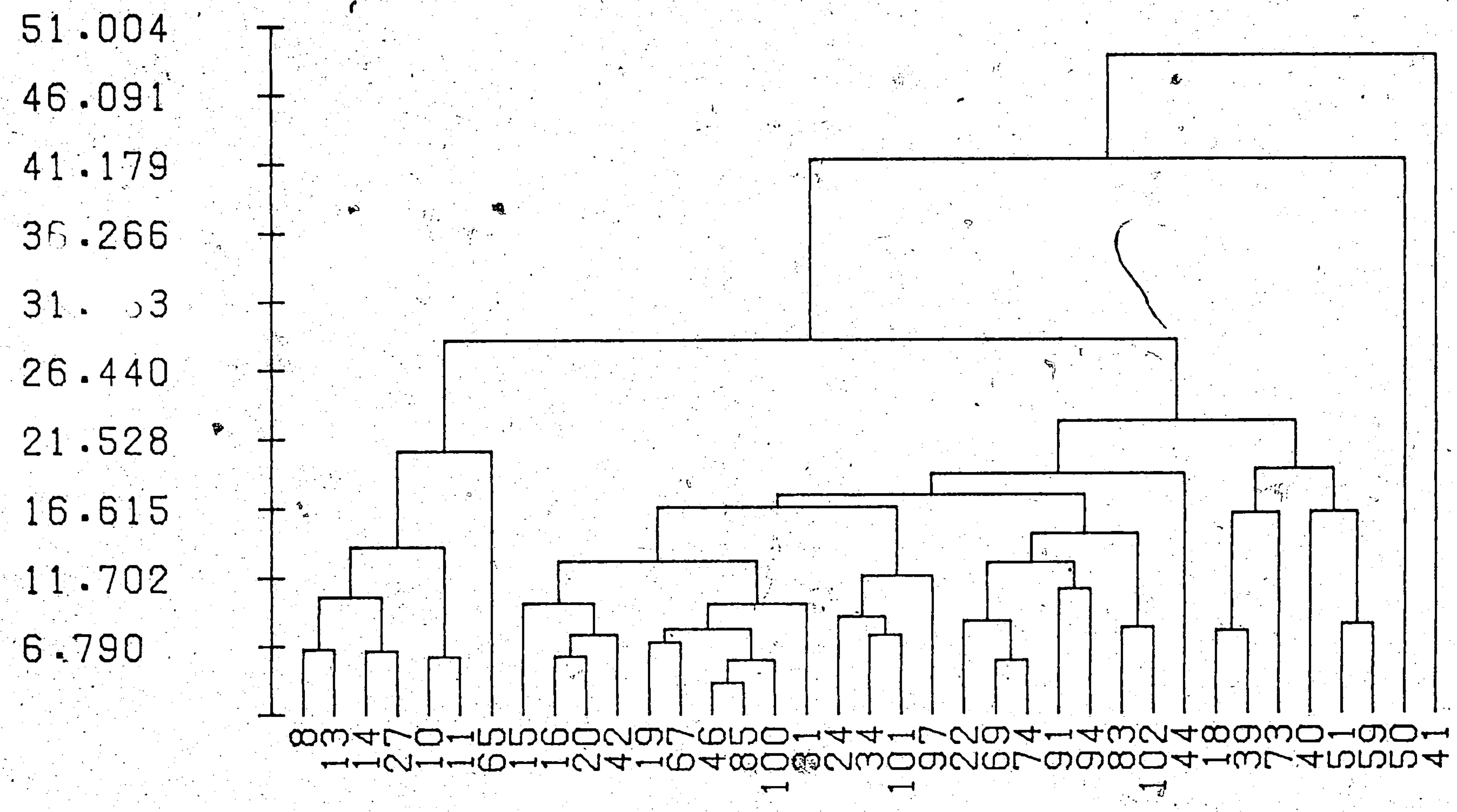


Figure 3B. UPGMA cluster analysis of male Couesius plumbeus generalized distances (D^2) (37 localities). Scale is generalized distance (D^2). Locality labels as in Table 1.

Figure 4. Thirty-seven-group solution canonical variate scores along canonical axes I and II for A) female (34.6% and 16.9% of variance, respectively) and B) male (33.2% and 15.1% of variance, respectively) *Couesius plumbeus* from localities within or near postulated Wisconsin refugia. Square = Columbia River basin; triangle = Missouri River basin; circle = Atlantic coastal drainages. Locality labels as in Table 1.

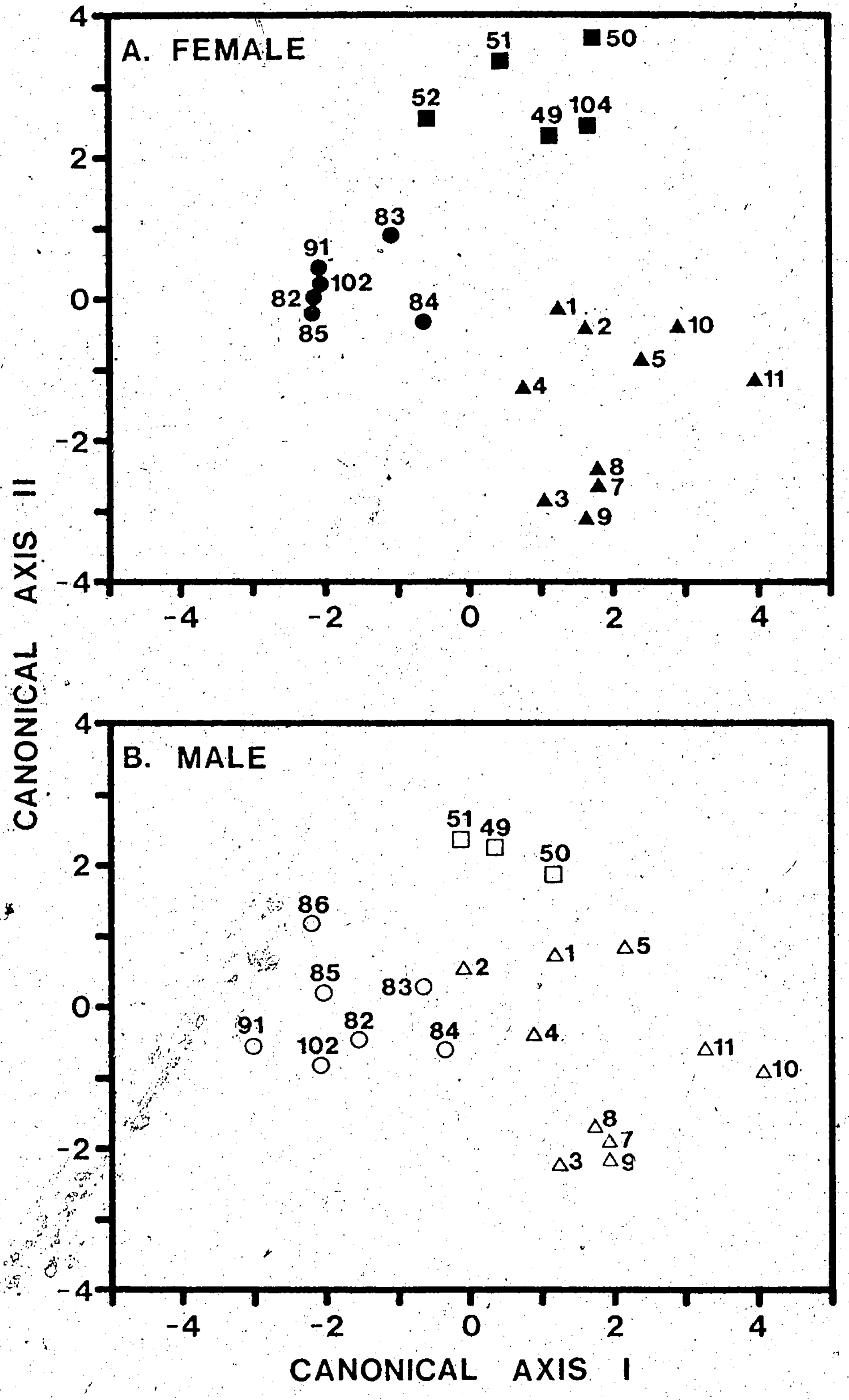

A. FEMALE
51
50
52
49
104
83
91
102
82
84
85
1
2
10
5
11
4
8
7
3
9
B. MALE
51
49
50
86
1
5
2
85
83
91
82
102
84
4
11
10
8
7
3
9
4
2
0
-2
-4
-4
-2
0
2
4
CANONICAL AXIS II
CANONICAL AXIS I

Figure 5. Character vector magnitude and direction based on three-group solution for A) female and B) male *Couesius plumbeus*. Character labels as in Table 2.

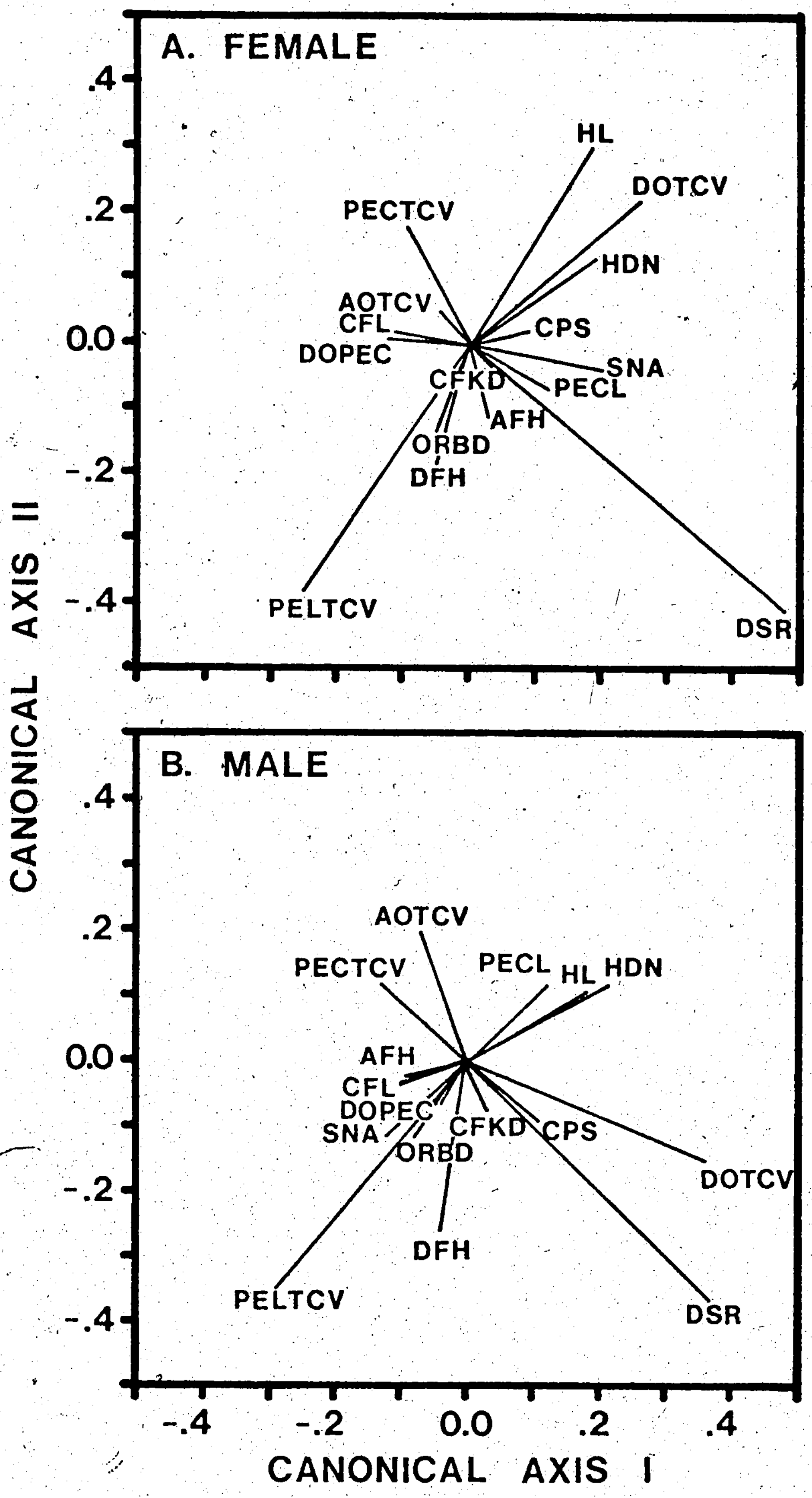

A. FEMALE
HL
DOTCV
PECTCV
HDN
AOTCV
CFL
CPS
DOPEC
SNA
CFKD
PECL
AFH
ORBD
DFH
PELTCV
DSR
B. MALE
AOTCV
PECTCV
PECL
HL
HDN
AFH
CFL
DOPEC
SNA
CFKD
CPS
ORBD
DOTCV
DFH
PELTCV
DSR
.4
.2
0.0
-.2
-.4
CANONICAL AXIS II
-.4
-.2
0.0
.2
.4
CANONICAL AXIS I

Figure 6. Three-group solution canonical variate scores along canonical axes I and II for A) female and B) male Couesius plumbeus from localities within or near postulated Wisconsin refugia. Square = Columbia River basin; triangle = Missouri River basin; circle = Atlantic coastal drainages. Generalized distance (D^2) and 95% confidence radius of centroid are indicated. The two axes account for 100% of the variance.

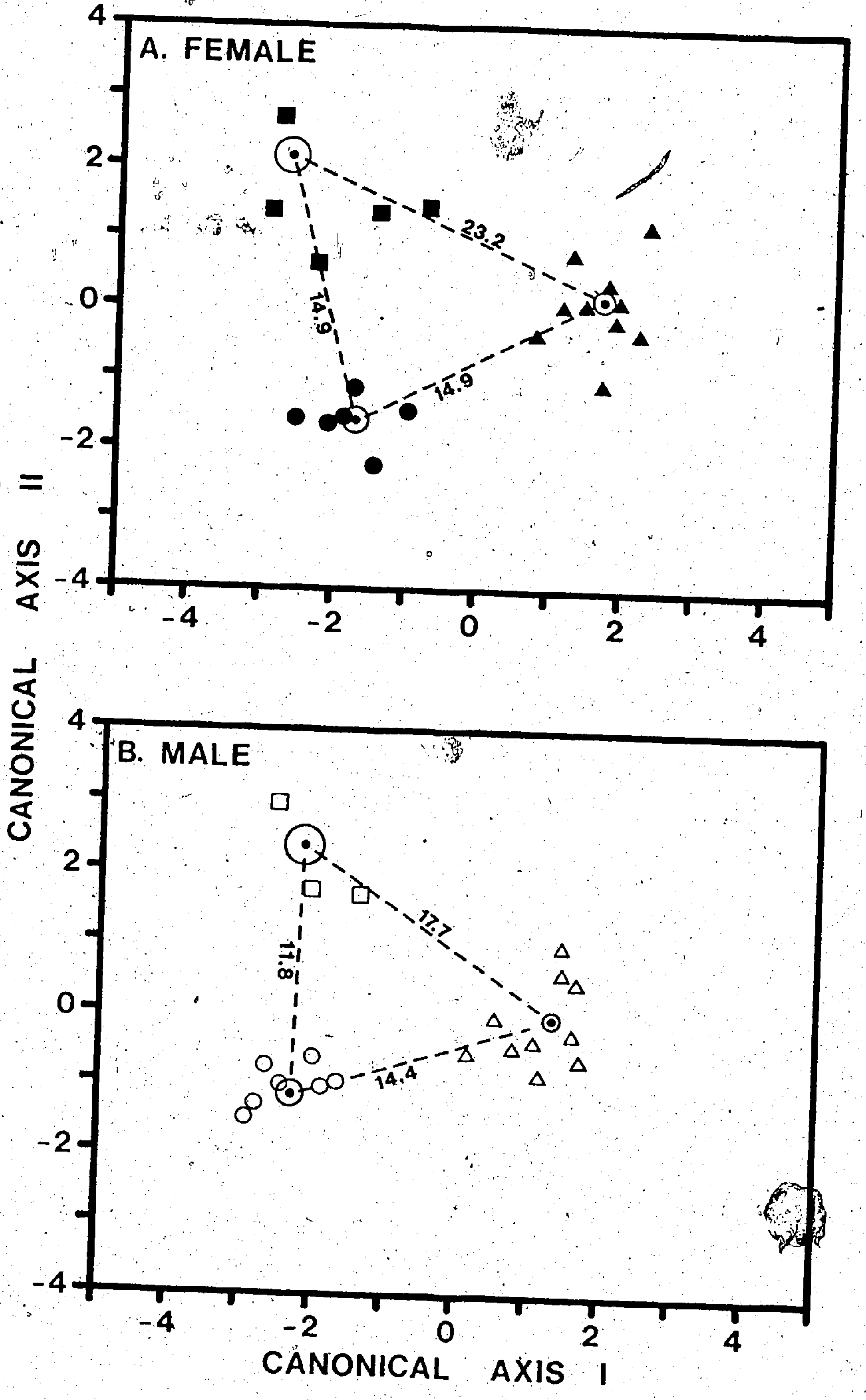

A. FEMALE
B. MALE
23.2
14.9
14.9
12.7
11.8
14.4
CANONICAL AXIS II
CANONICAL AXIS I
4
2
0
-2
-4
-4
-2
0
2
4

Figure 7A. Three-group solution canonical variate scores along canonical axes I and II for female *Couesius plumbeus* from all localities. Locality labels as in Table 1. The two axes account for 100% of the variance.

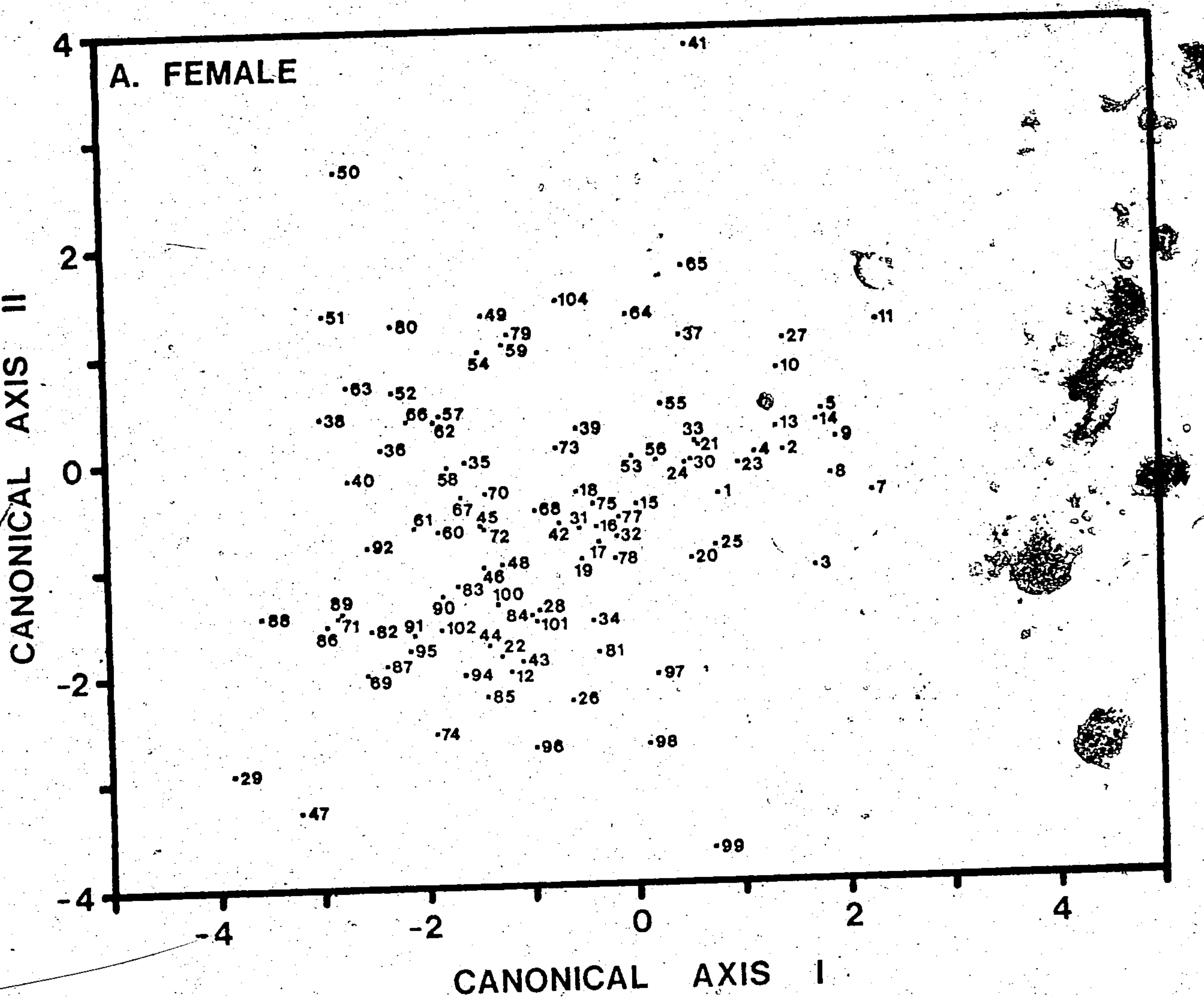
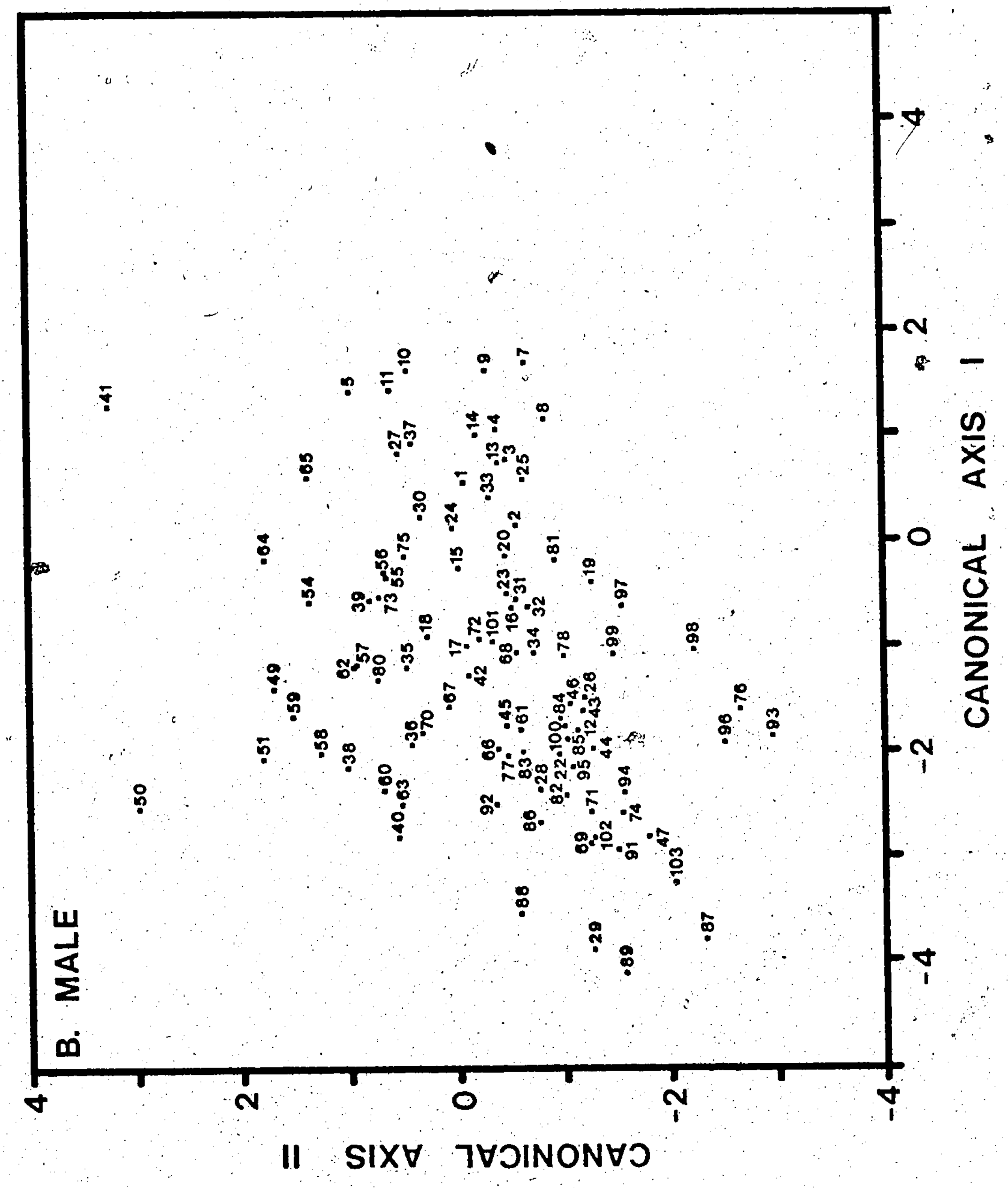

A. FEMALE
CANONICAL AXIS II
CANONICAL AXIS I
4
2
0
-2
-4
-4
-2
0
2
4
41
50
65
104
64
11
51
80
49
79
37
27
59
54
10
63
52
55
5
14
13
66
57
38
62
39
33
9
21
36
73
56
4
2
35
53
30
23
8
24
40
58
70
18
1
7
75
15
67
68
61
45
31
77
60
72
42
16
32
25
92
17
48
78
20
3
19
46
83
100
89
28
90
84
88
71
101
34
86
82
91
102
44
22
95
81
43
87
97
94
12
69
85
26
74
96
98
29
47
99

Figure 7B. Three-group solution canonical variate scores along canonical axes I and II for male *Couesius plumbeus* from all localities. Locality labels as in Table 1. The two axes account for 100% of the variance.


B. MALE
CANONICAL AXIS I
CANONICAL AXIS II
4
2
0
-2
-4
-4
-2
0
2
4
41
50
5
11
10
9
7
65
27
37
14
4
13
3
8
1
33
25
30
24
64
2
20
56
75
15
55
81
54
23
39
73
16
31
19
97
32
18
72
101
49
62
57
17
34
98
78
99
80
35
68
42
59
67
76
45
46
28
84
51
58
36
70
61
100
93
96
43
12
38
66
85
44
60
77
83
22
95
63
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28
94
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91
103
88
87
29
89

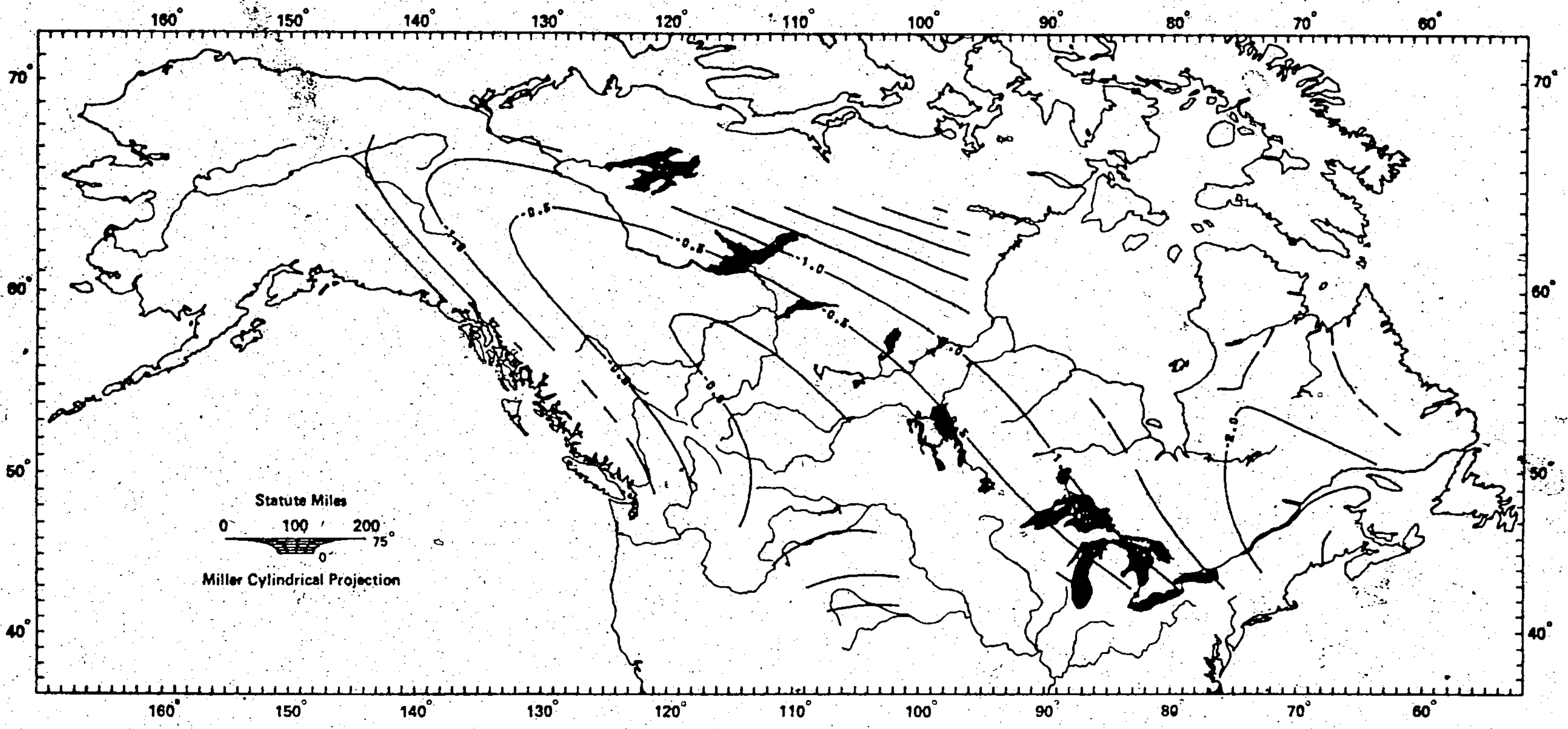


Figure 8A. Third degree polynomial trend surface of three-group solution canonical scores along canonical axis I for female Couesius plumbeus. Contour intervals = 0.5.

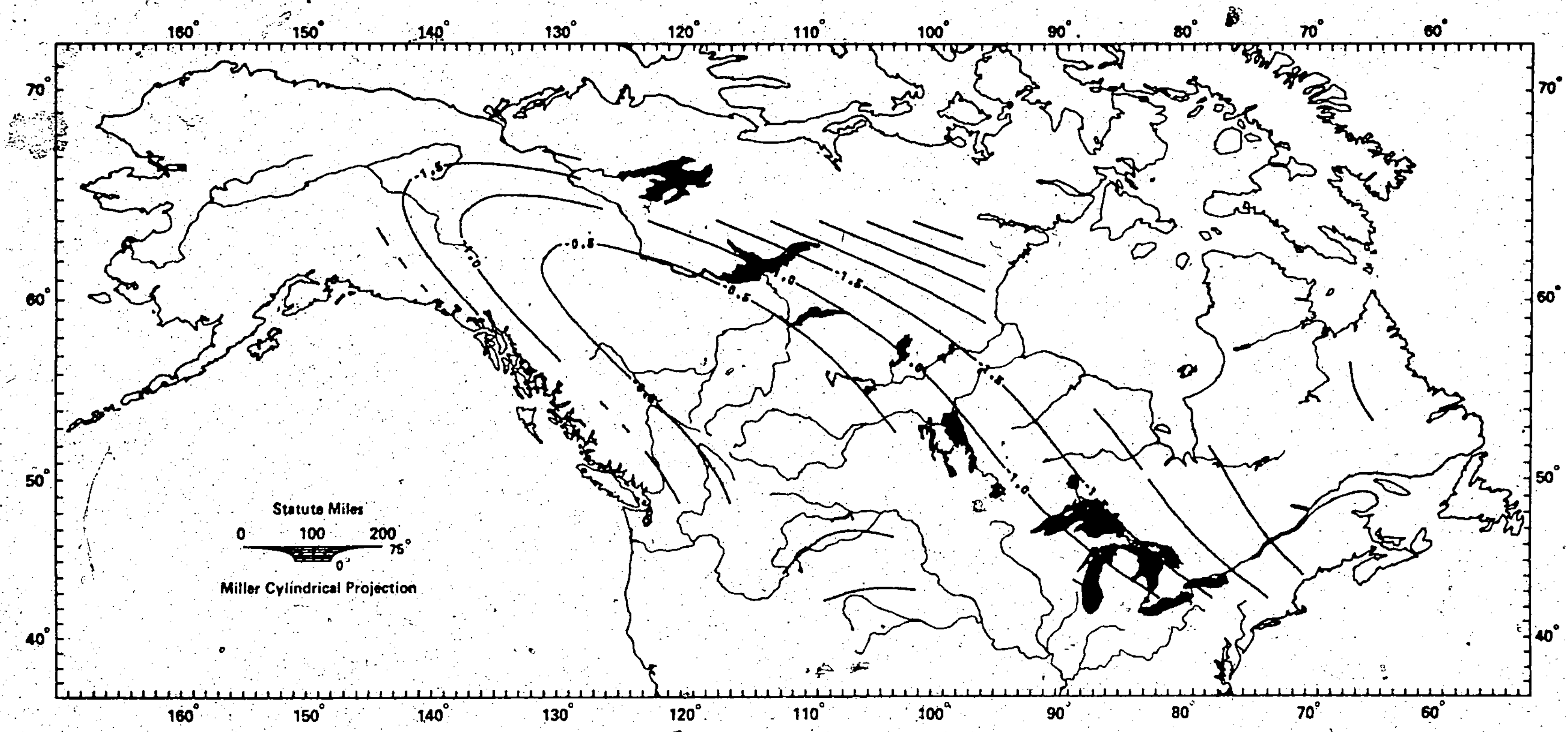


Figure 8B. Third degree polynomial trend surface of three-group solution canonical scores along canonical axis I for male *Couesius plumbeus*. Contour intervals = 0.5.

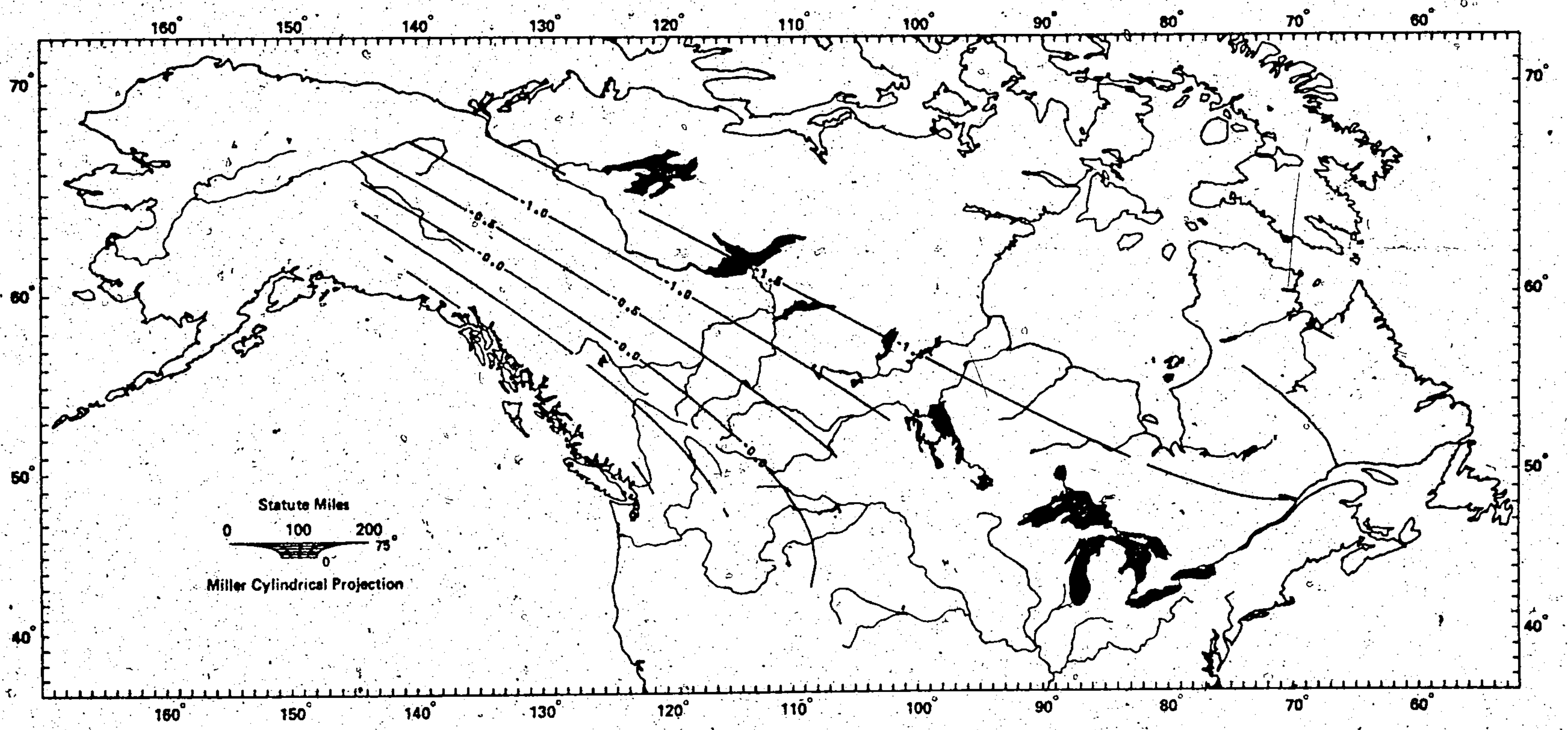


Figure 9A. Third degree polynomial trend surface of three-group solution canonical scores along canonical axis II for female Couesius plumbeus. Contour intervals = 0.5.

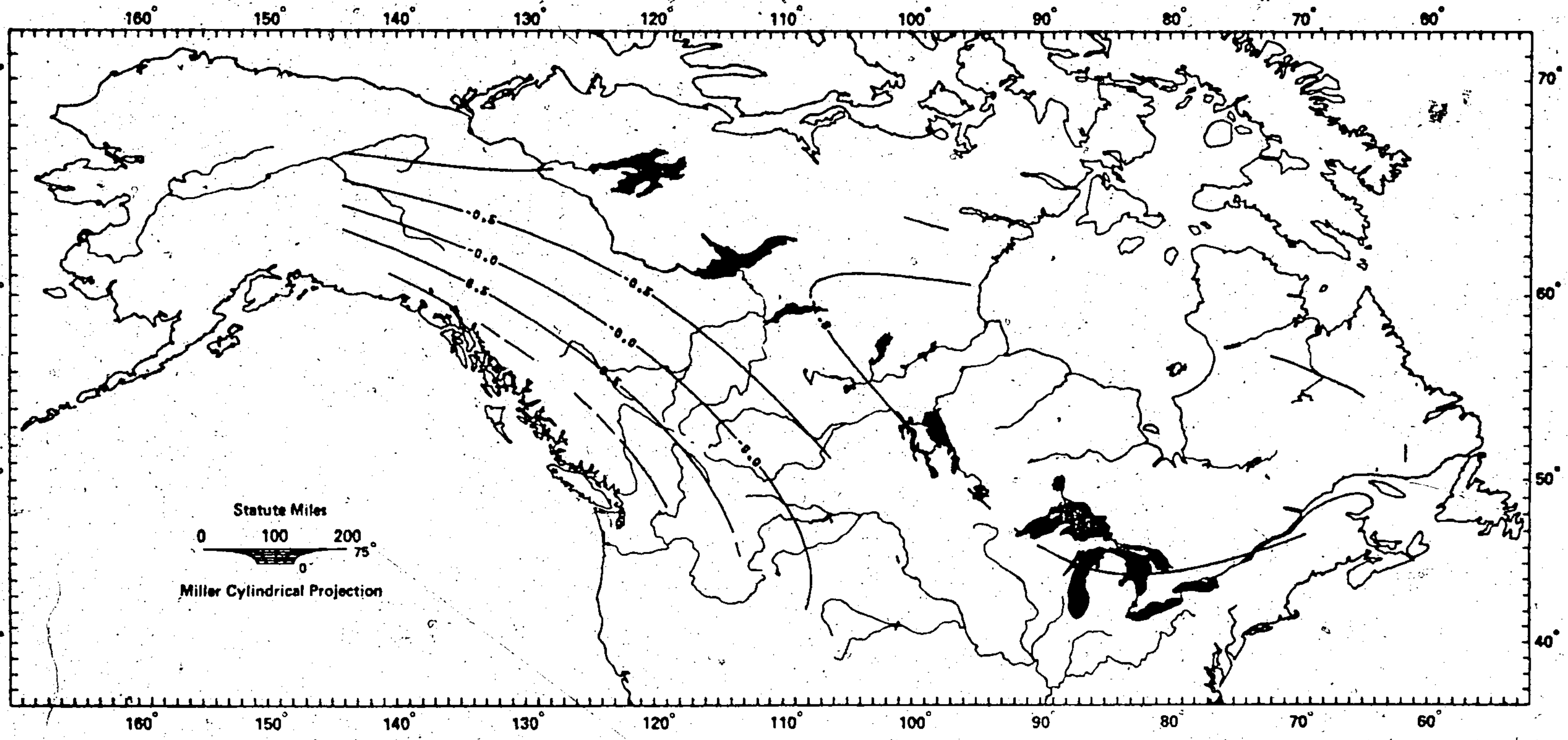


Figure 9B. Third degree polynomial trend surface of three-group solution canonical scores along canonical axis II for male Couesius plumbeus. Contour intervals = 0.5.

Figure 10. Ice margin position and postulated Wisconsin refugia for "greeni", "dissimilis", and "plumbeus" stocks of _Couesius plumbeus_ , ca. 17,000 YBP. (Partially after Prest, 1968; and McPhail and Lindsey, 1970).

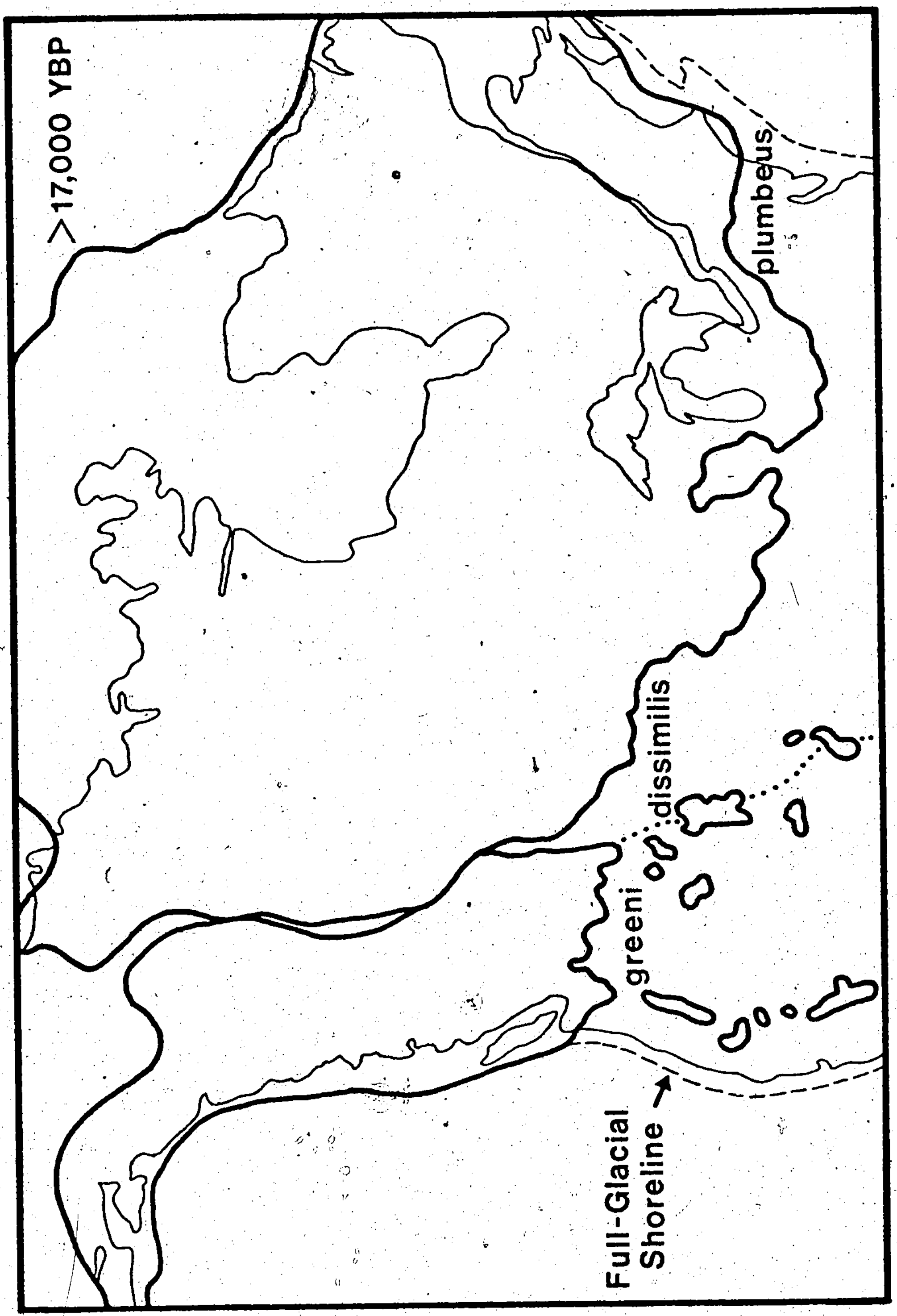

>17,000 YBP
plumbeus
dissimilis
greeni
Full-Glacial
Shoreline

Figure 11. Ice margin position and postulated dispersal routes of "greeni", "dissimilis", and "plumbeus" stocks of *Couesius plumbeus* , ca. 14,000 - 11,000 YBP. (Partially after Hough, 1958, 1963; Elson, 1967; Prest, 1968; McPhail and Lindsey, 1970; and Dadswell, 1974.) 1 = Lake McConnell; 2 = Lake Tyrrell; 3 = Lake Peace; 4 = Miette Lake 5 = Lake Edmonton; 6 = Lake Agassiz (Norcross phase); 7 = Warren River outlet; 8 = St. Croix River outlet; 9 = Lake Duluth; 10 = Lake Kirkfield; 11 = Early Lake Erie; 12 = Lake Iroquois; 13 = Trent Valley outlet; 14 = Champlain Sea.

