

THE UNIVERSITY OF MANITOBA

The Systematics of Ciscoes (Coregonidae)
in Central Canada

by
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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY



WINNIPEG, MANITOBA

FALL, 1973

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A dissertation submitted to the Faculty of Graduate Studies of
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ABSTRACT

Coregonus artedii, C. prognathus, C. autumnalis and C. sardinella were the only species of ciscoes judged to be valid in collections from 81 localities in central Canada. Sympatric forms (morphological types characteristic of localities) of ciscoes, definitely found at 35 localities, were separated by mean square distance, discriminant analysis and gillraker counts; forms from all localities were grouped by factor analysis, mean square distance and information analysis. Gillraker counts, upper jaw length, mandible length, snout length, eye diameter and interorbital width were of most use in separating the species, but all 19 characters studied showed interspecific differences. Sexual dimorphism was not significant at the three localities where it was tested.

C. autumnalis and C. sardinella were found only in the Mackenzie R. where they were sympatric with C. artedii; there, C. autumnalis was distinguished from C. sardinella and C. artedii by an eye diameter of less than 4.0% fork length, and C. sardinella from C. artedii by an interorbital width of less than 4.7% fork length. There was no character or combination of characters that separated all C. prognathus from all C. artedii, but in central Canada all populations of C. prognathus had a mean gillraker count of 40.2 or less, and

C. artedii of 40.9 or more. Where C. prognathus was sympatric with C. artedii, all individuals were separable by gillraker counts. Two or more sympatric forms of C. artedii were found in 26 localities, but their differences were not consistent and were associated mainly with size differences. Differences between the gillraker counts of sympatric C. prognathus and C. artedii were not correlated to size differences, but differences between the gillraker counts of sympatric forms of C. artedii were correlated to size differences. Differences between populations of C. artedii were associated with environmental and size differences. The four species differed in the shape of their dentary, maxilla, supraethmoid and supralingual plates. A partial key to the ciscoes of central Canada is given, but a multivariate approach is more effective because of the problems of allometric growth and intraspecific variation.

Suggested new synonyms for C. artedii are C. hoyi (except from the Great Lakes and George L.), C. n. nigripinnis, C. nipigon, C. zenithicus from Attawapiskat L., C. athabascae, C. entomophagus, C. macrognathus, C. churchillensis and C. nueltinensis. Suggested new synonyms for C. prognathus are C. zenithicus (except from Attawaspiskat L.), C. cyanopterus, C. reighardi, C. hoyi from George L., C. artedii from Deer L. and some C. artedii from Lac Seul and Sandy L. It is suggested that C. alpenae, C. johanna and C. bartletti may be

be conspecific with C. prognathus, that C. hubbsi is conspecific with C. artedii, and that Great Lakes C. hoyi and C. kiyi are conspecific and may be conspecific with C. artedii.

From their morphology and distribution it was concluded that each species is monophyletic and survived the Wisconsin glaciation in one refugium; C. autumnalis and C. sardinella in the Bering refugium, and C. artedii and C. prognathus in the Mississippi refugium. The lack of morphological equivalence between sympatric forms of C. artedii suggests that they arose postglacially by either microgeographic or sympatric differentiation; probably they behave as elementary populations which do not interbreed at some localities but do interbreed at others. Intraspecific variation in coregonids suggests that the selective regime is more important than reproductive isolation in the differentiation of coregonids.

ACKNOWLEDGEMENTS

I wish to express my appreciation of the supervision, advice and stimulation of Dr. C. C. Lindsey, and the advice, discussion and final supervision of Dr. K. W. Stewart. Dr. R. H. Green suggested and patiently explained some statistical techniques, and Dr. K. Patalas suggested the use of some environmental variables. Thanks are due to Dr. W. B. Scott and Dr. E. J. Crossman of the Royal Ontario Museum and to Dr. D. E. McAllister of the National Museum of Canada for allowing me to examine museum specimens. The Manitoba Department of Mines, Resources and Environmental Management, Dr. F. M. Atton and the Saskatchewan Department of Natural Resources, Mr. M. J. Paetz and the Alberta Department of Lands and Forests, the Ontario Department of Lands and Forests, and numerous conservation and fish and wildlife officers provided great assistance. Many thanks to Bill Franzin, Erich Kliever, John Loch, Bob Manness, Tetsuya Narita, Pat Rakowski and Alex Tretiak for help in the field work, and to Mel Falk and A. H. Kooyman for providing specimens. Mr. W. Heck took the photographs and advised in the preparation of the figures. Finally, many thanks to my wife, Pauline, for support and help in all aspects of the work.

Financial support was provided by a University of

Manitoba Graduate Fellowship and a National Research Council Scholarship. Field work was financed by grants from the National Research Council and the Aquatic Biology Research Unit of the University of Manitoba to Dr. C. C. Lindsey.

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INTRODUCTION

The ciscoes, bloaters, chubs, lake herrings and tullibees are a group of sibling species placed, with the whitefish, in the genus Coregonus. Their taxonomy is complicated by phenotypic plasticity, which often results in there being greater differences between allopatric populations of the same species than between sympatric populations of different species. This was not recognised fully by early workers and led to the description of 39 species of ciscoes from North America, of which only twelve were recognised as valid by Bailey et al. (1970). A total of twelve species have been described from central Canada (defined as the Arctic and Hudson Bay drainages of mainland Canada as shown in Fig. 1); five of these were considered valid by Bailey et al. (1970).

To date cisco taxonomy in North America has been based on Koelz's (1929, 1931) work in the Great Lakes basin and northeastern U.S.A., and Dymond's (1943) work on the ciscoes of northwestern Canada. Koelz's (1929) keys to the ciscoes of the Great Lakes and L. Nipigon, Hubbs and Lagler's (1964) key to the ciscoes of the Great Lakes region, and the key to Manitoban ciscoes (Hinks 1957) are not satisfactory within the geographical areas for which they were intended, and are even less satisfactory outside of these areas, chiefly because of the phenotypic plasticity of the ciscoes.

In the last decade several new techniques of analysis have been introduced into taxonomy (Sokal and Sneath 1963). Some of these techniques are used, together with some traditional techniques, to elucidate the systematics of ciscoes in central Canada and their relationship to the ciscoes of the Great Lakes basin and to the arctic ciscoes (the ciscoes of the Arctic Ocean, Bering Sea, Yukon R. system, and the anadromous ciscoes of the Mackenzie R.). The study is based on collections made by the author from 42 new localities, and on examination of new or old material from another 56 localities.

THE SEPARATION OF SYMPATRIC FORMS OF CISCOES
FROM CENTRAL CANADA

Materials

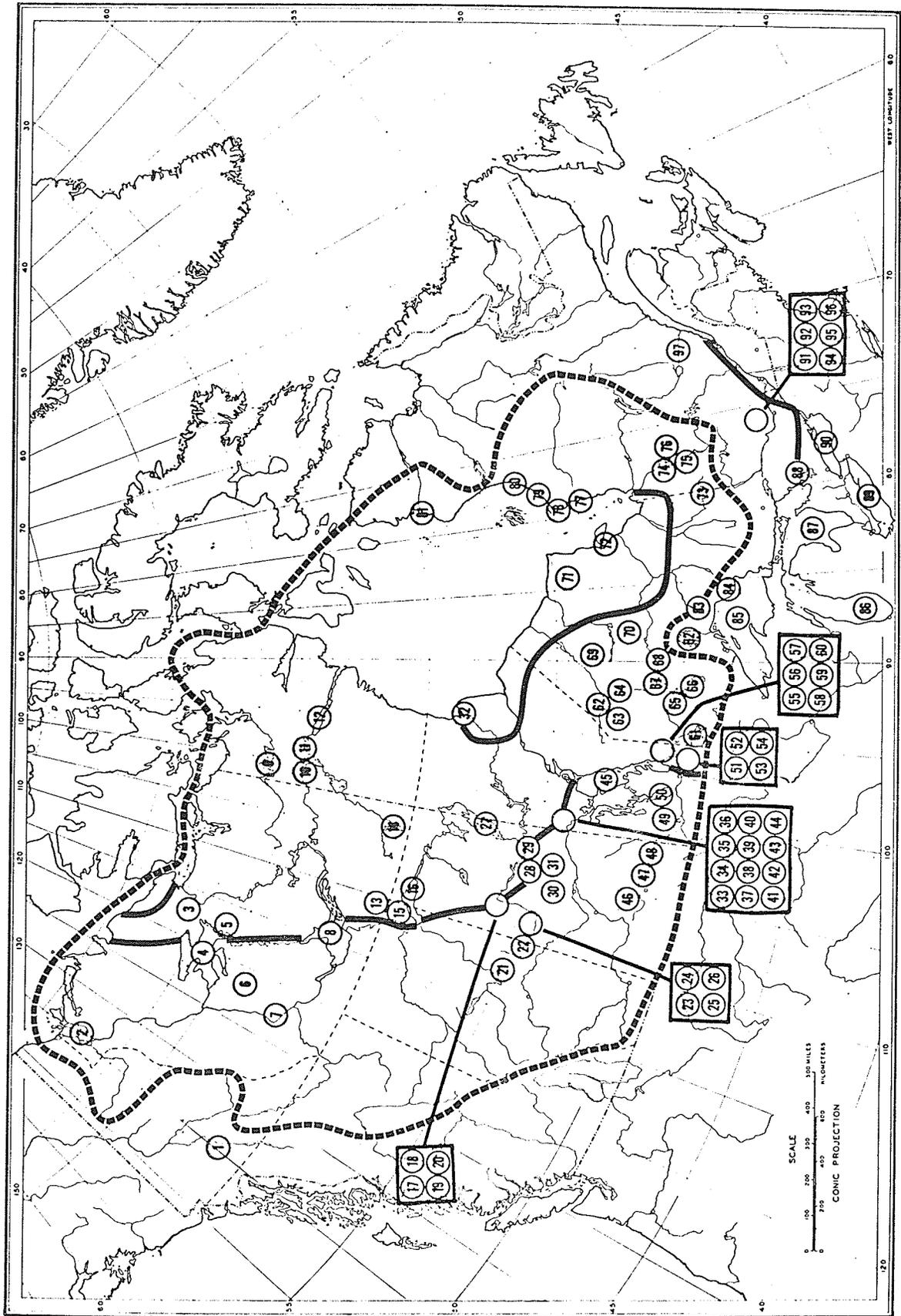
A total of 1493 ciscoes from 81 localities in central Canada (Fig. 1 and Appendix 1) were examined. The localities in Fig. 1, including the localities of extra-limital material used in later analyses, were numbered from the north-west to the south-east and the names corresponding to the numbers are given in the accompanying key. The sequence of localities in all tables is alphabetic and the corresponding location numbers are given in Table II and Appendix 1. Sample sizes are also given in Table II and Appendix 1. 1355 specimens from 49 localities, mainly collected from the Prairie provinces and northwestern Ontario by the author between 1967 and 1970, were examined at the University of Manitoba; these fish were preserved in formalin and then transferred to isopropyl alcohol. An additional 138 preserved specimens from 38 localities were examined at the Royal Ontario Museum or the National Museum of Canada. Fish from Fort Simpson and the Mackenzie Delta were combined into one sample for analysis, referred to as the Mackenzie R. sample.