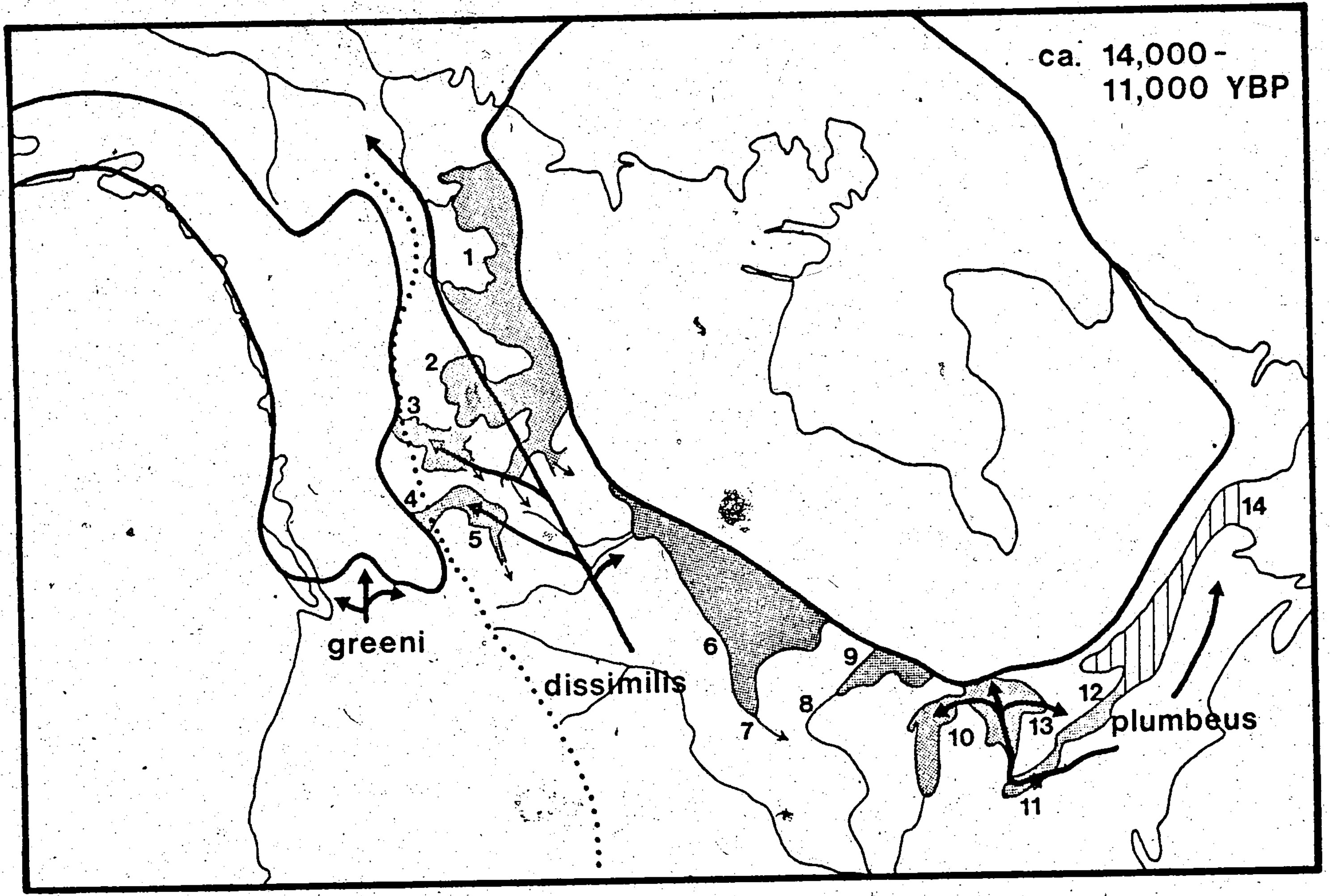

ca. 14,000-
11,000 YBP
1
2
3
4
5
6
7
8
9
10
11
12
13
14
greeni
dissimilis
plumbeus

Figure 12. Ice margin position and postulated dispersal routes of "greeni", "dissimilis", and "plumbeus" stocks of *Couesius plumbeus*, ca. 10,000 - 9,000 YBP. (Partially after Hough, 1958, 1963; Elson, 1967; Prest, 1968; McPhail and Lindsey, 1970; and Dadswell, 1974.) 1 = Great Bear Lake; 2 = Great Slave Lake; 3 = Lake Athabasca; 4 = Lake Agassiz (Campbell phase); 5 = Lake Minong; 6 = Lake Payette; 7 = Fox River outlet; 8 = Early Lake Erie; 9 = Lake Barlow - Ojibway; 10 = Ottawa River outlet; 11 = Champlain Sea.

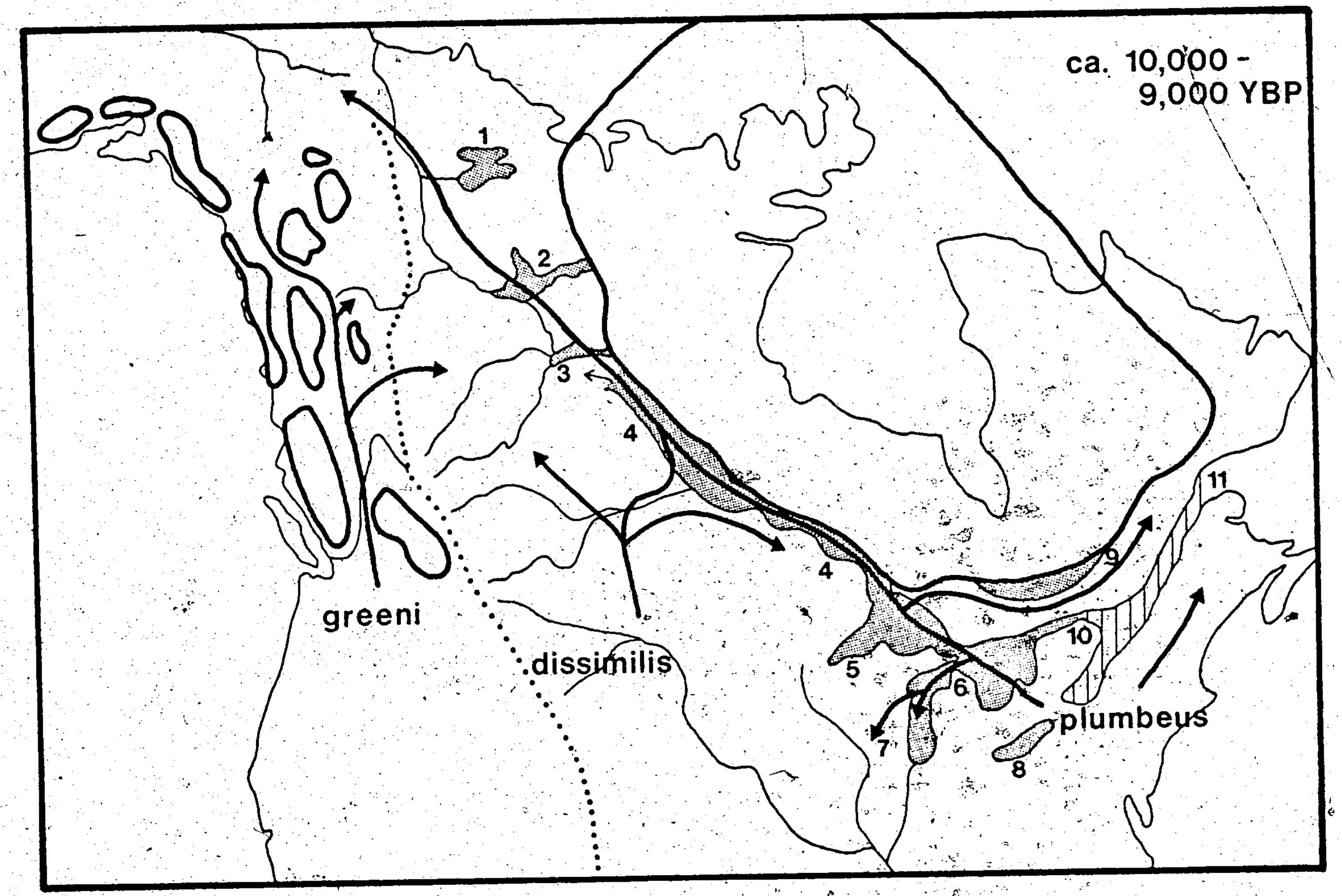
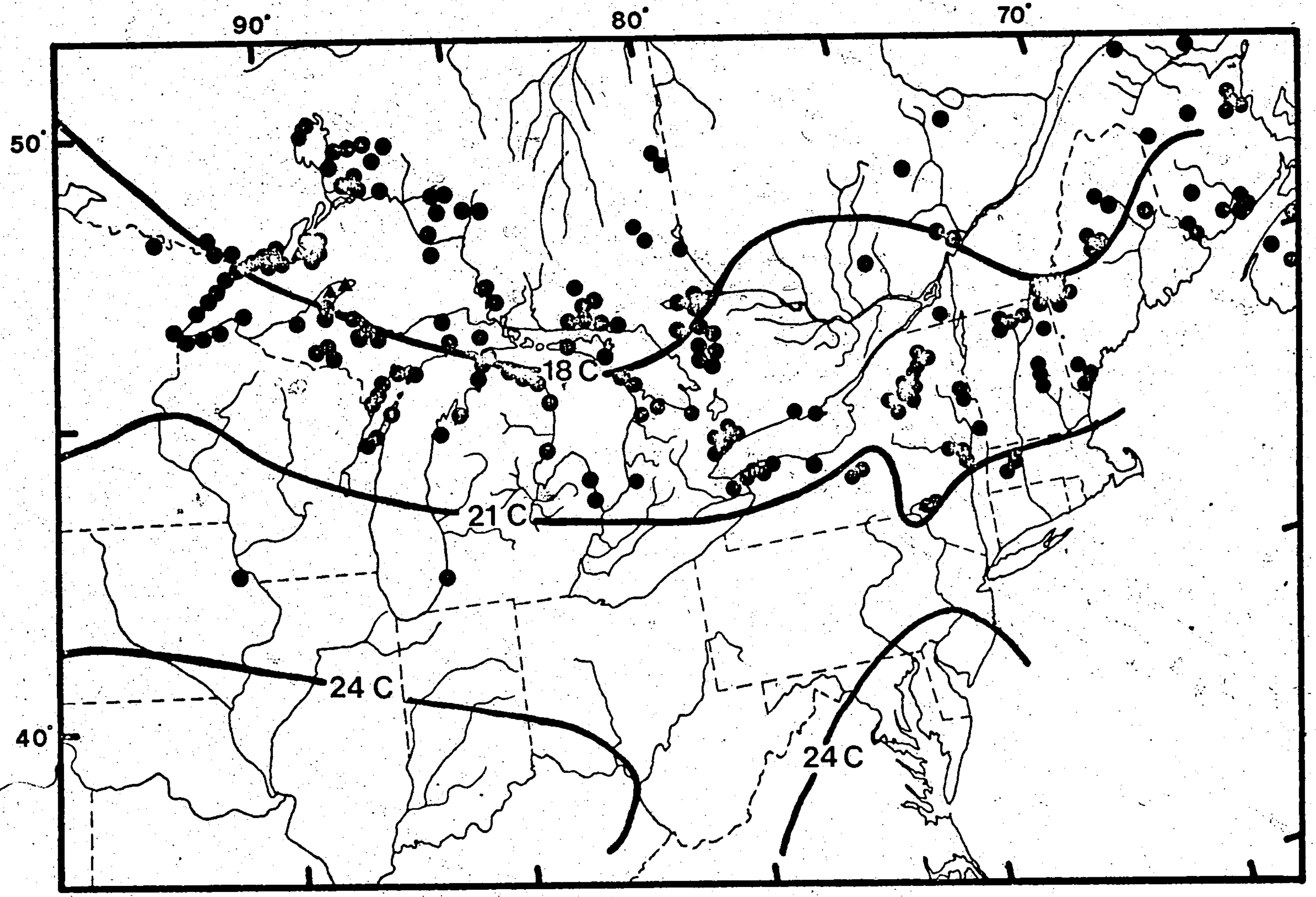

ca. 10,000 -
9,000 YBP
1
2
3
4
4
5
6
7
8
9
10
11
greeni
dissimilis
plumbeus

Figure 13. Distribution of <u>Couesius plumbeus</u> in the Great Lakes region in relation to July - August surface water isotherms. Triangles on Isle Royale and Keweenaw Peninsula represent "dissimilis" stock; circles represent "plumbeus" stock. Isotherms based on Geraghty, et al. (1973).


90°
80°
70°
50°
40°
18 C
21 C
24 C
24 C

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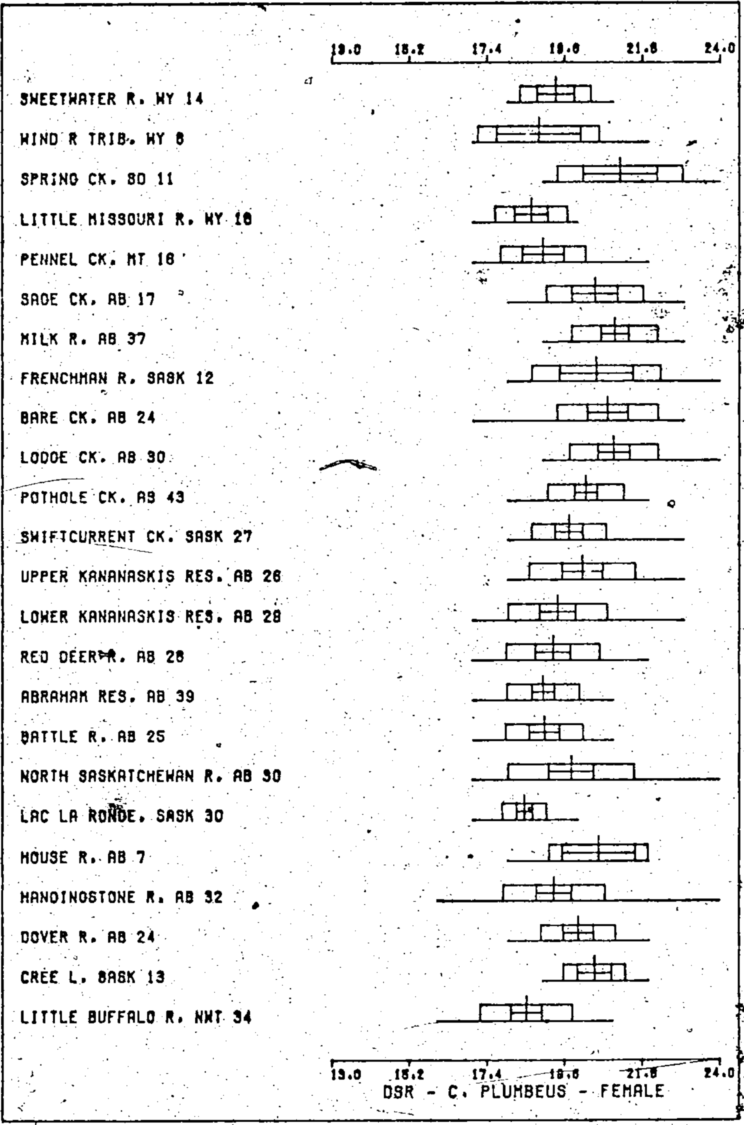
APPENDIX A

Univariate descriptive statistics (range, one standard deviation, two standard errors of mean, and mean) of selected characters (diagonal scale rows, head length, orbit diameter, head depth at nostril, and dorsal fin height), multivariate statistics, and selected trend surfaces for female and male _Couesius plumbeus_.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PENNEL CK. MT 16
SAGE CK. AB 17
MILK R. AB 37
FRENCHMAN R. SASK 12
BARE CK. AB 24
LODGE CK. AB 30
POTHOLE CK. AB 43
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 26
LOWER KANANASKIS RES. AB 28
RED DEER R. AB 28
ABRAHAM RES. AB 39
BATTLE R. AB 25
NORTH SASKATCHEWAN R. AB 30
LAC LA RONGE. SASK 30
MOUSE R. AB 7
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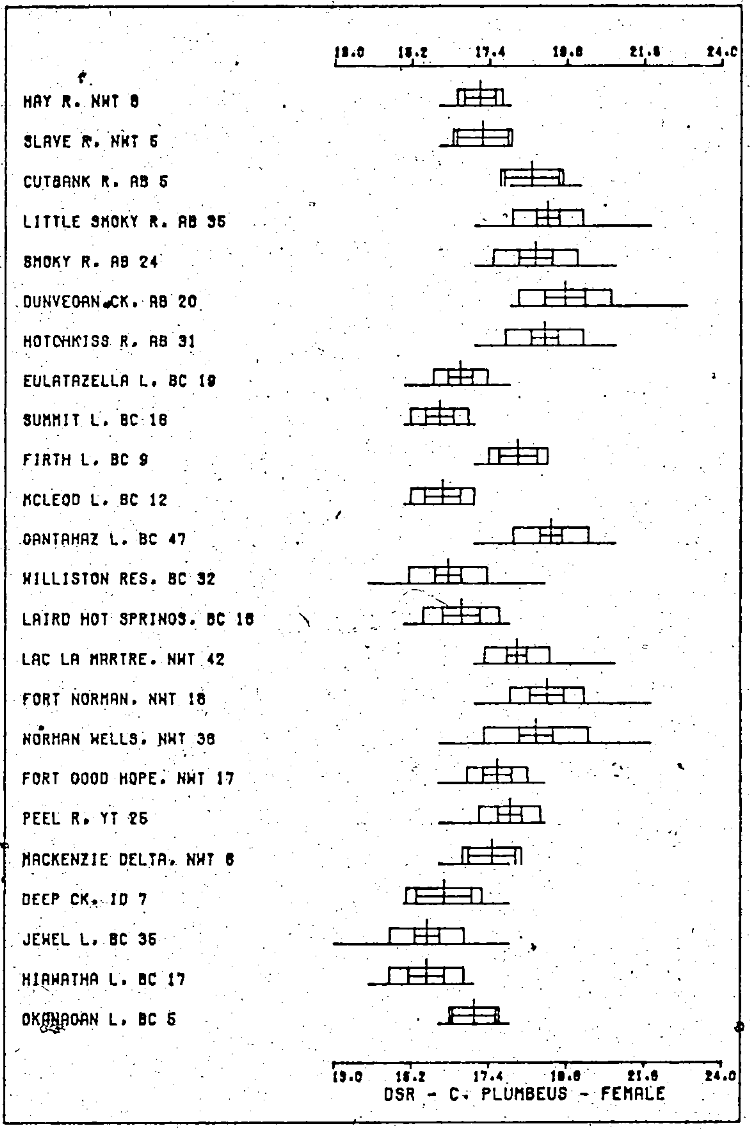
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DUNVEGAN CK. AB 20
HOTCHKISS R. AB 31
EULATAZELLA L. BC 19
SUMMIT L. BC 18
FIRTH L. BC 9
MCLEOD L. BC 12
OANTAHAZ L. BC 47
WILLISTON RES. BC 32
LAIRD HOT SPRINGS. BC 18
LAC LA MARTRE. NWT 42
FORT NORMAN. NWT 18
NORMAN WELLS. NWT 38
FORT GOOD HOPE. NWT 17
PEEL R. YT 25
MACKENZIE DELTA. NWT 8
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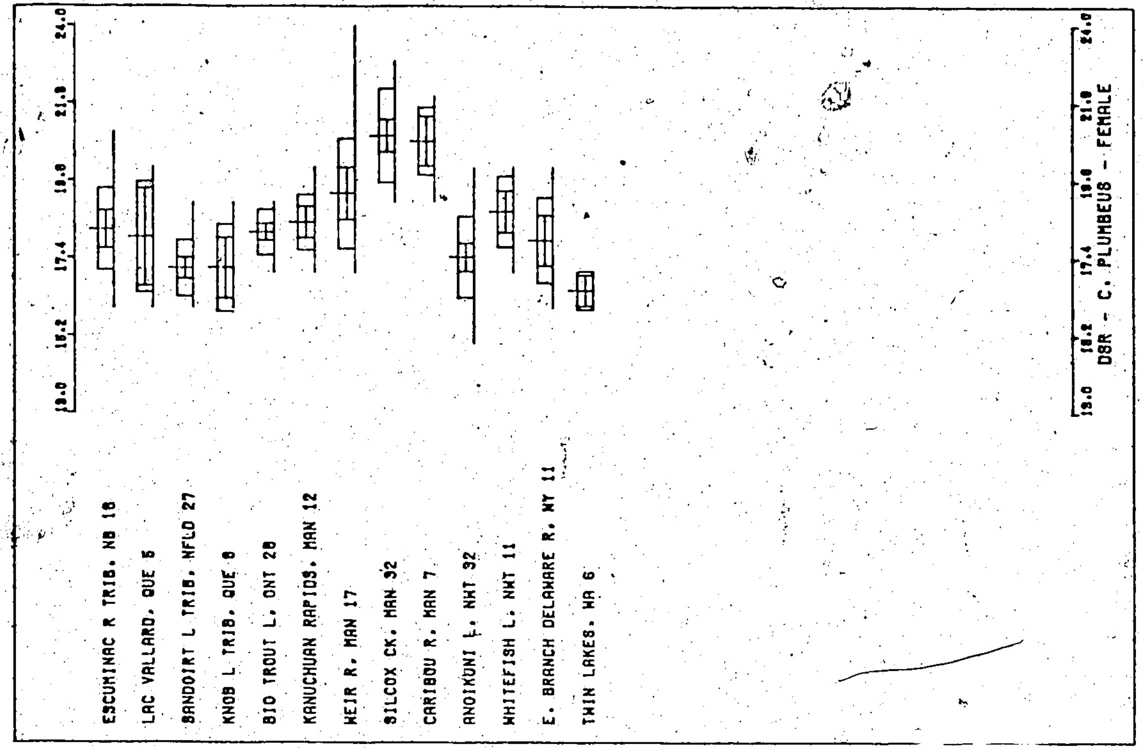
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WEIR R. MAN 17
SILCOX CK. MAN 32
CARIBOU R. MAN 7
ANOIKUNI L. NWT 32
WHITEFISH L. NWT 11
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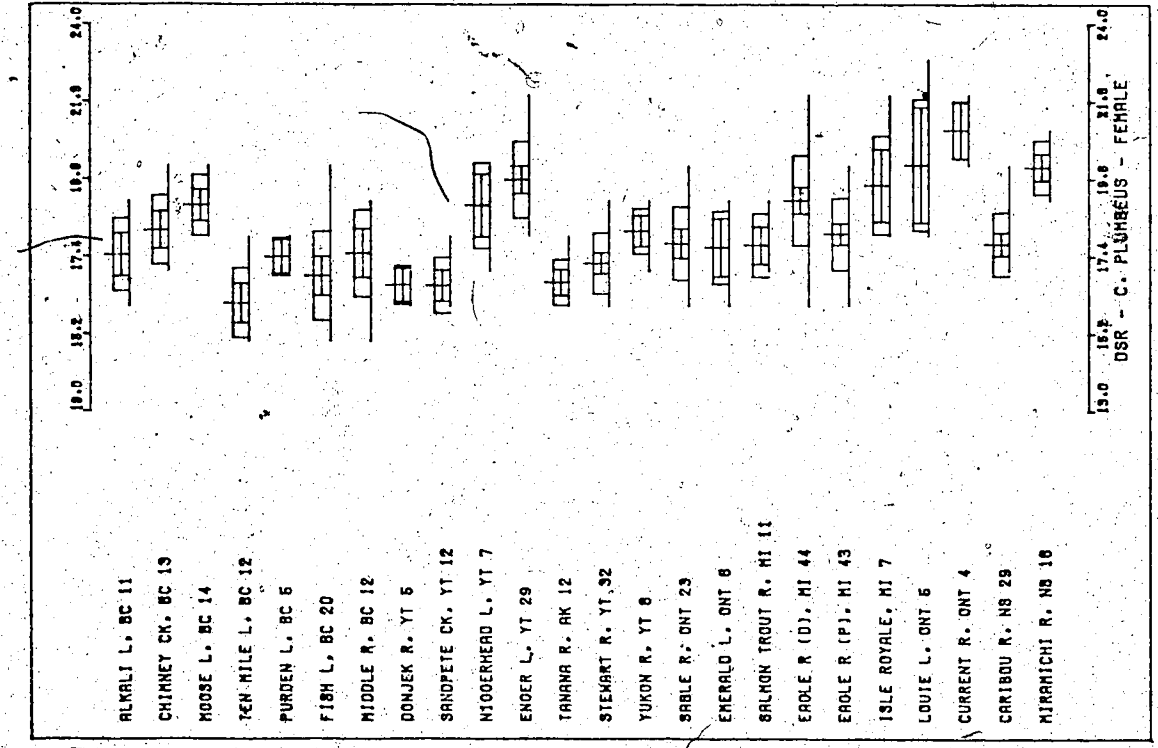
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DONJEK R. YT 5
SANDPETE CK. YT 12
NIDDERHEAD L. YT 7
ENDER L. YT 29
TANANA R. AK 12
STEWART R. YT 32
YUKON R. YT 8
SABLE R. ONT 23
EMERALD L. ONT 8
SALMON TROUT R. MI 11
EAGLE R (D). MI 44
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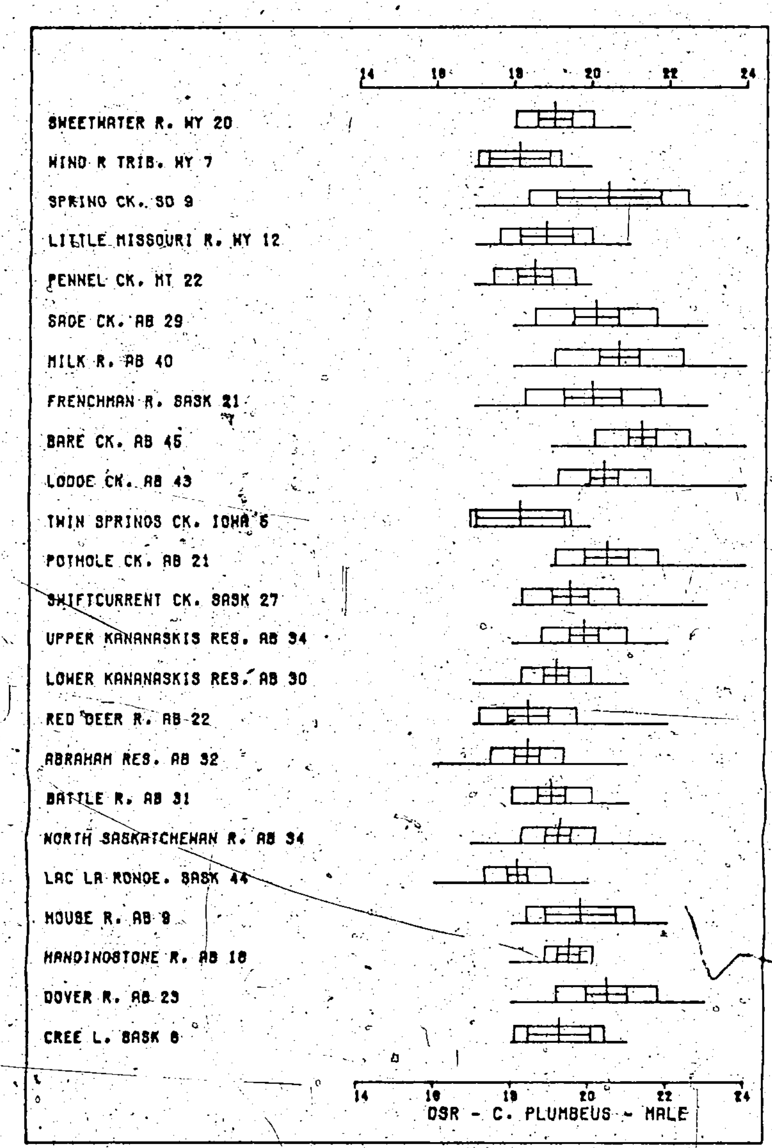
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MILK R. AB 40
FRENCHMAN R. SASK 21
BARE CK. AB 45
LODGE CK. AB 43
TWIN SPRINGS CK. IOWA 6
POTHOLE CK. AB 21
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 34
LOWER KANANASKIS RES. AB 30
RED DEER R. AB 22
ABRAHAM RES. AB 32
BATTLE R. AB 31
NORTH SASKATCHEWAN R. AB 34
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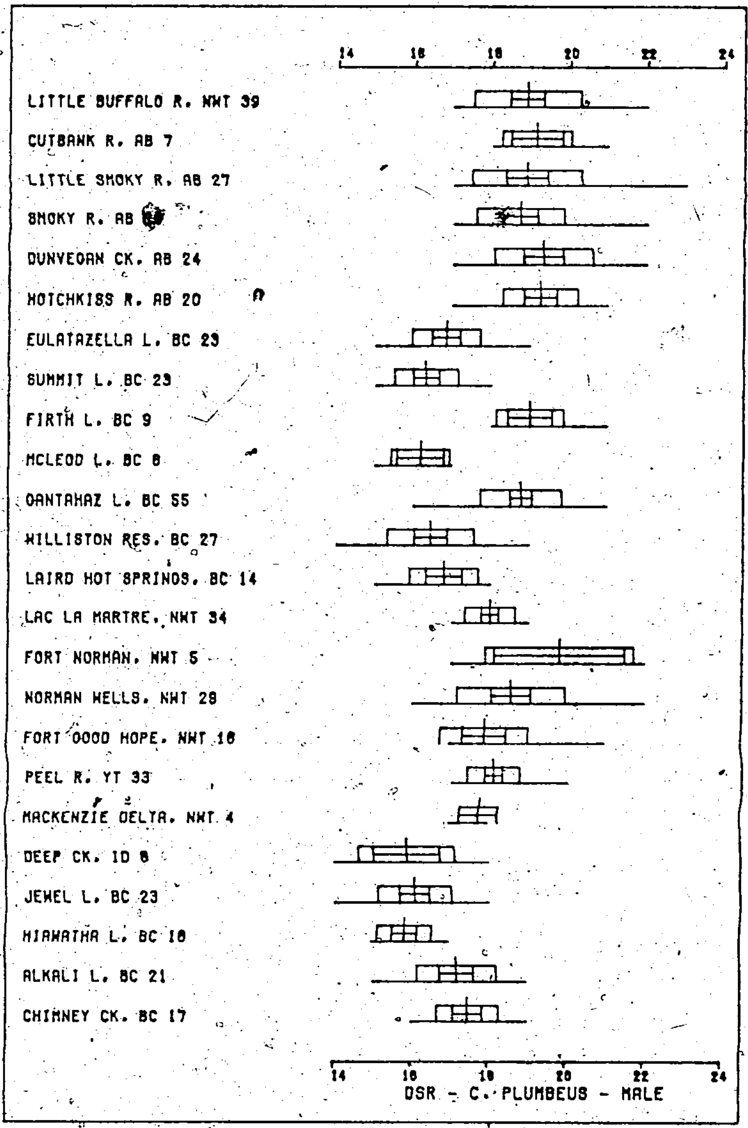
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LITTLE SMOKY R. AB 27
SMOKY R. AB
DUNVEGAN CK. AB 24
HOTCHKISS R. AB 20
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SUMMIT L. BC 23
FIRTH L. BC 9
MCLEOD L. BC 8
OANTAHAZ L. BC 55
WILLISTON RES. BC 27
LAIRD HOT SPRINGS. BC 14
LAC LA MARTRE. NWT 34
FORT NORMAN. NWT 5
NORMAN WELLS. NWT 28
FORT GOOD HOPE. NWT 16
PEEL R. YT 33
MACKENZIE DELTA. NWT 4
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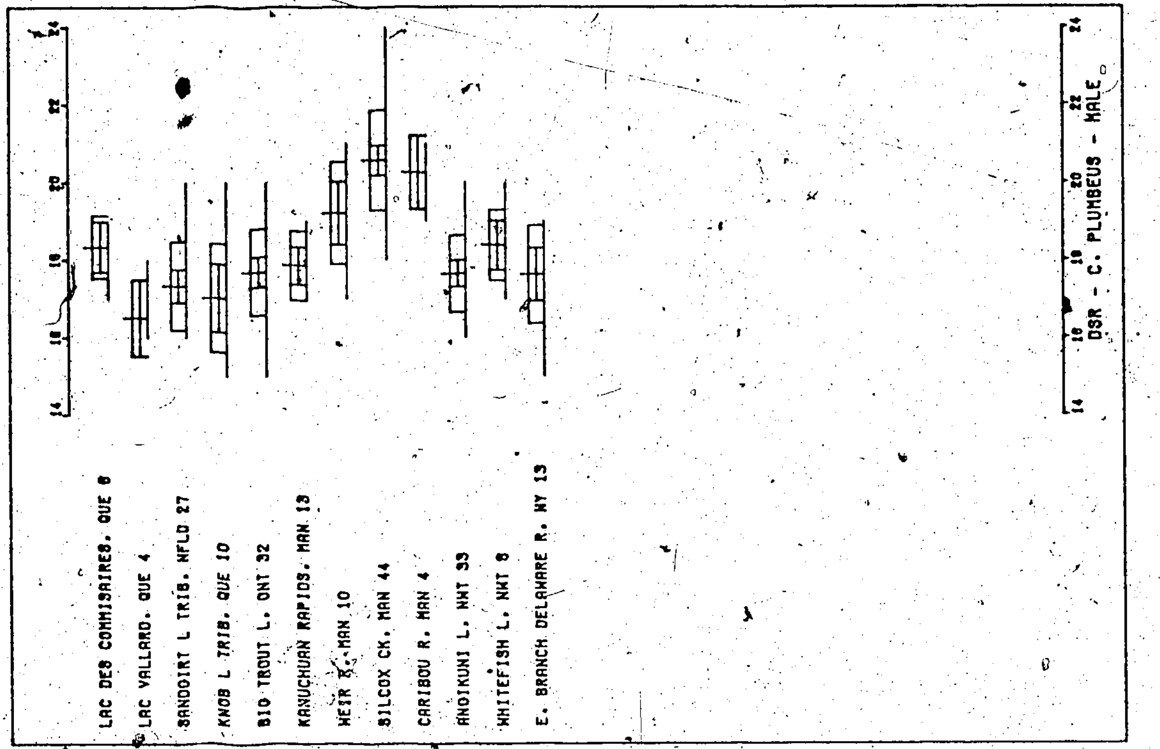
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WEIR R. MAN 10
SILCOX CK. MAN 44
CARIBOU R. MAN 4
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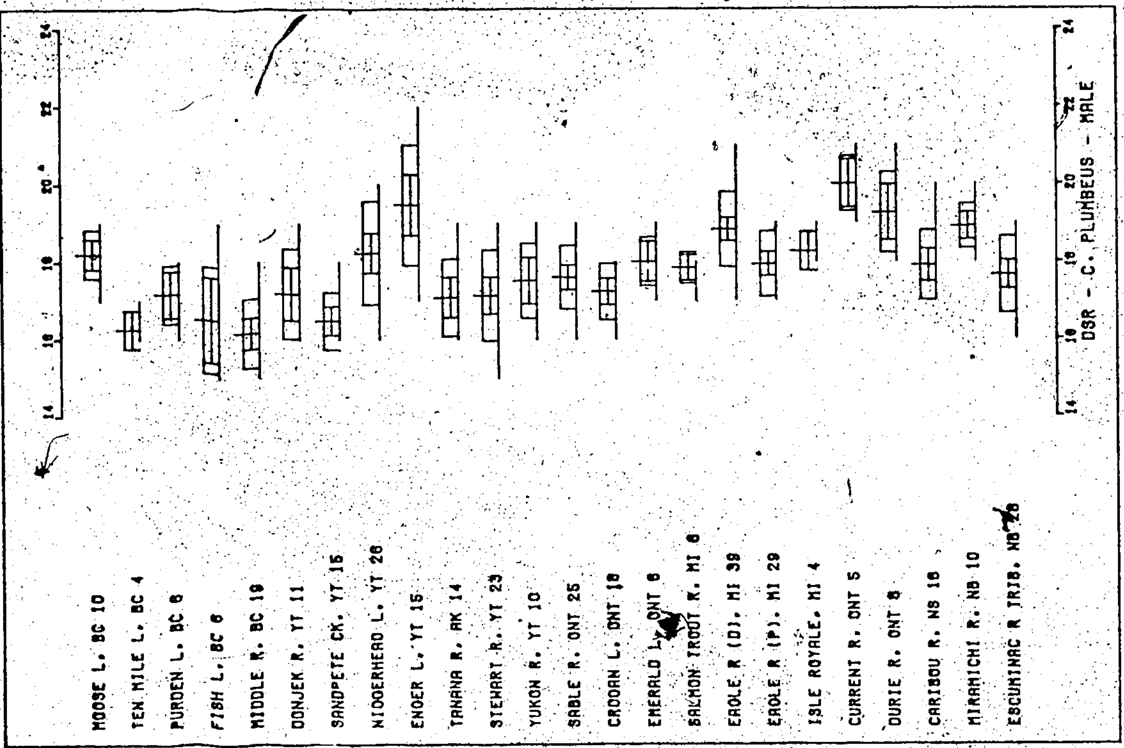
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YUKON R. YT 10
SABLE R. ONT 25
CROOAN L. ONT 18
EMERALD L. ONT 6
SALMON TROUT R. MI 6
EROLE R (D). MI 39
EROLE R (P). MI 29
ISLE ROYALE, MI 4
CURRENT R. ONT 5
DURIE R. ONT 8
CARIBOU R. NS 16
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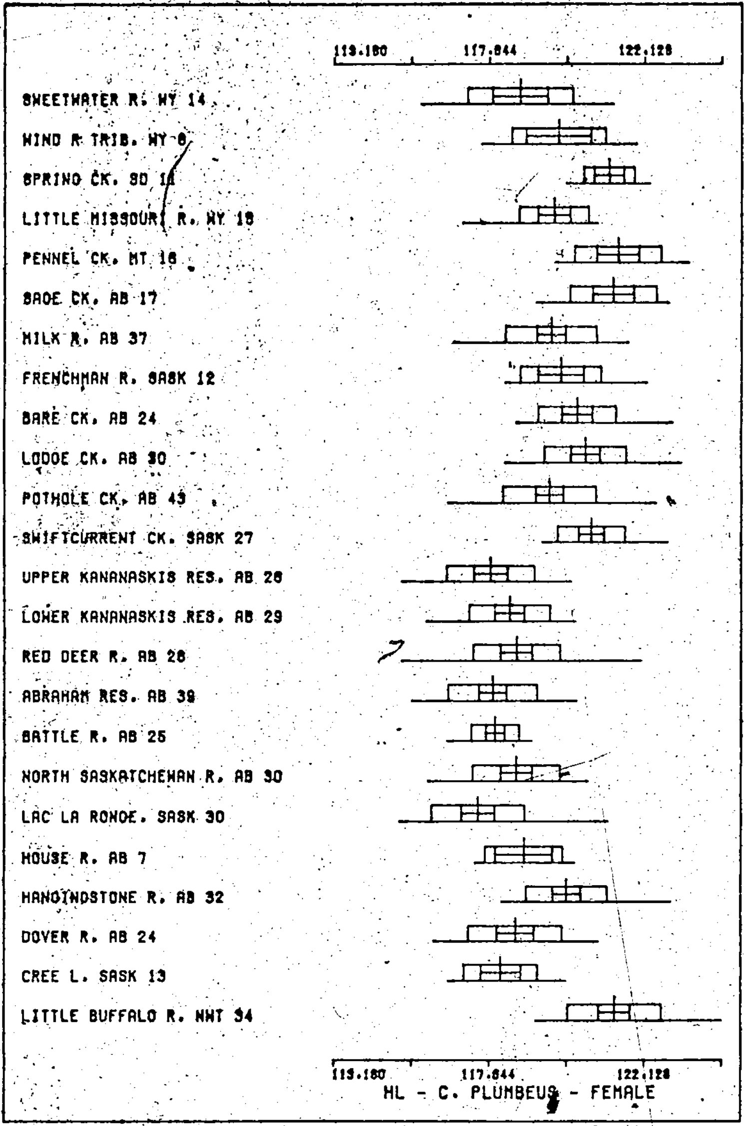
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MILK R. AB 37
FRENCHMAN R. SASK 12
BARE CK. AB 24
LODGE CK. AB 30
POTHOLE CK. AB 43
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 26
LOWER KANANASKIS RES. AB 29
RED DEER R. AB 26
ABRAHAM RES. AB 39
BATTLE R. AB 25
NORTH SASKATCHEWAN R. AB 30
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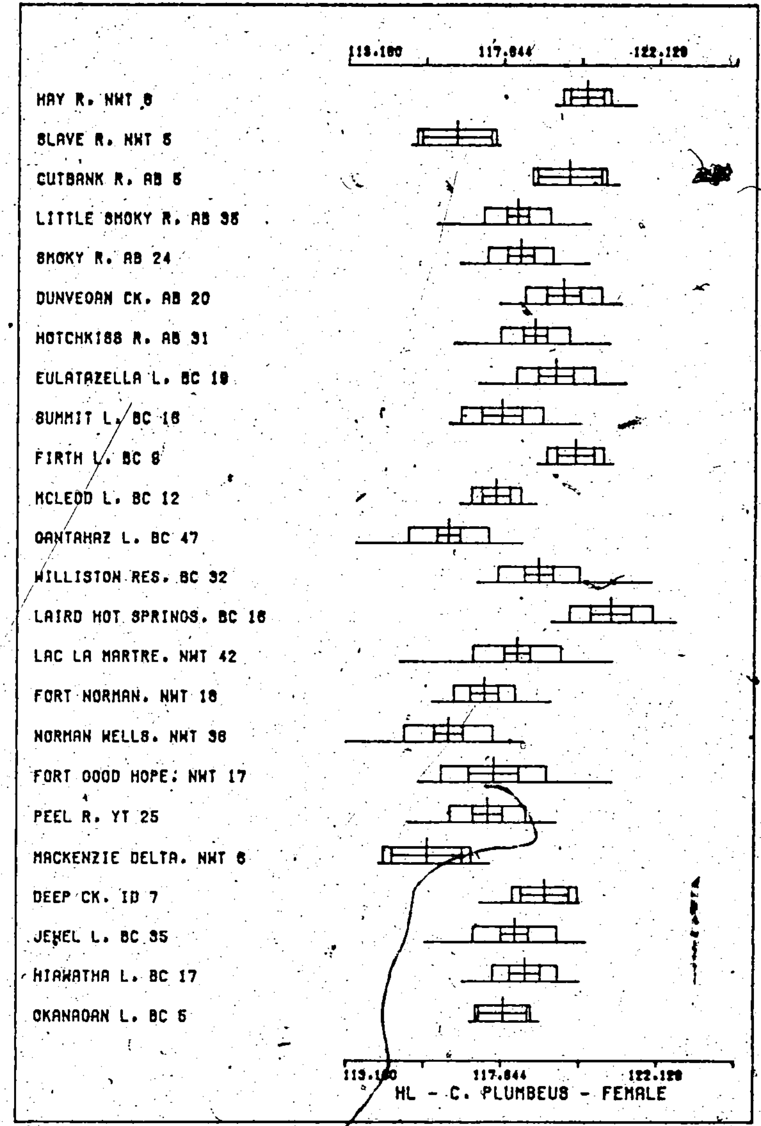
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MCLEOD L. BC 12
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WILLISTON RES. BC 32
LAIRD HOT SPRINGS. BC 16
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FORT NORMAN. NWT 18
NORMAN WELLS. NWT 36
FORT GOOD HOPE. NWT 17
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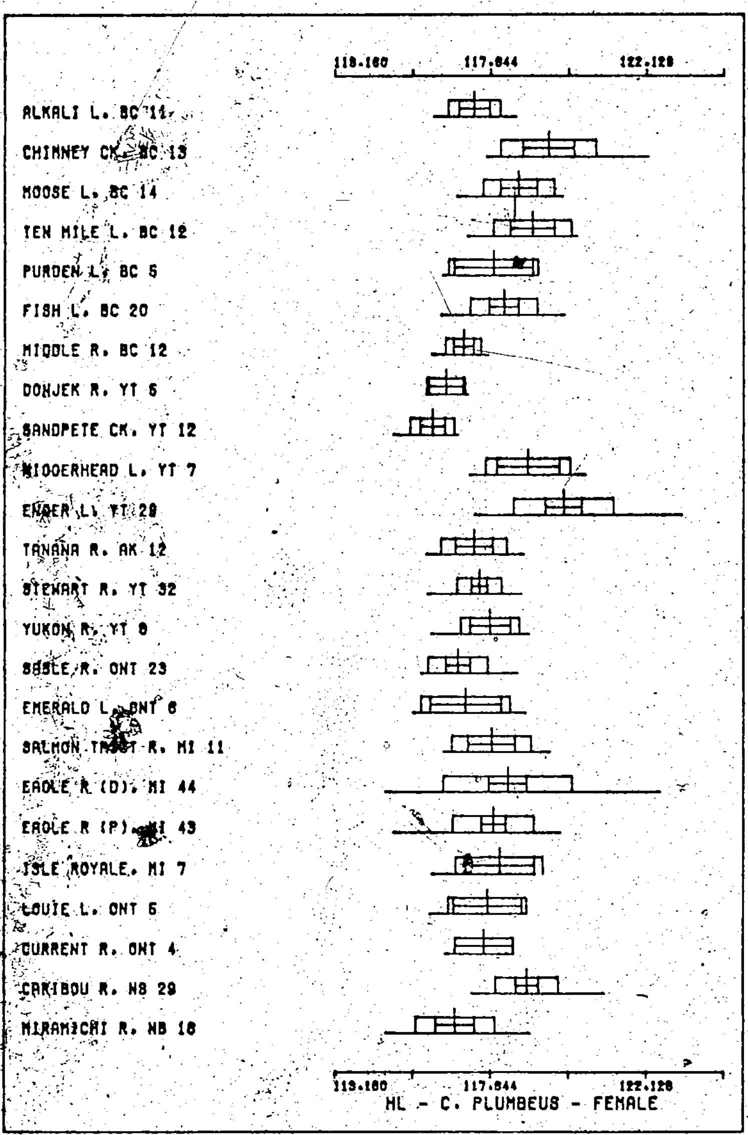
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ENGER L. YT 28
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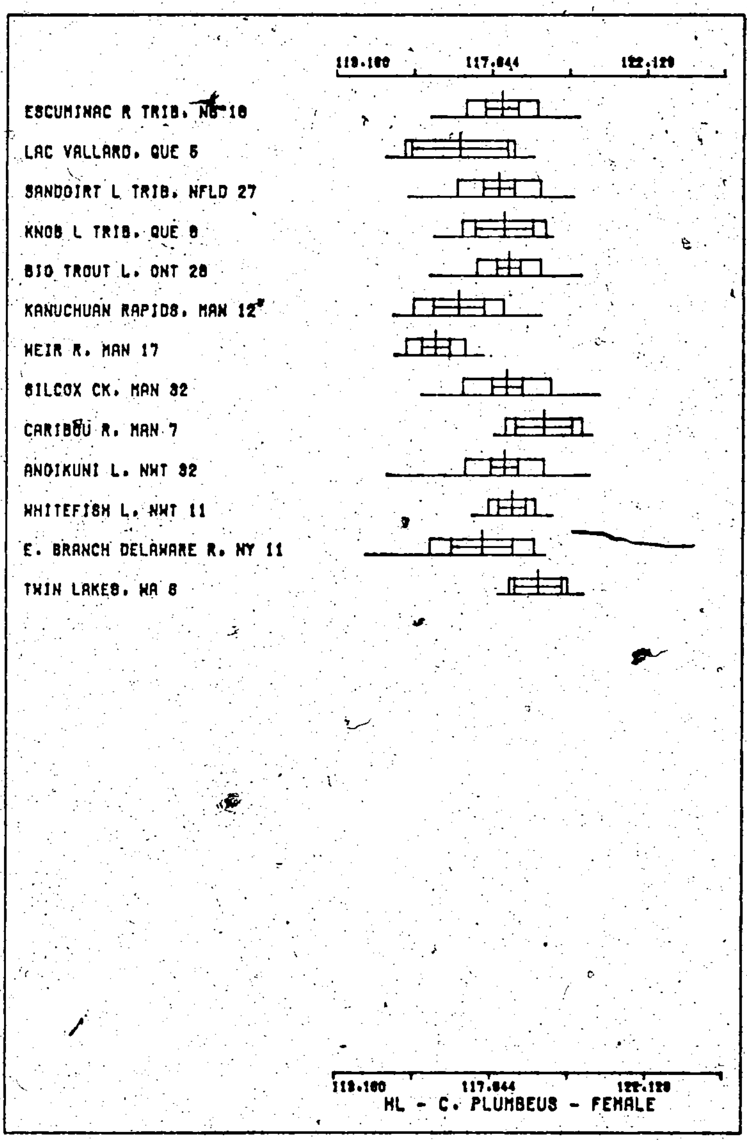
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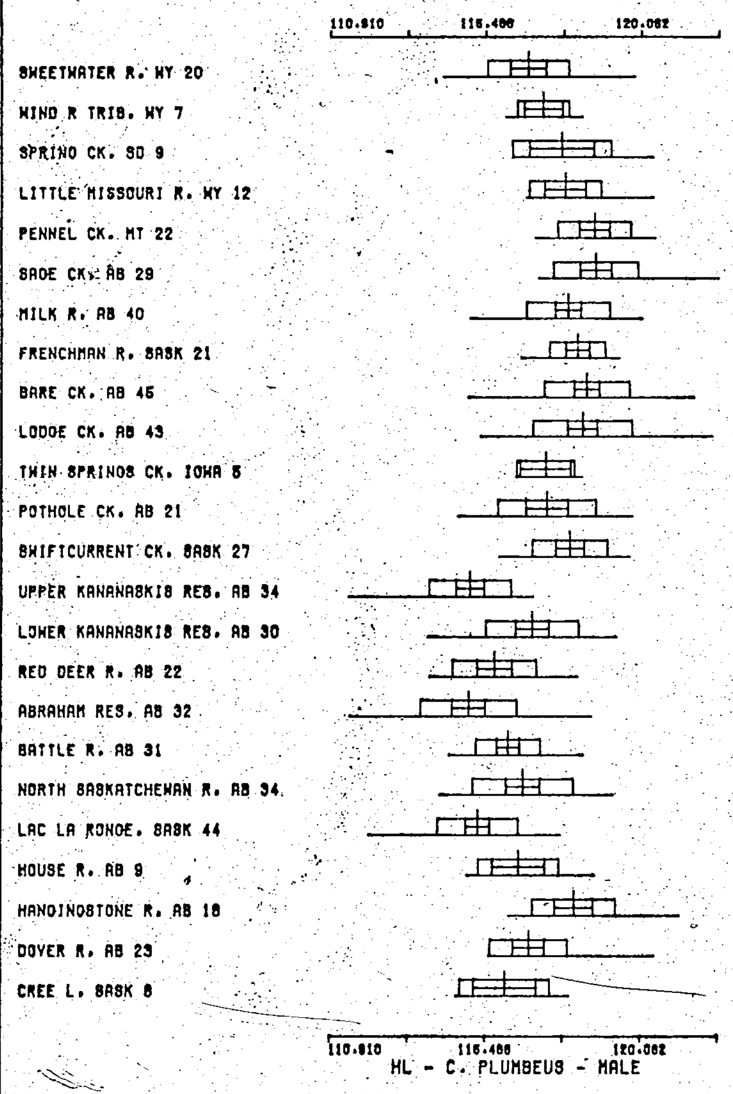
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FRENCHMAN R. SASK 21
BARE CK. AB 45
LODGE CK. AB 43
TWIN SPRINGS CK. IOWA 5
POTHOLE CK. AB 21
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 34
LOWER KANANASKIS RES. AB 30
RED DEER R. AB 22
ABRAHAM RES. AB 32
BATTLE R. AB 31
NORTH SASKATCHEWAN R. AB 34
LAC LA RONGE. SASK 44
HOUSE R. AB 9
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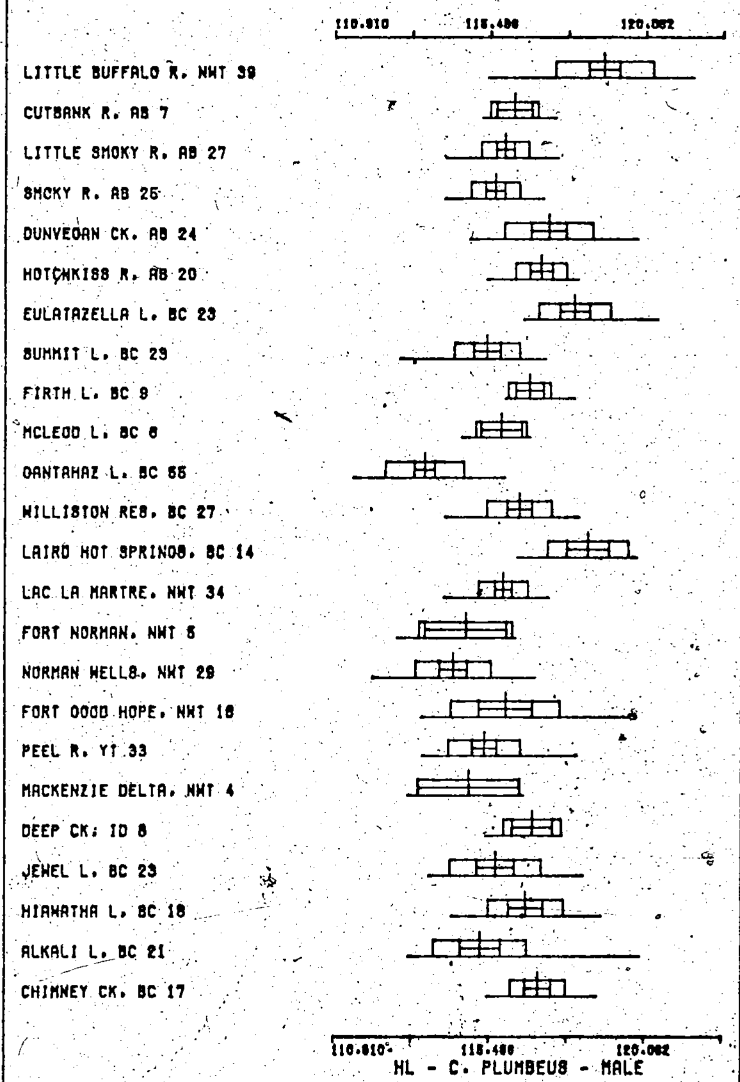
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EULATAZELLA L. BC 23
SUMMIT L. BC 29
FIRTH L. BC 9
MCLEOD L. BC 6
GANTAHAZ L. BC 55
WILLISTON RES. BC 27
LAIRD HOT SPRINGS. BC 14
LAC LA MARTRE. NWT 34
FORT NORMAN. NWT 5
NORMAN WELLS. NWT 29
FORT GOOD HOPE. NWT 18
PEEL R. YT 33
MACKENZIE DELTA. NWT 4
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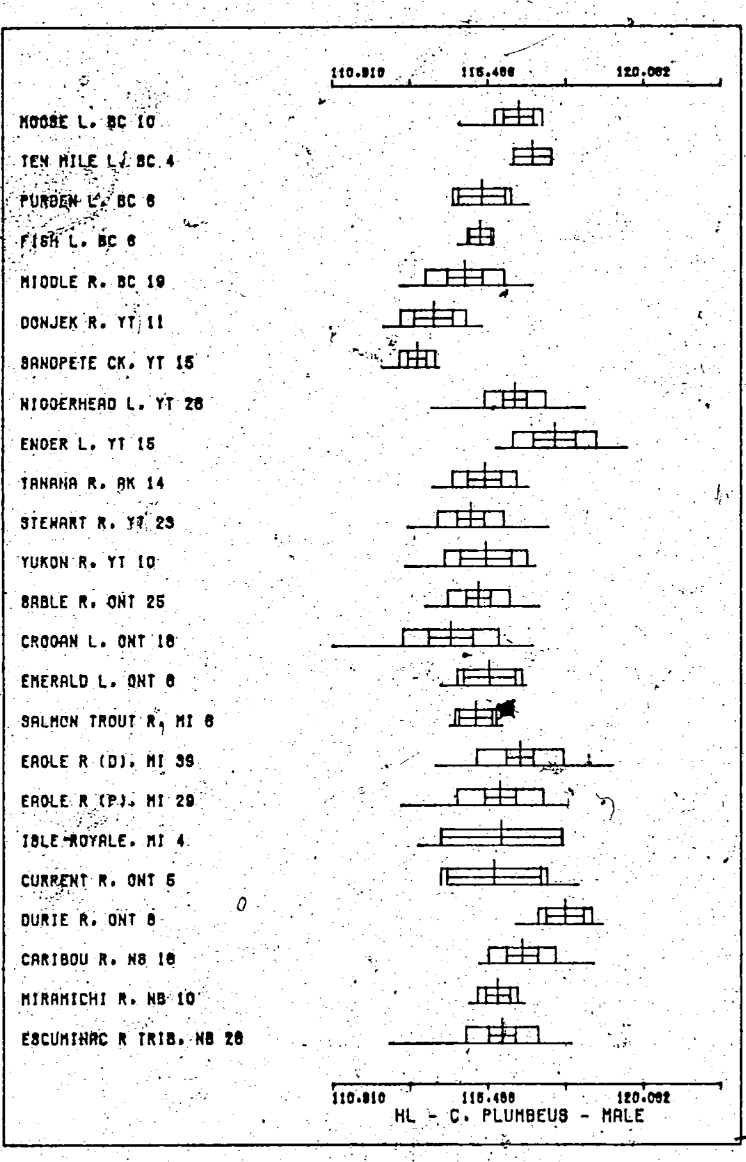

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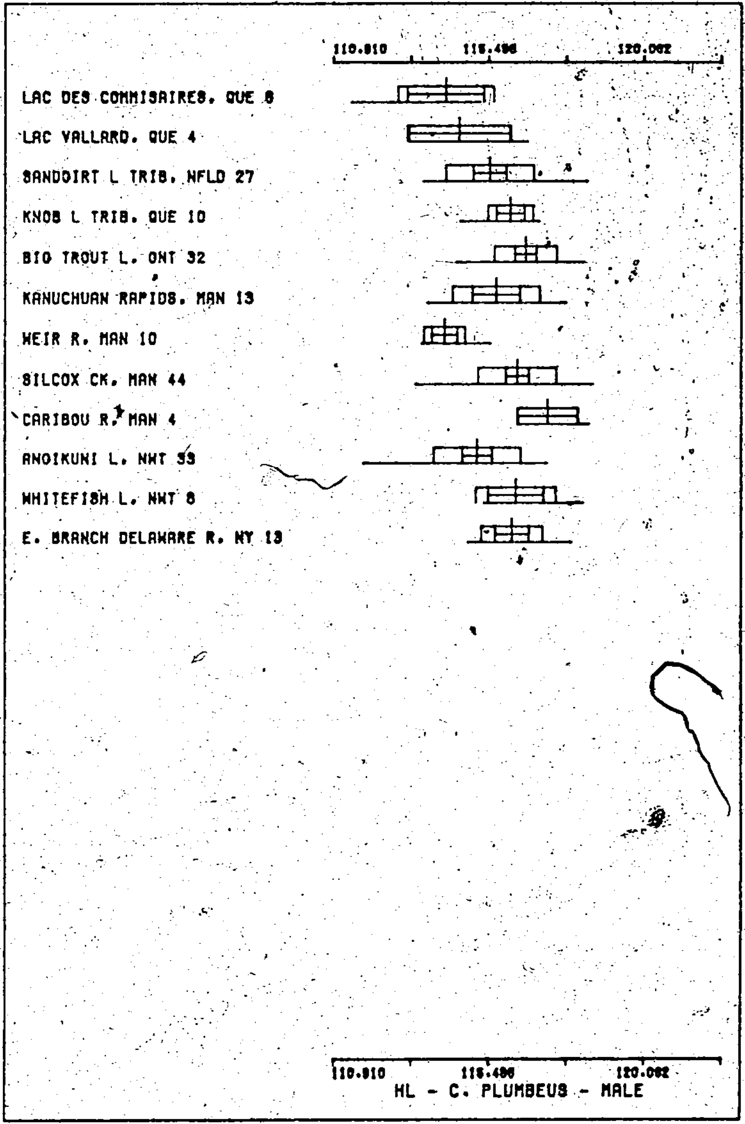

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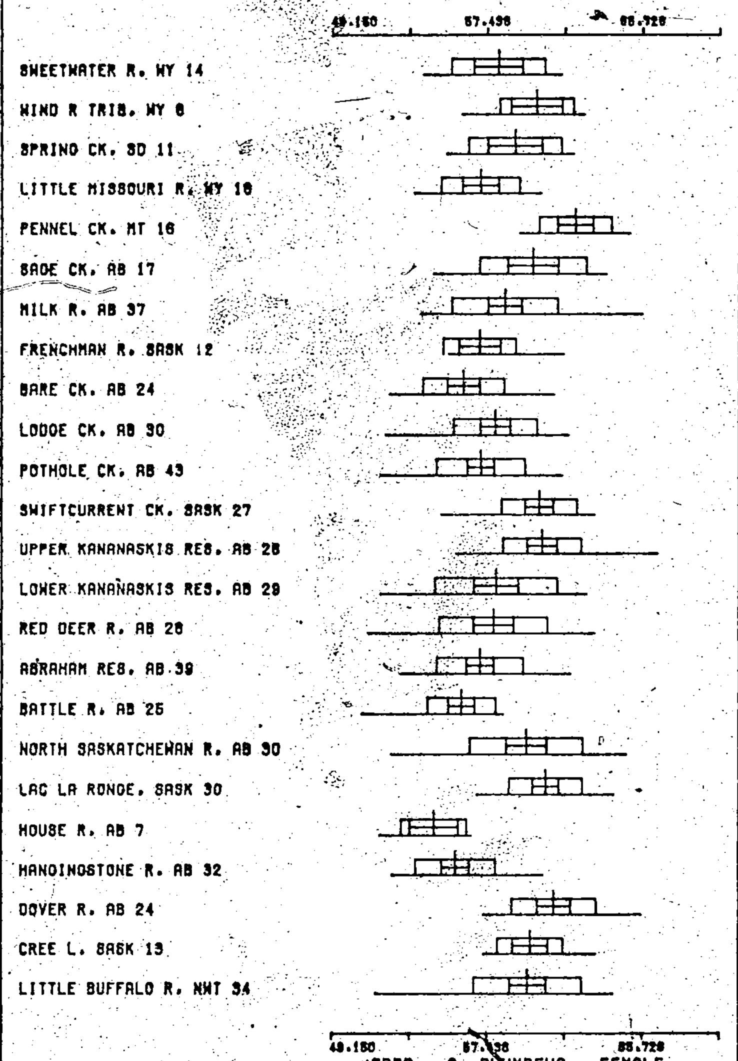

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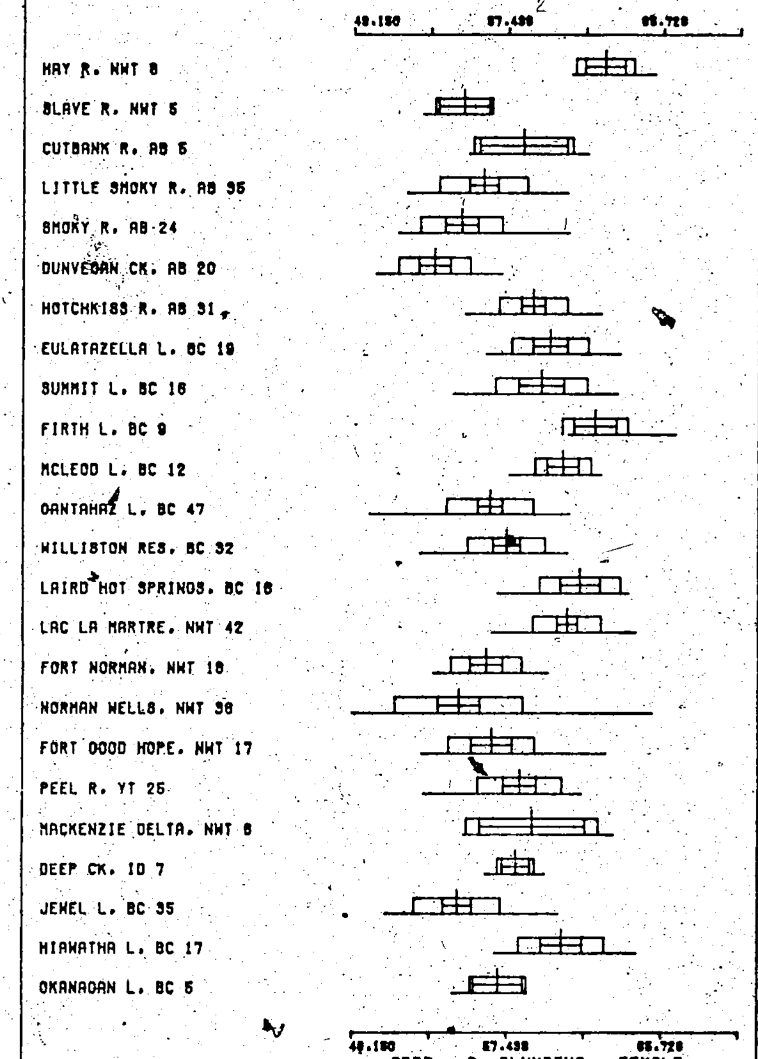

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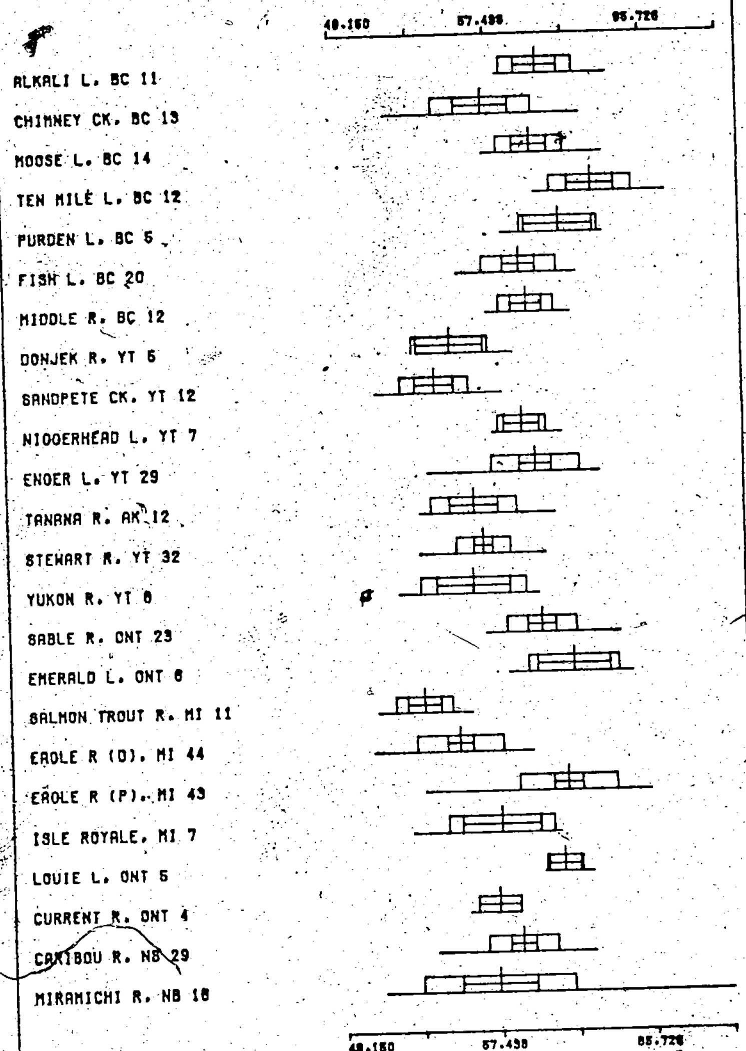

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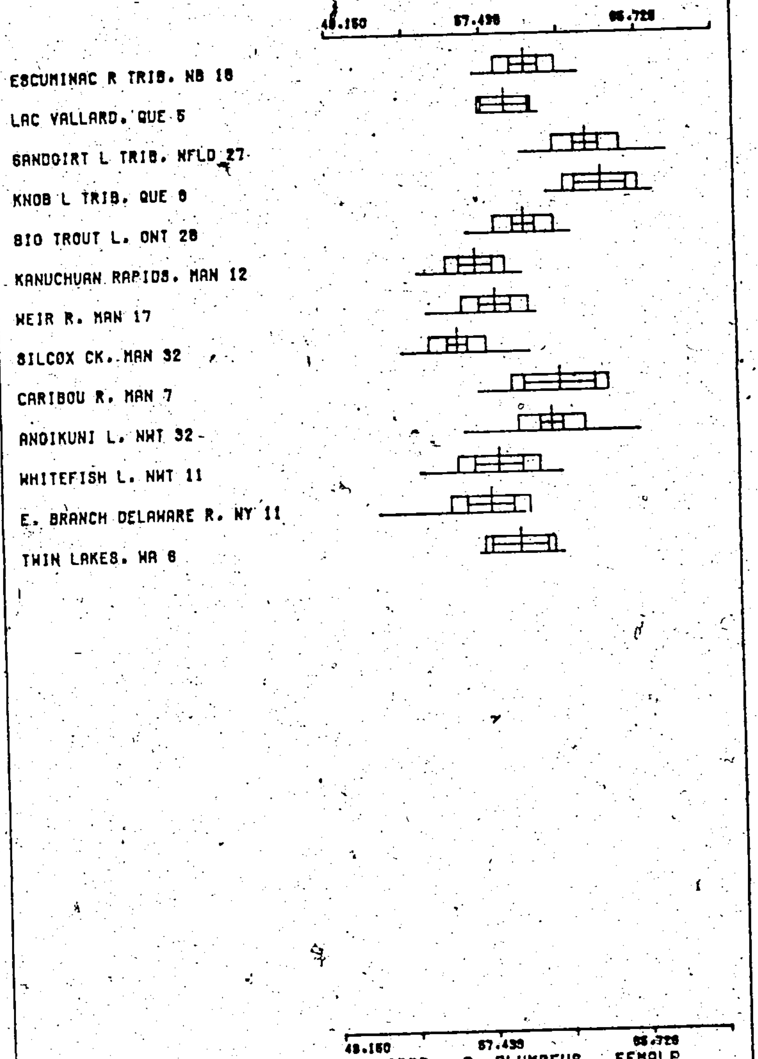

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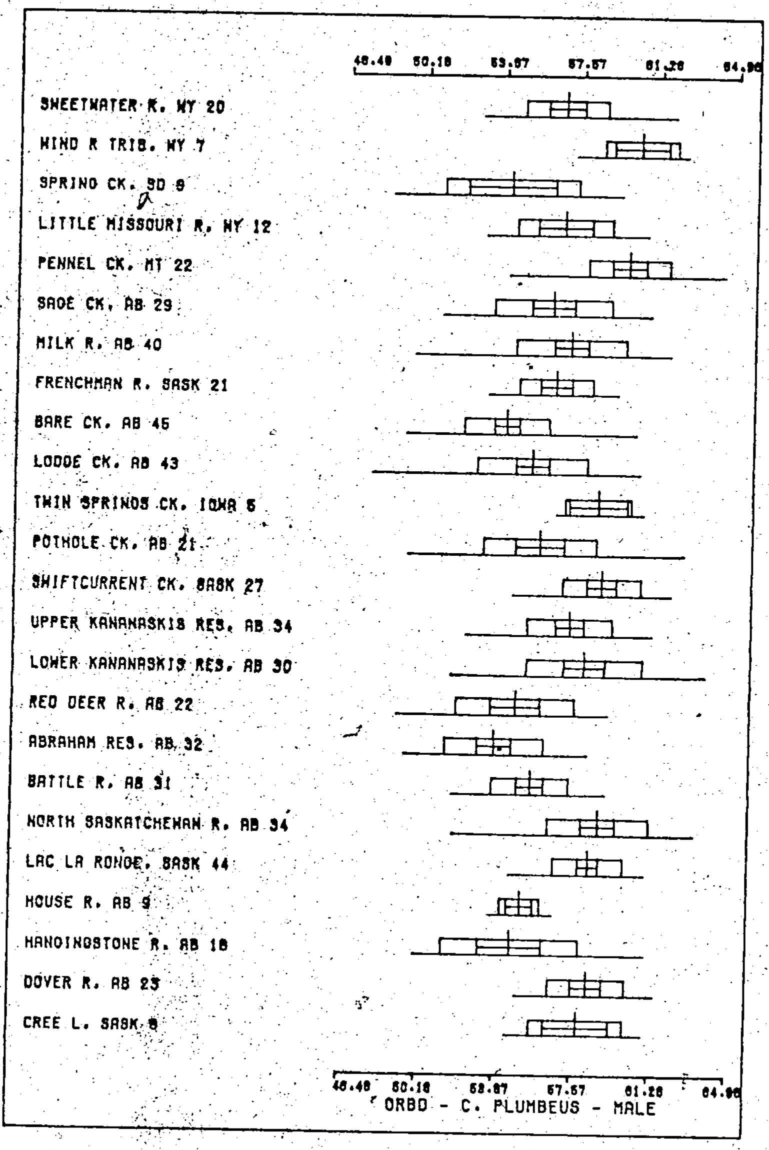
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LITTLE MISSOURI R. WY 12
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SAGE CK. AB 29
MILK R. AB 40
FRENCHMAN R. SASK 21
BARE CK. AB 45
LODGE CK. AB 43
TWIN SPRINGS CK. IOWA 5
POTHOLE CK. AB 21
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 34
LOWER KANANASKIS RES. AB 30
RED DEER R. AB 22
ABRAHAM RES. AB 32
BATTLE R. AB 31
NORTH SASKATCHEWAN R. AB 34
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CREE L. SASK 8
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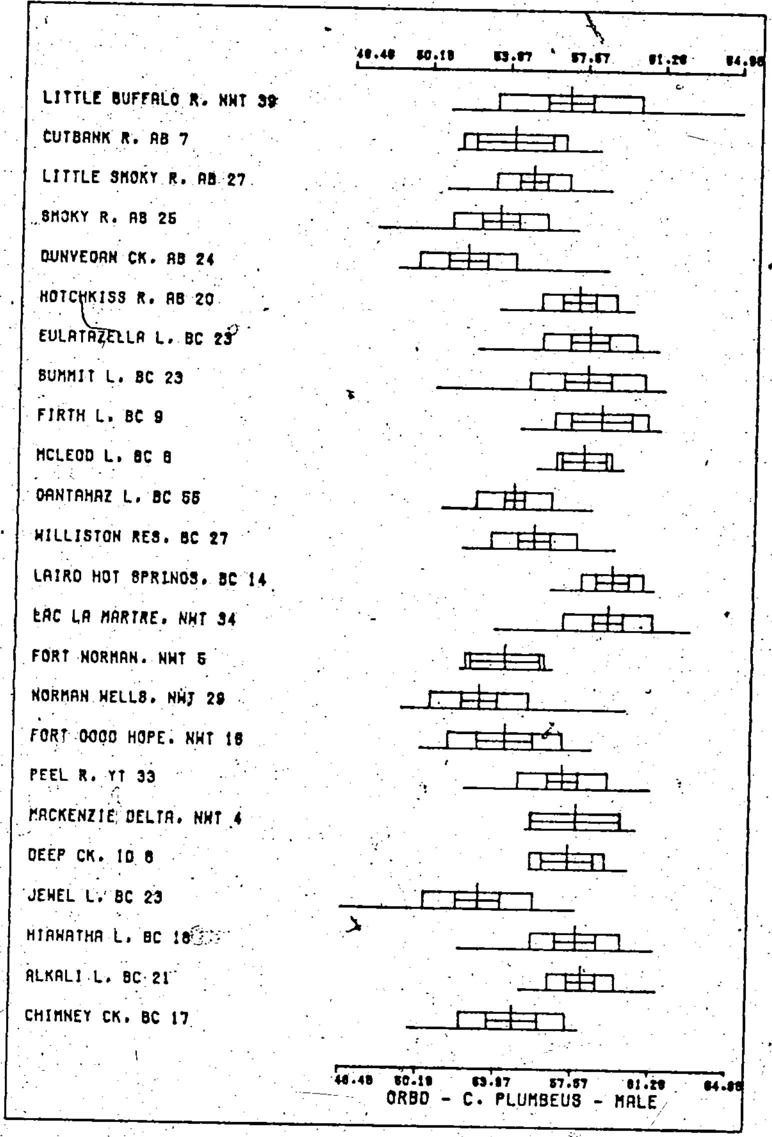
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EULATAZELLA L. BC 23
SUMMIT L. BC 23
FIRTH L. BC 9
MCLEOD L. BC 8
GANTAHAZ L. BC 55
WILLISTON RES. BC 27
LAIRD HOT SPRINGS. BC 14
LAC LA MARTRE. NWT 34
FORT NORMAN. NWT 5
NORMAN WELLS. NWT 29
FORT GOOD HOPE. NWT 18
PEEL R. YT 33
MACKENZIE DELTA. NWT 4
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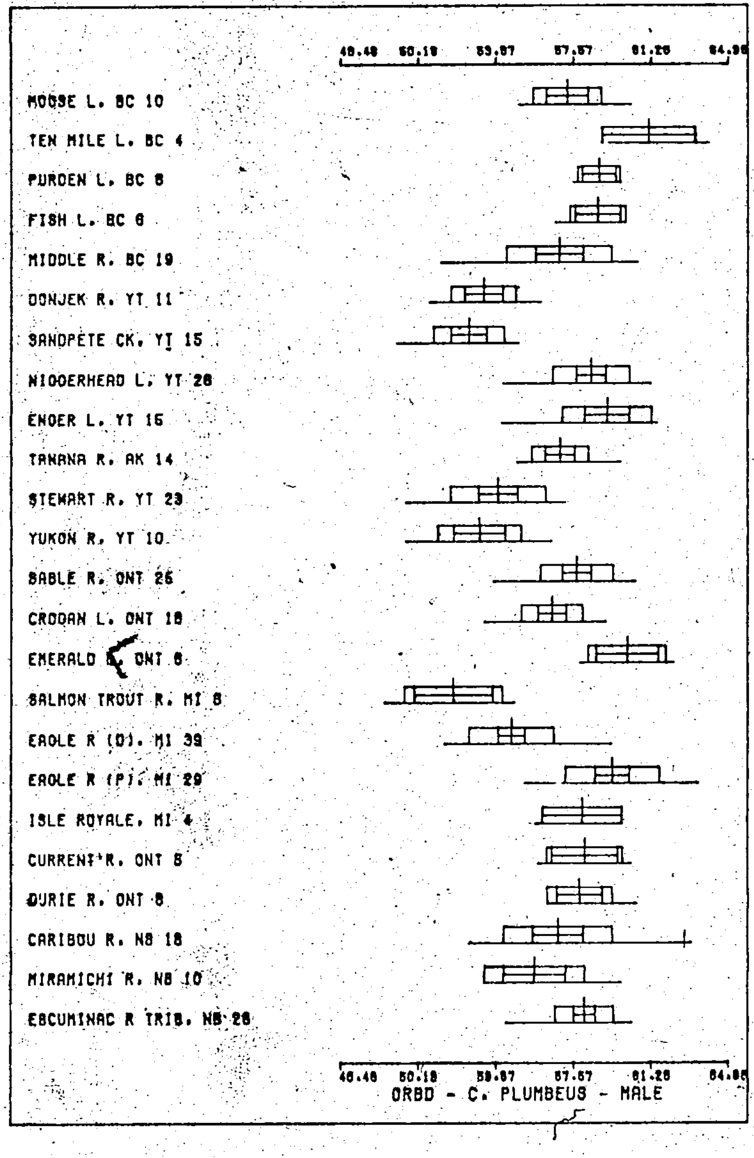
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NIDDERHEAD L. YT 28
ENDER L. YT 16
TANANA R. AK 14
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YUKON R. YT 10
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CRODAN L. ONT 18
EMERALD L. ONT 6
SALMON TROUT R. MI 6
EAGLE R (D). MI 39
EAGLE R (P). MI 29
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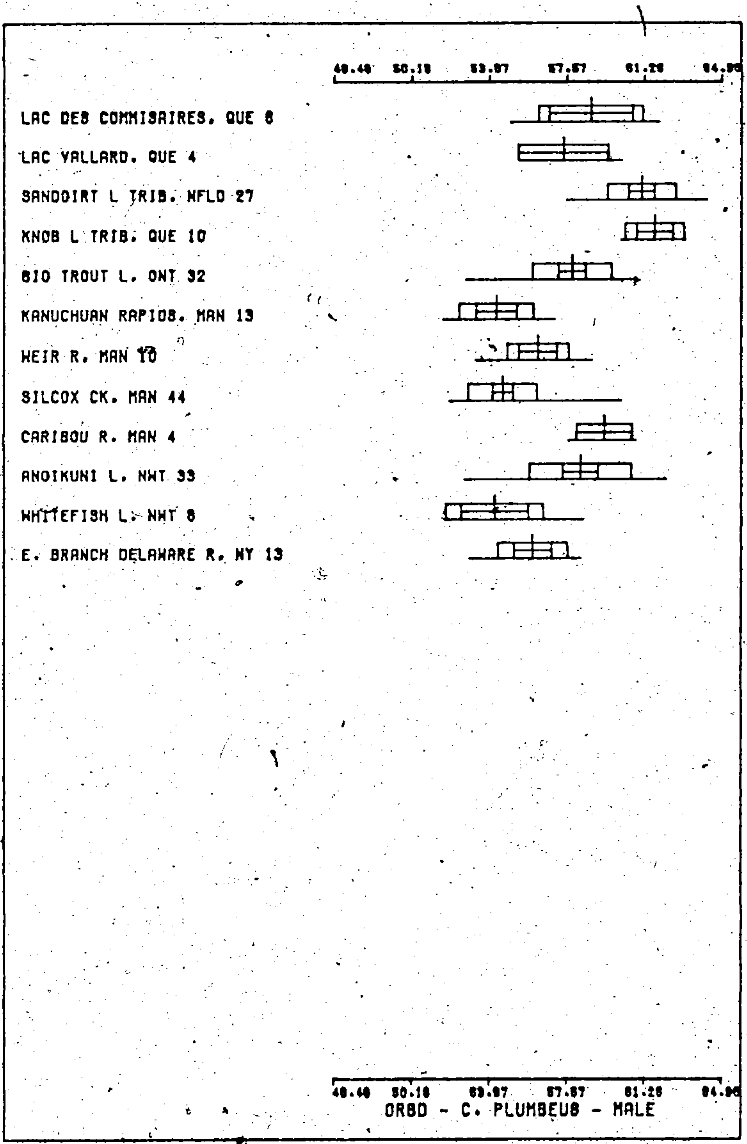
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BIG TROUT L. ONT 32
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WEIR R. MAN 10
SILCOX CK. MAN 44
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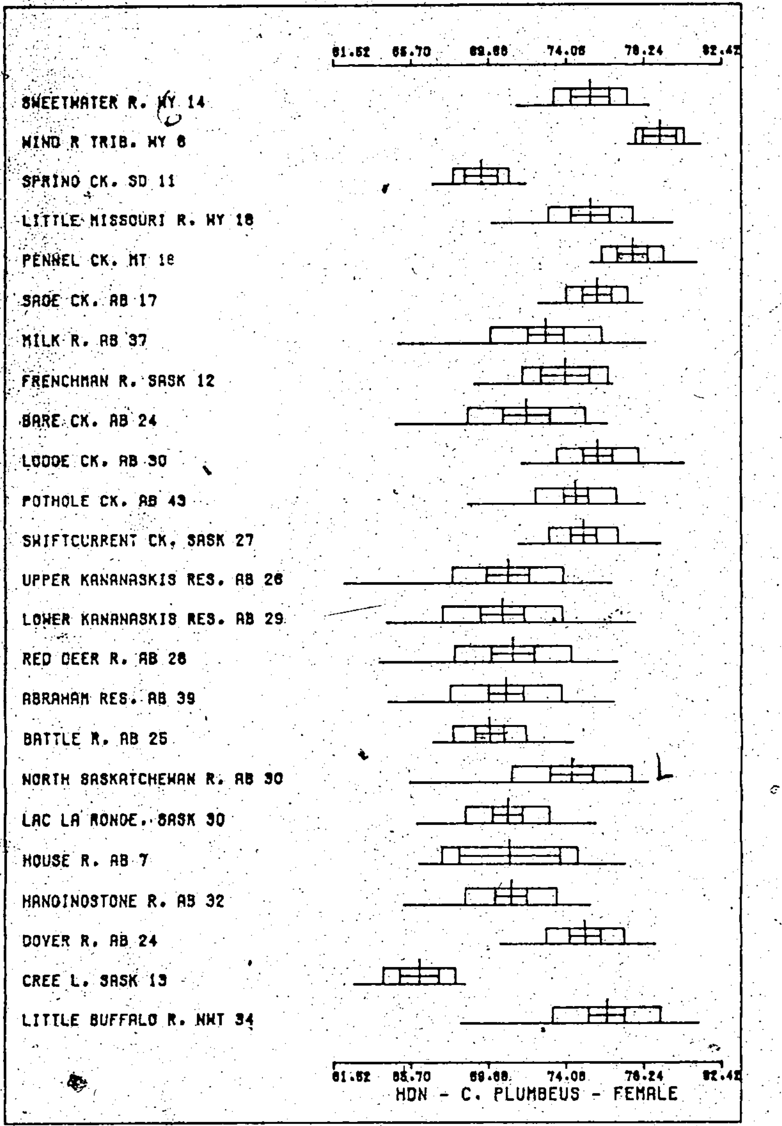
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LODGE CK. AB 30
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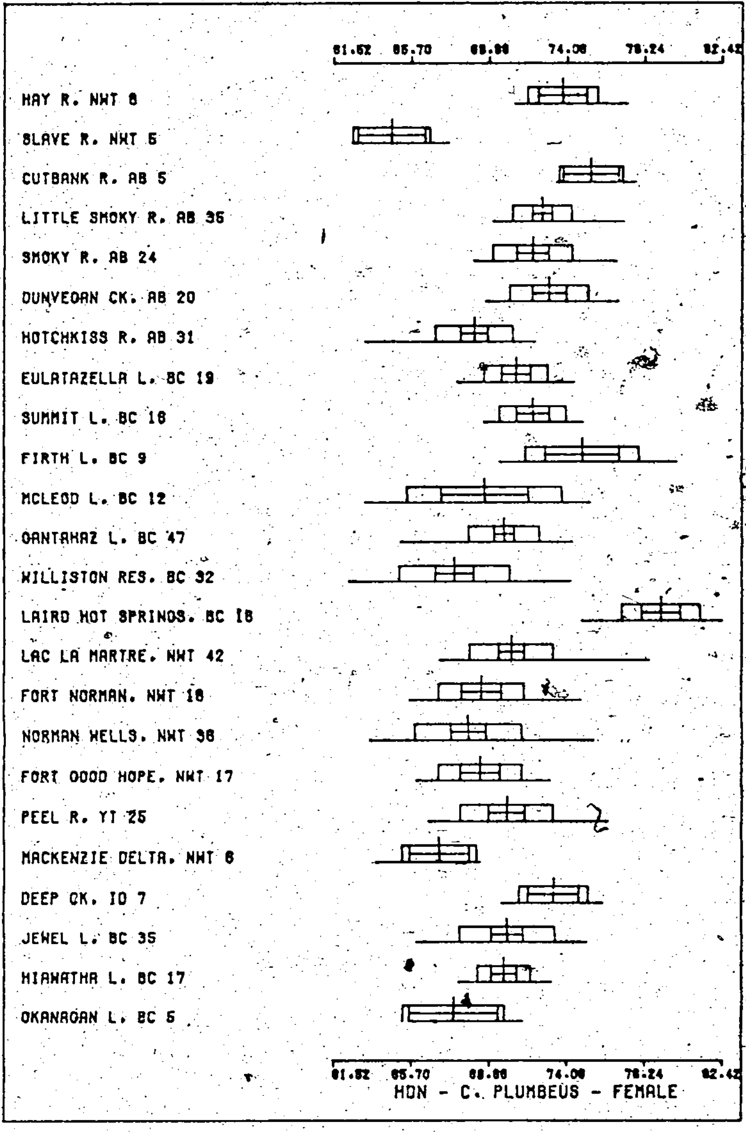
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FIRTH L. BC 9
MCLEOD L. BC 12
GANTAHAZ L. BC 47
WILLISTON RES. BC 32
LAIRD HOT SPRINGS. BC 18
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FORT GOOD HOPE. NWT 17
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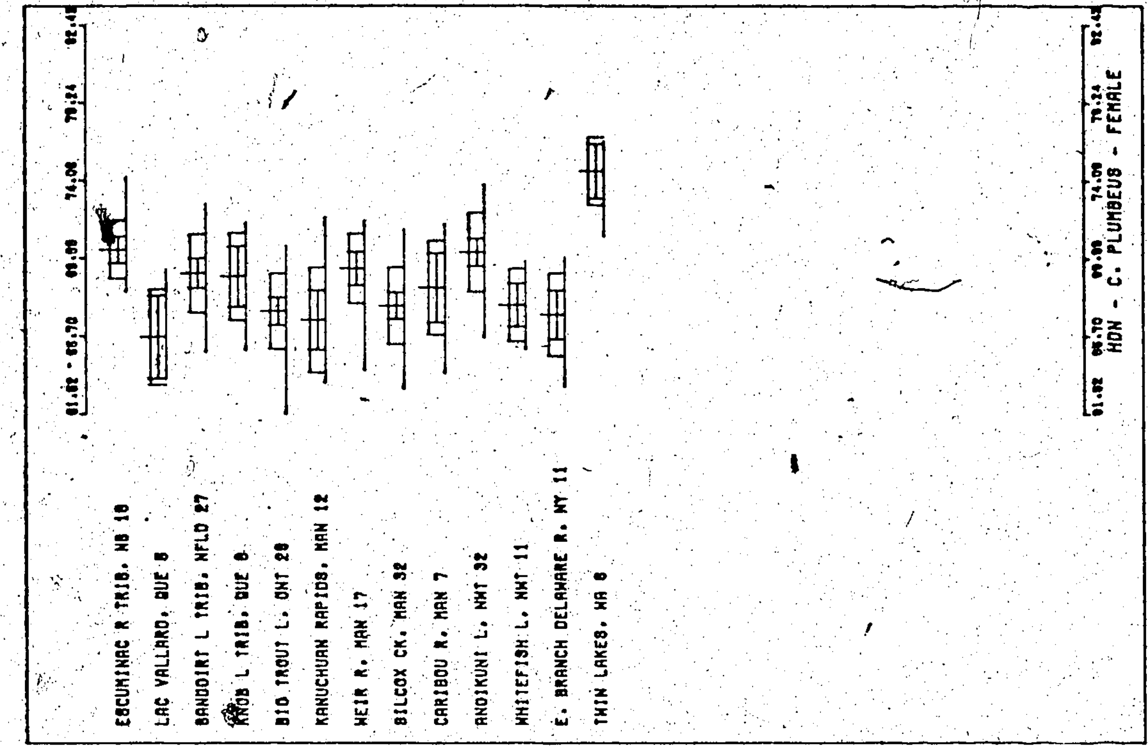
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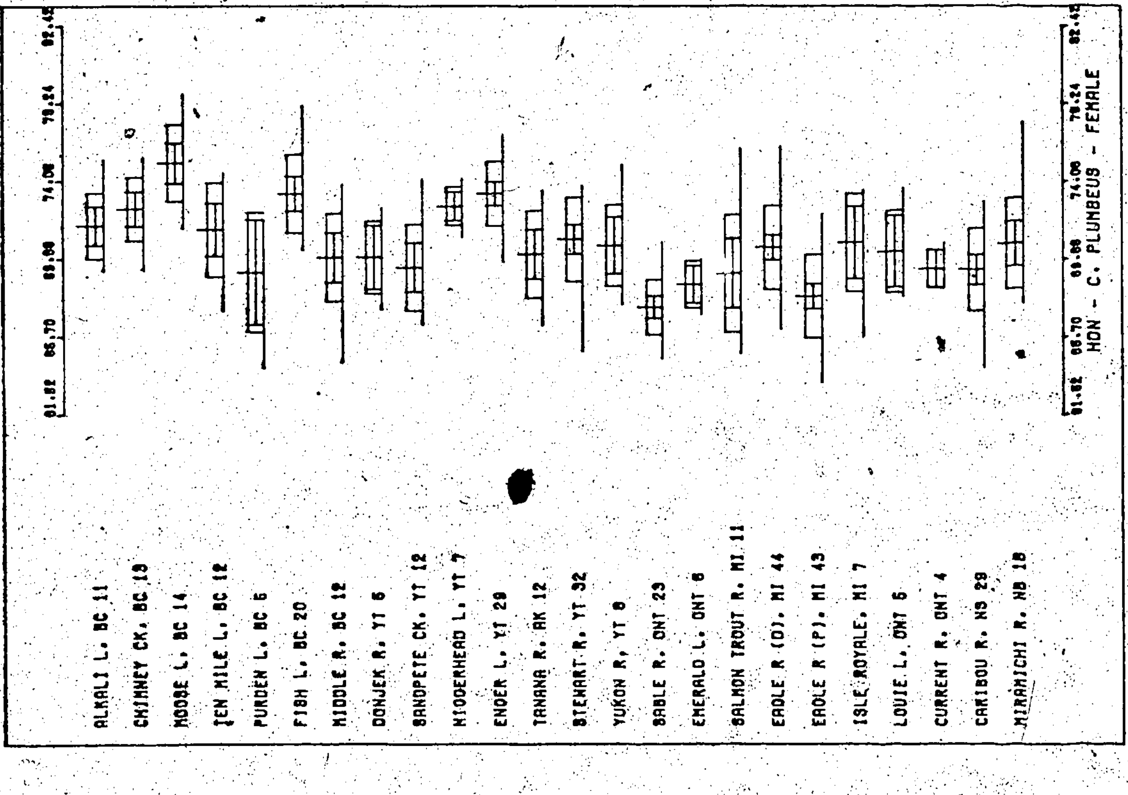
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LOUIE L. ONT 6
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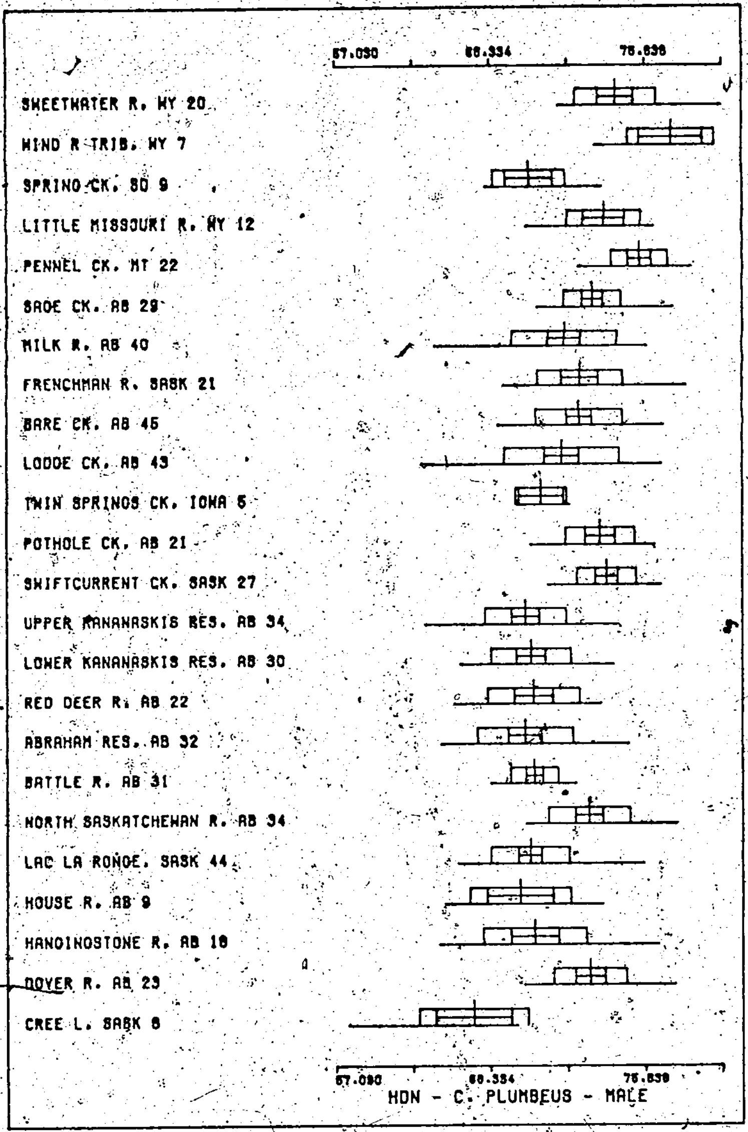
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LOWER KANANASKIS RES. AB 30
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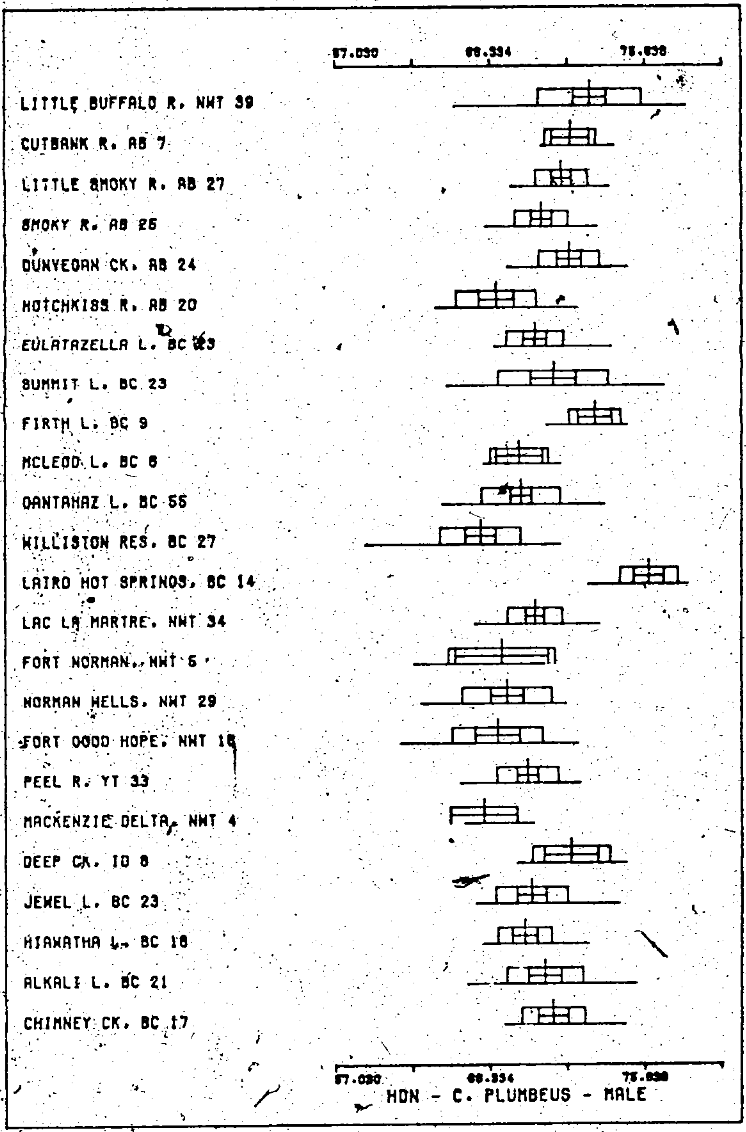
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SUMMIT L. BC 23
FIRTH L. BC 9
MCLEOD L. BC 8
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LAIRD HOT SPRINGS. BC 14
LAC LA MARTRE. NWT 34
FORT NORMAN. NWT 5
NORMAN WELLS. NWT 29
FORT GOOD HOPE. NWT 18
PEEL R. YT 33
MACKENZIE DELTA. NWT 4
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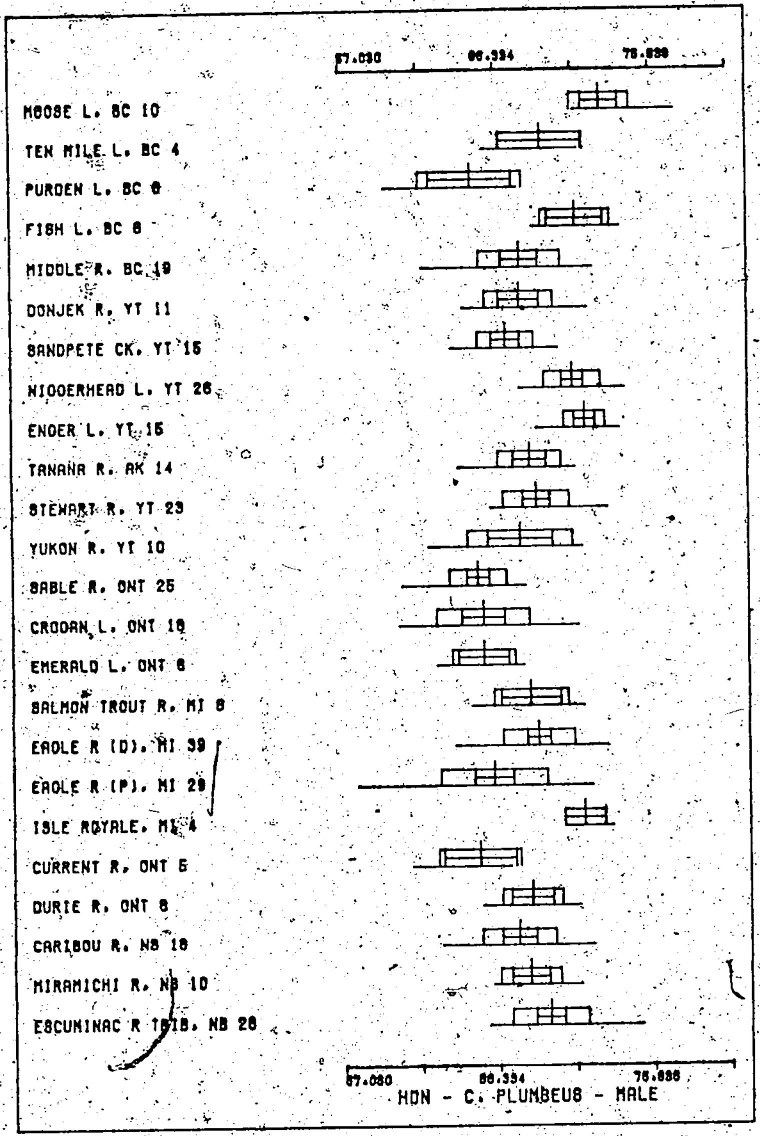