Morphological Characters

18 or 19 morphological characters were determined

Fig. 1. Map showing the localities from which ciscoes were examined.

Key: 1-Lac Laberge, 2-Mackenzie Delta, 3-Dismal L., 4-Great Bear L., 5-Spark Plug L., 6-Keller L., 7-Fort Simpson, 8-Great Slave L., 9-Pelly (or Garry) L., 10-Beverly L., 11-Aberdeen R., 12-Baker L., 13-Tazin R., 14-Wholdaia L., 15-Barrow L., 16-L. Athabasca, 17-Big Peter Pond, 18-Churchill L., 19-Little Peter Pond, 20-Ile-a-la-Crosse, 21-Lac la Biche, 22-Cold L., 23-Lac des Iles, 24-Flotten L., 25-Greig L., 26-Waterhen L., 27-Reindeer L., 28-Bigstone L., 29-Lac la Ronge, 30-Waskesiu L., 31-Montreal L., 32-Churchill, 33-Manistikwan (Big Island) L., 34-Neso L., 35-Big Twin L., 36-Little Twin L., 37-Payuk L., 38-Little Athapapuskow, 39-Mink Narrows, 40-Big Athapapuskow, 41-First Cranberry L., 42-Second Cranberry L., 43-Rocky L., 44-Clearwater L., 45-L. Winnipeg, 46-Last Mountain L., 47-Pasqua L., 48-Echo L., 49-Fishing L., 50-L. Manitoba, 51-Big Whiteshell L., 52-George L., 53-Falcon L., 54-West Hawk L., 55-Wanipigow L., 56-Quesnell (Caribou) L., 57-Beresford L., 58-Pine Falls, 59-Bird (Oiseau) L., 60-Davidson L., 61-L. of the Woods, 62-Sandy L., 63-Deer L., 64-Nikip L., 65-Lac Seul, 66-Minnitaki L., 67-L. St. Joseph, 68-Osnaburgh L., 69-Big Trout L., 70-Attawapiskat L., 71-Hawley L., 72-James Bay, 73-L. Abitibi, 74-L. Matagami, 75-Waswanipi L., 76-L. Olga, 77-Fort George, 78-Cape Jones, 79-Great Whale R., 80-Richmond Gulf, 81-Povungnituk, 82-L. Nipigon, 83-Long L., 84-Dunc L., 85-L. Superior, 86-L. Michigan, 87-L. Huron, 88-Baby L., 89-L. Erie, 90-L. Ontario, 91-Lac du Loups, 92-Lac Heney, 93-L. Simon, 94-Wilson's L., 95-Meach L., 96-Little Whitefish L., 97-Saguenay Fjord. Location unknown-Kapsawi R., N.W.T. Black and white line encloses area defined as central Canada. Solid line shows limits of the Precambrian Shield.



for each fish, on the left side whenever possible. The twelve external measurements and two angles are shown in Fig. 2; fork length and profile were measured on a measuring board graduated to lmm., and the other measurements were made with dial callipers graduated to 0.05mm. Angles were measured by placing the fish on a board, marked in degrees. The following counts were made: lateral line scales (all the pored scales; if scales were missing, scale pockets were counted); gillrakers of the first gill arch (counted under a binocular microscope and including all bony rudiments; counts of the upper and lower limbs were recorded separately; a gillraker straddling the angle of the arch was included in the upper count). Gillraker length (distance from the tip to base on the ventral side of the second raker from the angle on the lower limb of the first gill arch) was also measured.

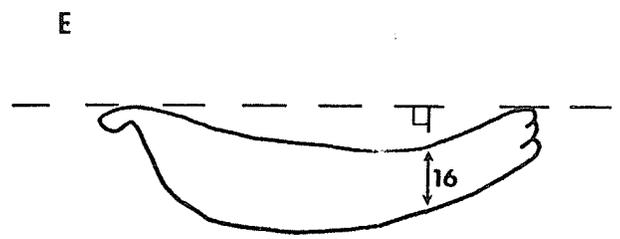
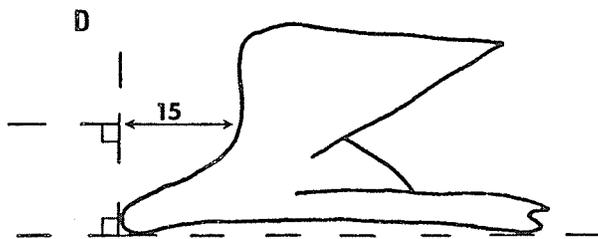
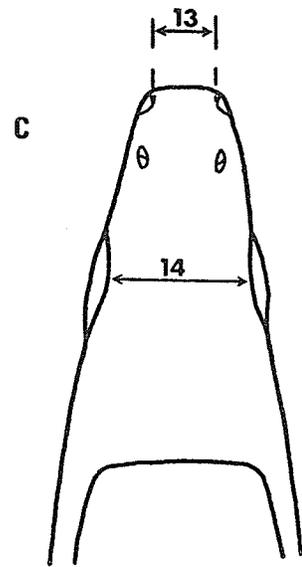
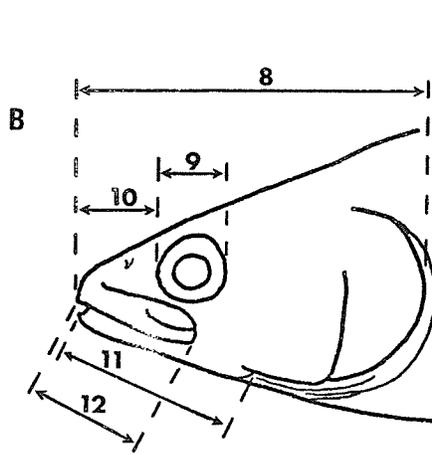
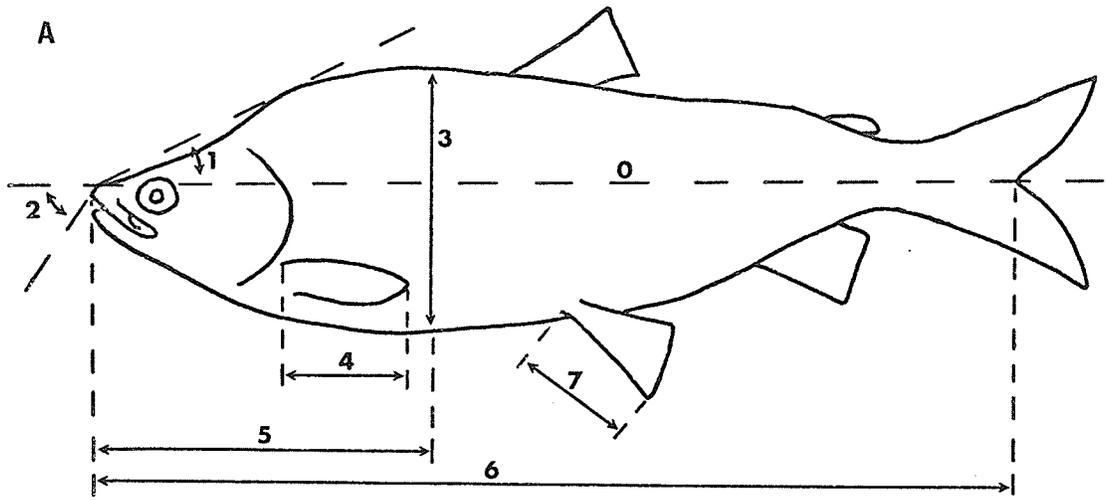
Analysis

Gillraker counts, appearance, and a numerical taxonomic method were used to detect sympatric forms (morphological types characteristic of a locality) of ciscoes in each lake, and to separate the forms if more than one form was present. The samples from each lake may not have included every form present in that lake, or, if only a few individuals of a form were samples, that form may have escaped detection.

Numerical Taxonomy. - The following process was

Fig. 2. Diagrams showing external measurements and angles, and measurements made on the dentary and maxilla. Measurements follow Hubbs and Lagler (1964) except where stated.