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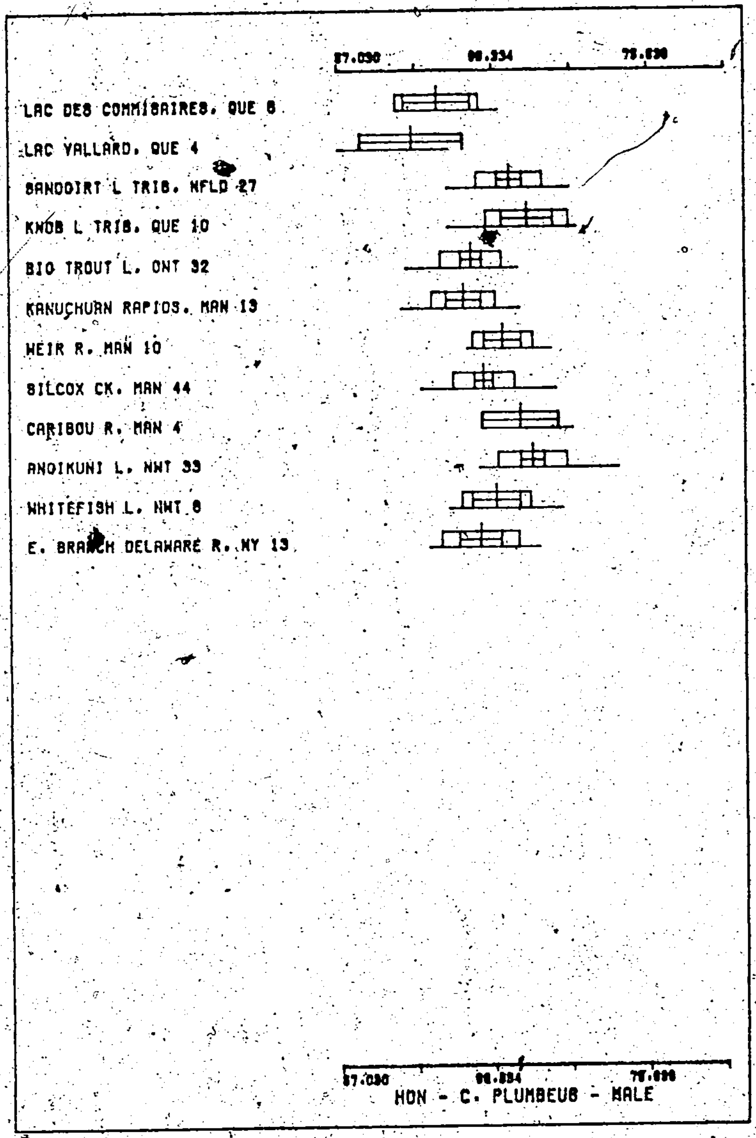

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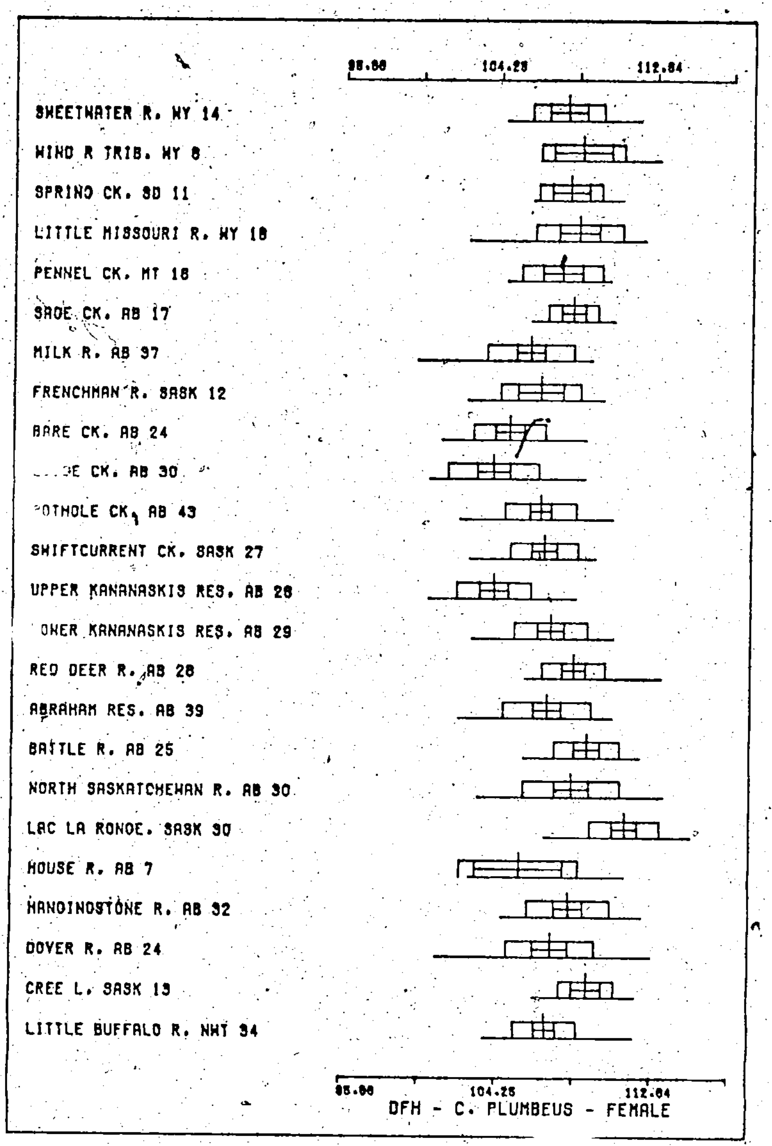

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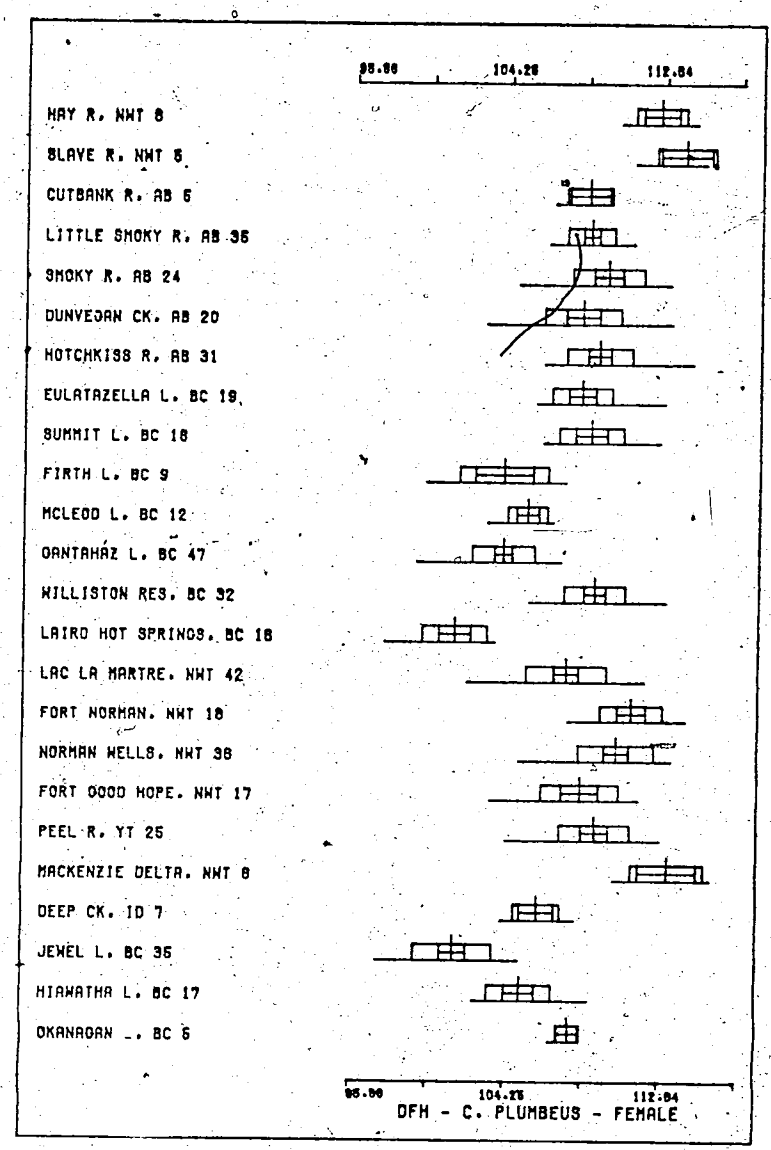
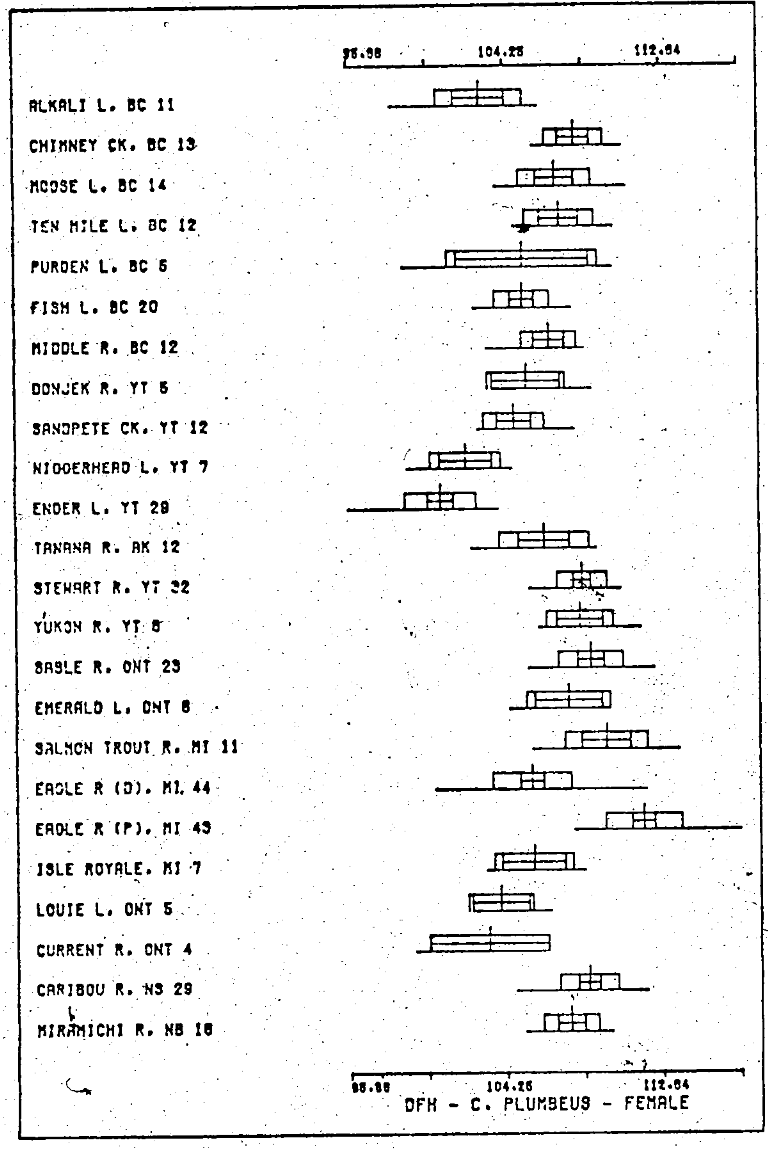


DFH - C. PLUMBEUS - FEMALE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112.64
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MIDDLE R. BC 12
DONJEK R. YT 5
SANDPETE CK. YT 12
NIDDERHERD L. YT 7
ENDER L. YT 29
TANANA R. AK 12
STEWART R. YT 32
YUKON R. YT 5
SABLE R. ONT 23
EMERALD L. ONT 8
SALMON TROUT R. MI 11
EAGLE R (D). MI 44
EAGLE R (P). MI 43
ISLE ROYALE. MI 7
LOUIE L. ONT 5
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CARIBOU R. NS 29
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104.25
112.64
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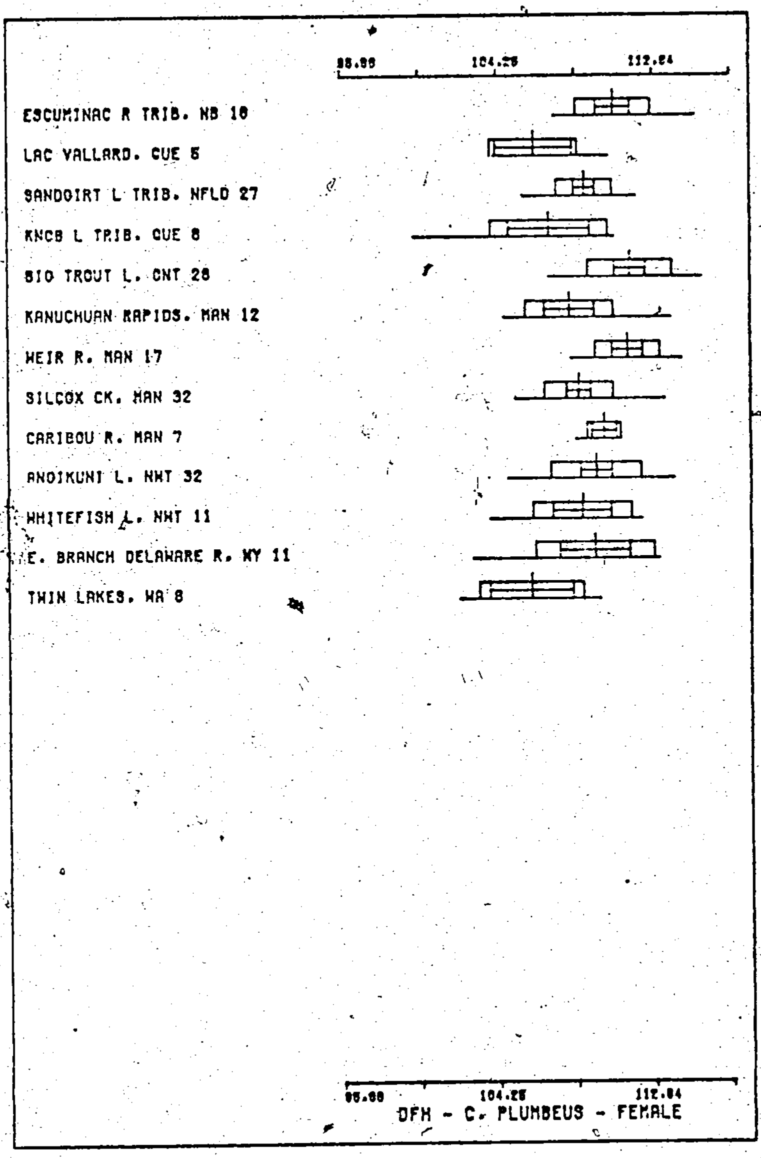
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BIG TROUT L. ONT 28
KANUCHUAN RAPIDS. MAN 12
WEIR R. MAN 17
SILCOX CK. MAN 32
CARIBOU R. MAN 7
ANGIKUNI L. NWT 32
WHITEFISH L. NWT 11
E. BRANCH DELAWARE R. NY 11
THIN LAKES. WA 8
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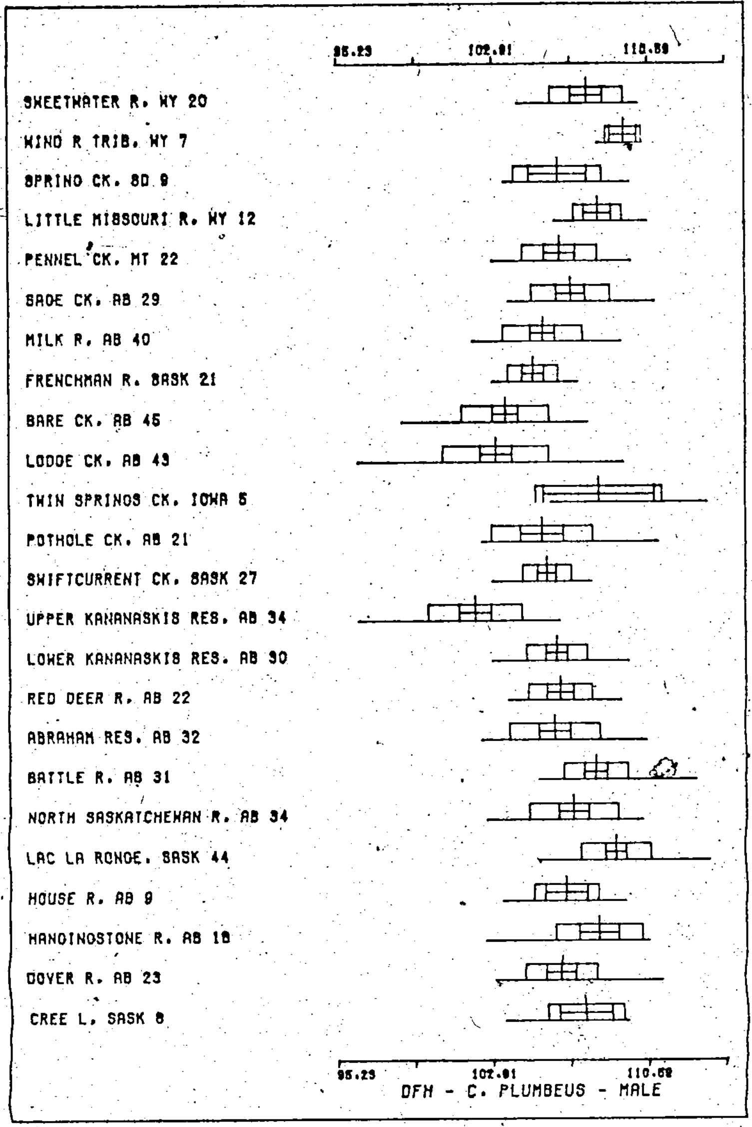
104.25
112.64
DFH - C. PLUMBEUS - FEMALE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SAGE CK. AB 29
MILK R. AB 40
FRENCHMAN R. SASK 21
BARE CK. AB 45
LODGE CK. AB 43
TWIN SPRINGS CK. IOWA 5
POTHOLE CK. AB 21
SWIFTCURRENT CK. SASK 27
UPPER KANANASKIS RES. AB 34
LOWER KANANASKIS RES. AB 30
RED DEER R. AB 22
ABRAHAM RES. AB 32
BATTLE R. AB 31
NORTH SASKATCHEWAN R. AB 34
LAC LA RONGE. SASK 44
HOUSE R. AB 9
HANGINGSTONE R. AB 18
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102.91
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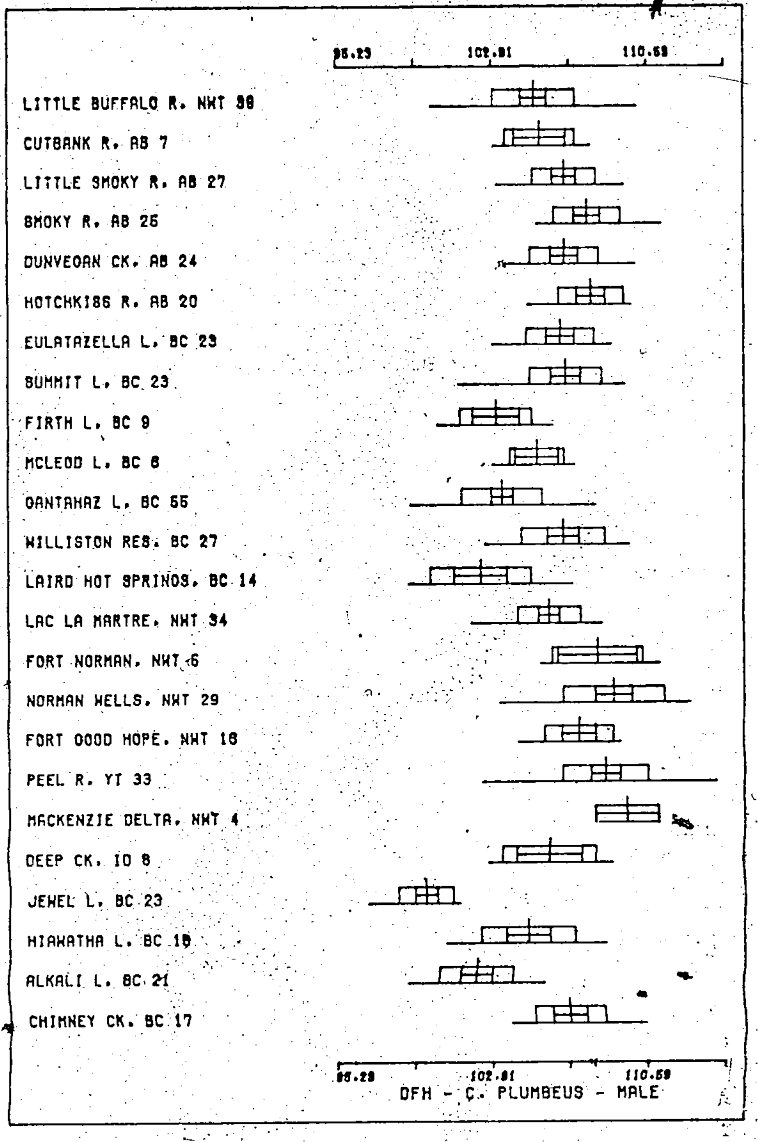
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DUNVEGAN CK. AB 24
HOTCHKISS R. AB 20
EULATAZELLA L. BC 23
SUMMIT L. BC 23
FIRTH L. BC 9
MCLEOD L. BC 6
GANTAHAZ L. BC 55
WILLISTON RES. BC 27
LAIRD HOT SPRINGS. BC 14
LAC LA MARTRE. NWT 34
FORT NORMAN. NWT 6
NORMAN WELLS. NWT 29
FORT GOOD HOPE. NWT 18
PEEL R. YT 33
MACKENZIE DELTA. NWT 4
DEEP CK. ID 8
JEWEL L. BC 23
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CHIMNEY CK. BC 17
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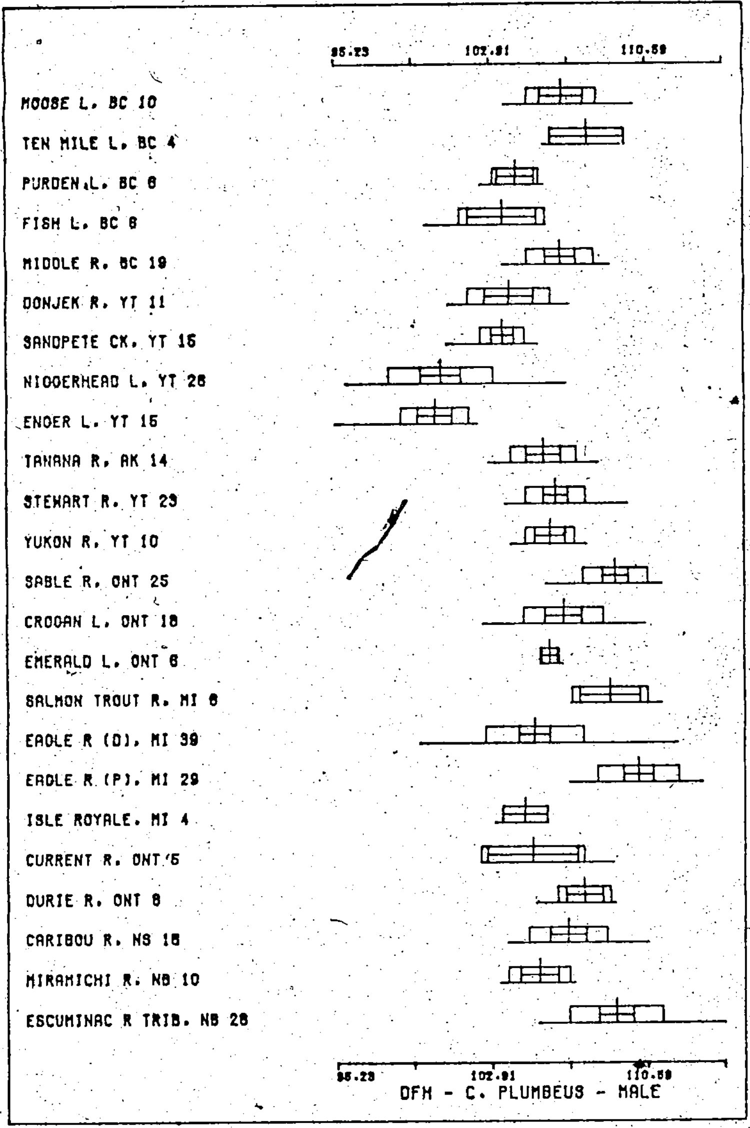
102.91
110.59
DFH - C. PLUMBEUS - MALE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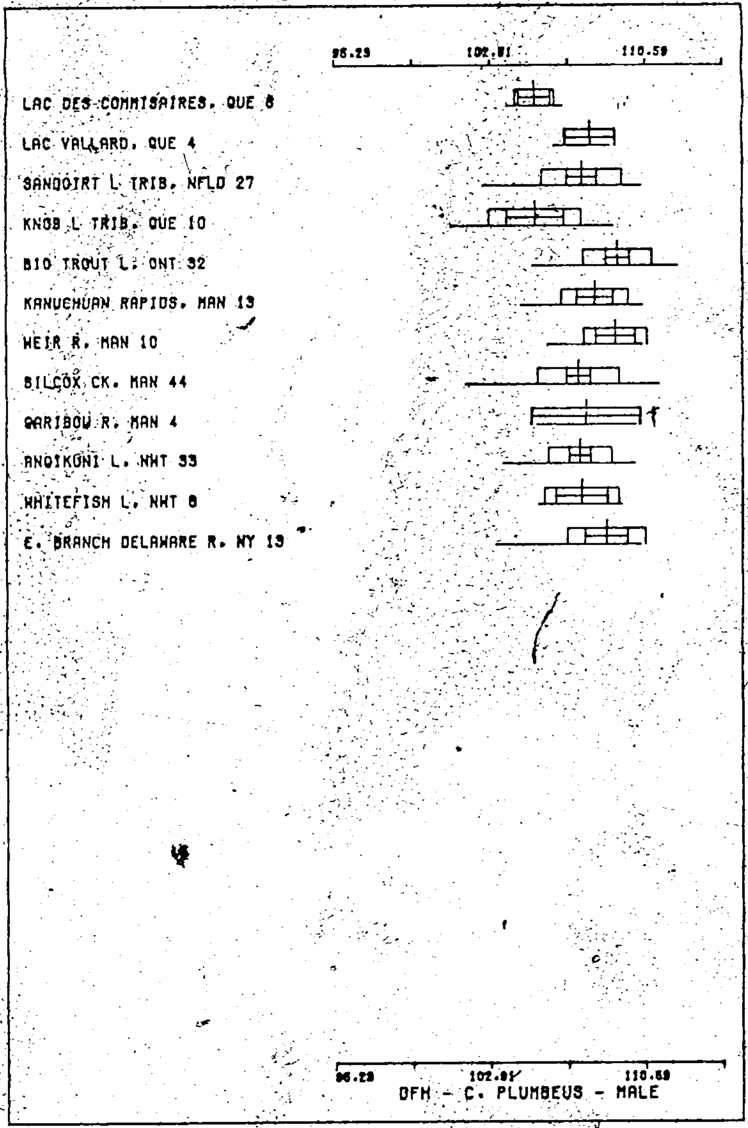
PURDEN L. BC 6
FISH L. BC 6
MIDDLE R. BC 19
DONJEK R. YT 11
SANDPETE CK. YT 15
NIOOERHEAD L. YT 26
ENOER L. YT 15
TANANA R. AK 14
STEWART R. YT 23
YUKON R. YT 10
SABLE R. ONT 25
CROOAN L. ONT 18
EMERALD L. ONT 6
SALMON TROUT R. MI 6
EAOLE R (D). MI 39
EAOLE R (P). MI 29
ISLE ROYALE. MI 4
CURRENT R. ONT 5
DURIE R. ONT 8
CARIBOU R. NS 18
MIRAMICHI R. NB 10
ESCUMINAC R TRIB. NB 26
95.23
102.91
110.59
DFM - C. PLUMBEUS - MALE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102.91
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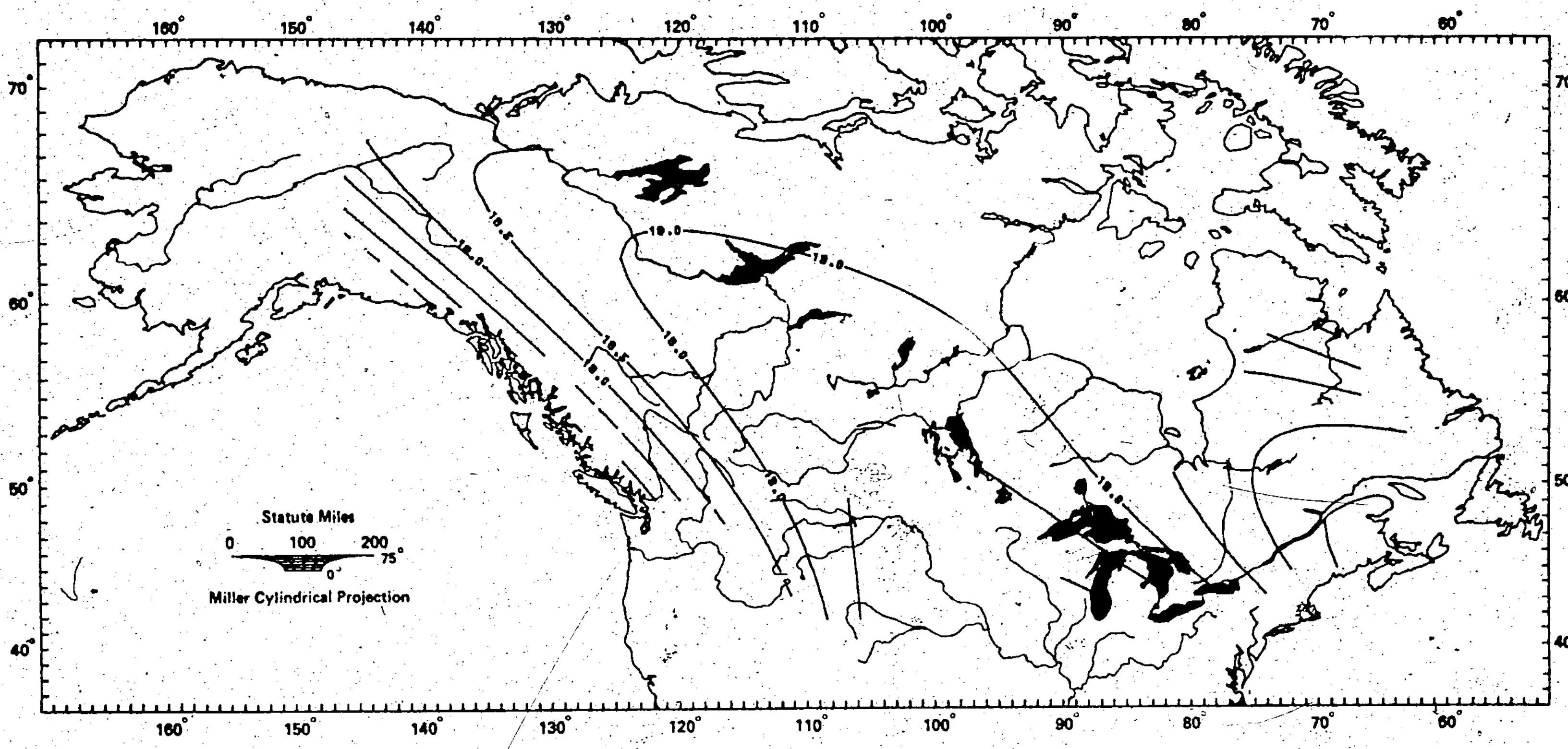
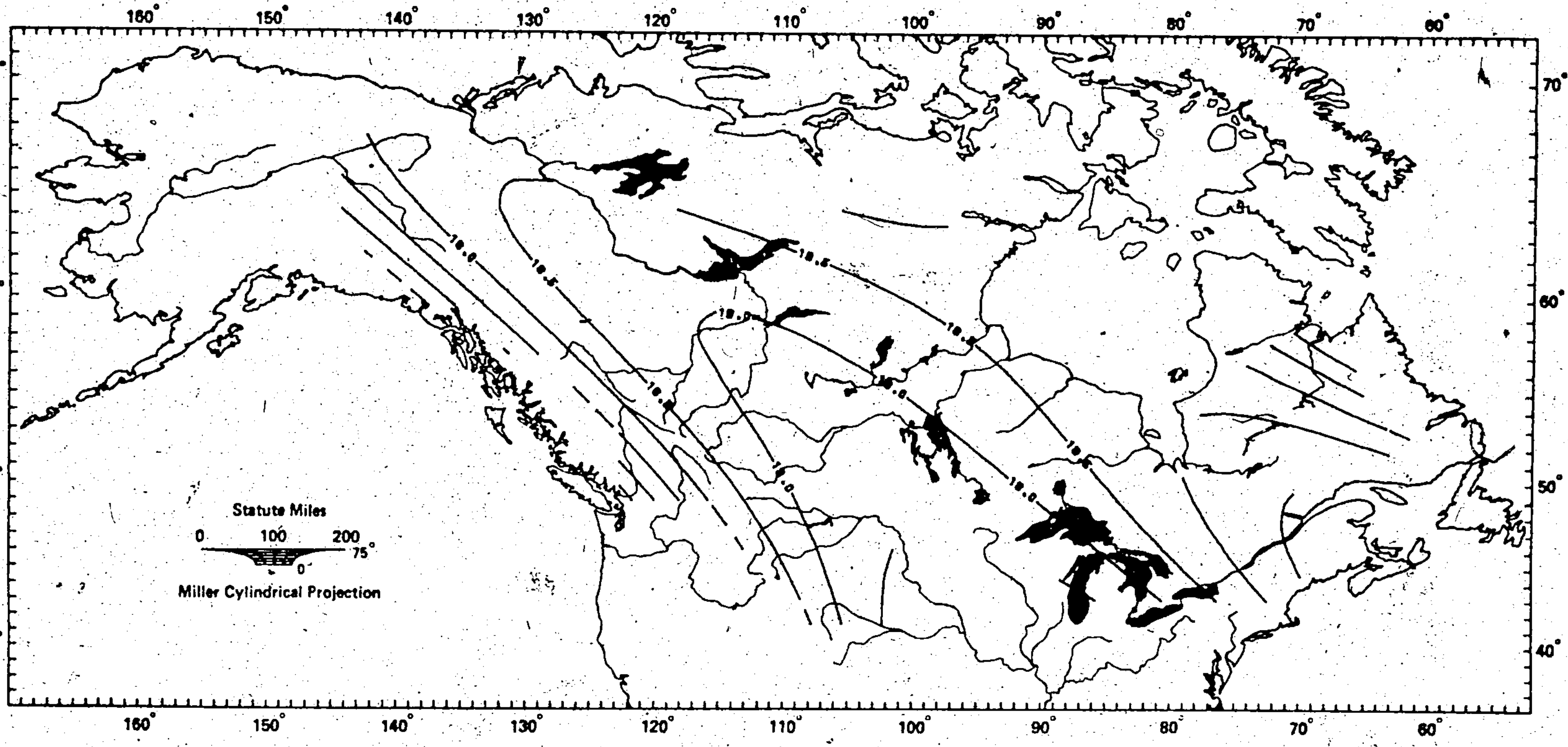
LAC VALLARD. QUE 4
SANDOIRT L TRIB. NFLD 27
KNOB L TRIB. QUE 10
BIO TROUT L. ONT 32
KANUCHUAN RAPIDS. MAN 13
WEIR R. MAN 10
BILCOX CK. MAN 44
CARIBOU R. MAN 4
ANOIKONI L. NWT 33
WHITEFISH L. NWT 8
E. BRANCH DELAWARE R. NY 13
95.23
102.91
110.59
DFM - C. PLUMBEUS - MALE

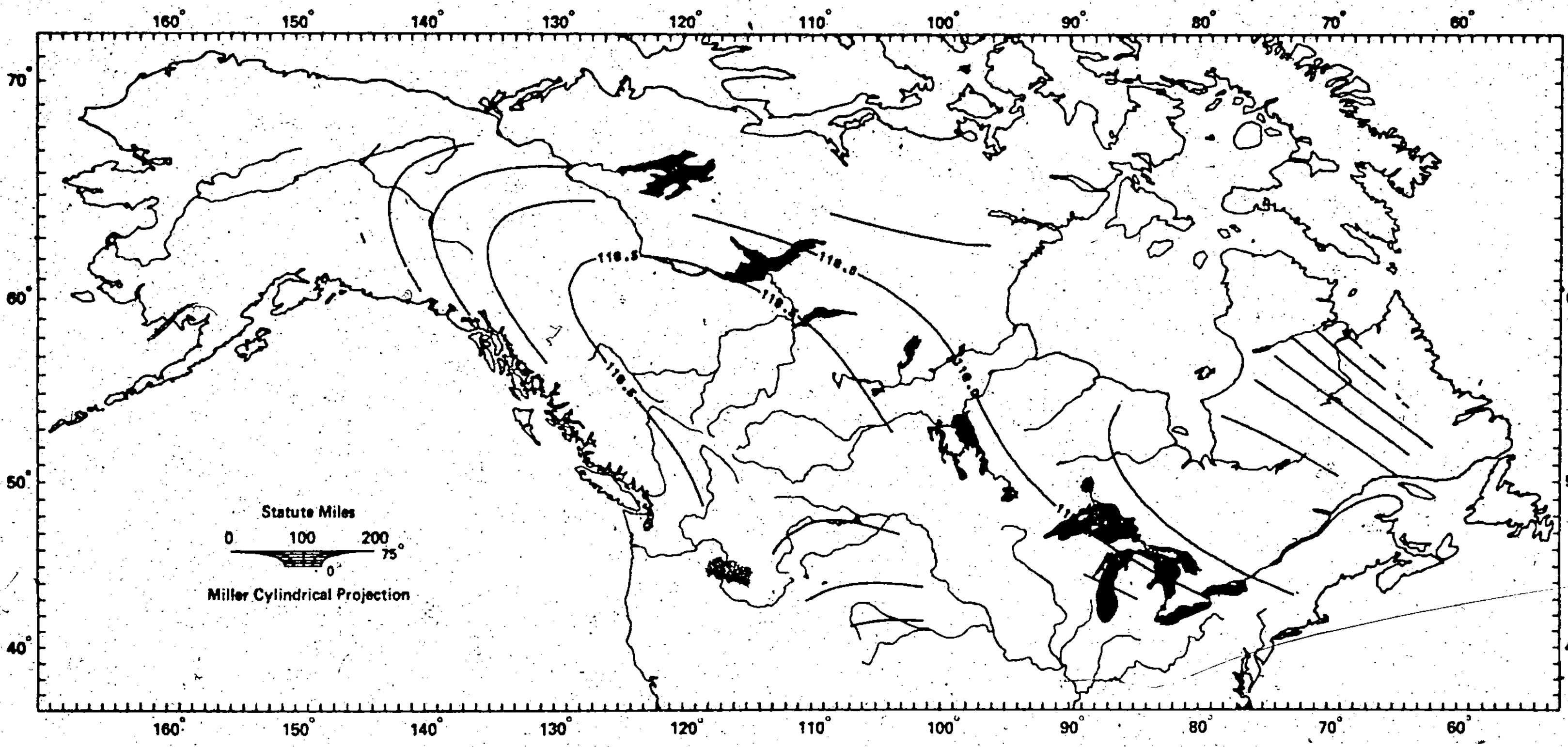


Appendix A. Figure 1A. Third degree polynomial trend surface of diagonal scale rows (DSR) for female Couesius plumbeus. Contour interval = 0.5.

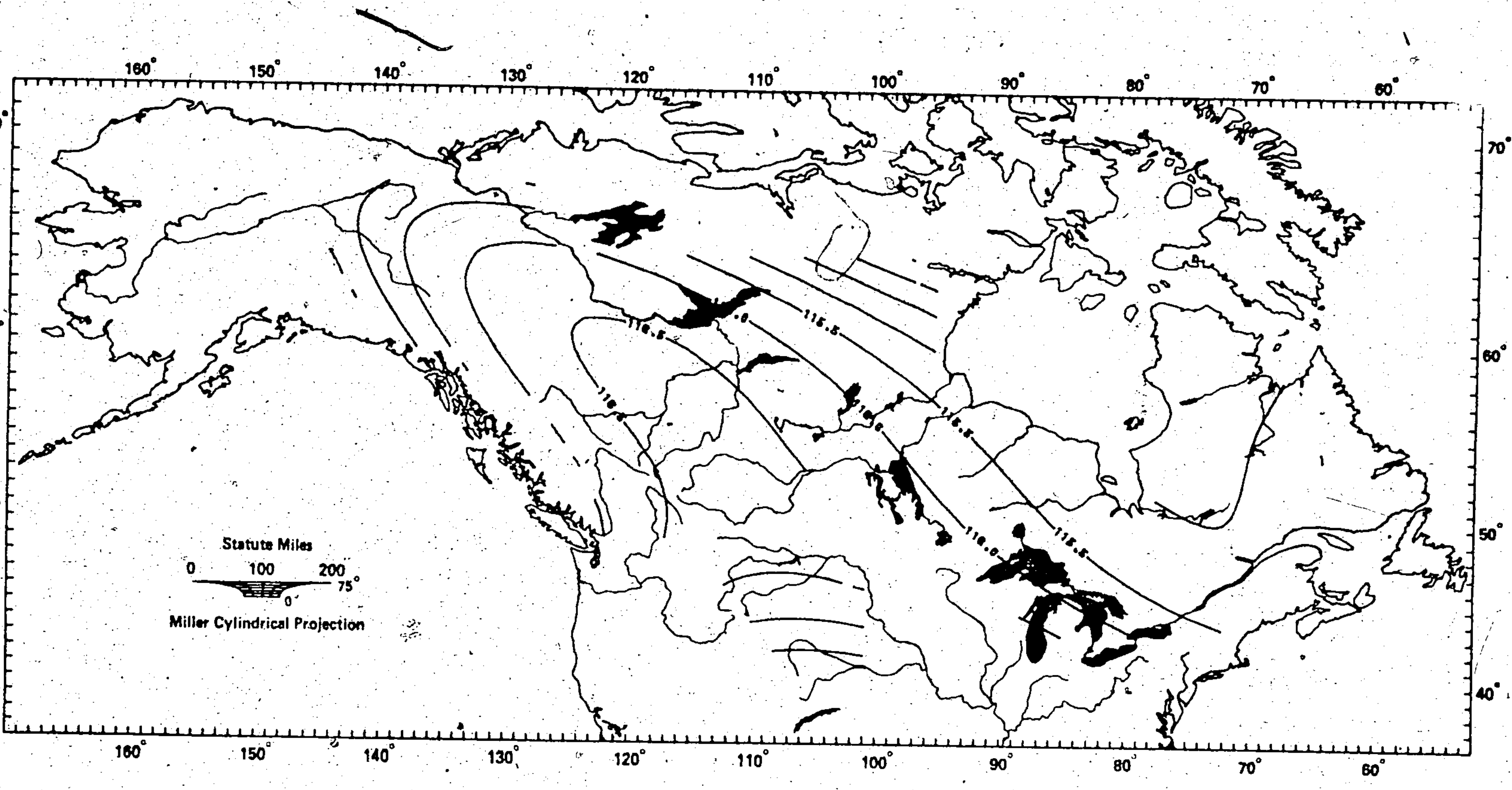


Appendix A. Figure 1B. Third degree polynomial trend surface of diagonal scale rows (DSR) for male *Couesius plumbeus*. Contour interval = 0.5.

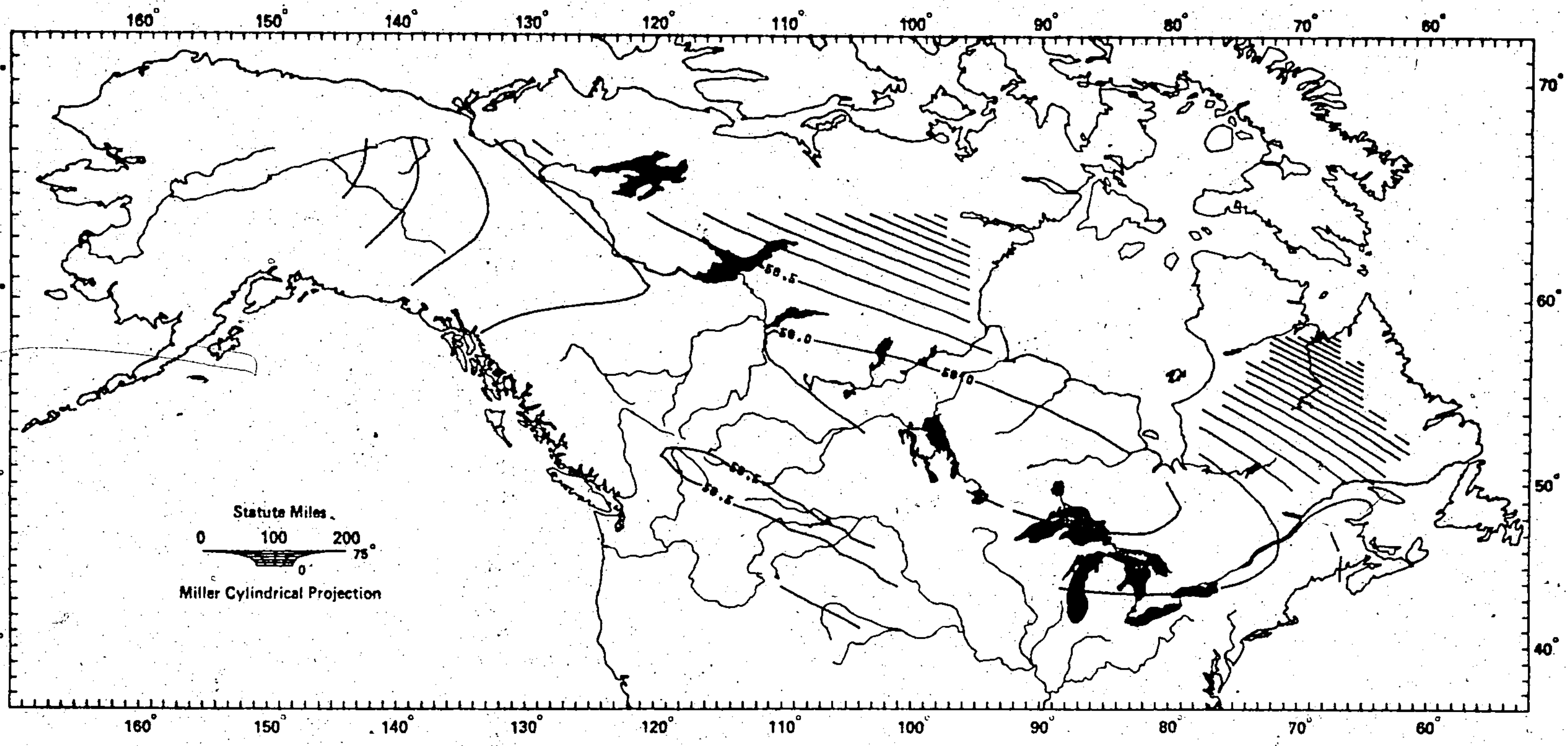
]



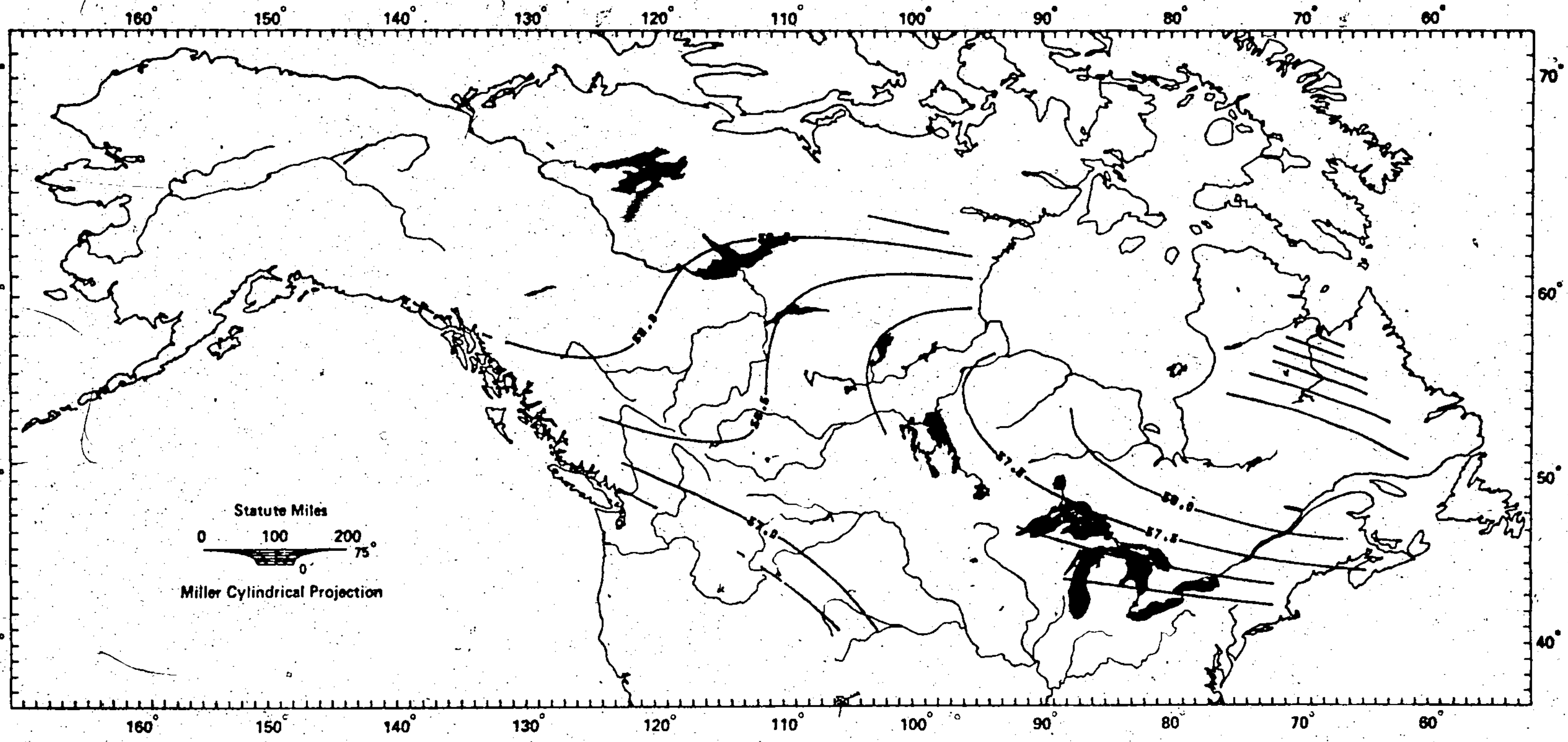
Appendix A. Figure 2A. Third degree polynomial trend surface of head length (HL) for female <u>Couesius plumbeus</u>. Contour interval = 0.5.



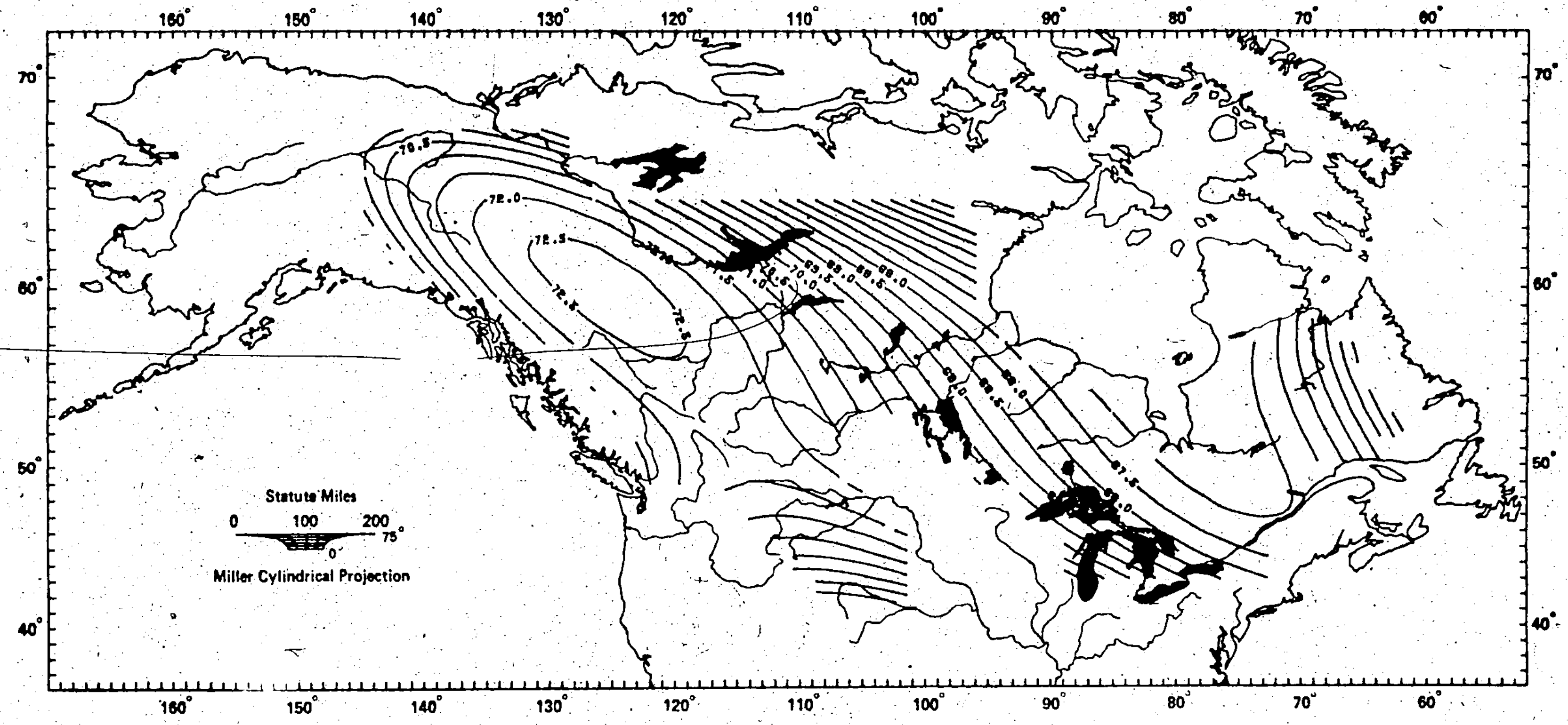
Appendix A. Figure 2B. Third degree polynomial trend surface of head length (HL) for male <u>Couesius plumbeus</u>. Contour interval = 0.5.



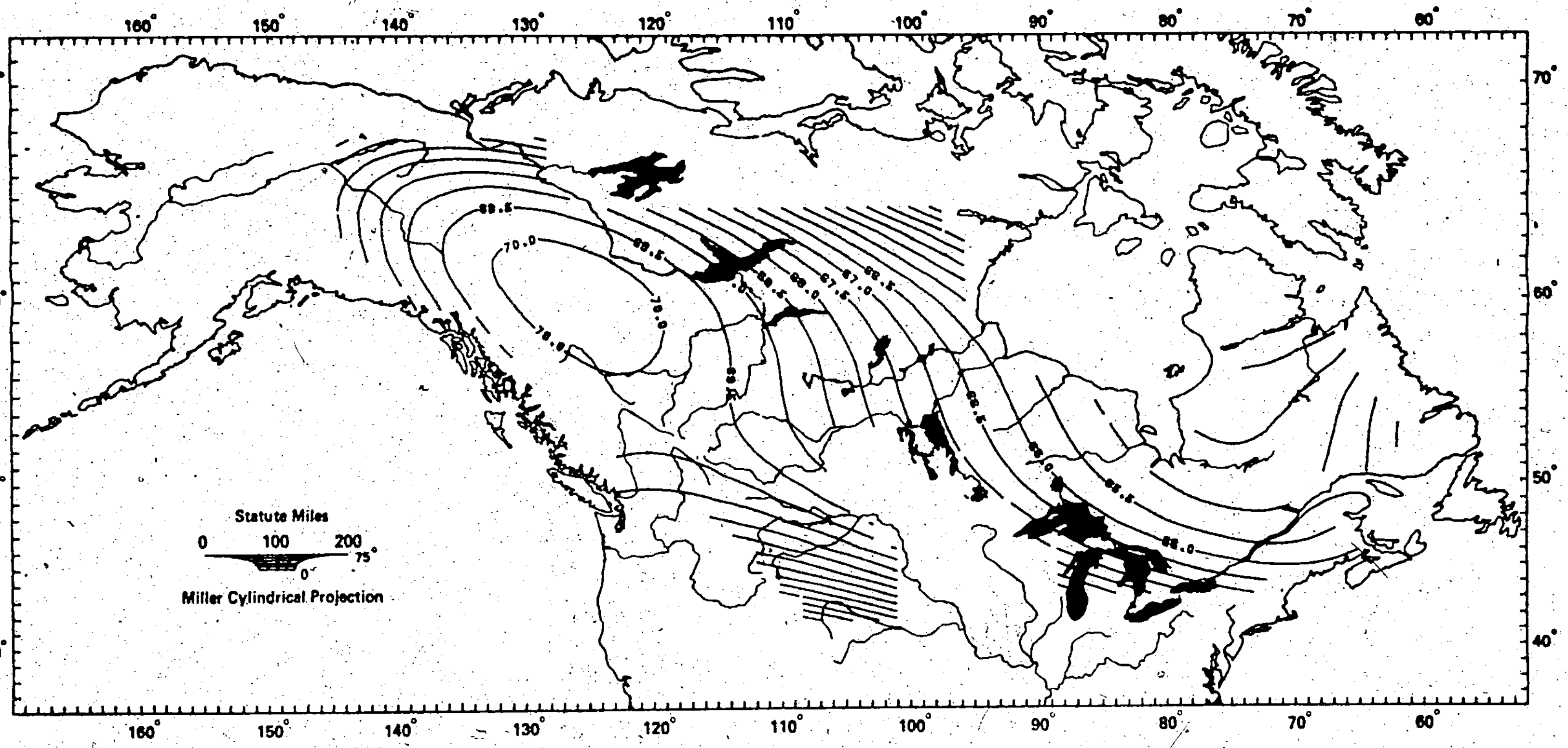
Appendix A. Figure 3A. Third degree polynomial trend surface of orbit diameter (ORBD) for female Couesius plumbeus. Contour interval = 0.5.



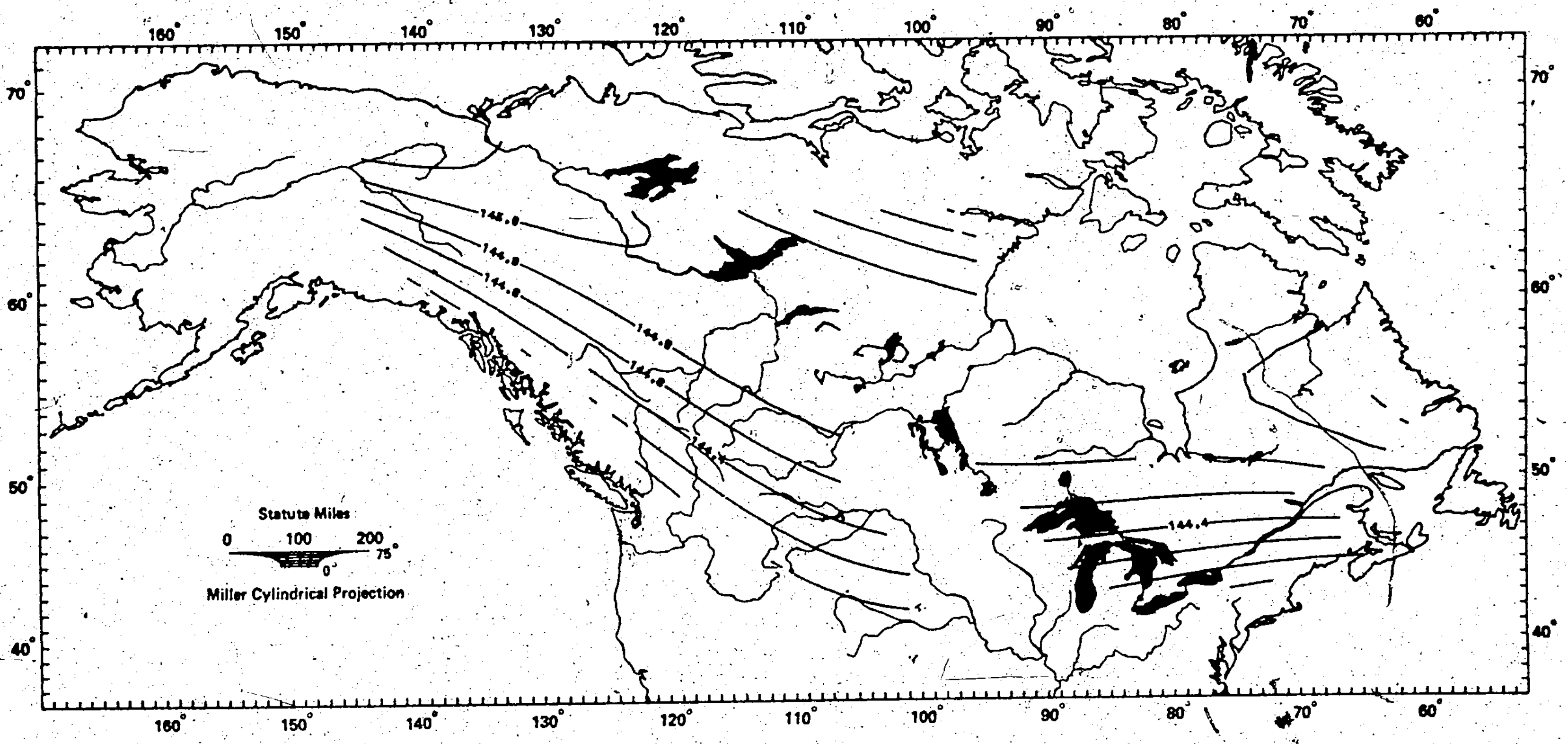
Appendix A. Figure 3B. Third degree polynomial trend surface of orbit diameter (ORBD) for male *Couesius plumbeus*. Contour interval = 0.5.



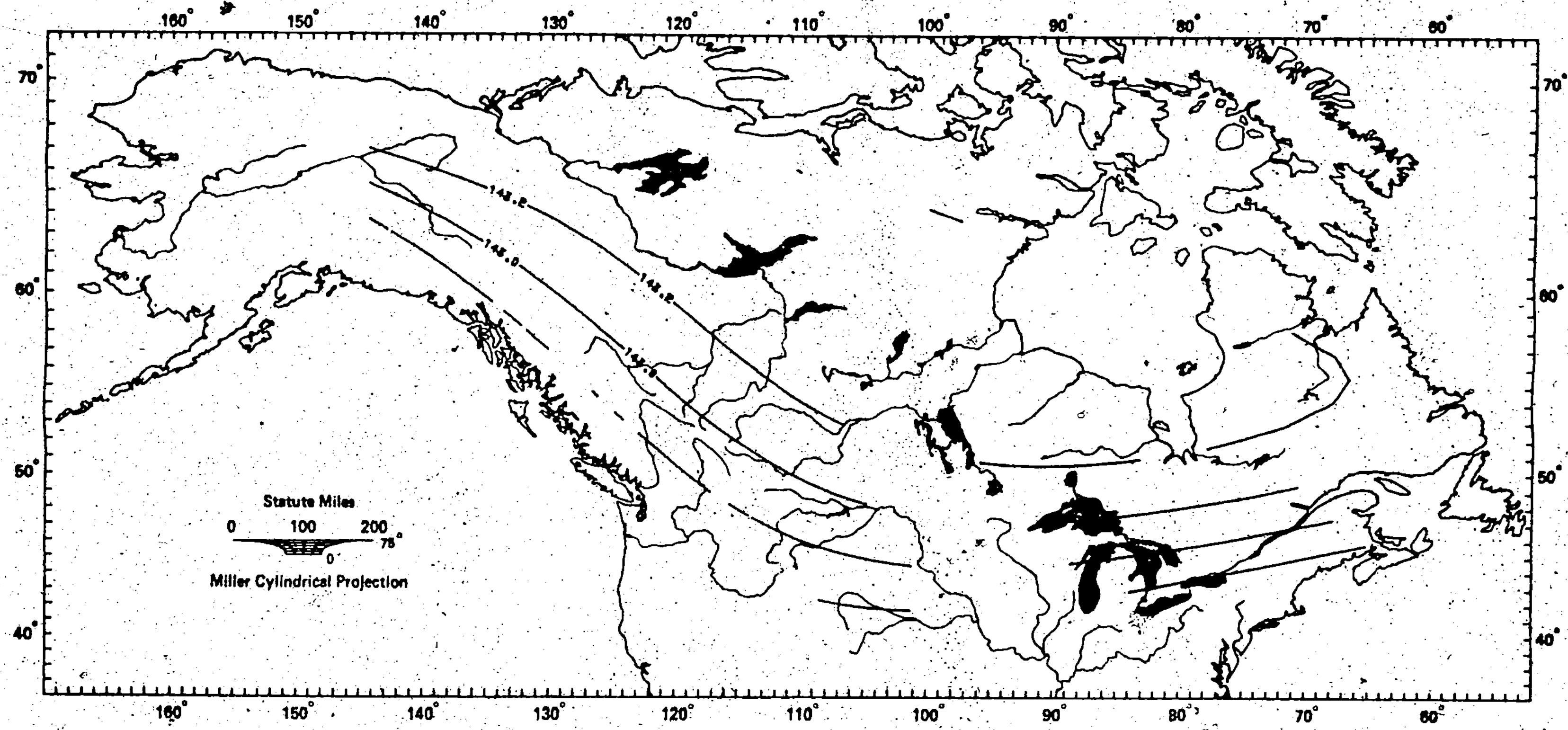
Appendix A. Figure 4A. Third degree polynomial trend surface of head depth at nostril (HDN) for female <u>Couesius plumbeus</u>. Contour interval - 0.5.



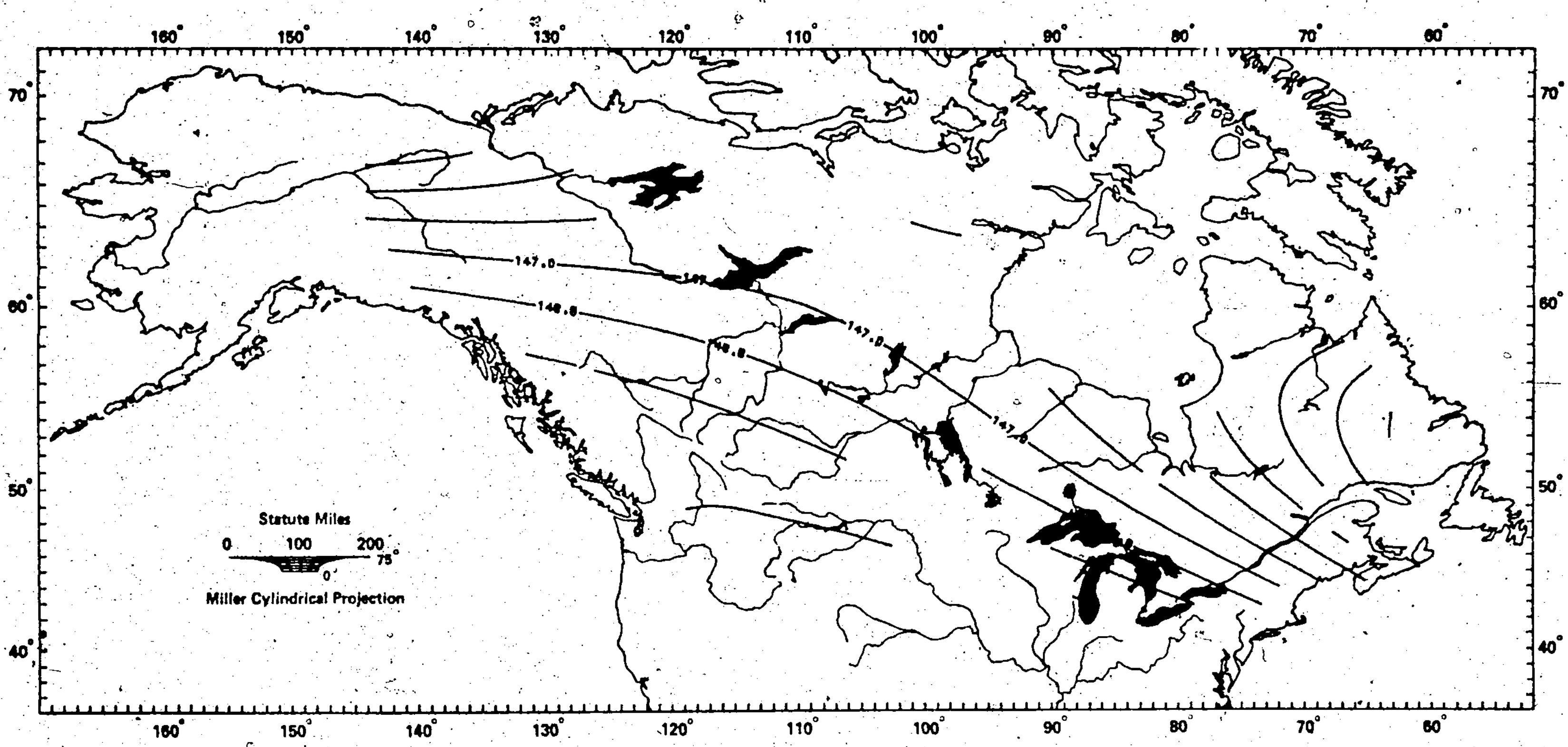
Appendix A. Figure 4B. Third degree polynomial trend surface of head depth at nostril (HDN) for male <u>Couesius plumbeus</u>. Contour interval = 0.5.



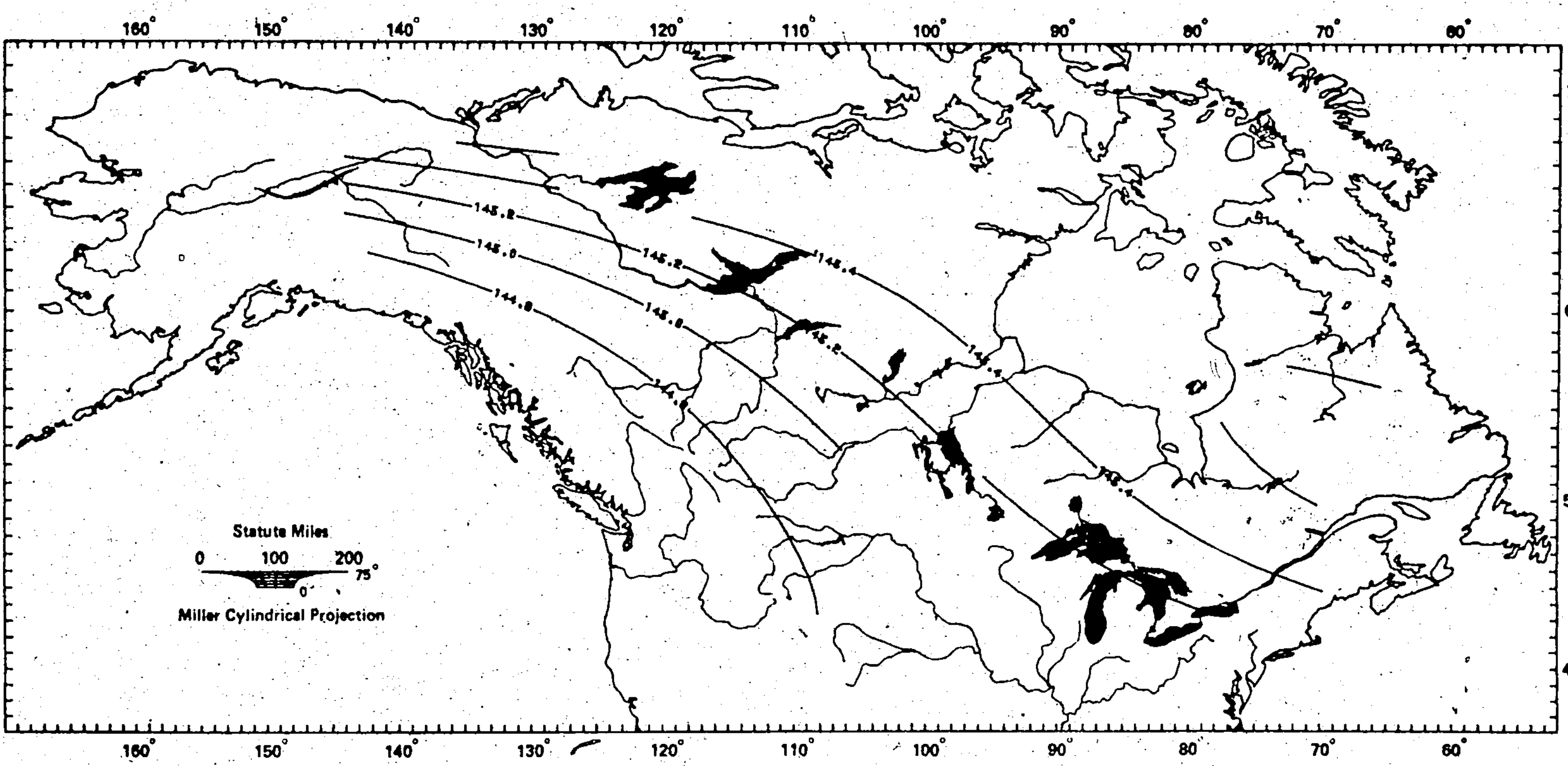
Appendix A. Figure 5A. Third degree polynomial trend surface of dorsal fin origin to TCV (DOTCV) for female Couesius plumbeus. Contour interval = 0.2.



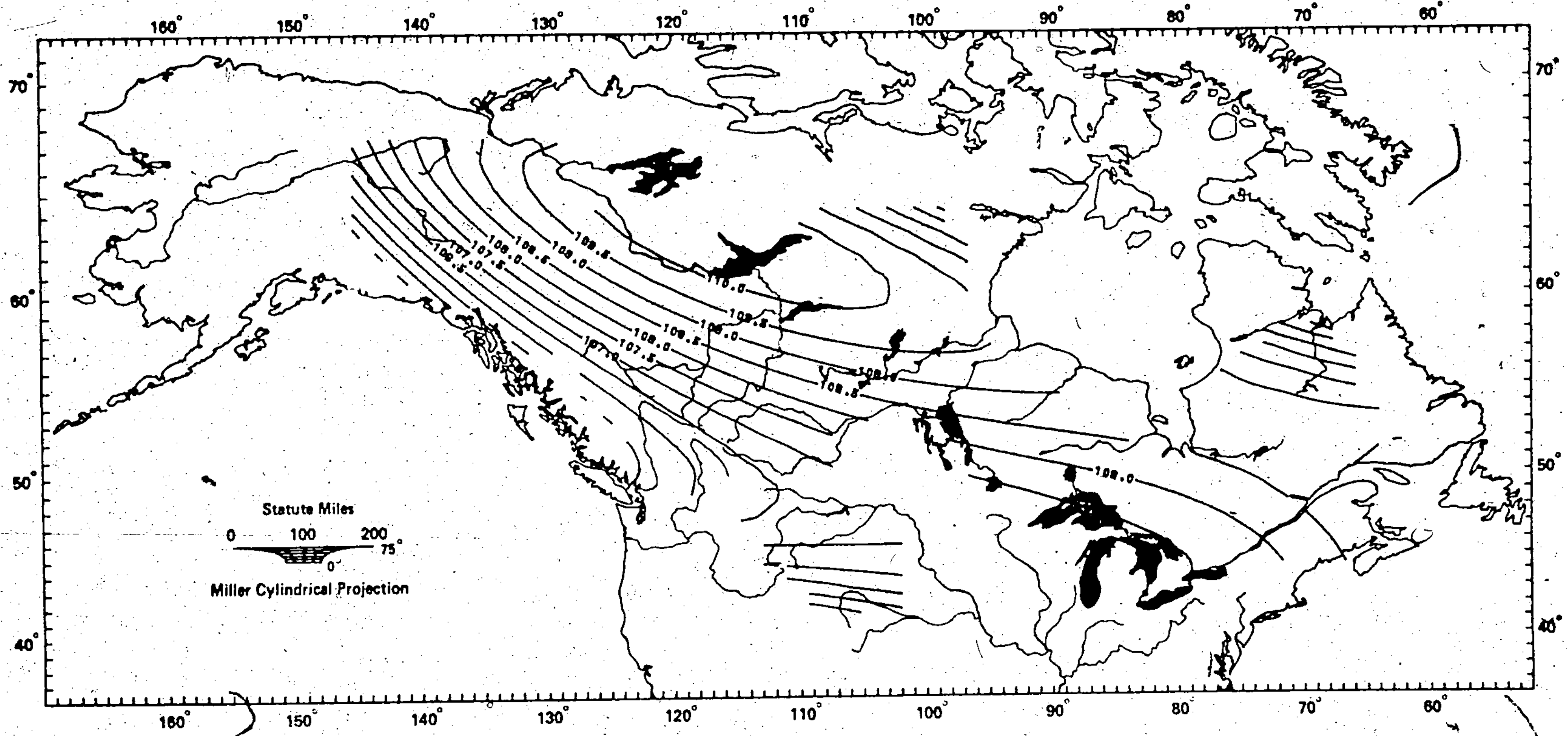
Appendix A. Figure 5B. Third degree polynomial trend surface of dorsal fin origin to TCV (DOTCV) for male <u>Couesius plumbeus</u>. Contour interval = 0.2.



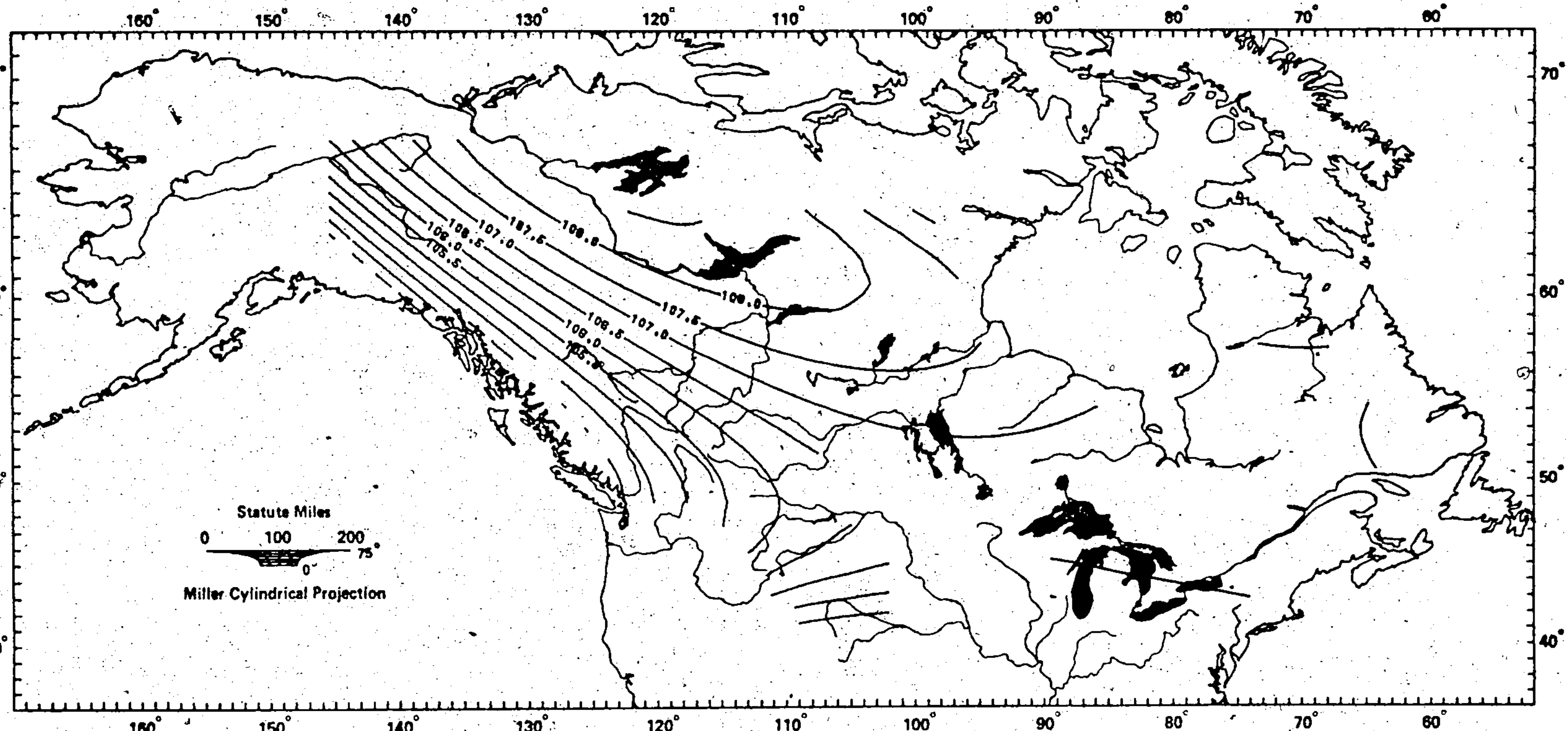
Appendix A. Figure 6A. Third degree polynomial trend surface of pelvic fin origin to TCV (PELTCV) for female _Couesius plumbeus_. Contour interval = 0.2.



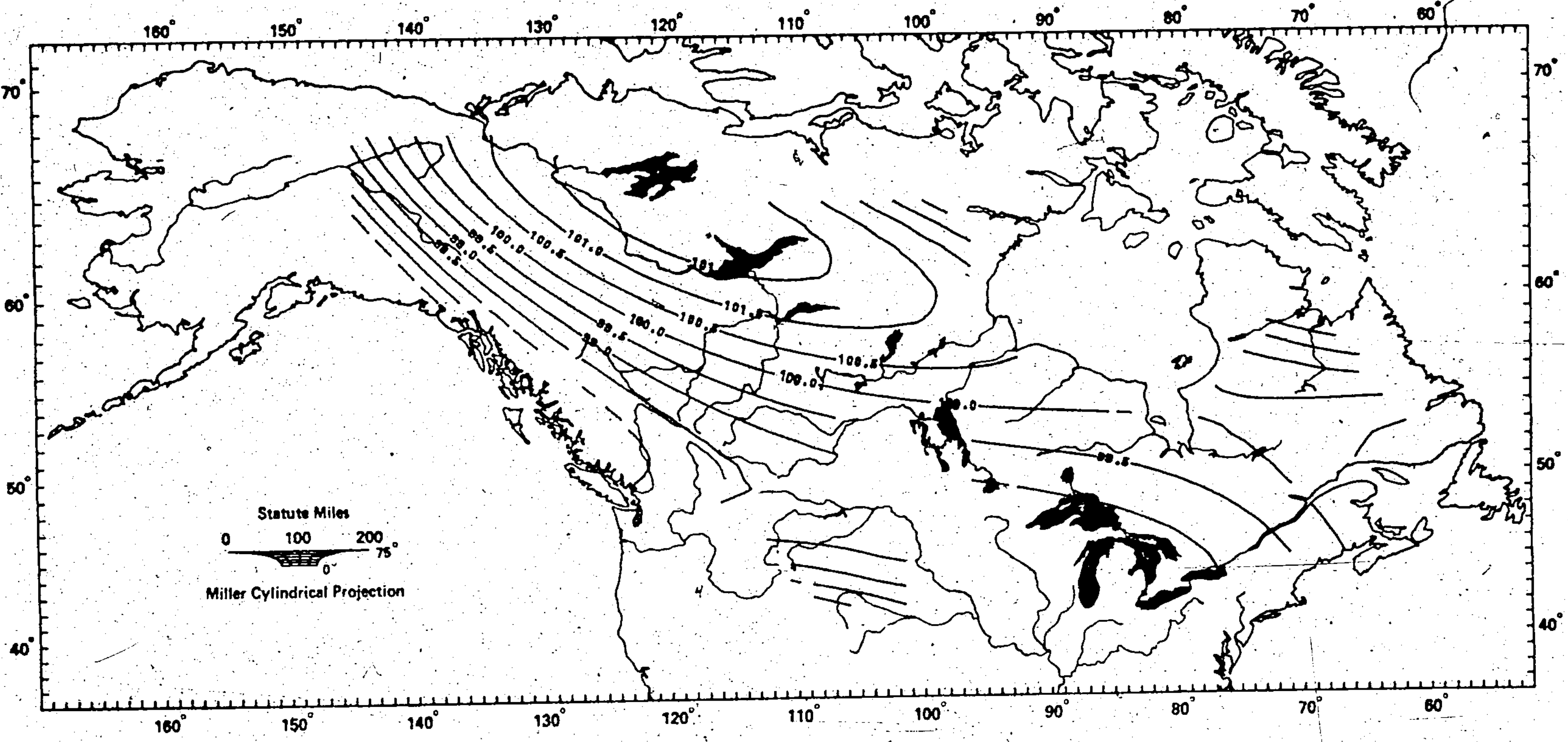
Appendix A. Figure 6B. Third degree polynomial trend surface of pelvic fin origin to TCV (PELTCV) for male <u>Couesius plumbeus</u>. Contour interval = 0.2.