Key. A: 0-horizontal axis (line from the fork of the caudal fin to the premaxillae-ethmoid joint), 1-profile angle (the greatest angle between the horizontal axis and the nuchal hump; not measured for all localities), 2-premaxilla angle (angle between the horizontal axis and the premaxillae), 3-body depth, 4-pectoral length, 5-profile (anterior tip of snout to greatest body depth), 6-fork length, 7-pelvic length. B: 8-head length (excluding opercular membrane), 9-eye diameter (greatest horizontal distance across the cornea), 10-snout length, 11-mandible length, 12-upper jaw length. C: 13-premaxillae width (width of snout between the two premaxilla-maxilla joints, 14-interorbital width (least bony width). D: 15-dentary (maximum distance from the most anterior point to the anterior edge of the coronoid plate). E: 16-maxilla (minimum vertical height at the junction of the anterior and posterior portions of the distal plate).



repeated for 48 localities where the sample size was greater than four. The data of measurements, counts and angles were transformed to \log_{10} . The effect of overall size differences was removed from the measurements by calculating the regression line for each measurement against fork length, and then using the deviation of each cisco's measurements from the corresponding regression line. A matrix of mean square distance coefficients (Sokal and Sneath 1963) was calculated after the deviations and other characters had been standardised. Separate gillraker counts for the upper and lower limbs were included; the total number of gillrakers and fork length were omitted. This matrix showed the similarity of each cisco to the other ciscoes from the same locality. Each cisco was grouped with the ciscoes to which it was most similar. If this method showed that there was more than one form of cisco, the ciscoes were arranged in their respective forms (see Appendix 2). If there were more than five individuals in each sympatric form, discriminant analysis (Cooley and Lohnes 1962; Seal 1964) was used on the same standardised data that were used in the calculation of mean square distance coefficients, except that fork length was included. Discriminant scores showed whether any ciscoes had been grouped wrongly by mean square distance; if ciscoes had been grouped wrongly, they were regrouped by their discriminant scores and discriminant analysis was repeated. Discriminant coefficients showed which of the standardised variables were

of use in the separation of sympatric forms. Chi-square values indicated the degree of morphological difference between sympatric forms. No statistical significance was placed on these chi-square values since the same data were used in discriminant analysis and to separate the sympatric forms, and discriminant scores were used to regroup ciscoes. In the tests for sexual dimorphism and intra-lake variation, statistical significance was placed on the results of discriminant analysis since separation of the groups was by data not included in the analysis.

The use of deviations to negate size differences in the measurements and their subsequent use in numerical taxonomy requires that sympatric forms of ciscoes have similar size ranges, and that the regression lines for each form are parallel.

Further details of the numerical taxonomic method are given in Appendix 4. All these calculations and all subsequent calculations were carried out on the University of Manitoba IBM 360-65 computer, using programmes available at the computer centre or written by the author. The discriminant analysis programme was modified from Lee (MS 1971).

Results

Numerical Taxonomy

Amongst the 48 localities with sample size over four, examination of the matrices of mean square distance coefficients suggested that there were three sympatric forms of ciscoes at six localities, two forms at 26 localities, and one form at 16 localities.

Amongst the 32 localities thus indicated as having more than one form of cisco, discriminant analysis showed considerable morphological difference among the three sympatric forms in the same six localities, and among the two sympatric forms in 18 lakes (chi-square values of 22.9 or larger; see Table I). The two sympatric forms in Second Cranberry L. differed very little in their morphology (chi-square = 5.6) and it was concluded that there was insufficient evidence from mean square distance and discriminant analysis to warrant the separation of these ciscoes into two distinct sympatric forms. Discriminant analysis was not used on the sympatric forms in seven lakes (Attawapiskat, Falcon, First Cranberry, Flotten, Montreal, Sandy, West Hawk) since one or both forms contained less than five ciscoes.

Of the 24 localities thus shown to have morphologically different forms, discriminant scores completely separated the two or three forms at 20 localities. The scores never completely separated the two sympatric forms in Cold L., Echo L., and Last Mountain L.; the scores and coefficients

were not calculated for Big Whiteshell L. The discriminant scores showed that an average of 11.1% of the ciscoes had been grouped wrongly by the mean square distance coefficients. At the 20 localities where there was a complete separation of the forms, nine per cent had been grouped wrongly, compared to 22.5% in the three lakes where separation was not complete.

Table I gives the results of the discriminant analyses, the discriminant coefficients and the mean score for each sympatric form (lower, medium and higher refer to gillraker counts - see Table II and below) for the 24 localities where morphologically different forms were found.

The discriminant coefficients show which of the standardised variables were of most use in separating sympatric forms at each locality. The coefficients for each variable, except profile angle, were squared and summed over all the discriminant functions; the resultant sums of squares for the variables were normalised. This showed how much of the total variability between the morphologically different sympatric forms at the 23 localities (coefficients were not calculated for Big Whiteshell L.) was accounted for by each variable. Gillraker counts were the only characters that completely separated any sympatric forms.

Gillraker Counts

Since gillraker counts within a population are largely

TABLE I

The results of discriminant analysis used to separate sympatric pairs (or trios) of forms of ciscoes. Coefficients greater than 0.30 are underlined.

Locality	Chi-square	Discriminant coefficients for each variable														Mean discriminant scores for each form						
		Fork 1.	Pectoral 1.	Body d.	Pelvic 1.	Head 1.	Profile	Eye diam.	Premaxilla ang.	Snout 1.	Lateral line	Interorbital w.	Upper rakers	Upper jaw 1.	Lower rakers	Mandible 1.	Profile ang.	Premaxilla w.	Gillraker 1.	Lower	Med	Higher
L. Athabasca	111.0	.22	.12	.04	-.23	.16	.05	.15	-.08	.04	.04	-.15	.11	-.41	.72	.21	.06	.13	-.93	.65		
Big Athapapuskow	199.3	.35	-.12	.08	.43	.07	-.14	-.01	-.15	.32	-.13	.27	.12	-.34	.42	-.05	-.21	.05	-.86	.39		
Big Peter Pond	62.9	.57	-.23	.03	.20	.35	-.10	.31	.18	-.17	.19	-.19	.14	-.29	.33	-.00	-.09	-.03	.00	-.16	.21	
Big Whiteshell L.	93.9	.52	-.03	.05	.15	-.23	-.19	.22	.23	.24	-.23	-.54	.15	.01	.19	.02	-.06	-.15	-.16	-.22	.26	
Bird L.	41.4	-.65	.28	-.03	-.05	-.27	.28	.05	-.00	.45	-.04	.21	.19	.15	-.13	-.15	-.02	-.04	-.44	.37		
Churchill L.	59.0	-.19	.25	-.13	.18	-.38	-.17	.00	.04	-.02	-.16	.60	.23	.18	.06	-.19	-.09	-.32	-.03	-.29	.26	

(cont.)

TABLE I (cont'd)

Discriminant coefficients for each variable

Locality	Chi-square	Discriminant coefficients for each variable														Mean discriminant scores for each form				
		Fork 1.	Pectoral 1.	Body d.	Pelvic 1.	Head 1.	Profile	Eye diam.	Premaxilla ang.	Snout 1.	Lateral line	Interorbital w.	Upper rakers	Upper jaw 1.	Lower rakers	Mandible 1.	Profile ang.	Premaxilla w.	Gillraker 1.	Lower Med. Higher
Cold L.	63.2	<u>-.36</u>	<u>.54</u>	<u>-.13</u>	<u>-.23</u>	<u>-.40</u>	<u>-.25</u>	<u>-.04</u>	<u>.06</u>	<u>.37</u>	<u>.12</u>	<u>.19</u>	<u>.01</u>	<u>.20</u>	<u>.12</u>	<u>-.07</u>	<u>-.18</u>	<u>-.06</u>	<u>-.19</u>	<u>.19</u>
Echo L.	33.3	<u>.59</u>	<u>.18</u>	<u>.05</u>	<u>-.63</u>	<u>.13</u>	<u>-.24</u>	<u>-.14</u>	<u>-.03</u>	<u>-.11</u>	<u>-.07</u>	<u>-.06</u>	<u>.04</u>	<u>.25</u>	<u>-.04</u>	<u>-.10</u>	<u>-.09</u>	<u>-.07</u>	<u>.12</u>	<u>-.53</u>
Lac des Iles	35.1	<u>.26</u>	<u>-.46</u>	<u>-.07</u>	<u>-.14</u>	<u>.22</u>	<u>.54</u>	<u>.27</u>	<u>-.15</u>	<u>.03</u>	<u>-.10</u>	<u>-.01</u>	<u>.15</u>	<u>-.25</u>	<u>-.16</u>	<u>-.37</u>	<u>.06</u>	<u>-.08</u>	<u>-1.61</u>	<u>.80</u>
Lac la Biche	78.0	<u>-.72</u>	<u>.24</u>	<u>-.01</u>	<u>.51</u>	<u>.03</u>	<u>-.06</u>	<u>.03</u>	<u>-.02</u>	<u>.13</u>	<u>.14</u>	<u>.05</u>	<u>.18</u>	<u>-.10</u>	<u>.15</u>	<u>-.01</u>	<u>.23</u>	<u>-.09</u>	<u>-.60</u>	<u>.54</u>
Lac Seul	131.2	<u>.16</u>	<u>-.07</u>	<u>.00</u>	<u>.02</u>	<u>.40</u>	<u>-.16</u>	<u>-.12</u>	<u>.11</u>	<u>-.22</u>	<u>-.04</u>	<u>.18</u>	<u>.35</u>	<u>-.19</u>	<u>.70</u>	<u>-.14</u>	<u>-.04</u>	<u>.03</u>	<u>-.34</u>	<u>.60</u>
Lake of the Woods	80.2	<u>-.15</u>	<u>.19</u>	<u>.06</u>	<u>.07</u>	<u>-.33</u>	<u>.15</u>	<u>-.27</u>	<u>-.12</u>	<u>-.07</u>	<u>-.02</u>	<u>.41</u>	<u>.08</u>	<u>-.32</u>	<u>.54</u>	<u>-.24</u>	<u>-.01</u>	<u>.29</u>	<u>-.88</u>	<u>.99</u>
Last Mountain L.	50.3	<u>-.84</u>	<u>.24</u>	<u>.03</u>	<u>.14</u>	<u>-.05</u>	<u>.33</u>	<u>-.04</u>	<u>.00</u>	<u>.03</u>	<u>.02</u>	<u>-.08</u>	<u>.06</u>	<u>.05</u>	<u>.00</u>	<u>-.14</u>	<u>.13</u>	<u>.07</u>	<u>-.20</u>	<u>.21</u>
Little Atha- papuskow	156.8	<u>-.31</u>	<u>.60</u>	<u>.08</u>	<u>-.28</u>	<u>-.33</u>	<u>.03</u>	<u>.07</u>	<u>-.01</u>	<u>-.18</u>	<u>.03</u>	<u>.21</u>	<u>.20</u>	<u>-.06</u>	<u>.34</u>	<u>.14</u>	<u>-.00</u>	<u>.30</u>	<u>-1.20</u>	<u>.16</u>
Little Peter Pond	89.2	<u>.28</u>	<u>-.29</u>	<u>-.02</u>	<u>-.44</u>	<u>.23</u>	<u>-.08</u>	<u>-.33</u>	<u>-.21</u>	<u>-.45</u>	<u>-.16</u>	<u>-.01</u>	<u>-.05</u>	<u>.06</u>	<u>.08</u>	<u>.10</u>	<u>.02</u>	<u>-.03</u>	<u>426.5</u>	<u>426.5</u>