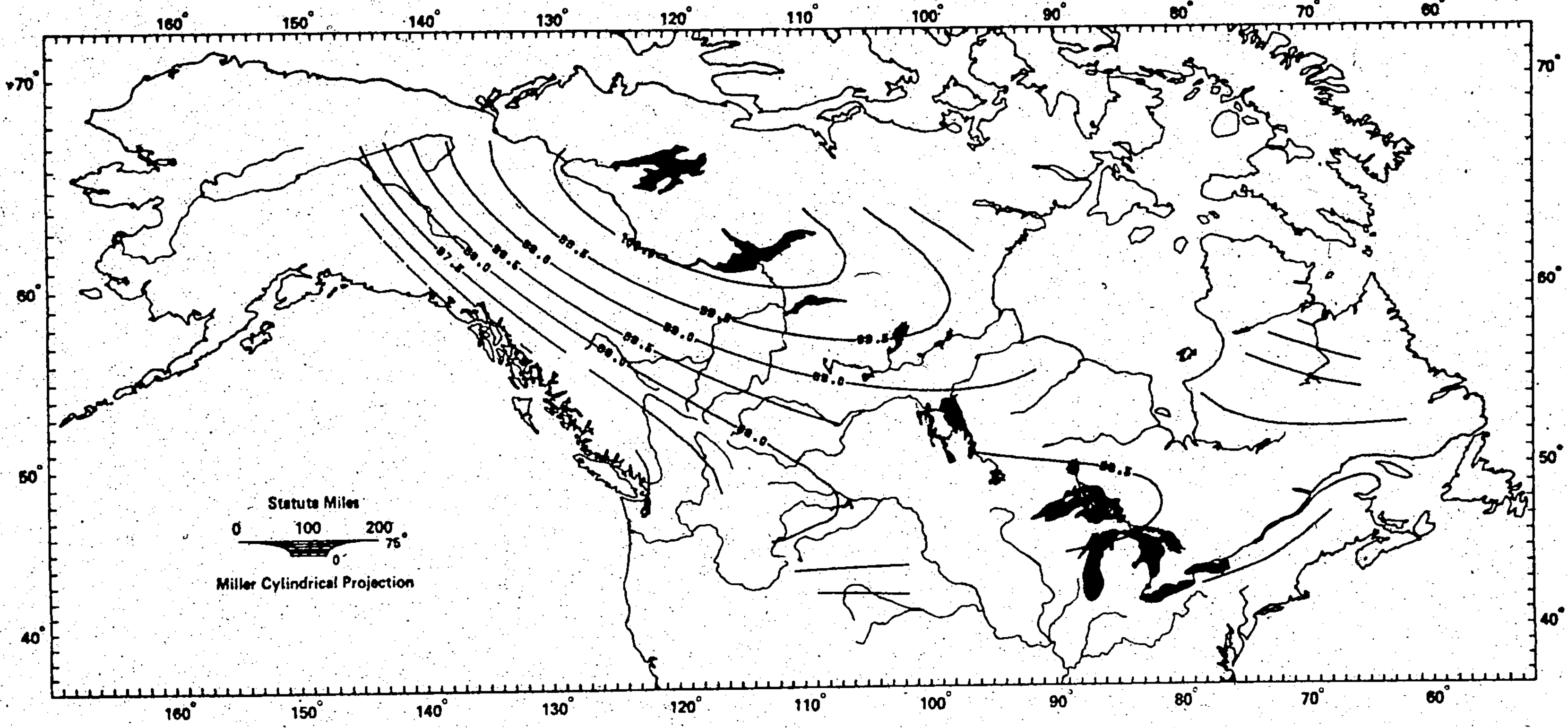
Appendix A. Figure 7A. Third degree polynomial trend surface of dorsal fin height (DFH) for female Couesius plumbeus. Contour interval = 0.5.



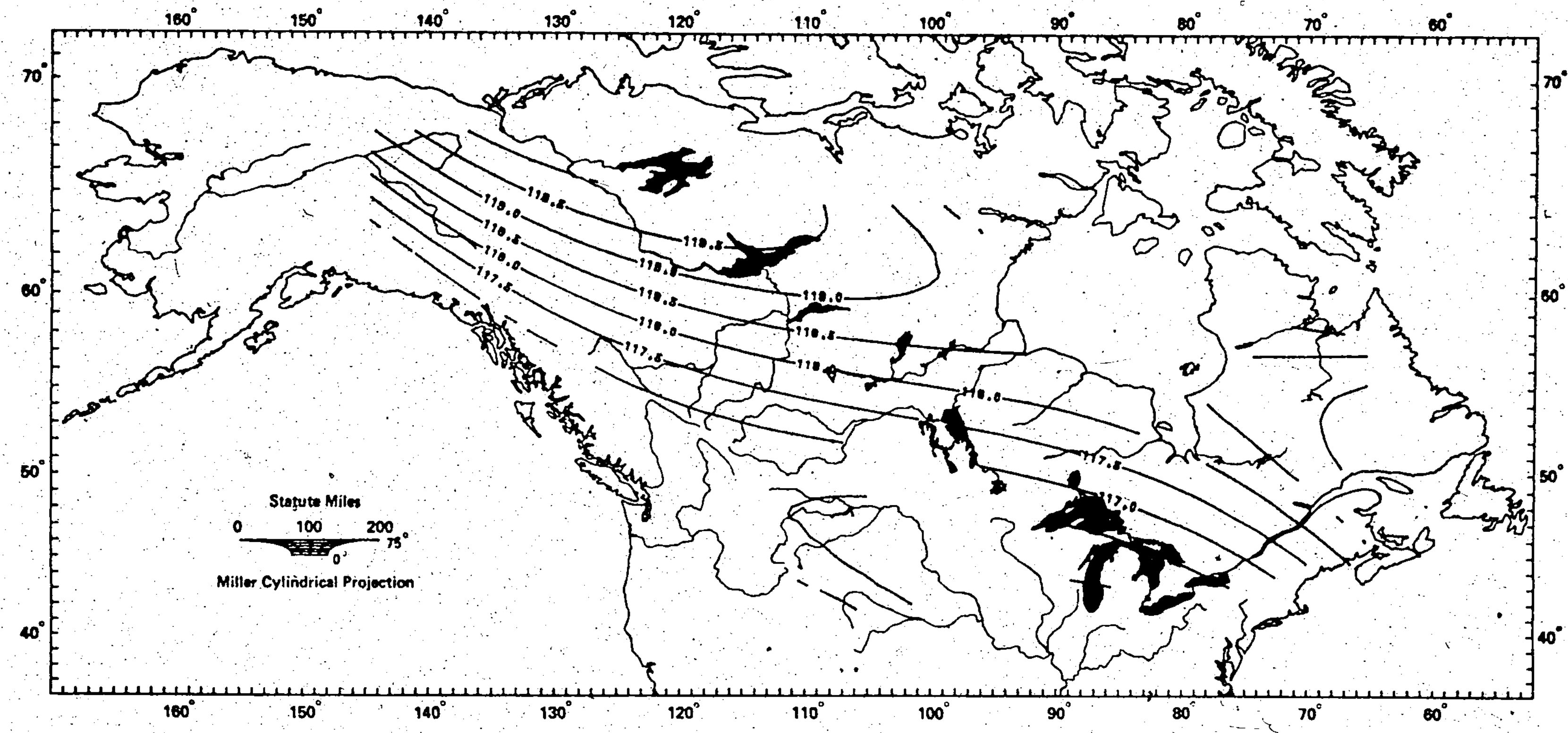
Appendix A. Figure 7B. Third degree polynomial trend surface of dorsal fin height (DFH) for male <u>Couesius</u> <u>plumbeus</u>. Contour interval = 0.5.



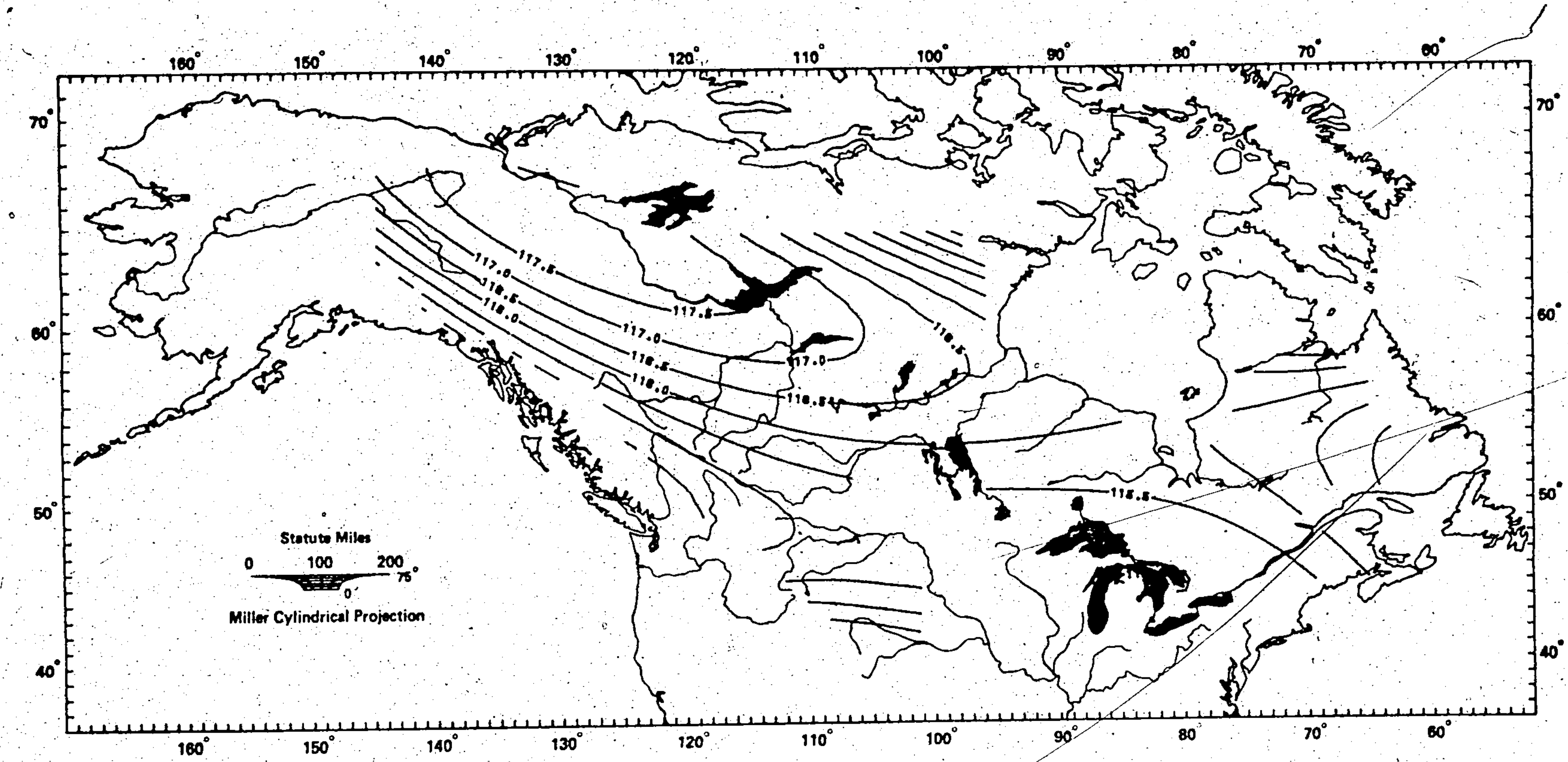
Appendix A. Figure 8A. Third degree polynomial trend surface of anal fin height (AFH) for female <u>Couesius plumbeus</u>. Contour interval = 0.5.



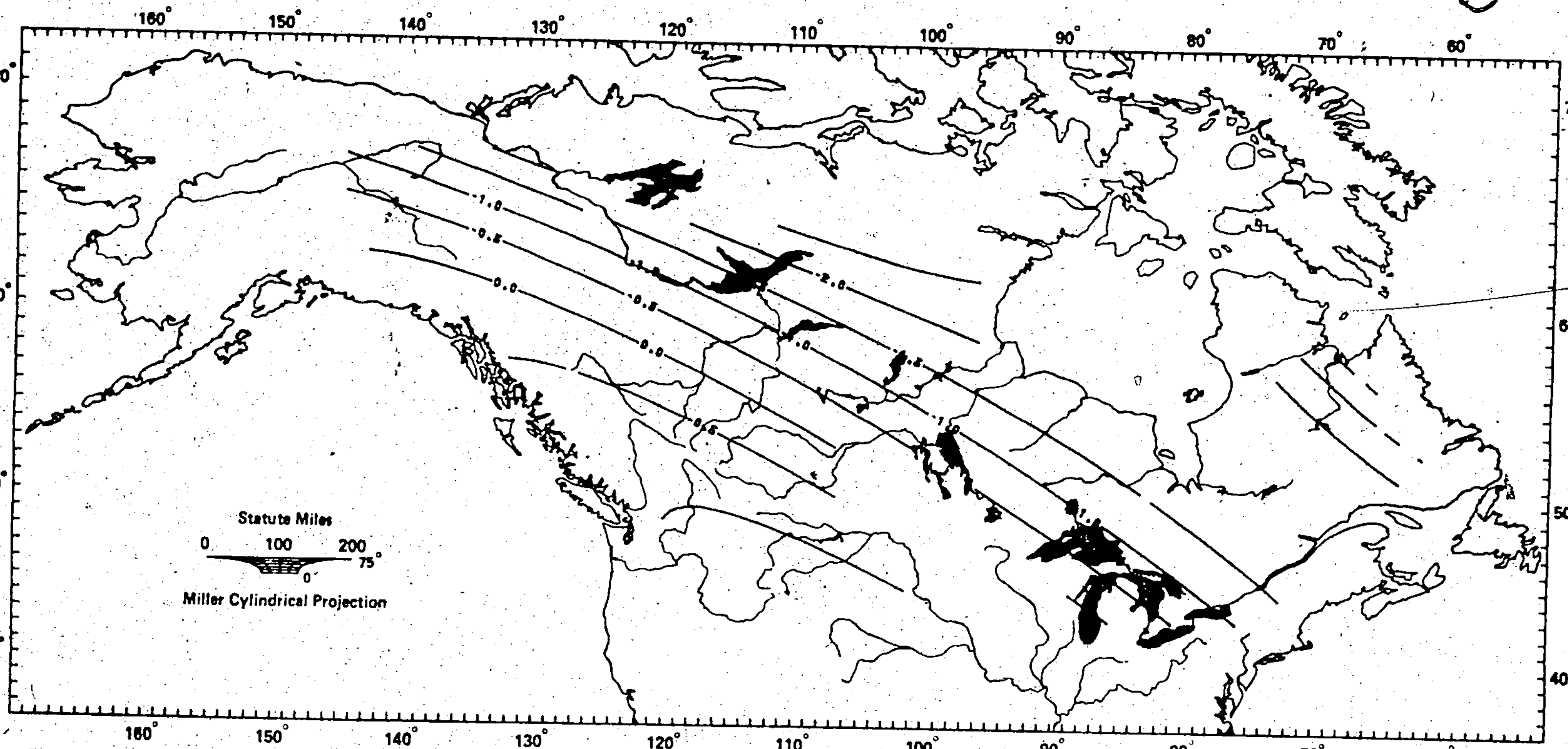
Appendix A. Figure 8B. Third degree polynomial trend surface of anal fin height (AFH) for male Couesius plumbeus. Contour interval = 0.5.



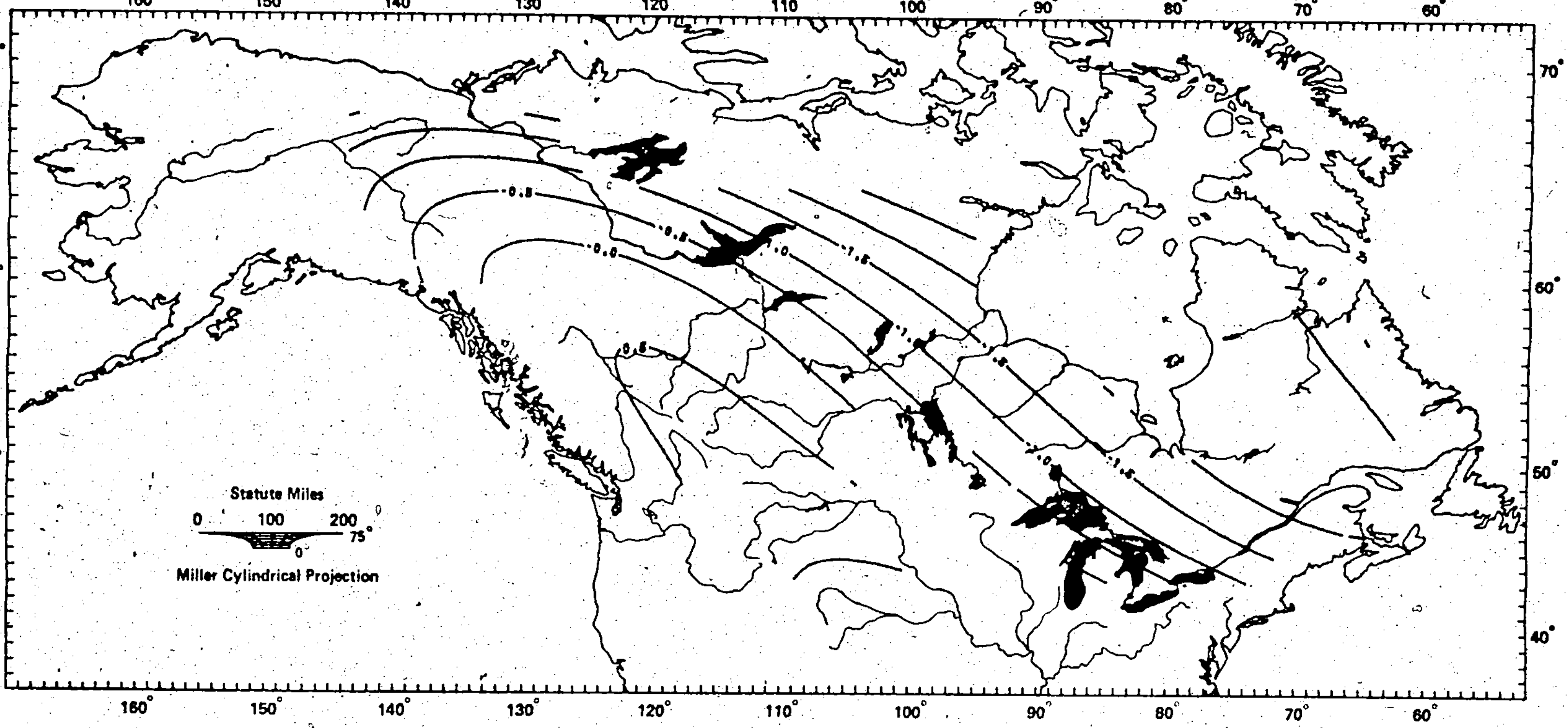
Appendix A. Figure 9A. Third degree polynomial trend surface of caudal fin length (CFL) for female *Couesius plumbeus*. Contour interval = 0.5.



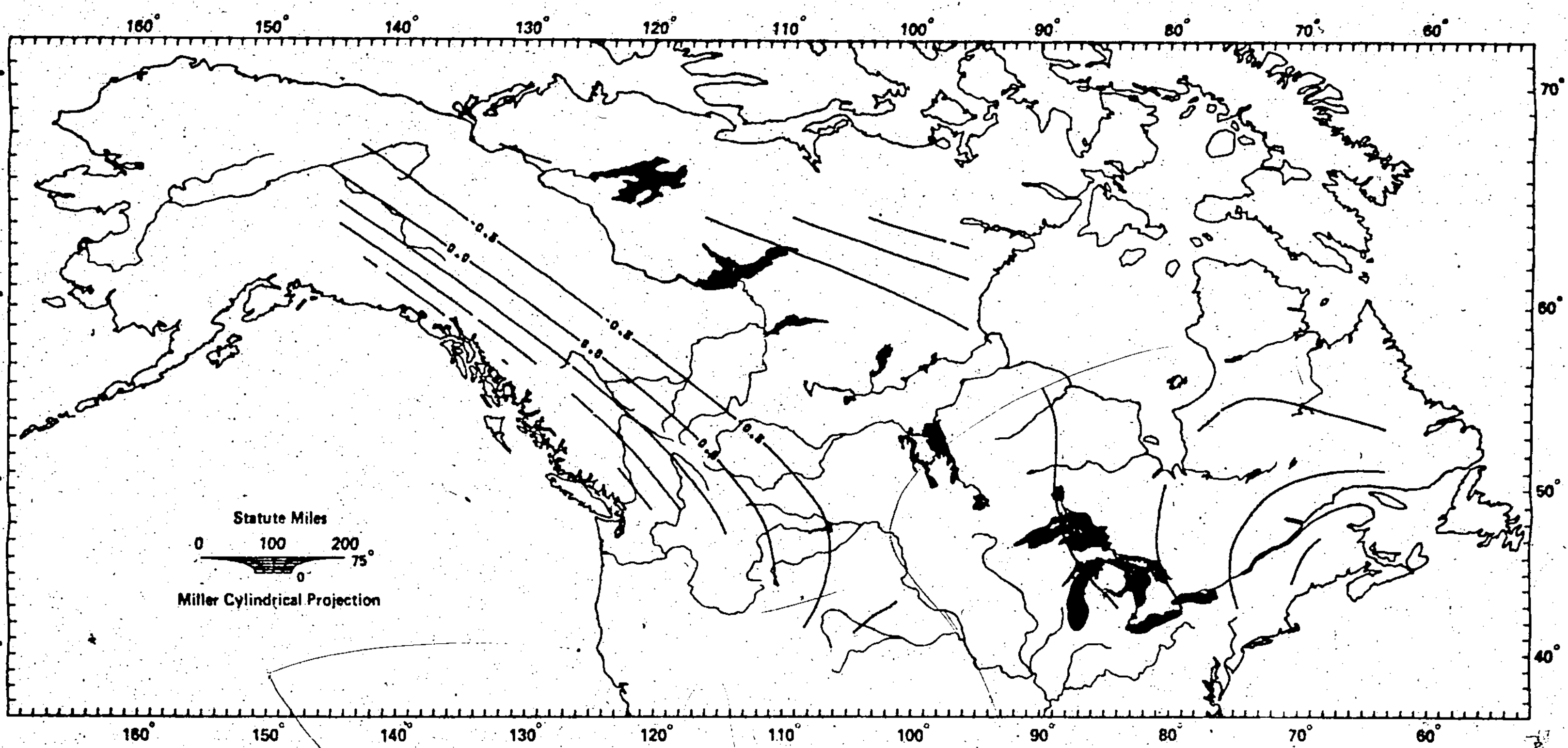
Appendix A. Figure 9B. Third degree polynomial trend surface of caudal fin length (CFL) for male Couesius plumbeus. Contour interval = 0.5.



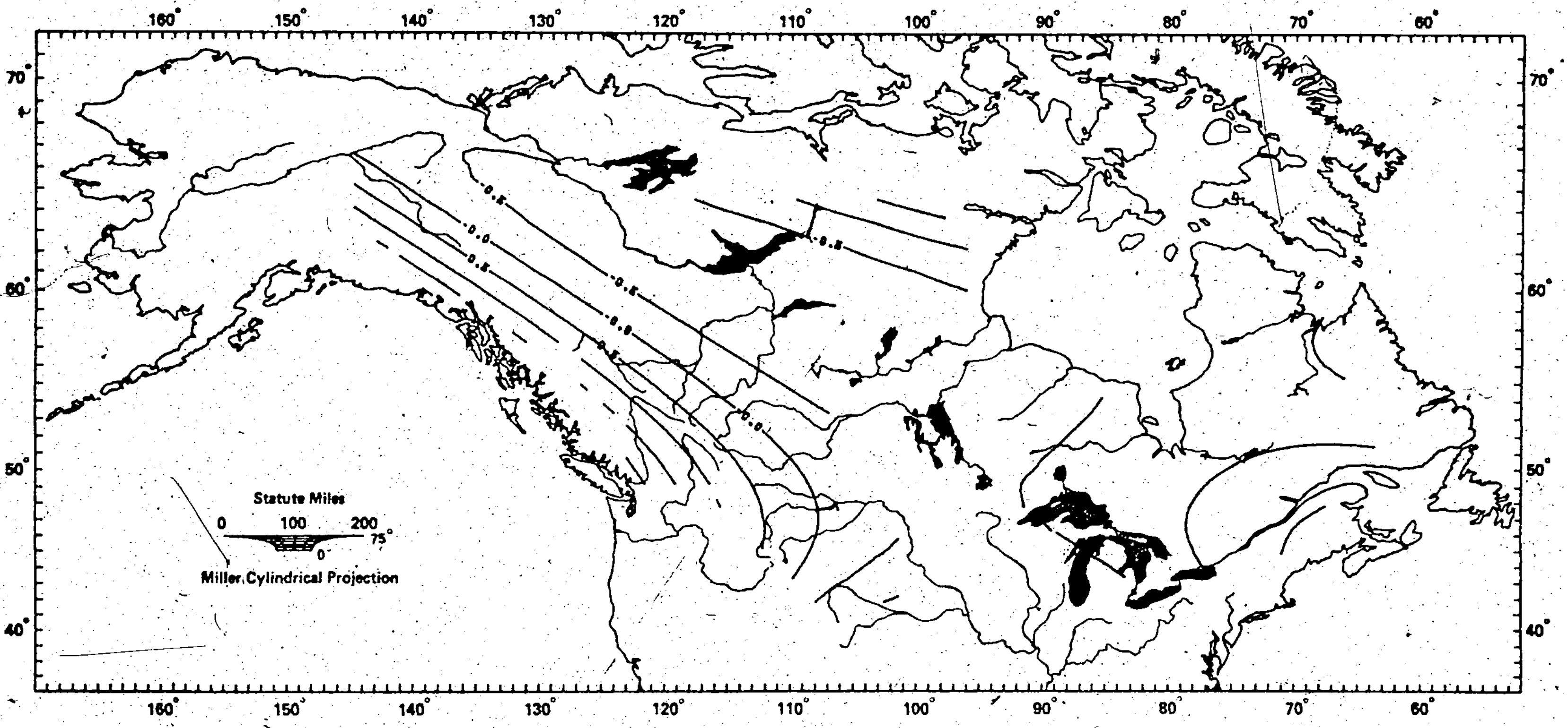
Appendix A. Figure 10A. Third degree polynomial trend surface of 37-group solution canonical variate scores along canonical axis I for female <u>Couesius</u> <u>plumbeus</u>. Contour interval = 0.5.



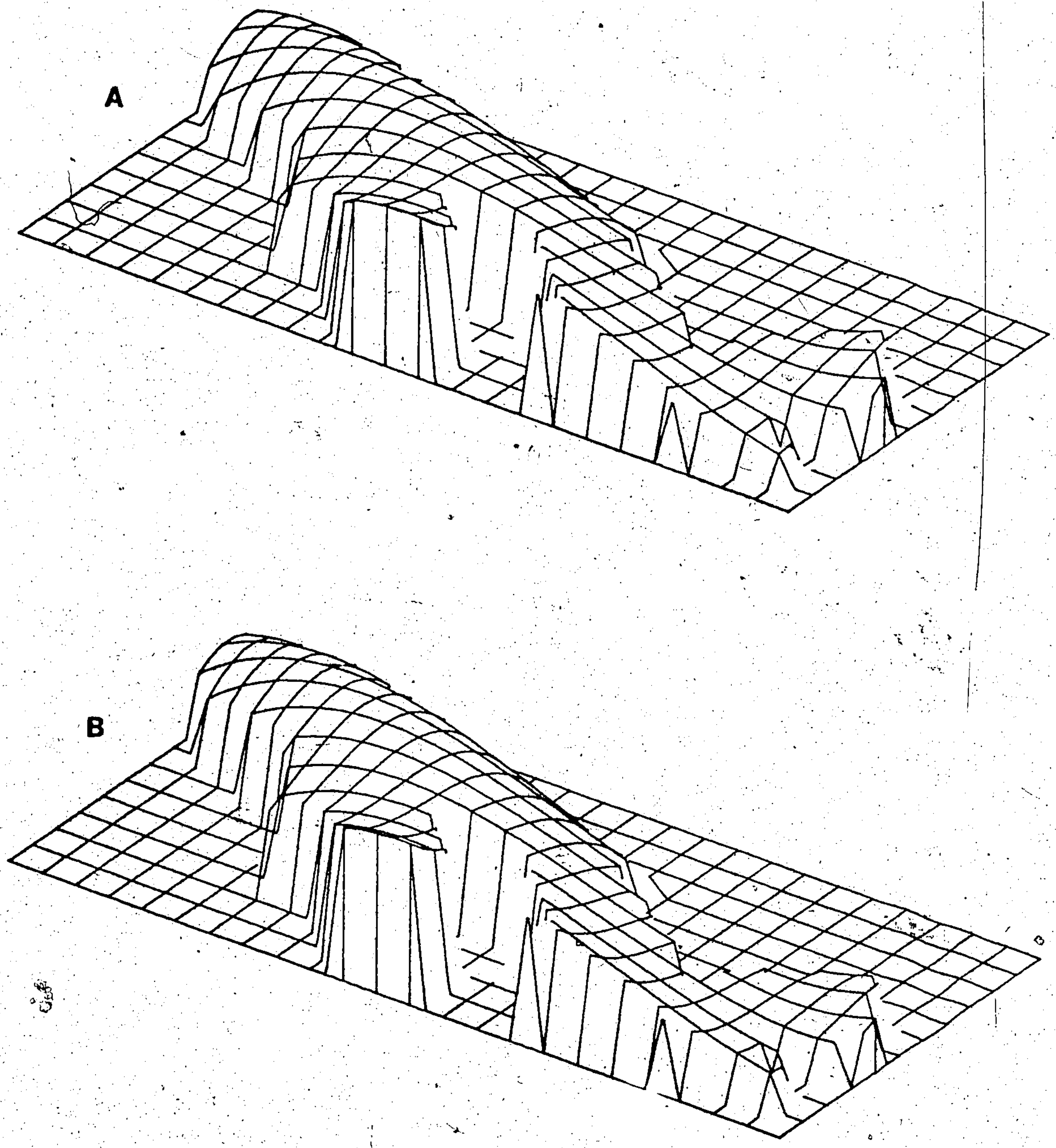
Appendix A. *Figure 10B. Third degree polynomial trend surface of 37-group solution* canonical variate scores along canonical axis I for male Couesius plumbeus. Contour interval = 0.5.



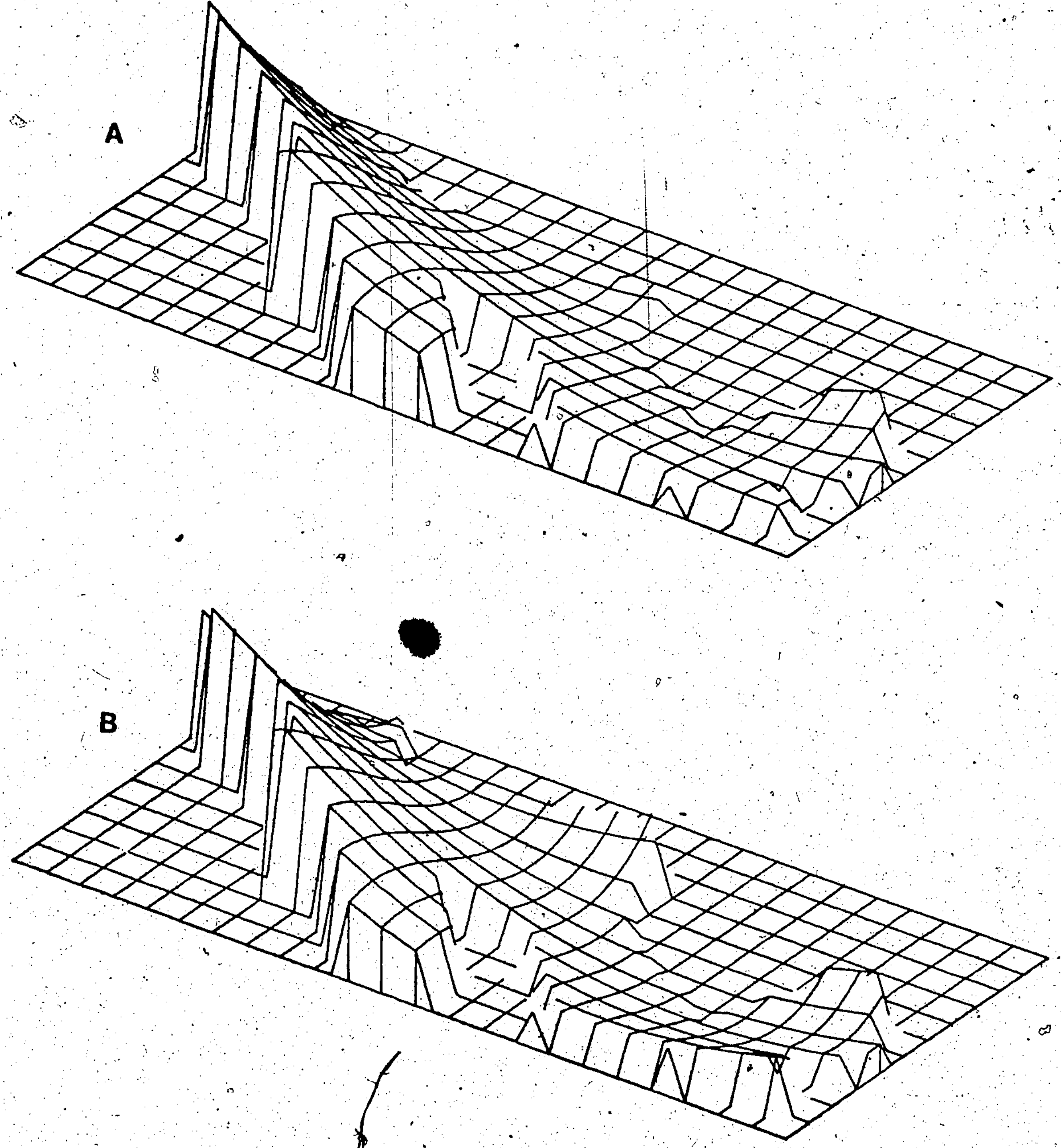
Appendix A. Figure 11A. Third degree polynomial trend surface of 37-group solution canonical variate scores along canonical axis II for female <u>Couesius plumbeus</u>. Contour interval = 0.5.



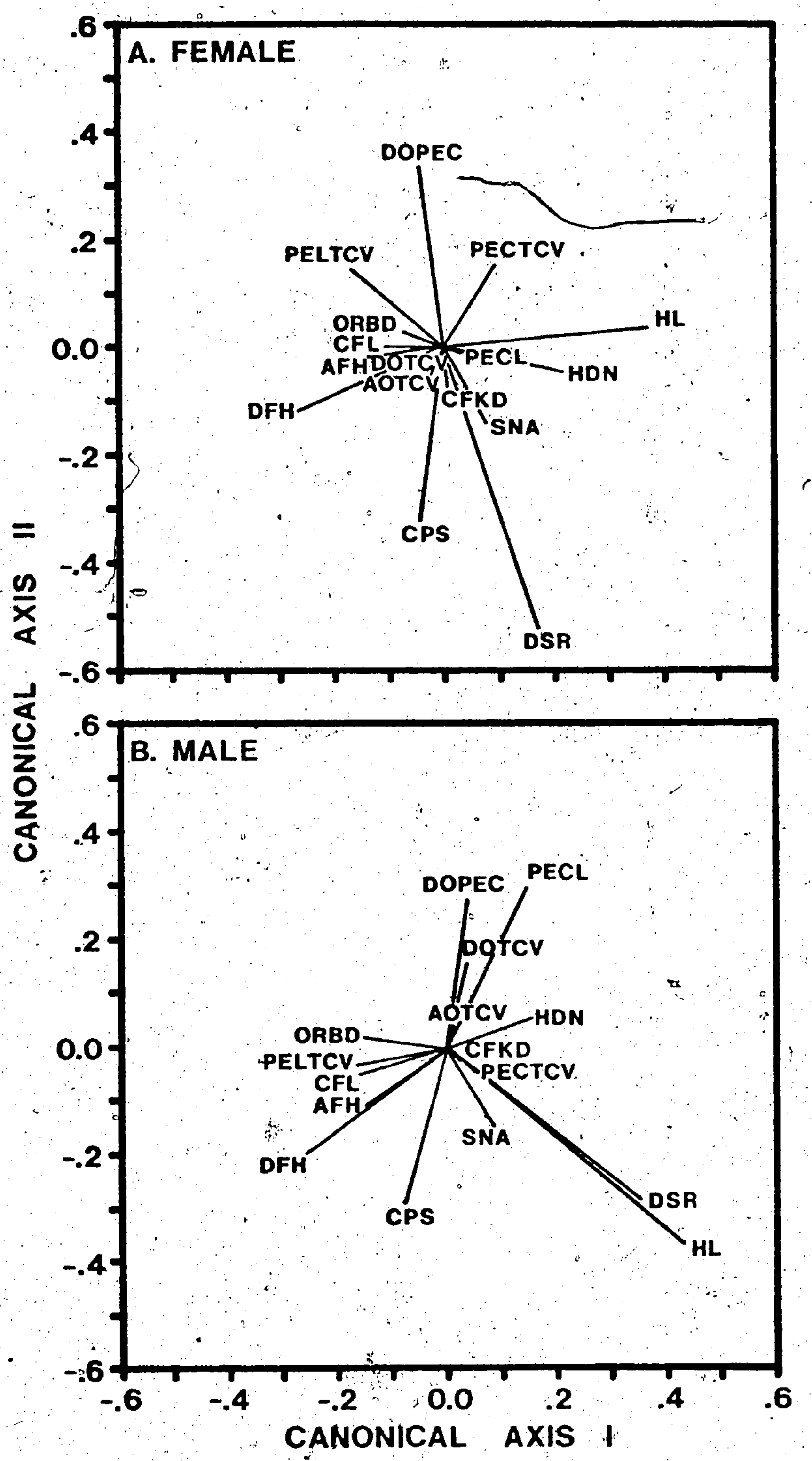
Appendix A. Figure 11B. Third degree polynomial trend surface of 37-group solution canonical variate scores along canonical axis II for male <u>Couesius plumbeus</u>. Contour interval = 0.5.



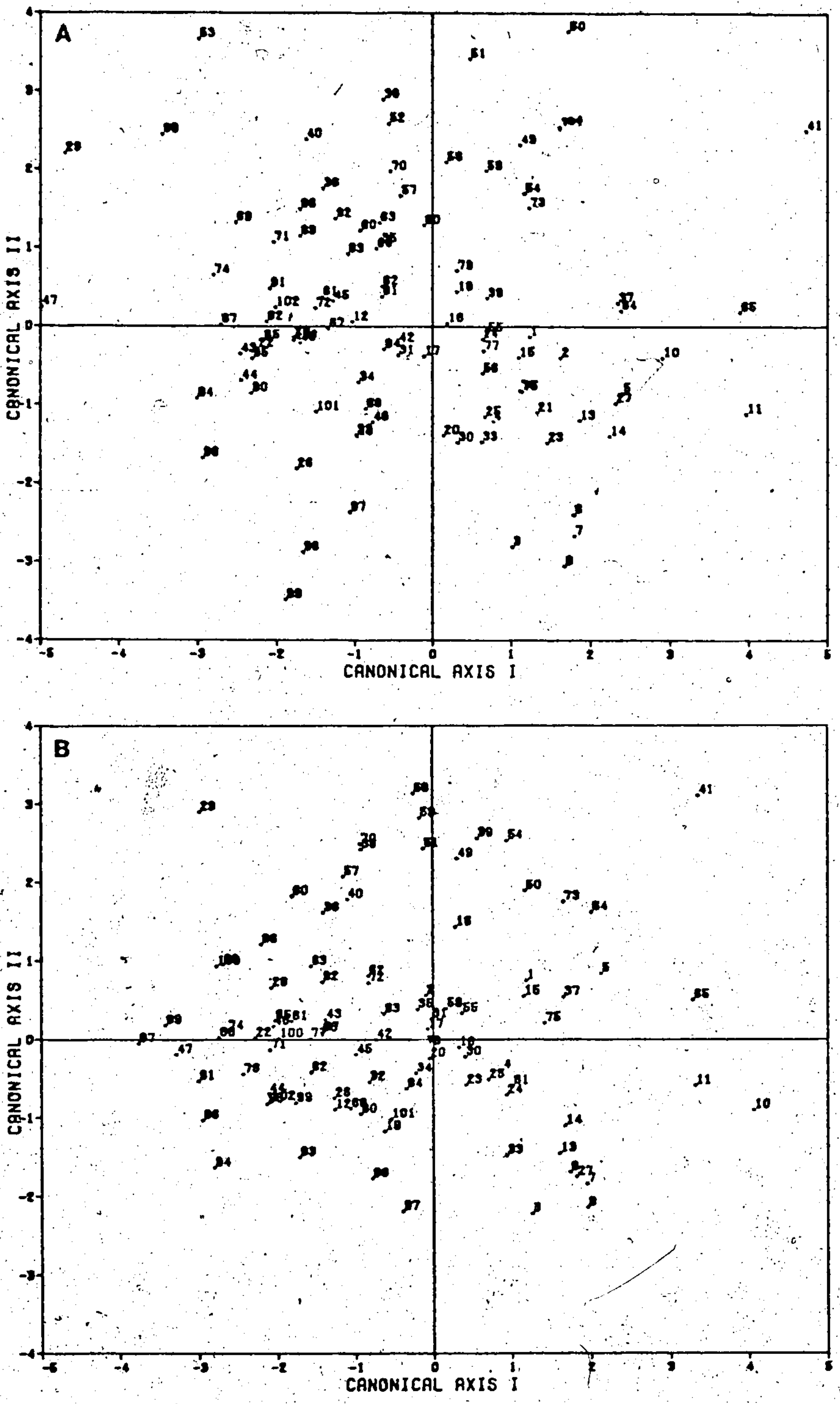
Appendix A. Figure 12. Isometric plots of third degree polynomial trend surface of three-group solution canonical variate scores along canonical axis I for A) female and B) male <u>Couesius plumbeus</u>. Raised surface represents geographic range viewed from 35° azimuth, 30° elevation, and 10,000 map units.



Appendix A. Figure 13. Isometric plots of third degree polynomial trend surface of three-group solution canonical variate scores along canonical axis II for A) female and B) male Couesius plumbeus. Raised surface represents geographic range viewed from 35° azimuth, 30° elevation, and 10,000 map units.



Appendix A. Figure 14. Character vector magnitude and direction based on 37-group solution for A) female and B) male *Couesius plumbeus*. Character labels as in Table 2.



Appendix A. Figure 15. Thirty-seven-group solution canonical variate scores along canonical axes I and II for A) female (34.6% and 16.9% of variance, respectively) and B) male (33.2% and 15.2% of variance, respectively) <u>Couesius plumbeus</u> from all localities. Locality labels as in Table 1.

APPENDIX B

Environmental Correlations.

Appendix B. Table 1. Couesius plumbeus environmental correlations - Latitude.

Character	Missouri Female (18)	Missouri Male (18)	Columbia Female (12)	Columbia Male (12)	Atlantic Female (26)	Atlantic Male (27)	Combined Female (100)	Combined Male (97)
DSR	-0.009	-0.016	-0.480	-0.442	0.141	-0.011	0.161	0.104
CPS	0.352	0.461*	-0.476	-0.465	-0.060	-0.233	0.053	0.075
HL	0.687**	0.612**	0.378	0.305	0.342*	0.178	0.018	-0.025
ORBD	0.281	0.252	-0.190	-0.122	0.570**	0.519*	0.205*	0.195*
HDN	0.266	0.372	0.368	0.317	-0.316	0.251	-0.391**	-0.341**
DOTCV	-0.264	-0.277	-0.473	-0.537*	-0.615**	-0.425*	-0.008	0.066
DOPEC	-0.171	-0.179	0.180	0.037	0.301	0.084	0.170*	-0.076
AOTCV	-0.494*	-0.336	-0.147	0.084	-0.377*	-0.278	-0.012	0.079
PELTCV	-0.429*	-0.365	0.249	0.166	-0.082	-0.021	0.186*	0.325**
PECTCV	-0.776**	-0.857**	-0.124	-0.316	-0.544**	-0.454**	0.047	-0.136
SNA	0.385	0.151	0.358	0.276	0.408*	0.386*	0.084	0.155
DFH	0.225	0.172	-0.412	-0.327	-0.238	-0.206	0.206*	0.241**
AFH	0.165	0.081	-0.549*	-0.382	-0.285	-0.154	0.164	0.146
PECL	0.263	0.441*	-0.706**	-0.239	-0.202	0.021	0.067	-0.084
CFKD	0.085	0.206	0.503*	-0.413	-0.519**	-0.475**	-0.156	-0.127
CFL	0.002	0.143	-0.633*	-0.548*	-0.409*	-0.408*	0.040	-0.012
CS37-1	0.276	0.266	0.657**	0.557*	0.162	0.052	-0.282**	-0.272**
CS37-2	-0.359	-0.243	0.632*	0.216	0.320	0.184	-0.045	-0.251**
CS37-3	-0.200	0.337	0.011	0.441	-0.093	0.416*	0.203*	-0.021
CS3-1	0.563**	0.554**	-0.213	-0.060	-0.131	-0.390*	-0.171*	-0.184*
CS3-2	0.139	0.123	0.755**	0.724**	-0.139	-0.013	-0.433**	-0.406**

* = p<0.05; ** = p<0.01

Appendix B. Table 2. *Couesius plumbeus* environmental correlations - Longitude.