(cont.)

TABLE I (cont'd)

Locality	Chi-square	Discriminant coefficients for each variable														Mean discriminant scores for each form					
		Fore L.	Pectoral L.	Body d.	Pelvic L.	Head L.	Profile	Eye diam.	Premaxilla ang.	Snout L.	Lateral line	Interorbital w.	Upper rakers	Upper jaw L.	Lower rakers	Mangle L.	Profile ang.	Premaxillae w.	Gillraker L.	Lower Med	Higher
Mackenzie R.	107.4	<u>-.53</u>	<u>-.02</u>	<u>.25</u>	<u>.59</u>	<u>-.12</u>	<u>-.11</u>	<u>.22</u>	<u>-.23</u>	<u>-.18</u>	<u>-.12</u>	<u>-.02</u>	<u>-.06</u>	<u>.07</u>	<u>.25</u>	<u>-.19</u>	<u>.03</u>	<u>-.19</u>	<u>-1.87</u>	<u>.17</u>	<u>1.32</u>
Mink Narrows	42.1	<u>.67</u>	<u>-.03</u>	<u>-.33</u>	<u>.35</u>	<u>.07</u>	<u>-.10</u>	<u>.17</u>	<u>-.07</u>	<u>-.12</u>	<u>.27</u>	<u>-.16</u>	<u>.04</u>	<u>-.20</u>	<u>-.25</u>	<u>-.16</u>	<u>.04</u>	<u>-.18</u>	<u>.24</u>	<u>-.54</u>	<u>.34</u>
Minnitaki L.	51.4	<u>.18</u>	<u>-.21</u>	<u>-.06</u>	<u>-.53</u>	<u>.19</u>	<u>-.03</u>	<u>-.13</u>	<u>.47</u>	<u>.10</u>	<u>-.16</u>	<u>.38</u>	<u>.47</u>	<u>-.05</u>	<u>.36</u>	<u>.14</u>	<u>.12</u>	<u>.13</u>	<u>-1.26</u>	<u>.51</u>	
Neso L.	49.0	<u>.52</u>	<u>.09</u>	<u>.18</u>	<u>.06</u>	<u>-.27</u>	<u>-.27</u>	<u>.10</u>	<u>-.04</u>	<u>.11</u>	<u>-.05</u>	<u>-.29</u>	<u>.01</u>	<u>.20</u>	<u>.07</u>	<u>-.27</u>	<u>-.37</u>	<u>.42</u>	<u>-.38</u>	<u>.28</u>	
Quesnell L.	34.2	<u>.32</u>	<u>-.44</u>	<u>.01</u>	<u>.14</u>	<u>.01</u>	<u>.40</u>	<u>.04</u>	<u>-.04</u>	<u>-.24</u>	<u>.07</u>	<u>-.11</u>	<u>.01</u>	<u>-.52</u>	<u>.01</u>	<u>.32</u>	<u>.05</u>	<u>.03</u>	<u>-.55</u>	<u>.34</u>	
Rocky L.	31.5	<u>.03</u>	<u>.12</u>	<u>-.15</u>	<u>.40</u>	<u>-.39</u>	<u>-.21</u>	<u>.09</u>	<u>.09</u>	<u>.63</u>	<u>-.02</u>	<u>.02</u>	<u>.18</u>	<u>-.04</u>	<u>.07</u>	<u>-.34</u>	<u>.00</u>	<u>-.20</u>	<u>-.41</u>	<u>.52</u>	
Waskesiu L.	45.4	<u>-.71</u>	<u>-.07</u>	<u>.08</u>	<u>.50</u>	<u>.09</u>	<u>.24</u>	<u>.09</u>	<u>.04</u>	<u>.18</u>	<u>-.02</u>	<u>.06</u>	<u>.04</u>	<u>.02</u>	<u>.06</u>	<u>.00</u>	<u>.20</u>	<u>-.14</u>	<u>-.57</u>	<u>.31</u>	
Waterhen L.	59.8	<u>-.53</u>	<u>.02</u>	<u>.06</u>	<u>-.05</u>	<u>.05</u>	<u>.53</u>	<u>-.01</u>	<u>.06</u>	<u>-.11</u>	<u>.05</u>	<u>-.12</u>	<u>.09</u>	<u>.58</u>	<u>-.05</u>	<u>-.20</u>	<u>-.13</u>	<u>-.00</u>	<u>-.28</u>	<u>.27</u>	
L. Winnipeg	36.7	<u>.71</u>	<u>.10</u>	<u>-.01</u>	<u>-.08</u>	<u>-.04</u>	<u>.24</u>	<u>-.02</u>	<u>.06</u>	<u>-.31</u>	<u>-.03</u>	<u>-.12</u>	<u>.06</u>	<u>-.17</u>	<u>-.04</u>	<u>.27</u>	<u>-.04</u>	<u>-.27</u>	<u>-.75</u>	<u>.44</u>	
	82.5	<u>-.32</u>	<u>.01</u>	<u>-.22</u>	<u>.33</u>	<u>-.49</u>	<u>.20</u>	<u>.00</u>	<u>.04</u>	<u>-.05</u>	<u>.04</u>	<u>.09</u>	<u>.18</u>	<u>-.02</u>	<u>.05</u>	<u>.32</u>	<u>.26</u>	<u>-.49</u>	<u>-.45</u>	<u>.33</u>	<u>1.00</u>
	22.9	<u>-.30</u>	<u>-.05</u>	<u>.16</u>	<u>-.34</u>	<u>.58</u>	<u>.32</u>	<u>.06</u>	<u>-.01</u>	<u>.20</u>	<u>-.10</u>	<u>.30</u>	<u>-.06</u>	<u>-.10</u>	<u>.05</u>	<u>-.34</u>	<u>-.04</u>	<u>-.23</u>	<u>.06</u>	<u>-.29</u>	<u>.24</u>

(cont.)

TABLE I (cont.)

Locality	Chi-square	Discriminant coefficients for each variable										Mean discriminant scores for each form										
		Fork 1.	Pectoral 1.	Body d.	Pelvic 1.	Head 1.	Profile	Eye diam	Premaxilla ang.	Snout 1.	Lateral line	Interorbital w.	Upper rakers	Upper jaw 1.	Lower rakers	Mandible 1.	Profile ang.	Premaxillae w.	Gillraker 1.	Lower	Med	Higher
		21.7	7.7	1.4	10.6	8.7	6.2	2.2	1.1	6.0	1.3	6.0	2.6	5.9	8.1	4.0	2.9	3.6				

Amount of variance (%) between sympatric forms accounted for by each variable (except profile angle)

independent of body size above 120 mm. (Svardson 1957; McCart and Andersen 1967), and are convenient taxonomically, the use of this character was examined as a means of discriminating and equating forms previously sorted by numerical taxonomy.

A form will be referred to as a lower, medium or higher form, depending on the relationship of its mean gill-raker number to the means of other sympatric forms. If only one form occurs in a lake, it will be referred to as a medium form; if two, as lower and higher forms; if three, as lower, medium and higher forms. The means and ranges of the gill-raker counts found for each form at each locality are given in Table II. The term "bimodal" will be used to describe gillraker distributions that suggest the presence of sympatric forms, but do not clearly separate the forms found by numerical taxonomy. Similarly the term "normal" will be used to describe distributions that suggest a single form.

The range of gillraker counts clearly separated two sympatric forms in 11 lakes, and three sympatric forms in three lakes (Table II). In Big Athapapuskow the gillraker counts separated the lower form from the other two forms, whose combined counts were "bimodal". The counts were "bimodal" in 14 localities where two forms had been found by numerical taxonomy, and in Pasqua L., Payuk L. and at Churchill where there was no firm evidence for the existence of two sympatric forms. "Normal" combined counts were found for the Mackenzie R. where three forms were found, and in four

TABLE II

Gillraker counts of ciscoes from central Canada arranged according to their relationship to counts of sympatric forms. Counts that distinguish sympatric forms are underlined.

Locality (name and number)	Gillraker counts								
	Lower			Medium			Higher		
	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean
Aberdeen R. (11) ¹				2	44-46	45.0			
L. Abitibi (73)				5	55-60	57.4			
L. Athabasca (16)	18	<u>34-43</u>	<u>38.7</u>				26	<u>49.57</u>	<u>52.6</u>
Attawipiskat L. (70)	6	<u>38-44</u>	<u>41.6</u>				6	<u>53-56</u>	<u>54.1</u>
Baker L. (12) ¹				2	40-41	40.5			
Barrow L. (15) ^{1,2}	15	<u>37-41</u>	<u>39.5</u>				21	<u>44-51</u>	<u>47.8</u>
Beresford L. (57)				18	42-48	43.6			
Beverly L. (10)				5	42-46	44.4			
Big Athapapuskow (40)	16	<u>24-36</u>	<u>29.4</u>	24	38-47	42.3	19	42-49	45.6
Big Peter Pond (17)	38	42-49	45.9				32	43-50	47.4
Bigstone L. (28)				20	46-56	47.3			
Big Trout L. (69) ¹	1	<u>35</u>	<u>35</u>				2	<u>40-45</u>	<u>42.5</u>

(cont'd)

Table II (cont'd)

Locality (name and number)	Gillraker counts								
	Lower			Medium			Higher		
	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean
Big Twin L. (35)				14	45-51	47.8			
Big Whiteshell L. (51)	7	48-51	49.3				9	46-53	49.3
Bird L. (59)	15	41-47	44.9				18	42-50	45.8
Cape Jones (78) ¹				1	42	42			
Churchill (32) ⁵				19	38-46	43.4			
Churchill L. (18)	23	43-50	46.0				26	45-51	48.0
Clearwater L. (44) ¹	2	<u>33</u>	<u>33.0</u>				28	<u>38-49</u>	<u>42.9</u>
Cold L. (22)	32	37-46	40.9				32	36-46	41.4
Davidson L. (60)				3	43-47	44.6			
Deer L. (63) ¹	2	<u>35</u>	<u>35.0</u>				2	<u>50-52</u>	<u>51.0</u>
Dismal L. (3) ¹				4	46-49	47.7			
Echo L. (48)	11	47-54	50.1				19	49-55	51.6
Falcon L. (53) ⁵				14	48-54	51.0			
First Cranberry L. (41) ⁵				15	48-57	52.5			
Fishing L. (49) ¹				1	41	41			
Flotten L. (24) ³	1	<u>38</u>	<u>38</u>				16	<u>43-52</u>	<u>46.8</u>
Fort George (77) ¹				3	41-43	42.0			

(cont'd)

Table II (cont'd)

Locality (name and number)	Gillraker counts								
	Lower			Medium			Higher		
	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean
George L. (52)				5	33-37	35.4			
Great Bear L. (4) ¹				5	43-49	45.4			
Great Slave L. (8) ³	1	<u>38</u>	<u>38</u>				5	<u>42-49</u>	<u>45.8</u>
Great Whale R. (79)				4	41-46	42.9			
Greig L. (25) ¹				2	44-46	45.0			
Hawley L. (71)				5	43-49	44.8			
Ile-a-la Crosse (20)				4	44-48	46.5			
James Bay (72) ¹				1	43	43			
Kapsawi R. (unknown) ¹				1	48	48			
Keller L. (6) ¹				2	45-47	46.0			
Lac des Iles (23)	7	45-51	47.0				14	44-50	48.0
Lac la Biche (21)	19	43-51	46.8				21	47-53	49.9
Lac la Ronge (29) ⁴	5	<u>48-53</u>	<u>50.2</u>				1	<u>57</u>	<u>57</u>
Lac Seul (65) ⁴	39	<u>31-37</u>	<u>33.8</u>	22	<u>41-48</u>	<u>44.2</u>	2	<u>54-57</u>	<u>55.5</u>
Lake of the Woods (61)	18	30-41	36.3				16	41-51	46.0
Last Mountain L. (46)	27	46-56	51.7				26	47-57	51.8
Little Athapapuskow (38)	14	<u>32-37</u>	<u>34.5</u>	13	<u>40-46</u>	<u>42.7</u>	19	<u>48-54</u>	<u>51.4</u>

(cont'd)

Table II (cont'd)

Locality (name and number)	Gillraker Counts								
	Lower			Medium			Higher		
	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean	<u>n</u>	Range	Mean
Little Peter Pond (19)	9	45-49	47.7				9	44-51	47.8
Little Twin L. (36)				11	49-53	51.1			
Mackenzie R. (2, 7)	8	40-44	42.4	10	39-44	42.5	10	41-47	44.4
Manistikwan L. (33) ¹				24	38-45	41.6			
L. Manitoba (50)				20	46-56	50.5			
L. Matagami (74)				3	59-67	62.9			
Mink Narrows (39) ⁴	8	<u>34-40</u>	<u>37.1</u>	20	<u>43-47</u>	<u>44.7</u>	1	<u>58</u>	<u>58</u>
Minnitaki L. (66)	17	38-50	43.7				23	41-49	44.4
Montreal L. (31)	71	39-48	43.2				3	48-53	50.6
Neso L. (34)	11	46-53	49.7				18	48-57	51.1
Nikip L. (64)				4	42-44	43.2			
L. Olga (76) ¹				1	56	56			
Osnaburgh L. (68) ¹				1	42	42			
Pasqua L. (47) ⁵				28	47-58	51.0			
Payuk L. (37) ⁵				35	48-57	52.5			
Pelly L. (9)				4	41-44	42.2			
Pine Falls (58) ¹				7	41-46	44.0			
Povungnituk (81) ¹				1	46	46			

(cont'd)

Table II (cont'd)

Locality (name and number)	Gillraker Counts								
	Lower			Medium			Higher		
	n	Range	Mean	n	Range	Mean	n	Range	Mean
Quesnell L. (56)	15	44-50	46.2				12	46-52	48.7
Reindeer L. (27)				5	34-38	35.6			
Richmond Gulf (80) ¹				1	41	41			
Rocky L. (43)	12	41-46	43.4				22	42-49	45.3
L. St. Joseph (67)				16	38-46	41.3			
Sandy L. (62)	7	<u>37-43</u>	<u>40.2</u>				3	<u>51.54</u>	<u>53.0</u>
Second Cranberry L. (42)	15	<u>45-51</u>	<u>47.6</u>				1	<u>56</u>	<u>56</u>
Spark Plug L. (5) ¹				1	48	48			
Tazin R. (13)				1	37	37			
Wanipigow L. (55)				15	44-51	47.0			
Waskesiu L. (30)	24	42-50	45.6				25	44-52	47.6
Waswanipi L. (75) ¹				1	55	55			
Waterhen L. (26)	10	45-52	49.2				17	46-54	49.5
West Hawk L. (54) ^{1,5}				13	40-46	42.7			
Wholdaia L. (14) ¹				1	40	40			

(cont'd)

Table II (cont'd)

Locality (name and number)	Gillraker counts								
	Lower			Medium			Higher		
	n	Range	Mean	n	Range	Mean	n	Range	Mean
L. Winnipeg (45)									
U.M.	9	38-47	42.1	20	41-47	44.0	6	42-48	44.4
R.O.M.	5	<u>37-43</u>	<u>39.3</u>	1	<u>50</u>	<u>50</u>	1	<u>61</u>	<u>61</u>

¹None used in numerical taxonomic analysis

²From Paterson (1969)

³Lower form not used in numerical taxonomic analysis

⁴Higher form not used in numerical taxonomic analysis

⁵Possibly two forms present

lakes (Big Peter Pond, Big Whiteshell, Little Peter Pond, Waterhen) where there were two forms, and in 26 localities where there was only one form. "Normal" counts occurred in Falcon L., First Cranberry L. and West Hawk L. where two forms had been suggested by numerical taxonomy but not tested. There was only one specimen from twelve localities.

Three sympatric forms were found in L. Winnipeg. The counts were "bimodal" for the specimens examined at the University of Manitoba, but the three forms found in the specimens examined at the Royal Ontario Museum had separate ranges (Table II). The relationship between the University and Museum samples is not clear.

Appearance

The appearance distinguished sympatric forms at five localities. In Barrow L. (also see Paterson 1969) and Flotten L. the lower forms were much larger and deeper-bodied than the higher forms, and usually had more vertical premaxillae. The higher form in Montreal L. was much slimmer and had a longer head than the lower form. The lower form in Big Athapapuskow had a greenish colouration above the lateral line, and, usually, the premaxillae were nearly vertical and the lower jaw was included. In the Mackenzie R. the medium form had the deepest body; the lower form had

least pigmentation, and the premaxillae were nearly vertical with an included lower jaw; the premaxillae were nearest the horizontal in the higher form, which usually had a protruding lower jaw.

Other morphological differences between sympatric forms are shown by the discriminant coefficients for the localities where significant differences were found between the forms (Table I). Where discriminant analysis was not used or the results were not significant, the following morphological differences were noted. In Clearwater L. the lower form had shorter gillrakers than the higher form; in Big Trout L. and Deer L. the lower forms had shorter gillrakers and shorter paired fins; in Second Cranberry L. the lower form had longer gillrakers and shorter paired fins. The lower form in Sandy L. was slimmer with a longer snout and longer paired fins; the lower form in Great Slave L. had a more ovate profile and a shorter head than the higher form. In Mink Narrows the higher form had shorter gillrakers and a deeper body than the medium form, and a deeper body and less vertical premaxillae than the lower form. The higher form from Lac Seul had a deeper body than the medium and lower forms, and longer gillrakers and shorter upper jaw than the lower form. The higher forms in Attawapiskat L. and Lac la Ronge were longer than the lower forms, but the lack of overlap in size range between the two forms prevented the

discovery of any morphometric differences.