	Localities							
	Missouri		Columbia		Atlantic		Combined	
Character	Female (18)	Male (18)	Female (12)	Male (12)	Female (26)	Male (27)	Female (100)	Male (97)
DSR	0.112	0.199	0.551*	0.541*	-0.257	-0.072	-0.100	-0.114
CPS	-0.167	-0.297	0.438	0.416	0.025	0.244	0.081	0.047
HL	-0.395	-0.280	-0.447	-0.402	-0.300	-0.151	-0.165	-0.174*
ORBD	-0.239	-0.205	0.190	0.123	-0.396*	-0.415*	-0.036	-0.119
HDN	-0.397	-0.531*	-0.395	-0.367	0.331*	0.386*	-0.073	-0.039
DOTCV	0.478*	0.289	0.600*	0.648*	0.631**	0.448**	0.295**	0.287**
DOPEC	-0.269	-0.326	-0.047	0.067	-0.347*	-0.025	-0.345**	-0.060
AOTCV	0.777**	0.637**	0.041	0.007	0.500**	0.401*	0.359**	0.336**
PELTCV	0.329	0.237	-0.261	-0.034	0.019	0.119	0.175*	0.092
PECTCV	0.291	0.411*	0.264	0.396	0.492**	0.542**	0.073	0.328**
SNA	-0.827**	-0.660**	-0.194	-0.210	-0.344*	-0.309	-0.336**	-0.353**
DFH	-0.212	-0.170	0.433	0.336	0.336*	0.214	0.105	-0.006
AFH	-0.017	0.027	0.491	0.335	0.405*	0.198	0.172*	0.047
PECL	-0.147	-0.391	0.650*	0.300	0.271	-0.063	0.109	-0.110
CFKD	-0.118	-0.257	0.458	0.372	0.645**	0.594**	0.319**	0.237**
CFL	-0.046	-0.232	0.586*	0.503*	0.580**	0.534**	0.381**	0.280**
CS37-1	-0.278	-0.193	-0.659**	-0.532**	-0.286	-0.126	-0.228*	-0.153
CS37-2	0.112	-0.035	-0.624*	-0.030	-0.318	-0.196	-0.105	-0.011
CS37-3	0.179	-0.302	0.091	-0.584*	-0.084	-0.300	-0.242**	-0.071
CS3-1	-0.408*	-0.384	0.238	0.086	0.035	0.291	-0.161	-0.125
CS3-2	-0.169	-0.081	-0.784**	-0.772**	-0.035	-0.010	-0.097	-0.003

* = $p<0.05$; ** = $p<0.01$

Appendix B. Table 3. *Couesius plumbeus* environmental correlations - Temperature.

	Localities							
	Missouri		Columbia		Atlantic		Combined	
Character	Female (18)	Male (18)	Female (12)	Male (12)	Female (26)	Male (27)	Female (100)	Male (97)
DSR	0.061	0.050	-0.284	-0.405	0.273	0.068	0.058	0.089
CPS	0.237	0.400*	-0.331	-0.331	-0.105	-0.359*	-0.132	-0.030
HL	0.606**	0.577**	0.226	0.155	0.156	0.335*	0.260**	0.375**
ORBD	0.206	0.153	-0.345	-0.292	-0.217	-0.214	-0.092	-0.118
HDN	0.343	0.445*	0.250	0.285	-0.181	-0.183	0.289**	0.313**
DOTCV	-0.121	-0.160	-0.638*	-0.597*	-0.590**	-0.553**	-0.345**	-0.306**
DOPEC	-0.113	-0.094	-0.023	-0.135	0.494	0.361*	0.199*	0.143
AOTCV	-0.612**	-0.473	0.056	0.000	-0.348*	-0.491**	-0.392**	-0.277**
PELTCV	-0.227	-0.270	0.145	-0.159	-0.152	-0.356*	-0.272**	-0.209*
PECTCV	-0.559**	-0.607**	-0.297	-0.250	-0.185	-0.058	-0.168*	-0.295**
SNA	0.547**	0.440*	0.119	0.199	0.258	0.467**	0.374**	0.394**
DFH	0.206	0.086	-0.380	-0.214	-0.077	0.044	-0.086	0.031
AFH	0.056	-0.070	-0.343	-0.201	-0.148	0.003	-0.092	0.006
PECL	0.150	0.307	-0.418	-0.219	0.004	0.224	0.002	0.153
CFKD	0.073	0.166	-0.358	-0.172	-0.369*	-0.369*	-0.184*	-0.058
CFL	0.132	0.275	-0.462	-0.349	-0.437*	-0.331*	-0.250**	-0.118
CS37-1	0.321	0.342	0.542*	0.363	0.188	0.387*	0.311**	0.328**
CS37-2	-0.312	-0.254	0.365	0.022	0.194	0.178	0.041	0.007
CS37-3	-0.163	0.290	0.108	0.295	0.650**	-0.292	0.218*	0.018
CS3-1	0.560**	0.570**	-0.064	-0.072	0.091	-0.025	0.275**	0.335**
CS3-2	0.174	0.069	0.579*	0.612*	-0.040	0.188	0.207*	0.219*

* = $p<0.05$; ** = $p<0.01$

Appendix B. Table 4. Couesius plumbeus environmental correlations - Elevation.

	Localities							
	Missouri		Columbia		Atlantic		Combined	
Character	Female (18)	Male (18)	Female (12)	Male (12)	Female (26)	Male (27)	Female (100)	Male (97)
DSR	-0.194	-0.260	-0.173	0.047	-0.207	-0.276	0.117	0.100
CPS	-0.040	0.015	-0.018	0.184	-0.011	-0.044	0.050	0.076
HL	-0.070	-0.096	0.253	0.345	0.310	0.171	0.385**	0.339**
ORBD	-0.045	0.052	-0.103	0.215	0.307	0.383*	0.082	-0.003
HDN	0.262	0.371	-0.207	-0.269	0.177	0.050	0.516**	0.455**
DOTCV	-0.539*	-0.210	-0.285	-0.426	0.065	-0.005	-0.045	-0.129
DOPEC	0.605**	0.615**	-0.034	0.146	-0.231	-0.256	0.123	0.135
AOTCV	-0.612**	-0.560**	-0.207	0.019	-0.117	-0.045	-0.202	-0.195*
PELTCV	-0.261	-0.134	0.392	0.084	-0.084	-0.059	-0.185*	-0.349**
PECTCV	0.144	-0.001	0.015	0.054	0.035	-0.009	0.021	-0.079
SNA	0.766**	0.716**	-0.048	-0.105	0.093	-0.017	0.335**	0.203*
DFH	0.094	0.219	-0.250	-0.407	-0.320	-0.234	-0.350**	-0.334**
AFH	-0.025	0.044	-0.333	-0.417	-0.354*	-0.124	-0.327**	-0.327**
PECL	0.049	0.301	-0.241	-0.322	-0.222	-0.144	-0.110	0.085
CFKD	0.038	0.207	-0.322	-0.425	-0.053	-0.057	-0.096	-0.127
CFL	-0.110	0.101	-0.141	-0.256	-0.300	-0.177	-0.359**	-0.235*
CS37-1	0.128	0.023	0.217	0.435	0.353*	-0.003	0.553**	0.519**
CS37-2	0.0173	0.264	0.261	-0.355	0.166	0.025	-0.018	0.131
CS37-3	0.062	0.022	0.001	0.180	-0.410*	0.487**	-0.025	0.175*
CS3-1	0.086	0.085	-0.244	-0.098	0.078	-0.129	0.402**	0.384**
CS3-2	0.129	0.002	0.283	0.313	0.442*	0.214	0.452**	0.411**

* = p<0.05; ** = p<0.01

Appendix B. Table 5. Couesius plumbeus environmental correlations - Water Type (lentic versus lotic).

	Localities							
	Missouri		Columbia		Atlantic		Combined	
Character	Female (18)	Male (18)	Female (12)	Male (12)	Female (26)	Male (27)	Female (100)	Male (97)
DSR	0.285	0.328	0.076	-0.183	-0.127	-0.127	0.091	0.167
CPS	0.281	0.314	0.106	0.117	0.058	-0.029	0.163	0.221*
HL	0.427*	0.584**	0.219	0.349	-0.052	0.353*	0.167*	0.337**
ORBD	0.156	0.343	-0.022	0.032	-0.297	-0.298	-0.178*	-0.118
HDN	0.299	0.330	0.244	0.253	0.464**	0.601**	0.190*	0.304**
DOTVC	0.213	-0.106	-0.248	-0.096	0.024	-0.113	0.205*	0.053
DOPEC	-0.410*	-0.384	-0.336	-0.568*	-0.058	0.384*	-0.226*	0.143
AOTCV	0.010	-0.069	-0.135	-0.470	-0.369*	-0.036	0.193*	0.012
PELTCV	0.068	-0.010	0.143	0.155	0.306	0.095	0.297**	0.068
PECTCV	-0.498*	-0.504*	-0.509*	-0.397	0.187	0.540**	-0.086	0.054
SNA	-0.130	-0.025	0.144	0.455	-0.142	0.174	0.039	0.039
DFH	0.030	0.041	0.264	0.330	0.352*	0.350*	0.373**	0.332**
AFH	0.054	-0.003	0.321	0.431	0.331*	0.359*	0.356*	0.336**
PECL	0.130	0.004	0.186	0.210	0.394*	0.069	0.435**	0.143
CFKD	-0.048	0.127	0.392	0.460	0.547**	0.432*	0.441**	0.319**
CFL	0.094	0.289	0.042	0.195	0.167	0.400*	0.243**	0.333**
CS37-1	0.282	0.230	-0.055	-0.099	-0.140	0.062	-0.103	0.079
CS37-2	-0.414*	-0.479*	-0.337	-0.514*	-0.262	-0.170	-0.325**	-0.371**
CS37-3	-0.177	0.421*	0.057	0.111	0.210	-0.238	0.210*	-0.216*
CS3-1	0.539*	-0.450	0.297	0.156	0.152	0.152	0.241**	0.092
CS3-2	0.092	-0.227	-0.227	-0.189	-0.160	-0.024	-0.228*	-0.190*

* = p<0.05; ** = p<0.01

Article 3. RELATIONSHIP OF COUESIUS TO CERTAIN OTHER NORTH AMERICAN CYPRINID GENERA

ABSTRACT

The relationship of *Couesius* to genera associated with *Hybopsis* sensu lato and *Semotilus* s.l. (including *Margariscus*) is examined using both phenetic and cladistic methodologies. Both analyses indicate that *Couesius* is most closely related to *Margariscus*. It is suggested that the two be considered congeneric. *Couesius* and *Margariscus* form a plesiomorphic sister group of *Semotilus* sensu stricto and *Nocomis*, while *Couesius*, *Margariscus*, *Semotilus* s.s., and *Nocomis* appear to form a plesiomorphic sister group of *Platygobio* and *Hybopsis* s.s.

INTRODUCTION

The taxonomic relationship of Couesius Jordan 1878 to other North American cyprinid genera has been unsettled since Bailey (1951) combined it with Hybopsis sensu stricto, Nocomis, Oregonichthys, Erimystax, Macrhybopsis, Extrarius, and Yuriria into an expanded Hybopsis. Couesius subsequently has been removed from Hybopsis (Bailey, et al., 1970) but the initial move stirred considerable controversy and served to emphasize the lack of understanding regarding the generic interrelationships of North American cyprinids in general and the Hybopsis association in particular (see Reno, 1969a).

Various authors (Jordan and Evermann, 1896; Bailey, 1951; Moore, 1968; Jenkins and Lachner, 1971) have characterized Hybopsis sensu lato as follows: 1) pharyngeal teeth in major row 4-4 and in minor row 0 to 2; 2) mouth subterminal to inferior, no frenum, 3) barbels present, their origin terminal or nearly terminal on maxillary, 4) intestine usually not whorled, and 5) scale radii restricted to posterior field. Jenkins and Lachner (1971) suggested that criteria 1, 2, 4, and 5 were of questionable value since most are shared with a large number of extant North American cyprinid species. The only feature that appears to unite Hybopsis s.l. and distinguish it from Notropis is the possession of a barbel. However, Jenkins and Lachner (1971) pointed out numerous examples of the labile nature of this character and suggested that it may not be uniquely derived within the group. Additionally, with the discovery of typically barbeled populations of *Notropis*, Gilbert and Bailey (1972) concluded that cyprinid barbels may have had as many as six independent origins in North America. This leaves little to justify the recognition of *Hybopsis* s.l. as a natural, or monophyletic, taxon. Several authors have expressed similar views (Hubbs and Crowe, 1956; Davis and Miller, 1967; Reno, 1969b).

In support of removal of *Nocomis* from *Hybopsis* s.l., Jenkins and Lachner (1971) stated that *Nocomis* was more closely related to the nest-building species of *Semotilus* (*S. atromaculatus* and *S. corporalis*). They added that *Couesius* showed an affinity to *Semotilus*, especially *Semotilus* (*Margariscus*) *margarita*, and that if *S. margarita* merits inclusion in the genus *Semotilus* (Bailey and Allum, 1962; Moore, 1968), then so does *Couesius*. The similarity of *Couesius* to *Semotilus*, especially *S. margarita*, has been discussed or implied by numerous authors (Girard, 1856; Cox, 1901; Hubbs, 1942; Raney, 1969; Reno, 1969b; McPhail and Lindsey, 1970; Paetz and Nelson, 1970; Sharpe, 1970; Jenkins, 1971).

Clarifying the taxonomic relationships of *Couesius* becomes important nomenclatorially if the "dissimilis" form of *Couesius* is to be recognized as a valid species or subspecies. If so, and if *Couesius* is combined with *Hybopsis*, then, as pointed out by Taylor (1954) and Lindsey

(1956), the name Hybopsis (Couesius) dissimilis (Girard) 1856 would become a junior secondary homonym of Hybopsis (Erimystax) dissimilis (Kirtland) 1841 and would, therefore, have to be changed.

Coad (1975), in his numerical cladistic treatment of North American cyprinid genera, added considerable new information and summarized much of the existing information on the interrelationships of Couesius, Semotilus, Hybopsis, and other related forms. However, some of his methods do not seem entirely satisfactory and appear to have led to unacceptable conclusions. This paper, using mostly data from Coad (1975) and other published sources, re-examines these relationships with both phenetic and cladistic methodologies.

MATERIALS AND METHODS

Most systematists believe that taxonomy should, in some way, reflect evolutionary history. Such a history, or phylogeny, involves at least two basic components: 1) the within line divergence, or anagenesis, and 2) the sequence of branching, or cladogenesis. A knowledge of one or both types of information, depending on the systematist's taxonomic philosophy, is therefore necessary to formulate a classification.

Phenetic methods, such as ordination and cluster analysis, measure the degree of similarity or dissimilarity between taxa. This provides a useful method of estimating the degree of anagenetic change. However, since cladogenetic events are ignored, differences between convergence and parallelism cannot be distinguished. Primarily for this reason, phenetic methods are considered by some as inappropriate for taxonomic analysis (Mayr, 1965; but see also Sneath and Sokal, 1973).

A careful cladistic analysis using the methodology of Hennig (1966), while ignoring anagenetic changes, can be useful in reconstructing cladogenetic events. Few find fault with the methodology of cladistic analysis, at least in theory, but many object to classifications derived from cladograms (Sneath and Sokal, 1973; Mayr, 1974; Colless, 1977; and numerous others).

In practice, cladistic methodologies are extremely difficult to apply to groups such as the North American Cyprinidae. First, as the number of Operational Taxonomic Units (OTU's) increases, the number of hypotheses to be tested quickly becomes unmanageable, even for a computer. The 18 OTU's with which this study is concerned would generate $6x10^{36}$ different rooted bifurcating trees (Felsenstein, 1978). An even greater number is generated if multifurcations are allowed. Clearly it is unreasonable to test all generated hypotheses for the 18 OTU's, let alone for all the approximately 250 species of North American cyprinids. Second, to dicotomize n OTU's, one needs at least n-1 uniquely derived character states. To date, there appears to be too few such known characters to fully express the relationships among the genera of North American minnows. Part of this problem lies with the failure to distinguish true homologies from convergences. Most taxonomic characters in cyprinids appear morphologically rather simple and subject to repeated evolution in divergent lines. This is further complicated by the fact that genetic variation in North American minnows is apparently within the lower portion of the range characteristic of vertebrates (Avise and Ayala, 1976). If so, North American cyprinids have undergone considerable cladogenesis without, seemingly, a great deal of anagenesis. This would make the discovery of evidence reflecting these cladogenetic events extremely difficult, if not impossible, to find. Third, as pointed out by Szalay (1977), the most crucial aspect of cladistic analysis is establishing character polarities. Although some characters within the North American Cyprinidae are fairly clear-cut in their evolutionary direction, most are not. If many characters are incorrectly coded, genera may be mistakenly united on the basis of shared primitive conditions (symplesiomorphies) rather than on the basis of shared derived conditions (synapomorphies).

In situations such as these, phenetic methods may prove useful in establishing initial hypotheses of phylogeny. Ordination and cluster analysis can be used to reduce the OTU's to a manageable number by indicating what may be "natural" units. Although problems created by parallelisms and convergences are still present, they are likely infrequent and suspected incidences may be readily tested by cladistic methods. Problems associated with character polarities can initially be ignored since phenetic methods do not require polarity estimates. Relationships derived through phenetic methods may, to some degree, be used to test postulated character polarities.

To answer questions concerning the relationships of *Couesius*, the possibilities were narrowed to groups which have been traditionally allied with *Couesius*, i.e. *Hybopsis* s.l. and *Semotilus* s.l. (Figure 1). *Exoglossum* and *Phenacobius* were included on the basis of Coad (1975). *Campostoma* was omitted because of its questionable relationship to the group and *Parexoglossum* was considered congeneric with *Exoglossum* also after Coad (1975). Whether this assemblage is holophyletic, paraphyletic, or even polyphyletic, can not as yet be definitely established. It is probably at least paraphyletic in that Campostoma does belong to this group (Jenkins, 1971). There appears to be no reason to suspect that the group is polyphyletic, although the inclusion of Oregonichthys is somewhat suspicious on zoogeographic grounds.

Eighteen species (Table 1) from 12 genera or subgenera were chosen to represent the groups in question. Oregonichthys, Couesius, Margariscus, Extrarius, and Platygobio were considered monotypic and were represented by the sole member of the genus or subgenus. Two of three species of Semotilus s.s., one of five species of Phenacobius, one of two species of Exoglossum s.l., two of seven species of Nocomis, two of six species of Erimystax, three of seven species of Hybopsis s.s., and both species of Macrhybopsis, representing the remaining genera, were chosen on the basis of the amount of published information. Monotypic Yuriria lacked sufficient information to be included. Although additional species of Hybopsis have been discovered or described (Jenkins, 1976), insufficient data made their inclusion unwarranted.

Information on 31 characters (Table 2) for the 18 species was compiled primarily from literature sources and is summarized in Table 3. Primary sources were Evans (1952), Davis and Miller (1967), Reno (1969b), Jenkins and Lachner (1971), Lachner and Jenkins (1971), and Coad (1975), as well as numerous regional works, such as Jordan and Evermann (1896), Baxter and Simon (1970), Scott and Crossman (1973), Clay (1975), Pflieger (1975), and Moyle (1976). For taxa with incomplete or conflicting characterizations, counts or measurements were made from specimens on hand or, if necessary, from published drawings or photographs. Data for characters 12, 13, 14, 26, 27, 28, and 29 were entirely from Coad (1975) and represent the typical state for the genus or subgenus rather than the selected species. Analyses excluding these characters showed that their inclusion produced artifically coherent intrageneric clusters, but the overall pattern of relationships was not significantly changed.

Phenetic relationships of the 18 OTU's were examined by principal co-ordinate analysis (Gower, 1966a; 1966b), using program PCOORD (Blackith and Reyment, 1971), and unweighted pair-group with arithmetic means (UPGMA) cluster analysis (see Sneath and Sokal, 1973), using the CLUSTAN 1C software package (Wishart, 1975). Gower's coefficient (Gower, 1971), which allows mixing of quantitative and qualitative multi-state characters, was used in both analyses. Principal co-ordinate analysis defines a set of orthogonal axes from an OTU x OTU association matrix (Q-technique) which accounts for successively lesser amounts of variance among OTU's. This allows a large amount of variation to be visualized in a reduced number of axes. Unfortunately, as in principal component analysis, distances between major groups may be faithfully represented while near neighbor distances may be greatly distorted. For this reason, cluster analysis, which generally exhibits opposite properties, was also used.

ANCESTRY

Determining the direction of evolution presents a major problem in phylogenetic reconstruction. Correct character polarity can often be established in reference to the fossil record (Criterion of geological character precedence - Hennig, 1966:95). The cyprinid fossil record is of little help in directly indicating primitive character states as many of the characters used in cyprinid systematics are not preserved in fossil material. However, it may be of value in establishing which extant species are likely to be near the primitive condition. The oldest known North American fossil cyprinids appear to represent western genera, especially *Gila* and *Ptychocheilus* (Figure 2).

Coad (1975) arbitrarily regarded the eastern genus *Notropis* as ancestral to North American forms. However, this choice seems unfortunate as the fossil record indicates that *Notropis* is likely of comparativley recent origin. A Lower Pliocene record of *Notropis* (Wilson, 1968) is highly questionable since it was based solely on a broken right infrapharyngeal. The tooth formula of this fragment (-4,2) cannot be considered diagnostic since this formula is found in many other genera. A Middle Pliocene specimen was questionably assigned to *Notropis* by Smith (1962) on the basis of large scales, general appearance, and absence of any other distinctive characters.

The fossil record suggests that a more likely choice of ancestors may be among the western genera, especially the Gila -like forms such as Gila, Siphateles, Ptychocheilus, Richardsonius, and Pogonichthys (see Miller, 1958; Uyeno, 1961; Uyeno and Miller, 1963, 1965; Miller, 1965; Avise and Ayala, 1976). Hopkirk (1973) believed that the western Pogonichthys represented the most primitive North American cyprinid genus, although he did not believe it to be derived from Gila or a Gila -like ancestor as did Uyeno and Miller (1965). He indicated that Pogonichthys was closely allied with the Asian Tribolodon and also with the North American genera Mylocheilus, Semotilus, and Platygobio. Coad (1975) also found a close link between Semotilus s.l. and several western genera, including Pogonichthys, on the basis of major row pharyngeal tooth count, supraorbital pore count, lateral line decurvature, and number of vertebrae, but attributed these similarities to parallelism. In view of these findings, likely character polarity estimates may be obtained by considering such genera as Pogonichthys, Acrocheilus, Mylocheilus, Mylopharodon, Gila, Ptychocheilus, and Tribolodon as near the ancestral condition.

CHARACTER ANALYSIS

DISTRIBUTION - North American cyprinids appear to fall into two rather distinctive groups, those of the Mississippi drainage system, and those in the more western drainages. The western genera are typically species-depauperate groups and include such genera as *Orthodon*, *Mylocheilus*, *Pogonichthys*, *Mylopharodon*, *Ptychocheilus*, and *Gila*, while the Mississippi, or eastern, groups are often speciose and include such genera as *Notropis*, *Hybopsis*, *Semotilus*, *Couesius*, *Hybognathus*, *Phoxinus*, *Pimephales*, and *Notemigonus*. However, all forms are generally referred to a single subfamily, Leuciscinae.

Within the *Hybopsis* - *Semotilus* complex all included species, except *Oregonichthys* and certain populations of *Couesius*, are found exclusively east of the Rocky Mountains. Coad (1975) considered a western distribution as derived, however, the fossil record seems to indicate the reverse. Although the decidedly eastern distribution of the *Hybopsis* - *Semotilus* complex may have important evolutionary significance and indicates a basic homogeneity among these species, the use of distribution patterns in establishing phylogenetic hypotheses should be discouraged as this can unknowingly lead to circularity when investigating zoogeographic patterns. For this reason distribution was not considered.

NUPTIAL COLORATION - Nuptial color patterns often take the form of yellow, orange, or red pigmentation usually along the ventral portion of the body and on the fins. *Semotilus* and *Nocomis* develop an overall reddish cast during spawning while male *Margariscus* develop an intense red flank stripe. Both male and female *Couesius* develop orange-reddish regions in the pectoral axils and around the mouth. Nuptial color patterns occur in many widely scattered groups. *Tribolodon* and *Mylocheilus* develop reddish coloration in the mouth region while *Pogonichthys* develops a red tinge on the fin tips. Therefore, the development of these color patterns should be considered as a primitive condition. A loss of this condition may be associated with habitats where vision is limited, such as turbid waters.

The exact degree of similarity between these color patterns may not be of great importance. It seems possible that, as these patterns form a basis for species recognition, a form of character displacement may occur. Closely related species might, therefore, have widely divergent color patterns.

NEST BUILDING - Nest building appears to be a derived behavior generally characterized by manipulation of the substrate by the male to form either a mound or depression. *Semotilus*, *Nocomis*, and *Exoglossum* are nest builders (Jenkins, 1971). Male *Margariscus* have been observed to defend a territory (Langlois, 1929) and thus may show a prerequisite of nest building. Reports of nesting behavior in *Couesius* are somewhat contradictory. Brown (1969) noted that spawning took place under rocks and observed no indication of nest building. However, he did cite a personal communication with V. C. Applegate that, in Michigan, Couesius builds pit-like nests. The situation is further complicated because the populations observed by Brown in northern Saskatchewan are very near the "plumbeus" form of Couesius. In Michigan both the "plumbeus" and "dissimilis" forms are sympatric and appear to be good biological species (Wells, 1978). As Brown (1969) suggested, it is possible that Applegate observed the "dissimilis" form. For the analysis, Couesius was considered as having a potential for nest building.

CEPHALIC NUPTIAL TUBERCLE SIZE - Small cephalic nuptial tubercles are present in Pogonichthys, Acrocheilus, Mylocheilus, Mylcpharodon, Ptychocheilus, and Tribolodon as well as most other cyprinids. Within the Hybopsis - Semotilus complex only Nocomis and Semotilus develop large tubercles. The possession of small cephalic nuptial tubercles should be considered as a primitive condition. Although tubercle histology and patterns are undoubtedly important in indicating phylogeny, there are insufficient detailed comparisons available (see Branson, 1962).

It should also be noted that reproductive male Couesius possess a roughened patch of scales on the breast region. Koster (1939), Hubbs (1942), and Fava and Tsai (1976) mentioned a similiar, but lesser, modification in the breast region of male Margariscus. This character was not included in the phenetic analysis but appears to be a shared derived state between only Couesius and Margariscus within the Hybopsis - Semotilus complex.

NUPTIAL CREST - Swelling of the dorsal region of the head appears to be a derived condition unique to Nocomis.

PHARYNGEAL TOOTH NUMBER (major and minor tooth rows) - Phyletics of pharyngeal tooth numbers are difficult to establish. The sometimes major differences within a genus and similarity between apparently unrelated genera indicate extreme plasticity in this character. Even within some species counts can be variable. Brown (1969), in a northern Saskatchewan population of Couesius, found 71% with the usual formula of 2,4-4,2; 9% with 1,4-4,1; 7% with 2,5-4,2 (typical of Semotilus and Margariscus); and 13% with counts ranging from 0,4-4,0 to 2,5-5,2. Typical pharyngeal tooth numbers of Pogonichthys (2,5-5,2), Mylocheilus (1,5-5,1), Mylopharodon (2,5-4,2), Gila (2,5-4,2), Ptychocheilus (2,5-4,2), and Tribolodon (2,5-4,2) indicate that the primitive condition is most likely 5-5 or 5-4 in the major row and 2-2 in the minor row. The extinct western genus Evomus may also have had a pharyngeal tooth count of 2,5-4,2 (Uyeno and Miller, 1965).

LATERAL STRIPE - A prominent, dark, lateral stripe is commonly associated with elongate body form (see Barlow, 1972). This character occurs widely throughout fishes in general and indicates repeated evolution. It should be considered primitive within the Hybopsis - Semotilus complex. A dark lateral stripe is best developed in Couesius, Margariscus, and young of Semotilus and Nocomis. Loss of the lateral stripe may be associated with habitats where vision is limited.

DORSAL, PELVIC, and ANAL FIN RAYS - Modal dorsal and pelvic fin ray counts for all members of the Hybopsis - Semotilus complex were invariable and therefore not considered. With respect to the hypothesized ancestral forms, the trend is toward a reduction in the number of dorsal, pelvic, and anal fin rays. This trend appears to be common among teleost fishes and numerous parallelisms may be expected. For this reason, these characters were used as phenetic evidence only.

BODY SIZE - The genera Pogonichthys, Mylocheilus, Mylopharodon, and Ptychocheilus contain among them the largest minnows in North America. Tribolodon is also a relatively large minnow (Coad, 1975). This would seem to indicate that a large body size is a primitive condition.

BARBEL - Within the Hybopsis - Semotilus complex at least two distinct types of barbels occur. Hybopsis, Erimystax, Macrhybopsis, Platygobio, Nocomis, Extrarius, and Oregonichthys possess a well developed barbel at the terminal end of the maxillary. That of Couesius, while similar, is generally less well developed and somewhat forward of this position (Moore, 1968). Semotilus and Margariscus possess a small flap-like barbel in the groove along the upper jaw. Phenacobius mirabilis lacks a barbel but was scored as having the potential to develop a Semotilus -like barbel since one occurs in all other members of Phenacobius. With reference to the hypothetical ancestral forms, terminal barbels are found in Pogonichthys and Mylocheilus. This suggests that possession of terminal barbels is a primitive condition in North American cyprinids and as such, cannot be used to unite the Hybopsis s.l. groups. Until the homologies of the other barbel types can be established, they are best regarded as phenetic evidence only.

THIRD URODERMAL BONE - I agree with Coad (1975) that the absence of the third urodermal is probably a derived character state. Presence of this bone in all the hypothesized ancestral forms supports this notion. However, derived states brought about by a loss of a simple structure should not be weighted heavily.

POSTEROVENTRAL METAPTERYGOID STRUT - Within the Hybopsis - Semotilus complex Coad (1975) found a single posteroventral metapterygoid strut, rather than the usual two struts, in Extrarius, Macrhybopsis, Nocomis, and Platygobio. A single strut would appear to be a derived condition but, again, this seems to be the result of a loss of a simple structure.

UROHYAL ARMS - Fusion of the urohyal arms to form a foramen appears to be unique to Exoglossum s.l. (Coad, 1975). Coad noted that large Phenacobius mirabilis occasionally approach this condition.

FEEDING TYPE - Davis and Miller (1967) classified species of Hybopsis s.l. into three feeding types on the basis of brain pattern and taste bud distribution. Group I, sight feeders, included Nocomis, Erimystax, Oregonichthys, Couesius, and some Extrarius. Group II, skin tasters, included Platygobio, Macrhybopsis, and some Extrarius while group III, mouth tasters, included most Hybopsis s.s. Evans (1952) found Semotilus atromaculatus to be a sight feeder. Since this character has been little studied in the remaining Cyprinidae, I somewhat arbitrarily consider sight feeding to be the primitive condition. An increased reliance on tasting may be associated with invasion of habitats with limited visibility. In the phenetic analysis, the evolution of sight feeding was scored independently from tasting.

PERITONEUM COLOR - A darkened peritoneum appears to be a derived state, usually associated with increased gut length and a herbivorous diet. Its presence in many widely scattered groups, even outside of the Cyprinidae, indicates multiple origins. A darkened peritoneum occurs in Nocomis and Erimystax. The recent inclusion of forms with a dark peritoneum and elongate gut, such as Dionda nubilis and Notropis mekistocholas, within Notropis indicates a lessening importance of this character in establishing generic relationships (see discussion in Hubbs and Miller, 1977).

LATERAL LINE DECURVATURE - Coad (1975) used the ratio of scales above the lateral line divided by scales below the lateral line to measure the degree of lateral line decurvature. He considered a non-decurved lateral line as the primitive condition but stated that the character was of only phenetic utility. With respect to the western and Asian ancestral types (mean ratio = 1.49) a clear trend toward a lessening of the decurvature is apparent (mean ratio = 1.23 for <u>Hybopsis</u> - <u>Semotilus</u> complex). I consider a non-decurved lateral line as derived.

SCALE COUNTS (above lateral line, below lateral line, predorsal, and along lateral line) - High scale counts (approximately 61-89 lateral line scales) are <u>typical of the</u> western and Asian ancestral genera. Low scale counts are therefore considered as derived. These characters are obviously intercorrelated since increased scale size would decrease each of these counts. A trend toward a decrease in scale size appears to be common among teleost fishes and is undoubtedly subject to numerous parallelisms and reversals.

SCALE RADII - Since all members of the <u>Hybopsis</u> - <u>Semotilus</u> complex, as well as most of the hypothesized ancestral forms, possess radii restricted to the posterior field, this character must be considered as a shared primitive character state and therefore of no value in describing the <u>Hybopsis</u>, <u>Couesius</u>, <u>Semotilus</u> relationships. The total number of scale radii may, however, be of some utility. The hypothesized ancestral forms typically possess a modal number of total scale radii less than approximately

25 (except *Ptychocheilus*) (Coad, 1975). Modal radii numbers greater than this are found in *Nocomis* and *Semotilus* and may be considered derived. It should also be noted that *Nocomis*, *Semotilus*, *Margariscus*, *Couesius*, and *Phenacobius* have previously been linked on the basis of several scale characters (Cockerell and Allison, 1909; Jenkins and Lachner, 1971).

VERTEBRAL COUNT - High modal vertebra counts are typical of the hypothesized ancestral group - *Pogonichthys* (43), *Acrocheilus* (45), *Mylocheilus* (45), *Mylopharodon* (47), *Ptychocheilus* (40-47), and *Tribolodon* (45-50) (Coad, 1975). Species in the *Hybopsis* - *Semotilus* complex generally have much lower counts (36-45). This would seem to indicate a trend toward a reduction in number of vertebrae. Again, this appears to be a widespread teleost trend and parallelisms may be common. This trend may also be associated with a reduction in body size.

CEPHALIC LATERAL LINE CANAL PORES (infraorbital/ preoperculomandibular/ supraorbital/ supratemporal) - With respect to *Pogonichthys* (26/21/18/10), *Acrocheilus* (25/16/13/11), *Mylocheilus* (26/17/15/10), *Mylopharodon* (27/20/16/12), *Gila* (29/22/16/11), and *Ptychocheilus* (46/38/24/19) (Coad, 1975), there appears to be a trend towards reduction of the number of cephalic lateral line canal pores. Low number of pores in each series may be considered derived. Reno (1969b) doubted the utility of the lateral line system in systematics since it is highly responsive to environmental factors such as turbidity and current velocity. However, he did note unique cephalic lateral line systems for Oregonichthys, Couesius, and Nocomis, while Erimystax, Macrhybopsis, and Extrarius appeared similar to one another, and Platygobio similar to turbid water Hybopsis s.s.

POSITION OF DORSAL FIN RELATIVE TO PELVIC FINS - Hopkirk (1973) believed that the dorsal fin in advance of the pelvic fins was the primitive condition for North American cyprinids since this is the position in Pogonichthys. The dorsal fin is also slightly in advance of the pelvic fins on Mylocheilus. This trend, if correct, is not readily apparent and would probably be subject to numerous parallelisms and reversals.

RATIO OF HEAD LENGTH TO TOTAL LENGTH - The head to body ratio was introduced entirely as a phenetic character, however, there may be a slight trend towards a proportionately larger head.

CHROMOSOME NUMBER (2n) - A diploid chromosome count of 50 is typical for North American and European cyprinids (Uyeno and Smith, 1972; Avise and Gold, 1977) and probably represents the ancestral number for North American cyprinids. Unfortunately, counts for most species involved in the Hybopsis - Semotilus question are unpublished. Counts for Semotilus (2n = 52), Margariscus (2n = 50), and Couesius (2n = 50) are from Legendre and Steven (1969). Other counts were replaced by the mean value (50.4).

RESULTS

Phenetic

The relationship among the 18 OTU's resulting from the principal co-ordinate analysis is displayed in Figure 3. The three-dimensional space accounts for 60.6% of the total variance between centroids. Platygobio, Macrhybopsis, and Extrarius form a closely knit cluster separate but nearest to the three representatives of Hybopsis. Both the Platygobio and Hybopsis clusters are distant from Nocomis, Semotilus, Couesius, and Margariscus. The nearest neighbor in full hyperspace to Couesius is Margariscus (Figure 4). These two are, in turn, nearest Semotilus. Nocomis is phenetically closest to Semotilus. Oregonichthys, Exoglossum, Erimystax, and Phenacobius are distant, but nearest Hybopsis.

Cladistic

The cladistic analysis considered only those species indicated by the phenetic analysis to be of major concern - Couesius, Margariscus, Semotilus (2 species), Nocomis (2 species), Platygobio, and Hybopsis (3 species). Extrarius, Macrhybopsis, Erimystax, and Phenacobius appear related to Hybopsis, but there are insufficient characters to fully resolve the relationships.

The least rejected hypothesis is summarized in Figure 5. No evolutionary reversals are noted. Parallelisms occur in development of a single metapterygoid strut, reduction of pharyngeal tooth number in both major and minor rows, reduction in number of vertebrae, reduction in number of scales, and loss of maxillary barbel. Parallelisms in these characters do not seem unusual (see CHARACTER ANALYSIS).

Phylogeny

A phylogeny of the Hybopsis - Semotilus complex was reconstructed from both the phenetic and cladistic analyses (Figure 6). The branching sequence was derived from the cladogram while the amount of divergence was based on the phenogram.

DISCUSSION

Both phenetic and cladistic analysis results are reasonably compatible. Each indicates that Couesius is most closely related to Margariscus. However, the association is based primarily on the mutual retension of primitive characters; only the shared derived occurrence of male breast tuberculation unites them. It should be noted that this pattern of breast tuberculation also occurs in Phoxinus (Starnes and Starnes, 1978) and Clinostomus (Koster, 1939), and a relationship between Phoxinus, Clinostomus, and Margariscus has been proposed by several workers (see Legendre, 1970). Couesius and Margariscus appear to form a plesiomorphic sister group of Semotilus and Nocomis. The similarity between Semotilus and Margariscus also appears to be based on the mutual retension of primitive characters. Divergence in the Nocomis lineage is most likely associated with reproductive adaptations. Platygobio appears to be a plesiomorphic sister group of Hybopsis and the Hybopsis - Platygobio lineage appears to be the result of several advanced trends (reduced vertebra numbers, enlarged scales, etc.) coupled with several adaptive trends associated with inhabiting turbid water environments (loss of coloration, development of skin and mouth tasting, etc.). This lineage probably represents a plesiomorphic sister group of Notropis and related genera, but in light of the current lack of knowledge regarding these groups, further speculation is unwarranted.

Following a phenetic philosophy, the results could suggest several different taxonomic interpretations. First, an extreme view would be to expand *Hybopsis* s.l. even further to include at least *Semotilus*, *Margariscus*, *Exoglossum*, and *Phenacobius*. However, this degree of lumping seems excessive, especially in view of arguments for lumping *Hybopsis* with *Notropis* (see Coad, 1975:473-475). A second interpretation would be to recognize *Hybopsis* in a more limited sense and recognize *Couesius* as a distinct genus, as presently done (Bailey, et al., 1970). If this course is followed, then it would appear unjustifiable to include *Margariscus* within *Semotilus* since *Margariscus* is closer to *Couesius*. A third interpretation would be to include *Couesius* within *Semotilus* s.l. as done by Raney (1969) and Sharpe (1970). This appears justifiable when one considers that if genera currently recognized as valid by the American Fisheries Society (Bailey, et al., 1970) are used to establish a generic phenon level; this level falls between approximately 0.68 and 0.50 in Figure 4. The *Semotilus* - *Couesius* - *Margariscus* similarity lies near the center of this region. This procedure also indicates that *Couesius* and *Margariscus*, considered together, are well below the level to be recognized as distinct genera.

The problem remains much the same using cladistic principals. Again, all *Hybopsis* - *Semotilus* groups could be combined into a single genus, but as mentioned previously, this seems unwise. *Couesius*, *Margariscus*, *Semotilus*, and *Nocomis* could be combined into a single genus, but this seems premature in that the relationships of the nest-building *Exoglossum* and *Campostoma* are still uncertain. Finally, *Semotilus* and *Nocomis* could ~~be~~ combined into a single genus while *Couesius* and *Margariscus* could be combined into another genus.

I suggest the best solution is to adopt an evolutionary or synthetic approach which recognizes the rapid divergence of the *Nocomis* lineage but also maintains monophyly in the *Semotilus* lineage. This may be accomplished by removing *Margariscus* from *Semotilus* s.l. and recognizing *Nocomis* as a distinct genus. The criteria which Bailey and Allum (1962) used to justify the inclusion of *Margariscus* within *Semotilus* appear to be, for the most part, based on shared primitive characters. *Margariscus*, more appropriately, should be placed in the genus *Couesius* following Cox (1901). The differences between them do not seem great enough to warrant the recognition of two monotypic genera.

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Table 1. Species used in analysis of *Hybopsis* - *Semotilus* complex.

Number	Species
1	*Hybopsis storeriana* (Kirtland) 1844
2	*Hybopsis rubrifrons* (Jordan) 1876
3	*Hybopsis amblops amblops* (Rafinesque) 1820
4	*Hybopsis* (*Erimystax*) *dissimilis dissimilis* (Kirtland) 1840
5	*Hybopsis* (*Erimystax*) *x-punctata x-punctata* (Hubbs and Crowe) 1956
6	*Hybopsis* (*Macrhybopsis*) *gelida* (Girard) 1856
7	*Hybopsis* (*Macrhybopsis*) *meeki* (Jordan and Evermann) 1896
8	*Hybopsis* (*Oregonichthys*) *crameri* (Snyder) 1907
9	*Couesius plumbeus* (Agassiz) 1850
10	*Nocomis biguttatus* (Kirtland) 1840
11	*Nocomis micropogon* (Cope) 1864
12	*Exoglossum maxillingua* (LeSueur) 1817
13	*Semotilus atromaculatus* (Mitchell) 1818
14	*Semotilus corporalis* (Mitchell) 1817
15	*Semotilus* (*Margariscus*) *margarita nachtriebi* (Cox) 1896
16	*Hybopsis* (*Platygobio*) *gracilis gracilis* (Richardson) 1836
17	*Hybopsis* (*Extrarius*) *aestivalis* (Girard) 1856
18	*Phenacobius mirabilis* (Girard) 1856

Table 2. Characters and coding used in *Hybopsis* - *Semotilus* phenetic comparison.

1. Nuptial coloration: 0 = No; 1 = Slight; 2 = Yes
2. Nest building: 0 = No; 1 = Potential; 2 = Mound or pit
3. Cephalic nuptial tubercle size: 0 = Very small; 1 = Small; 2 = Intermediate; 3 = Large; 4 = Very large
4. Nuptial crest: 0 = No; 1 = Slight; 2 = Yes
5. Minor row pharyngeal tooth number (sum)
6. Major row pharyngeal tooth number (sum)
7. Lateral stripe: 0 = No; 1 = Slight; 2 = Yes
8. Anal fin ray number (modal)
9. Body size (average maximum size in inches)
10. Terminal maxillary barbel: 0 = No; 1 = Yes
11. Flap-like barbel in maxillary groove: 0 = No; 1 = Potential; 2 = Yes
12. Third urodermal bone: 0 = No; 1 = Present or absent; 2 = Yes
13. Single posteroventral metapterygoid strut: 0 = Absent; 1 = Present

Table 2. Continued.

14. Fusion of urohyal arms: 0 = Yes; 1 = No

15. "Taster" feeding type: 0 = No; 1 = Mouth; 2 = Skin

16. "Sight" feeding type: 0 = No; 1 = Intermediate; 2 = Yes

17. Dorsal fin position: 0 = Before pelvics; 1 = Over pelvics; 2 = Slightly behind pelvics; 3 = Greatly behind pelvics

18. Peritoneum color: 0 = Light; 1 = Intermediate; 2 = Dark

19. Lateral line decurvature: 0 = Ratio 1.00 - 1.19; 1 = Ratio 1.20 - 1.39; 2 = Ratio 1.40 - 1.59

20. Scales below lateral line (modal)

21. Number of vertebrae (modal)

22. Lateral line scales (median)

23. Scales above lateral line (median)

24. Predorsal scales (modal)

25. Total scale radii (modal)

26. Infraorbital canal pores (modal)

27. Preoperculomandibular canal pores (modal)

Table 2. Continued.

28. Supraorbital canal pores (modal)

29. Supratemporal canal pores (modal)

30. Head length / Total length ratio (approximate percent)

31. Diploid chromosome number (missing data = 50.4)

Table 3. Data matrix for 18 species (numbers as in Table 1) and 31 characters (numbers as in Table 2) used to analyze the <u>Hybopsis</u> - <u>Semotilus</u> complex.

Character	Species																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0	1	0	0	0	0	0	0	2	2	2	0	2	2	2	0	0	1
2	0	0	0	0	0	0	0	0	1	2	2	2	2	2	1	0	0	0
3	1	1	0	1	1	1	2	2	1	4	4	0	3	2	1	1	1	1
4	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0
5	2	2	2	0	0	2	2	2	4	2	0	2	4	4	4	4	0	0
6	8	8	8	8	8	8	8	8	8	8	8	8	9	9	9	8	8	8
7	0	1	2	1	1	0	0	0	2	1	1	0	1	1	2	0	0	2
8	8	7	7	7	7	8	8	7	8	7	7	7	8	8	8	8	8	7
9	5	3	3	4	3	3	3	2	4	4	4	4	4	6	4	7	3	3
10	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0
11	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	1
12	2	2	2	2	2	2	2	1	2	1	1	2	0	0	2	2	2	2
13	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	1	1	0
14	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
15	1	1	1	0	0	2	2	0	0	0	0	0	0	0	0	2	2	0
16	0	0	0	2	2	0	0	2	2	2	2	2	2	2	2	0	1	2
17	0	1	1	0	0	1	0	1	1	1	1	1	3	2	2	0	1	0
18	0	0	0	2	2	0	0	0	0	1	2	0	0	0	0	0	0	0
19	0	0	0	1	1	0	0	1	2	1	1	1	1	1	1	2	0	0
20	4	3	4	5	5	5	7	5	8	5	6	7	6	5	9	5	4	6
21	39	38	36	40	39	39	43	36	42	40	41	38	42	43	39	45	36	41
22	40	36	38	44	44	44	44	36	66	42	40	54	57	47	70	53	36	47
23	5	5	5	6	6	6	7	6	12	7	7	8	9	8	12	8	6	7
24	14	13	16	17	16	17	17	17	26	16	15	31	30	22	43	25	14	20
25	19	14	19	12	8	14	10	11	19	33	41	21	33	33	23	15	7	13
26	15	15	15	14	14	15	15	19	17	16	16	17	19	19	18	17	17	14
27	13	13	13	9	9	10	10	16	11	10	10	11	14	14	13	14	13	7
28	9	9	9	8	8	9	9	9	9	9	9	10	13	13	12	8	9	9
29	4	4	4	4	4	5	5	10	7	6	6	6	8	8	7	7	5	7
30	19	21	22	19	21	22	18	19	21	23	23	20	23	22	21	18	19	20
31	x	x	x	x	x	x	x	x	50	x	x	48	52	52	50	x	x	x

x = missing data; replaced by mean (50.4).