Traditional Taxonomic Characters: Profile and Jaw Characteristics

Profile and jaw characteristics have been used extensively in cisco taxonomy (Koelz 1929, Hubbs and Lagler 1964), but, because of the variation of these characters within populations (briefly outlined below), they cannot be relied upon as key characters in the separation of sympatric forms of ciscoes, although statistical differences may exist between sympatric forms.

Large C. artedii from L. Erie and the larger ciscoes from Long L. had ovate profiles, (deeper forward than medially), whereas the smaller ciscoes had elliptical profiles (deepest medially). Although C. johannae and C. kiyi are normally ovate, some specimens examined were elliptical, and some C. reighardi from L. Nipigon were ovate, although this species is usually elliptical.

The lower jaw protruded beyond the tip of the snout in the large ciscoes from Little Twin L., but in Neso L. a greater proportion of smaller ciscoes had protruding lower jaws than did the larger ciscoes. In Big Athapapuskow, the lower jaw protruded in 44% of the medium form and in 30% of the higher form; the lower jaw was shorter than the upper jaw in 78% of the lower form (Clarke MS 1970).

Sexual Dimorphism

Discriminant analysis was used to test for sexual dimorphism in the lower forms from Big Peter Pond, Lac Seul and Montreal L. In no lake was there a significant difference between males and females, nor did the discriminant coefficients show a common pattern in the differences between the sexes.

Hile (1937) found that male ciscoes had longer fins, larger eyes, and slimmer, narrower bodies than females. In Big Peter Pond, Lac Seul and Montreal L., sexual dimorphism in fin lengths was not consistent between lakes; if the males had longer pectoral fins, they had shorter pelvic fins and vice versa. Males in all three lakes had slightly deeper bodies than the females. The data in this study does not permit validation or negation of Hile's (1937) observations.

Intra-lake Variation

Ciscoes were sampled from the north and south ends of Montreal L., about 30 miles apart. Although the lake is relatively uniform in its characteristics throughout (Mendis MS 1956), the higher form was caught only at the north end. Discriminant analysis showed that the lower form differed significantly ($p < 0.05$) between the two areas, with differences in size, profile and the length of the jaws.

Summary - In central Canada, three sympatric forms of ciscoes were found at six localities, two sympatric forms at 29 localities, and one form at 39 localities. Evidence was insufficient to decide if there was one or two forms at six localities. Gillraker count was the most useful single character in the separation of sympatric forms. Other characters of use in separating sympatric forms were fork length, pectoral and pelvic fin lengths, head length, profile, snout length, interorbital width and upper jaw length. The use of profile and jaw characteristics as key characters (Koelz 1929) was found to be unsatisfactory. Sexual dimorphism was not significant, but intra-lake variation in Montreal L. was significant.

THE EQUATING OF FORMS OF CISCOES
FROM CENTRAL CANADA

Once the numbers of sympatric forms present in each sample had been determined, the next task was to equate forms between different samples, in order to determine how many species are present in the whole area.

Materials

The same 1493 ciscoes from 81 localities in central Canada, that were examined for sympatric forms of ciscoes (Fig. 1 and Appendix 1) were used in the following analyses. The same morphological characters were studied as were used in the separation of sympatric forms of ciscoes, except that profile angle was not used.

Methods

Treatment of Data - Comparison of the forms of ciscoes from each locality required the calculation of one value for each character for every form. Mean values of fork length, premaxilla angle, lateral line scale numbers, and upper, lower and total numbers of gillrakers were calculated for each form. Values for the measurements of each form were obtained by simple linear regression, after the measurements were transformed to \log_{10} . Body depth, head length, pectoral length, pelvic length and profile were

regressed against fork length; eye diameter, snout length, interorbital width, upper jaw length, mandible length, premaxillae width and gillraker length were regressed against head length. The resultant regression equations were used to calculate the size of body parts at either 200mm. fork length or 45mm. head length (using \log_{10} values for 200mm. and 45mm.); the anti-logarithms of these values were used in subsequent analyses. The maximum fork length for each form was also included in the analyses.

As mean values and the regression technique were used to calculate values for the characters of each form, not all forms were included in the subsequent analyses. Nine forms were excluded from the analyses since their sample size was less than three. Forms with a sample size greater than three were included if the range in fork length of the form was at least 30mm. and if the regression gave credible estimates of the size of body parts at 200mm. fork length or 45mm. head length. At least one of the latter two criteria were not met by the Clearwater L. higher form, and the Dismal L., Fort George, Great Bear L., Manistikwan L., Pine Falls and West Hawk L. medium forms. It is questionable whether estimates of size of certain body parts for the lower form in Dunc L. (an extralimital form included because of its low mean gillraker count of 39.3) and for the lower form in Mink Narrows were accurate, but these forms were included in the analyses

except for R-mode factor analysis and the index. Table II shows, except for Dunc L., the 86 forms from 55 localities which were included in, and the 36 forms excluded from the analyses.

Numerical Taxonomy - The following analyses used the mean data; the data were transformed to \log_{10} for use in factor analysis and mean square distance. Since each method of analysis used the same data, these analyses do not give independent confirmation of results.

Correlations between the 19 morphological variables were investigated by R-mode factor analysis (Cattell 1965a, 1965b), which starts from the correlation matrix of the variables. Factor scores were calculated and used to group the 84 forms included in this analysis; the lower forms from Dunc L. and Mink Narrows were not included. No statistical significance can be attached to the differences between the groups, since the groups were constructed to be different. The F-test from analysis of variance (ANOVA) (Steel and Torrie 1960) indicated the degree of difference among the groups, rather than any formal statistical difference.

A simple index was constructed to separate groups found by R-mode analysis.

The overall similarity of the 86 forms was investigated by Q-mode factor analysis (Cattell 1965a, 1965b) which

starts from the correlation matrix of the samples, by mean square distance with the average linkage unweighted group pair method of clustering (Sokal and Sneath 1963) and also by information analysis using the mutual information statistic (Orloci 1968). Maximum fork length and the total number of gillrakers were not included in the distance and information analyses, but the values for average fork length, and lower and upper gillrakers were included.

Further details of the mean square distance and average linkage unweighted group pair method of clustering are given in Appendix 2, of factor analysis in Appendix 3, and of information analysis in Appendix 5.

Methods of Testing for Effects of the Environment -

R-mode factor analysis was used to investigate the association between 19 environmental parameters and i) the morphology of ciscoes; ii) the magnitude of differences between sympatric forms; and iii) the mean square distance between sympatric forms. The latitude, longitude and altitude of each locality was obtained from the appropriate maps and gazeteers. The following climatic data were obtained for each locality from the Atlas of Canada (Anon. 1957): mean January temperature, mean July temperature (both in degrees Fahrenheit), number of degree days above 42°F, number of frost-free days, number of days with greater than one inch

of snow cover and mean annual precipitation (inches). The following data for each lake were obtained from Rawson (1960), Johnson (1963), Ryder (1964, 1965), by measurement of the appropriate maps or from data available at the University of Manitoba: lake area (mi.²), length (mi.), width (mi.), shoreline length (mi.), drainage basin area (mi.²), maximum depth (m.) and total dissolved solids (ppm). Data for the latter two variables were not available for some lakes, which were excluded from the analysis. Values for shoreline development were calculated for each lake, as were values for a flushing index (drainage basin area/lake area) and for TDS/maximum depth. Lake area, frost-free days, degree days, TDS, maximum depth, average and maximum fork lengths were used to predict values for the morphological variables by multiple linear regression (Snedecor and Cochran 1964); the latter two variables were not used in the prediction of average and maximum fork lengths. The data were transformed to \log_{10} before use in factor analysis and multiple regression.

Results

R-mode Factor Analysis

Eight factors were extracted from the correlation matrix of the 19 characters for the 84 forms (86 forms minus the lower forms in Dunc L. and Mink Narrows). The factor loadings are shown in Table III. The first factor, which accounted for a third of the total variance, was most heavily loaded on mandible length, upper jaw length and body depth; long jaws were associated with a narrow interorbital width and a less deep body. The second factor was an association of head and paired fin lengths. The third factor was a gillraker factor; more gillrakers were associated with longer gillrakers. The fourth factor was mainly size, showing a tendency for large forms to have more scales. The fifth factor was a profile factor with an association between profile and gillraker length. The sixth factor showed an association between increased eye diameter and fewer lateral line scales. The seventh factor was loaded mainly on premaxilla angle. The last extracted factor showed that increased premaxillae width was associated with increased interorbital width and decreased snout length.

Factor scores for each form were calculated from the matrix of factor loadings. The factor scores had a

mean of 0.0 and a standard deviation of 1.0. The factor scores suggested that the forms should be arranged into four groups: the "Mackenzie R. low group," the "Mackenzie R. high group," and the "low group" and the "high group" (so named here on the basis of their gillraker counts), but not to be confused with the "lower" and "higher" columns in Table II which were based solely on the relative counts of two or three forms inhabiting the same lake. Table IV shows the range of factor scores, their means and standard deviations for the low and high groups, and the factor scores for the Mackenzie R. low and Mackenzie R. high groups. The overall difference between the four groups is shown by the F-value from ANOVA.

The two most atypical forms were the Mackenzie R. lower and higher forms. The Mackenzie R. lower form was outside of the range of factor scores of all other groups on factors VI and VIII, and the Mackenzie R. higher form was outside of the range of factor scores of the other three groups on factor VII (Table IV). A plot of the factor scores of factor VII against factor VIII showed the separation of the Mackenzie R. lower and higher forms from each other and from the low and high groups (Fig. 3). In addition the Mackenzie R. lower and higher forms were separated from each other and from the high and low groups on factor V, and the Mackenzie R. higher form from the high group on

Fig. 3. Plot of factor scores of each form from all localities, for factor VII (based mainly on premaxilla angle) and factor VIII (based mainly on premaxilla width, interorbital width and snout length). Note distinctiveness of the Mackenzie R. lower and higher forms. Key: low group ◦ , high group • , Mackenzie R. lower form ▲ , Mackenzie R. higher form △ .

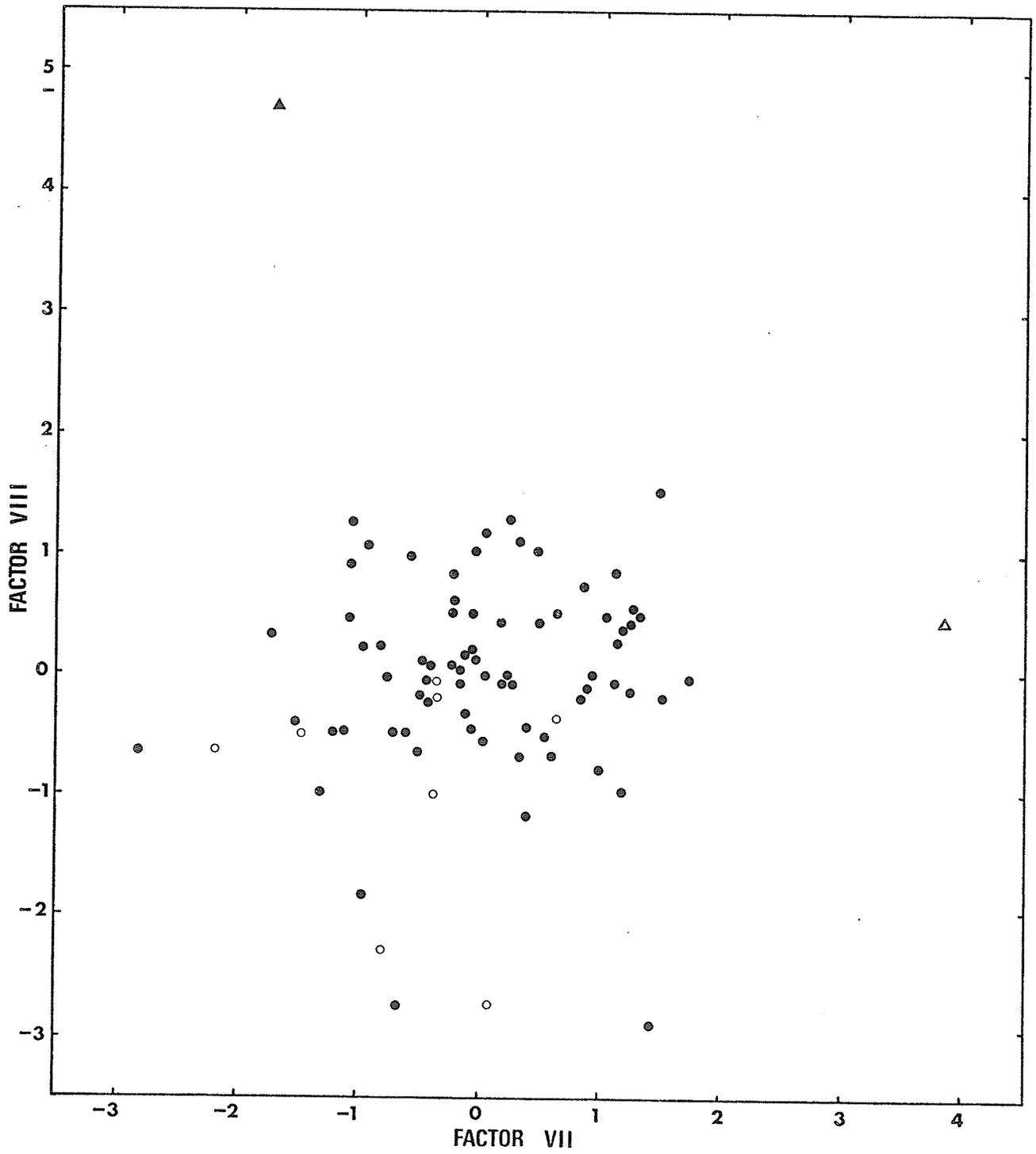


TABLE III

Rotated factor matrix of the morphological variables for the 84 forms.
Factor loadings greater than 0.30 are underlined.

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Cum. % variance	33.79	48.13	58.98	68.24	74.54	79.74	84.06	87.33
% variance	33.79	14.34	10.85	9.26	6.30	5.20	4.32	3.27
<u>Morphological variable</u>								
Av. fork l.	.11	.12	.28	<u>-.88</u>	.06	-.02	-.17	.12
Max. fork l.	<u>.42</u>	.08	.22	<u>-.76</u>	-.01	-.10	-.13	.12
Body d.	<u>.70</u>	<u>.37</u>	<u>.32</u>	-.07	-.05	.27	-.08	.18
Pectoral l.	.22	<u>.79</u>	.28	-.14	-.01	.26	.00	<u>.30</u>
Pelvic l.	.25	<u>.73</u>	.27	-.21	.01	.29	.06	<u>.31</u>
Head l.	-.26	<u>.87</u>	-.08	.06	-.18	-.10	-.03	-.07
Eye diam.	-.23	.10	-.17	-.03	.05	<u>.87</u>	.17	.05
Snout l.	<u>-.48</u>	.01	<u>-.37</u>	.15	-.25	-.12	.03	<u>-.52</u>
Upper jaw l.	<u>-.71</u>	.08	-.28	.24	-.05	.22	-.04	-.25
Mandible l.	<u>-.85</u>	.06	-.16	.09	-.19	.09	-.13	.10

(cont'd)

TABLE III (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
<u>Morphological variable</u>								
Interorbital w.	<u>.60</u>	.05	.14	-.17	-.09	-.25	-.07	<u>.53</u>
Premaxillae w.	.08	.29	-.06	-.14	-.15	-.03	-.20	<u>.81</u>
Gillraker l.	-.04	-.12	<u>.56</u>	.18	<u>-.59</u>	.21	.16	.28
Profile	-.13	.17	.02	-.00	<u>-.91</u>	-.06	-.09	.01
Premaxilla ang.	-.07	-.01	-.06	-.18	-.04	-.06	<u>-.92</u>	.16
Lateral line scales	-.12	-.19	-.01	<u>-.49</u>	.08	<u>-.67</u>	.22	.25
Upper rakers	.24	.08	<u>.91</u>	-.24	-.07	-.07	.00	.07
Lower rakers	.22	.12	<u>.94</u>	-.13	-.00	-.08	.03	-.01
Total rakers	.22	.11	<u>.94</u>	-.17	-.03	-.08	.02	.02

TABLE IV

Differences in the factor scores of the four groups.

There was only one sample from both the Mackenzie R.

lower and Mackenzie R. higher forms

Factor	Group	Range		Mean	Stand- ard Devia- tion	F-value from ANOVA
		Lower	Upper			
I	Low	-2.09	-0.25	-0.84	1.00	3.6
	High	-2.58	1.79	0.14	0.93	
	Mackenzie R. lower	-2.43				
	Mackenzie R. higher	-0.84				
II	Low	-1.02	1.75	0.53	1.01	2.0
	High	-2.66	1.99	-0.06	0.98	
	Mackenzie R. lower	-0.26				
	Mackenzie R. higher	-0.30				
III	Low	-3.95	-0.76	-2.12	0.95	2.4
	High	-1.02	2.57	0.24	0.70	
	Mackenzie R. lower	-0.94				
	Mackenzie R. higher	-0.06				
IV	Low	-0.77	1.83	0.13	0.83	3.3
	High	-2.22	2.77	0.04	0.99	
	Mackenzie R. lower	-1.67				
	Mackenzie R. higher	-1.97				

TABLE IV (cont'd)