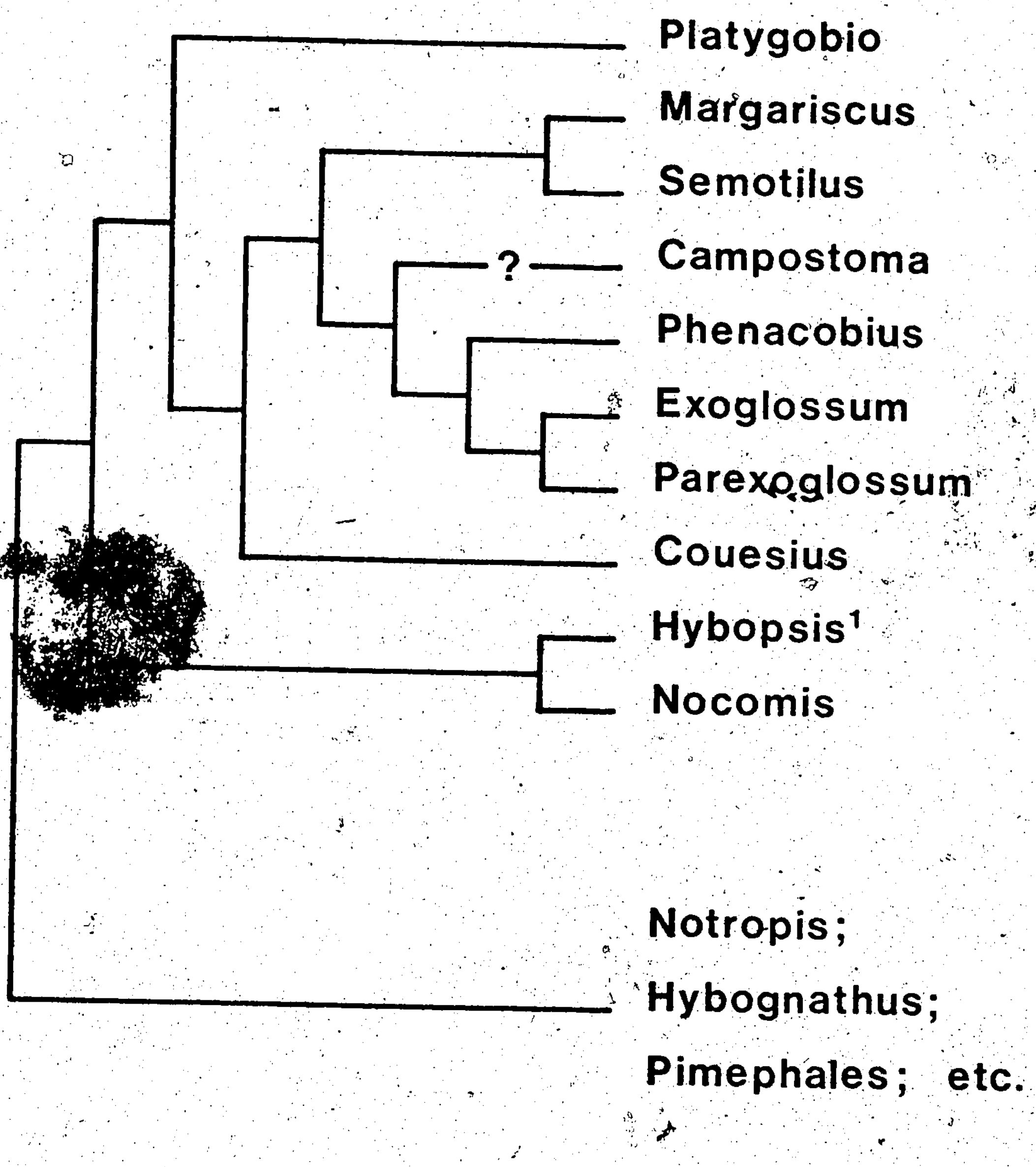


Figure 1. Relationships of Hybopsis, Semotilus, and related genera as proposed by Coad (After Coad, 1975:328; no similarity index given). Hybopsis = Hybopsis s.s., Erimystax, Macrhybopsis, Oregonichthys, and Extrarius.

Figure 2. Fossil record relevant to the origin of Cyprinidae in North America. Dot = oldest known occurrence. (Partially after Smith, 1962; Smith, 1963; Uyeno and Miller, 1963, 1965; Miller, 1965; Miller and Smith, 1967; Wilson, 1968; Coad, 1975; Casteel and Hutchison, 1973; Kimmel, 1975; and Smith, 1975).

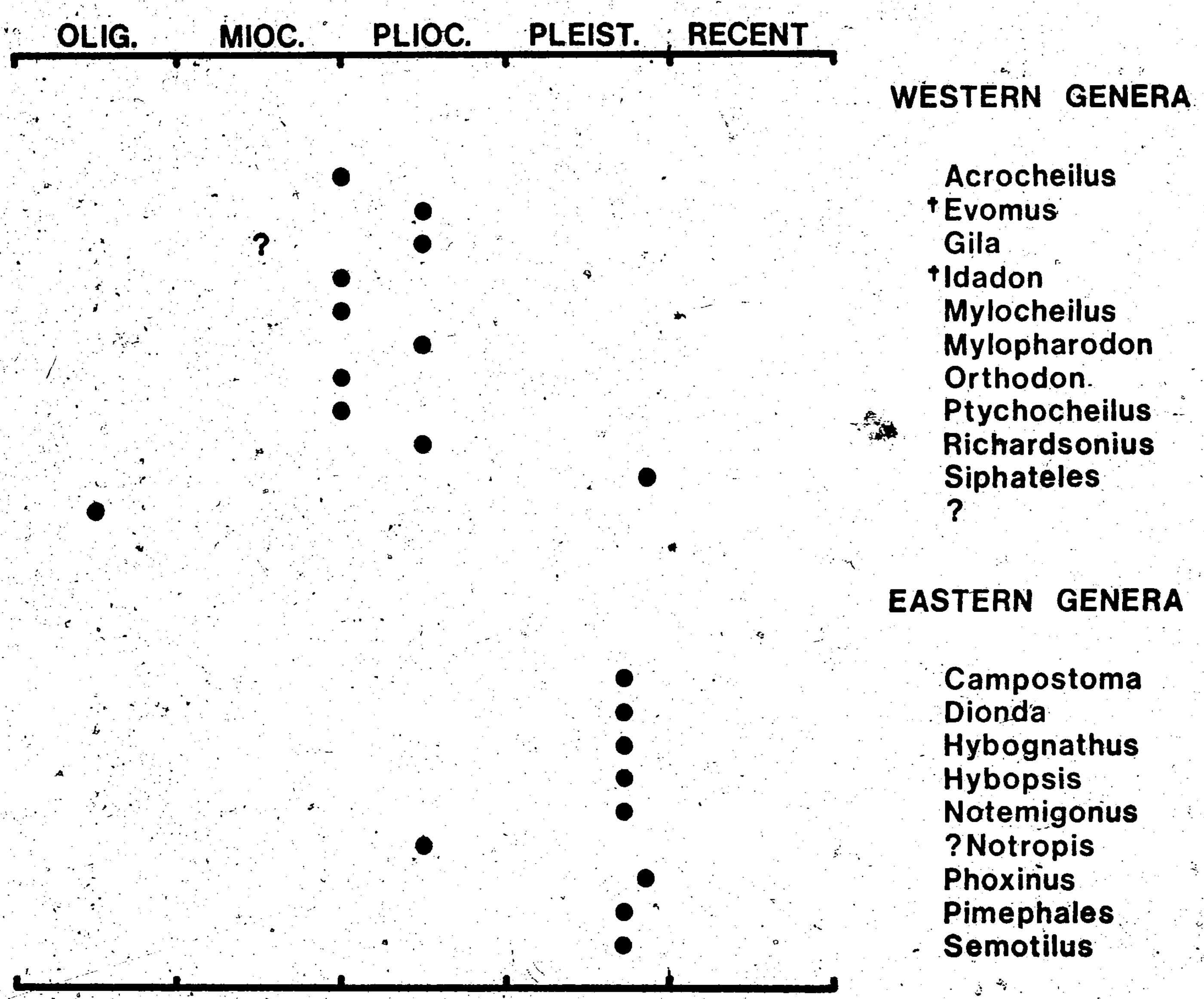

OLIG.
MIOC.
PLIOC.
PLEIST.
RECENT
WESTERN GENERA
Acrocheilus
†Evomus
Gila
†Idadon
Mylocheilus
Mylopharodon
Orthodon
Ptychocheilus
Richardsonius
Siphateles
?
?
EASTERN GENERA
Campostoma
Dionda
Hybognathus
Hybopsis
Notemigonus
?Notropis
Phoxinus
Pimephales
Semotilus

Figure 3. Principal co-ordinate ordination of *Hybopsis* - *Semotilus* complex on co-ordinate axes I, II, and III (32.5%, 15.7%, and 12.4% of variance, respectively). Species labels as in Table 1.

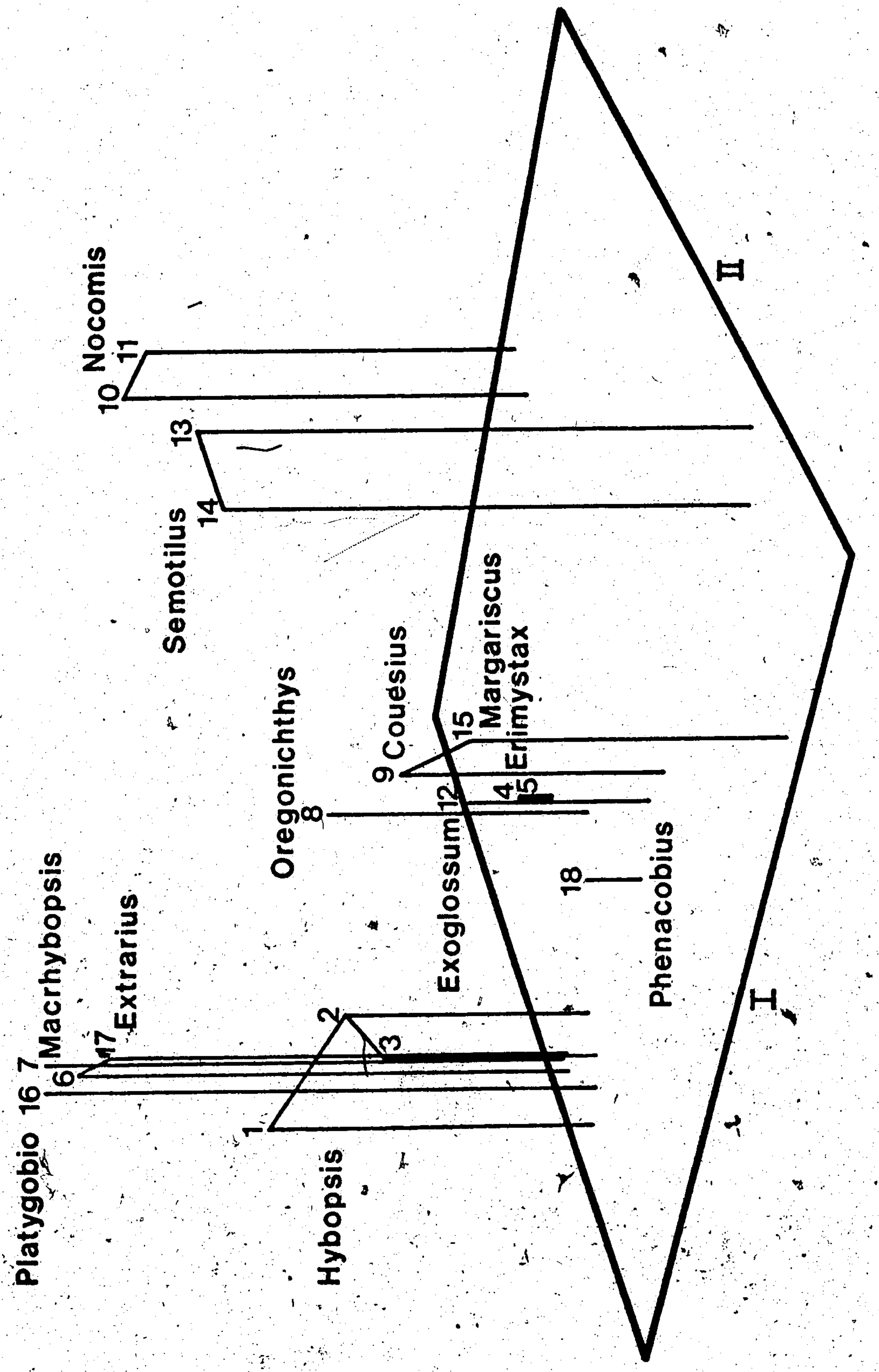

Platygobio
16
7
Macrhybopsis
6
17
Extrarius
1
2
3
Hybopsis
Oregonichthys
8
Exoglossum
12
9
Couesius
15
Margariscus
4
5
Erimystax
18
Phenacobius
Semotilus
14
13
10
11
Nocomis
I
II

Figure 4. Phenogram of <u>Hybopsis</u> - <u>Semotilus</u> complex. Shaded area represents approximate generic phenon level.

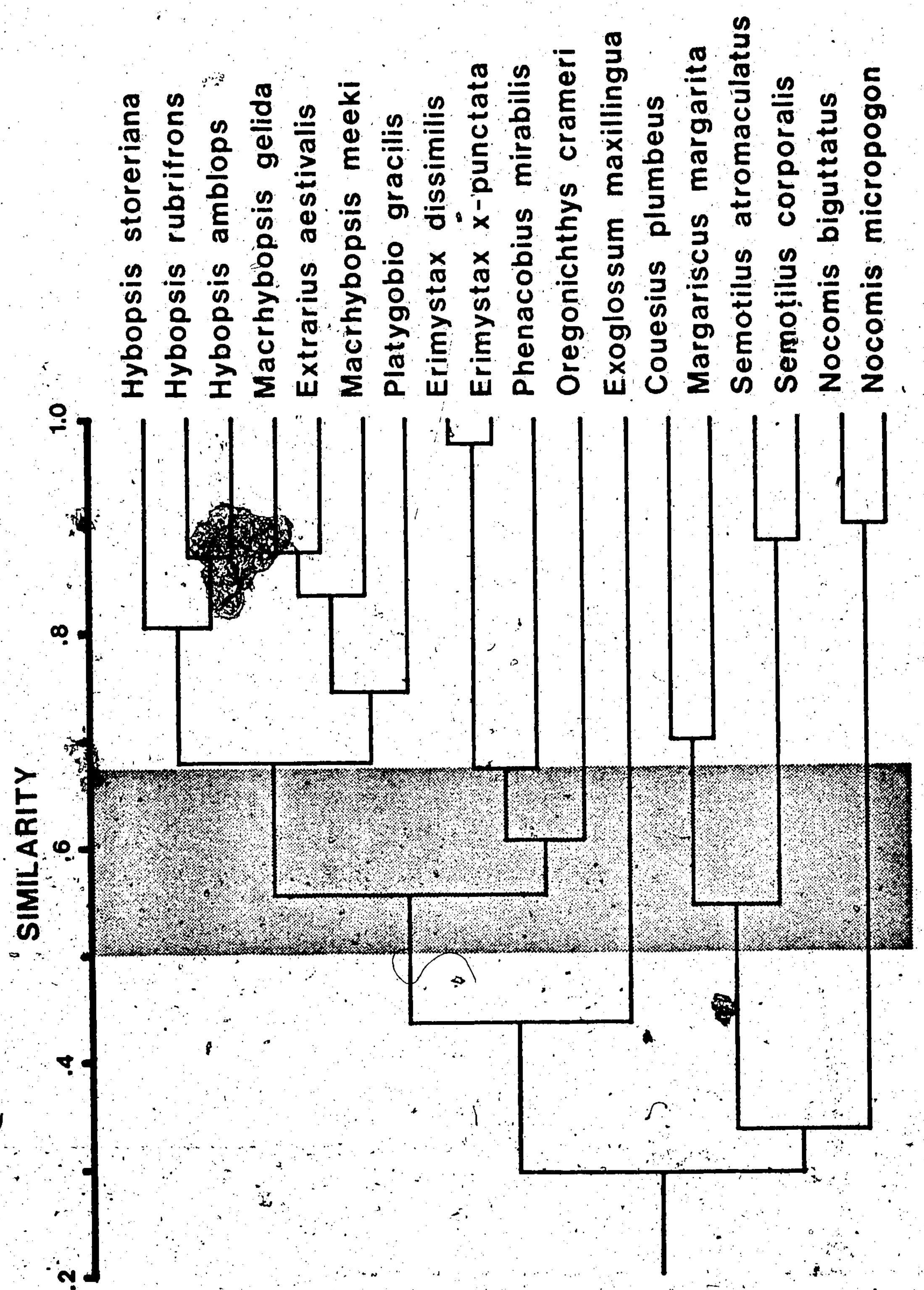

SIMILARITY
.2
.4
.6
.8
1.0
Hybopsis storeriana
Hybopsis rubrifrons
Hybopsis amblops
Macrhybopsis gelida
Extrarius aestivalis
Macrhybopsis meeki
Platygobio gracilis
Erimystax dissimilis
Erimystax x-punctata
Phenacobius mirabilis
Oregonichthys crameri
Exoglossum maxillingua
Couesius plumbeus
Margariscus margarita
Semotilus atromaculatus
Semotilus corporalis
Nocomis biguttatus
Nocomis micropogon

Figure 5. Cladogram of some genera within the _Hybopsis_ - _Semotilus_ complex. 1 = trend towards single metapterygoid strut; 2 = loss of nuptial coloration; 3 = reduction in major pharyngeal tooth row to 4-4; 4 = skin or mouth tasting; 5 = trend towards loss of lateral stripe; 6 = potential for nest building; 7 = trend towards dorsal fin origin behind pelvic fin origin; 8 = reduction in minor pharyngeal tooth row to one or zero; 9 = reduction in number of vertebrae to 40 or less; 10 = increase in scale size to 50 or less in lateral line; 11 = trend towards reduction in cephalic canal pore system, especially five or less supratemporal pores; 12 = reduction in lateral line decurvature ratio to less than 1.20; 13 = reduction in overall body size; 14 = increase in total scale radii to greater than 30; 15 = trend towards loss of third urodermal bone; 16 = large nuptial tubercles; 17 = mound or pit nest; 18 = development of breast tubercles in males; 19 = development of nuptial crest; 20 = increase in diploid chromosome number to 52; 21 = development of dark peritoneum; 22 = loss of terminal maxillary barbel. (Open = primitive; solid = uniquely derived; shaded = parallel derived).

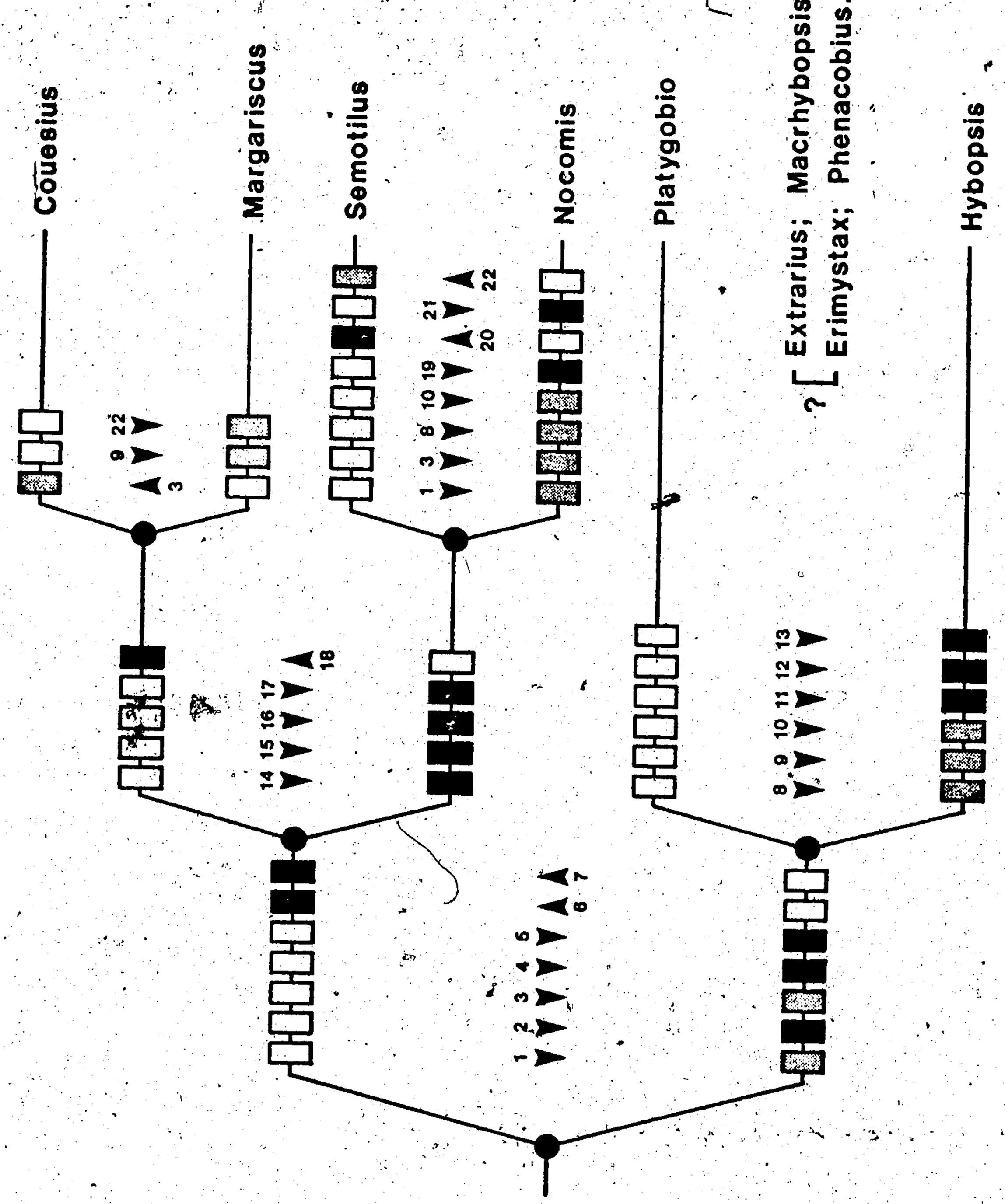
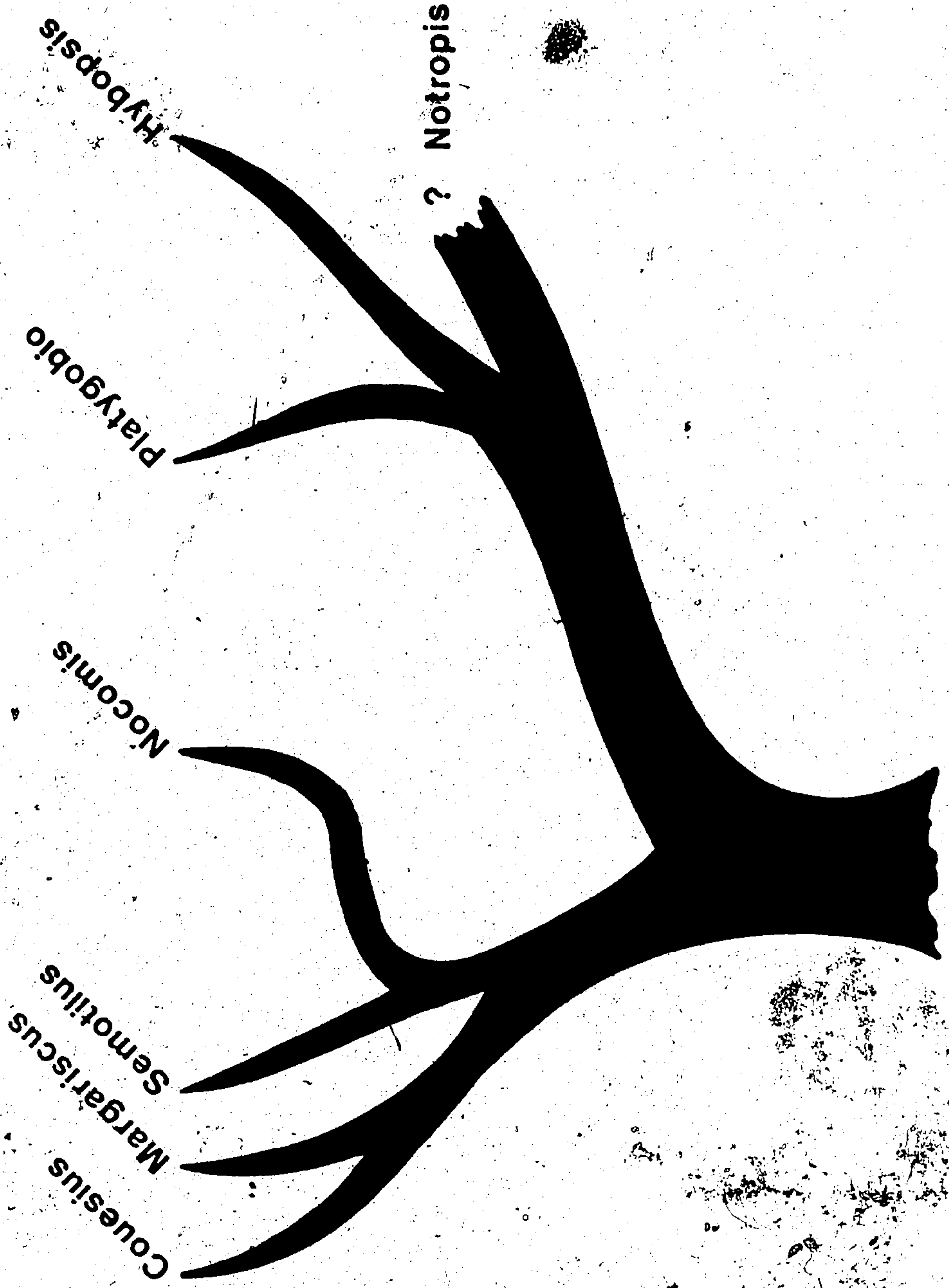

Couesius
Margariscus
Semotilus
Nocomis
Platygobio
? [Extrarius; Macrhybopsis; Erimystax; Phenacobius.
Hybopsis
9 22
3
1 3 8 10 19 21
20 22
14 15 16 17
18
8 9 10 11 12 13
1 2 3 4 5
6 7

Figure 6. Hypothesized phylogeny, derived from phenogram (Figure 4) and cladogram (Figure 5), of some genera within the *Hybopsis* - *Semotilus* complex.


Hybopsis
? Notropis
Platygobio
Nocomis
Semotilus
Margariscus
Couesius

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Article 4. NOTES ON POSSIBLE HYBRIDIZATION BETWEEN *COUESIUS PLUMBEUS* AND *SEMOTILUS MARGARITA*

While identifying specimens for the University of Alberta Museum of Zoology (UAMZ), it was noted that some of the specimens collected from the Sass River, Wood Buffalo National Park (60° 04'N; 113° 18'W), in 1977 by the Canadian Wildlife Service could be readily identified as either *Couesius plumbeus* or *Semotilus* (*Margariscus*) *margarita* while others, although appearing to be of one species or the other, were difficult to assign to either. Generally the two species, while similar in appearance, can be distinguished by several characters. For example, the barbel of *C. plumbeus* is moderately well developed and is situated near the terminal edge of the maxillary, while that of *S. margarita*, except when absent, is small, flap-like, located more anteriorly, and partially concealed in the groove above the maxillary. Trenchant differences occur in number of predorsal scales, ranging from about 25 to 27 in *C. plumbeus* and 38 to 48 in *S. margarita* (Coad, 1975). While some of the Sass River specimens possessed barbels typical of one species or the other, several possessed poorly developed, flap-like barbels near the terminal end of the maxillary. Additionally, although state of preservation and relatively small size (37-57 mm standard length, mean = 46.6) of the specimens made accurate scale counts difficult, predorsal scale counts appeared to bridge the two species.

Unfortunately, the range of variability in barbel position and development as well as in predorsal scale counts has not been well documented. Hubbs (1942) noted that a barbel may not be well developed on one or both sides of young C. plumbeus, while in S. margarita the barbel is sometimes absent on one or both sides (McPhail and Lindsey, 1970; Paetz and Nelson, 1970).

In an effort to identify these specimens the following nine morphometric characters were used to construct a discriminant function: standard length, predorsal distance, dorsal fin base length, caudal peduncle depth, interorbital distance, dorsal fin origin to terminal caudal vertebra distance, pelvic fin origin to terminal caudal vertebra distance, head length, and dorsal fin length. Characters chosen to distinguish the two species were either those that appeared to be of possible discriminating value or those used by McPhail and Lindsey (1970) and Hubbs (1942). Known parental types of approximately equal size to the 1977 Sass River material were selected from individuals judged to be representative of each species in previous Sass River collections [C. plumbeus, UAMZ 2153 (3); S. margarita, UAMZ 2165 (11)] and nearby Preble Creek [C. plumbeus, UAMZ 2152 (12); S. margarita, UAMZ 2163 (4)]. Forty-seven of the larger specimens from the 1977 Sass River collections (UAMZ 3905 and 3907) were considered as unknowns for classification by the discriminant analysis (BMD:07M; Dixon, 1973). Allometry and differences in mean length were not considered a problem since a narrow size range was involved and average standard lengths of the two known groups were not significantly different [F(1,28) = 0.34, p > 0.10]. Both sexes were included in the known groups and no sexual dimorphism was apparent in the characters involved in the analysis.

Position of the unknowns along the canonical axis (Figure 1) indicates that a majority of the 1977 Sass River specimens were probably _S. margarita_ and a few were _C. plumbeus_. However, an unexpectedly large number of specimens were intermediate to _C. plumbeus_ and _S. margarita_, which may indicate a hybrid origin for at least some of these individuals. Involvement of any species other than _C. plumbeus_ and _S. margarita_ seems unlikely since the only other cyprinids collected were _Phoxinus eos_, _Phoxinus neogaeus_, and _Pimephales promelas_. Presence of a barbel and a light peritoneum in the suspected hybrids makes these other species unlikely parental forms. Although _Notropis hudsonius_ has been reported from Sass River (Nelson and Paetz, 1972), none were present in the 1977 collections.

Hubbs (1942) noted no valid reports of hybridization between these two species. He considered Schultz's (1941) report of hybridization between _C. plumbeus dissimilis_ and _S. margarita nachtriebi_ to be erroneous and suggested that the impression hybridization had occurred was due to a failure to consider sexual dimorphism. As intergeneric cyprinid hybrids are relatively common (Hubbs, 1955), it seems unusual that this combination has not been previously reported (Schwartz, 1972), especially when one considers that *C. plumbeus* and *S. margarita* apparently share a close phylogenetic relationship (Jenkins and Lachner, 1971), are sympatric over a large portion of their respective ranges (Scott and Crossman, 1973), and have identical chromosome numbers (2n=50) (Legendre and Steven, 1969). However, the great morphological similarity between these two species may offer a partial explanation for the apparent failure to recognize hybridization, as a hybrid between two similar species may not be sufficiently distinct from one or both parentals to be recognized. This appears to be the situation with the 1977 Sass River material. A perfectly intermediate hybrid would be just beyond two standard deviations from either parental mean. It would be likely that a single hybrid individual would be recognized as only a slightly unusual *C. plumbeus* or *S. margarita*. It is only the unusually large number of nearly intermediate specimens that suggests hybridization has occurred.

The possibility of hybridization between *C. plumbeus* and *S. margarita* should be examined in greater detail. If hybridization between these two can be substantiated, the move to consider these species as congeners, as Raney (1969) and Sharpe (1970) have done, could have added validity.

ACKNOWLEDGMENTS

I wish to thank D.M. Wells for assistance in gathering data and preparing the manuscript, E. Kuyt of Canadian Wildlife Service for donating the 1977 collections, and W.E. Roberts for examining the specimens. I also thank J.S. Nelson for bringing the specimens to my attention.

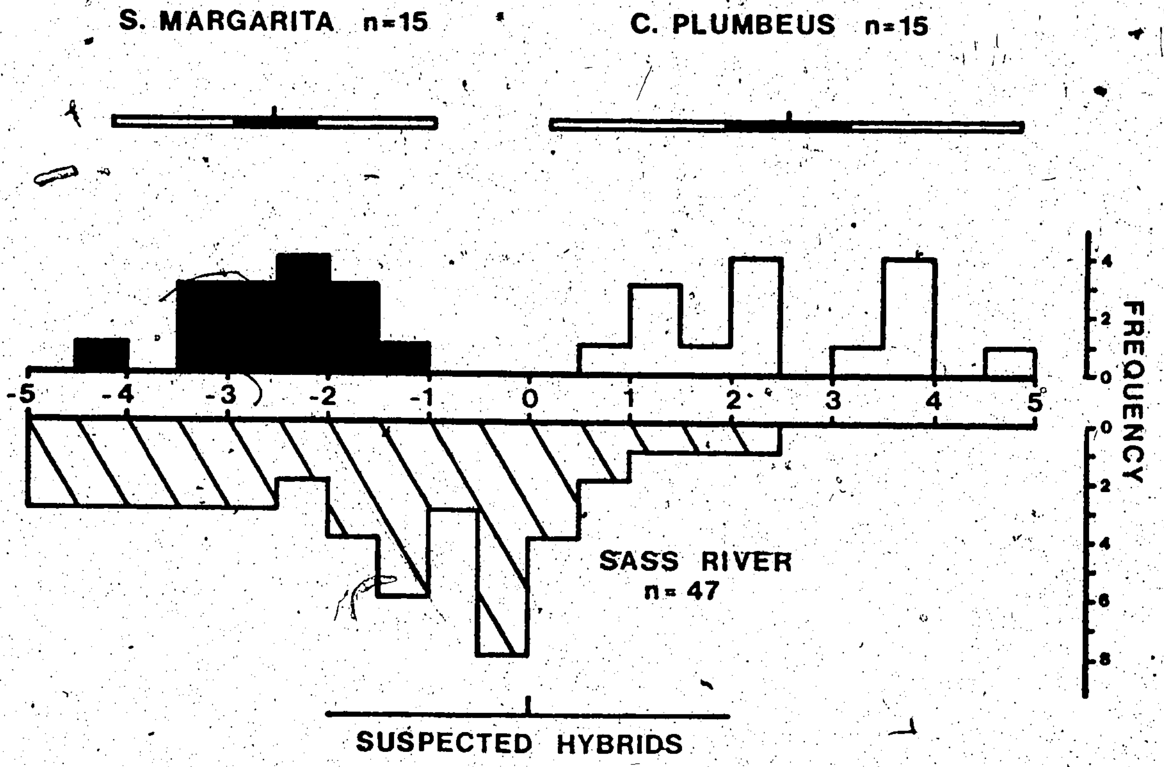

Figure 1. Position of known Couesius plumbeus (open) and Semotilus margarita (solid) from Sass River and Preble Creek and 1977 Sass River unknowns (barred) along canonical axis I. Mean, two standard errors, and two standard deviations are indicated for knowns. Expected mean and two standard deviations are indicated for suspected hybrids (unknowns).

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THESIS DISCUSSION

Aside from the specific conclusions reached in each article, this research, when considered as a whole, poses several questions and invites speculation along several lines. First, how does the intraspecific variability of Couesius plumbeus compare to that of Hybognathus hankinsoni? Second, what is the basis for the apparently similar pattern of morphological covariation between northeastern (Mississippi and Great Lakes basin) C. plumbeus and H. hankinsoni versus their southwestern (Missouri basin) counterparts? Third, can this study refine previous generalizations concerning the zoogeographic patterns of other North American freshwater fishes?

The relative degree of intraspecific variation within Couesius plumbeus and Hybognathus hankinsoni was assessed from square root transformed pair-wise generalized distances calculated from identical character sets. Average pair-wise generalized distance (D) and variance between populations of C. plumbeus (average D = 4.70; variance = 1.56; n = 666) (Figure 1) is significantly greater ($p < 0.05$) than that of between populations of H. hankinsoni (average D = 4.05; variance = 0.84; n = 231) (Figure 2). If rates of evolution in closely related organisms can be considered relatively constant over time, as suggested by several recent studies (Avise and Ayala, 1976; Gorman, Kim, and Rubinoff, 1976; Gorman and Kim; 1977; and others), then it might be expected that the average pair-wise intraspecific generalized distance between populations of C. plumbeus and H. hankinsoni may reflect their geologic age of origin. The greater the average generalized distance, the greater the period of divergence. This would seem to indicate that, while of relatively similar geologic age, C. plumbeus is an evolutionarily older species. This appears consistent with the postulated intergeneric relationships of C. plumbeus since H. hankinsoni appears closely related to Notropis, a derived group, through Dionda (Coad, 1975). However, this greater intraspecific variability within C. plumbeus may simply reflect its greater range and broader ecological tolerance, but then increased range and habitat diversity, in itself, may be a function of evolutionary time.

Generalizations concerning dispersal routes of fishes in northern North America may simultaneously explain the source of the similar trends in character variation within C. plumbeus and H. hankinsoni. Several species show a distribution pattern similar to that of the "plumbeus" form of Couesius plumbeus. These include Salvelinus namaycush, Coregonus hoyi, Coregonus johannae, Coregonus kiyi, Coregonus nigripinnis, Coregonus reighardi, Coregonus zenithicus, Coregonus clupeaformis, Prosopium coulteri, Prosopium cylindraceum, Phoxinus neogaeus, Catostomus catostomus, Pungitius pungitius, Cottus bairdi, Cottus cognatus, Cottus ricei, and Myoxocephalus quadricornis (see Scott and Crossman, 1973). The distribution of these species is characteristically throughout the Great Lakes, Labrador, Quebec, and northwestward through Ontario, but absent or rare from the upper Mississippi drainage system. McPhail (1963) and McPhail and Lindsey (1970) considered many of these species to be derived from the upper Mississippi refugium with subsequent extinction in this region brought about by postglacial climatic changes. However, an eastern lower Great Lakes refugium (of Underhill, 1957, or the eastern Ohio, upper Genesee River valley, and lower Hudson River valley region of Dadswell, 1974) better explains this pattern without postulating large scale extinctions. Since many of these species are associated with cold, deep, oligotrophic lakes, this may indicate evolution in a similar environment. The geographic proximity of the eastern lower Great Lakes refugium, as well as the upper Mississippi "Driftless Area", to the Pleistocence ice margin would be favorable for the creation of such lakes. Species evolving in this region might be expected to develop many of the characteristics listed by Hopkirk (1973) as lacustrine adaptations. These include numerous and fine gill rakers, a terminal to superior mouth, large eye diameter, increased intestine length, a narrow, compressed body, long fins, light color, and numerous, long gill filaments.

Species that show a distribution pattern similar to that of the "dissimilis" form of _C. plumbeus_ and the Missouri form of _H. hankinsoni_ include: _Hiodon alosoides_, *Hybopsis storeriana*, *Hybopsis gracilis*, *Hybopsis gelida*, *Hybopsis meeki*, *Notropis blennius*, *Hybognathus argyritis*, and *Ictiobus cyprinellus*. Their distribution generally includes the Missouri and middle Mississippi but with limited occurrence in the upper Mississippi and Great Lakes basin. This pattern appears associated with a Missouri, lower Mississippi, and "Preglacial Plains Stream" origin. These drainages were likely less intimately associated with the ice margin and of a more fluviatile nature. Species displaying this distribution pattern are generally associated with rivers, again possibly indicating evolution in a similar environment. Adaptations that might be expected under these conditions include: few, coarse gill rakers, inferior mouth, small eye diameter, a short intestine, deep body, short fins, dark color, and short, less numerous gill filaments.

These lacustrine versus fluviatile adaptations are precisely those evident between northeastern *Couesius plumbeus* and *Hybognathus hankinsoni* with respect to their more southwestern counterparts. Similar patterns of covariation might be expected in species that have distributions encompassing both of these patterns. Indeed, Metcalf (1966) has demonstrated this to be so for such species as *Semotilus atromaculatus*, *Notropis stramineus*, and *Catostomus commersoni*. Future work will most likely show similar patterns of variation in additional species.

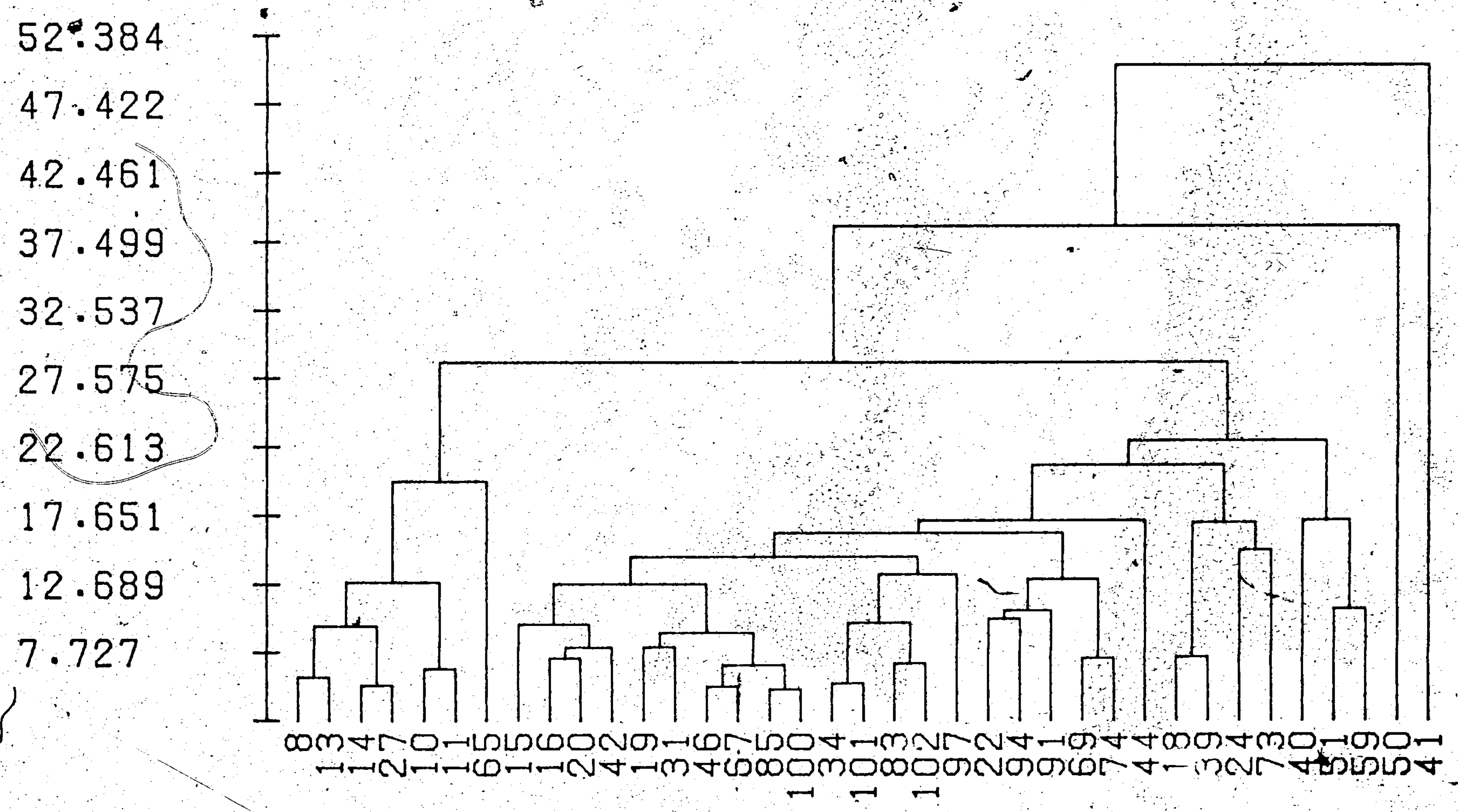

Figure 1. UPGMA cluster analysis for averaged female and male <u>Couesius plumbeus</u> interpopulation generalized distances (D²) based on 16 characters. Locality labels as in Article 2, Table 1.

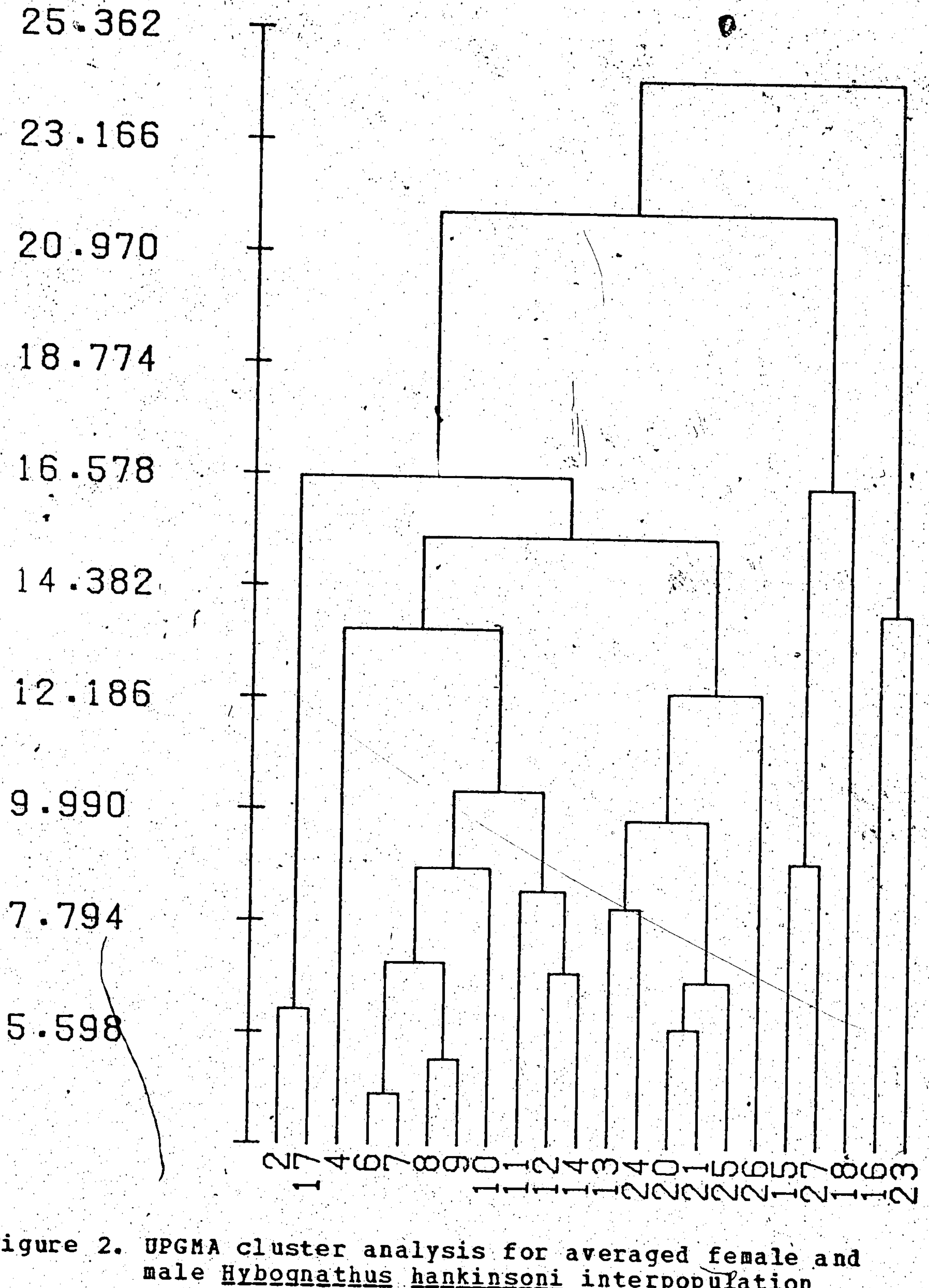

Figure 2. UPGMA cluster analysis for averaged female and male *Hybognathus hankinsoni* interpopulation generalized distances (D^2) based on 16 characters. Locality labels as in Article 1, Table 1.

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