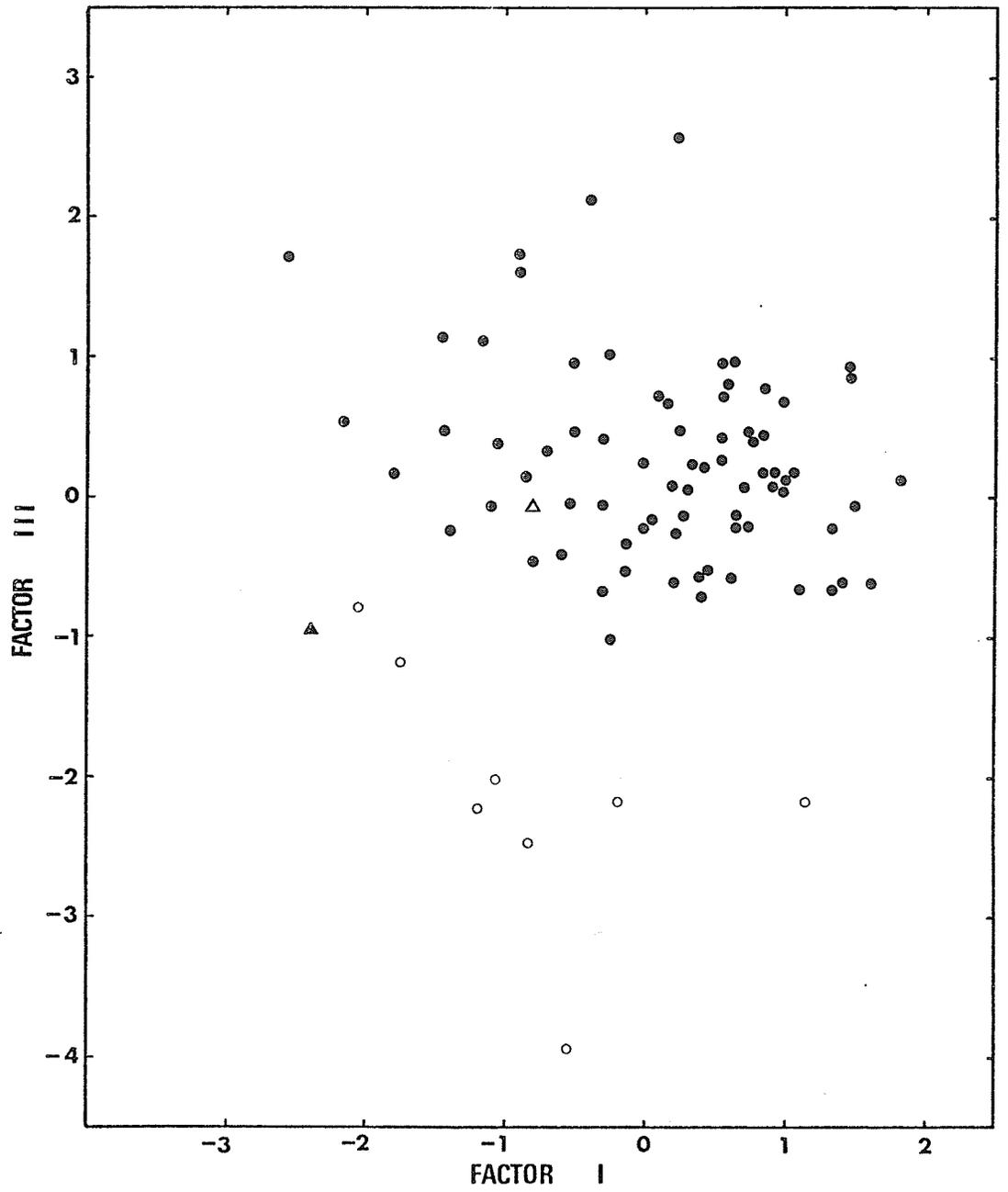
Factor	Group	Range		Mean	Stand- ard Devia- tion	F-value from ANOVA
		Lower	Upper			
V	Low	-1.49	4.63	0.19	1.85	5.1
	High	-1.78	2.99	-0.02	0.83	
	Mackenzie R. lower		-1.95			
	Mackenzie R. higher		2.20			
VI	Low	-0.83	0.93	0.14	0.70	7.2
	High	-2.17	3.07	-0.02	0.94	
	Mackenzie R. lower		-3.60			
	Mackenzie R. higher		1.23			
VII	Low	-2.20	0.63	-0.61	0.88	9.5
	High	-2.85	1.71	-0.04	0.88	
	Mackenzie R. lower		-1.73			
	Mackenzie R. higher		3.85			
VIII	Low	-2.73	-0.04	-0.95	1.02	13.4
	High	-2.90	1.51	0.03	0.79	
	Mackenzie R. lower		4.72			
	Mackenzie R. higher		0.46			

factor V, and the Mackenzie R. higher form from the high group on factor I and from the low and high groups on factor IV (Table IV). These differences indicate that the Mackenzie R. lower and higher forms are each distinctive from all other groups.

The low group was separated from the high group by a plot of factor I against factor III (Fig. 4). On factor III, the ranges of the two groups did not overlap, except that the L. St. Joseph medium form (high group) had a lower score than the Sandy L. lower form (low group). Differences occurred between the low and high groups on factors I, III, and VIII (Table IV). The following eight forms composed the low group: the lower forms from L. Athabasca, Big Athapapuskow, Lac Seul, Lake of the Woods, Little Athapapuskow and Sandy L.; and the medium forms from George L. and Reindeer L.

The remaining 74 forms were placed in the high group. It must be emphasised that 20 of the lakes are inhabited by two sympatric forms which both fall into this high group; L. Winnipeg has three sympatric forms in the high group. In each case the separation between the forms was established by the earlier analysis. One member of these sympatric forms has been listed in Table II under either "lower" or "medium," but according to the present analysis all members fall in the "high group."

Fig. 4. Plot of factor scores of each form from all localities, for factor I (based mainly on mandible length, upper jaw length, body depth and interorbital width) and factor III (based mainly on gillraker numbers and gillraker length), showing the separation of the low and high groups. Key as in Fig. 3.



There was a suggestion from the factor scores of factor III that the five forms with scores greater than 1.5 (the higher forms from L. Athabasca, L. Attawapiskat and Sandy L.; the medium forms from L. Abitibi and L. Matagami) might form a separate group, but there was no other evidence from the factor scores for this.

A simple index showed the separation of the low group from the high group. The best simple index was snout length + upper jaw length + mandible length - total number of gillrakers. The separation of the two groups was complete, with values for the high group ranging from -17.1 to 7.7, and for the low group from 12.3 to 20.6. An alternative way of showing this separation is to plot the total number of gillrakers against the sum of the values for snout length, upper jaw length and mandible length for each form; this is done in Fig. 5.

Mean Square Distance

A phenogram was constructed by the average linkage unweighted group pair method (Sokal and Sneath 1963) from the matrix of mean square distances of the 86 forms (the 84 forms plus the lower forms from Dunc L. and Mink Narrows). In drawing a phenogram, each form or cluster could be placed to the left or right of the cluster which it joined. In Fig. 6, each form or cluster was placed on the side of the main

Fig. 5. Separation of the low and high groups by a plot of mean total numbers of gillrakers against a simple index (snout l. + upper jaw l. + mandible l.).
Key as in Fig. 3.

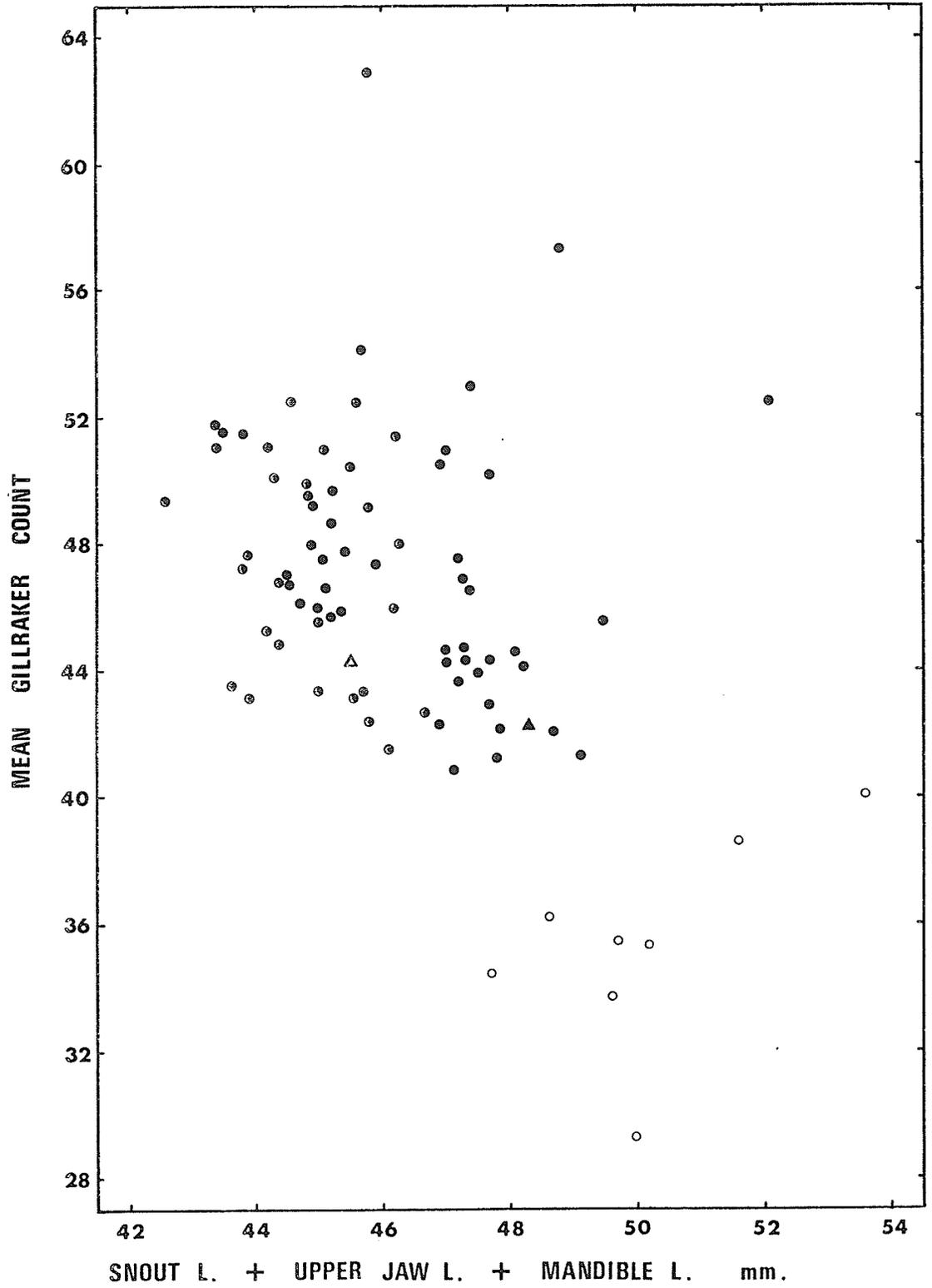
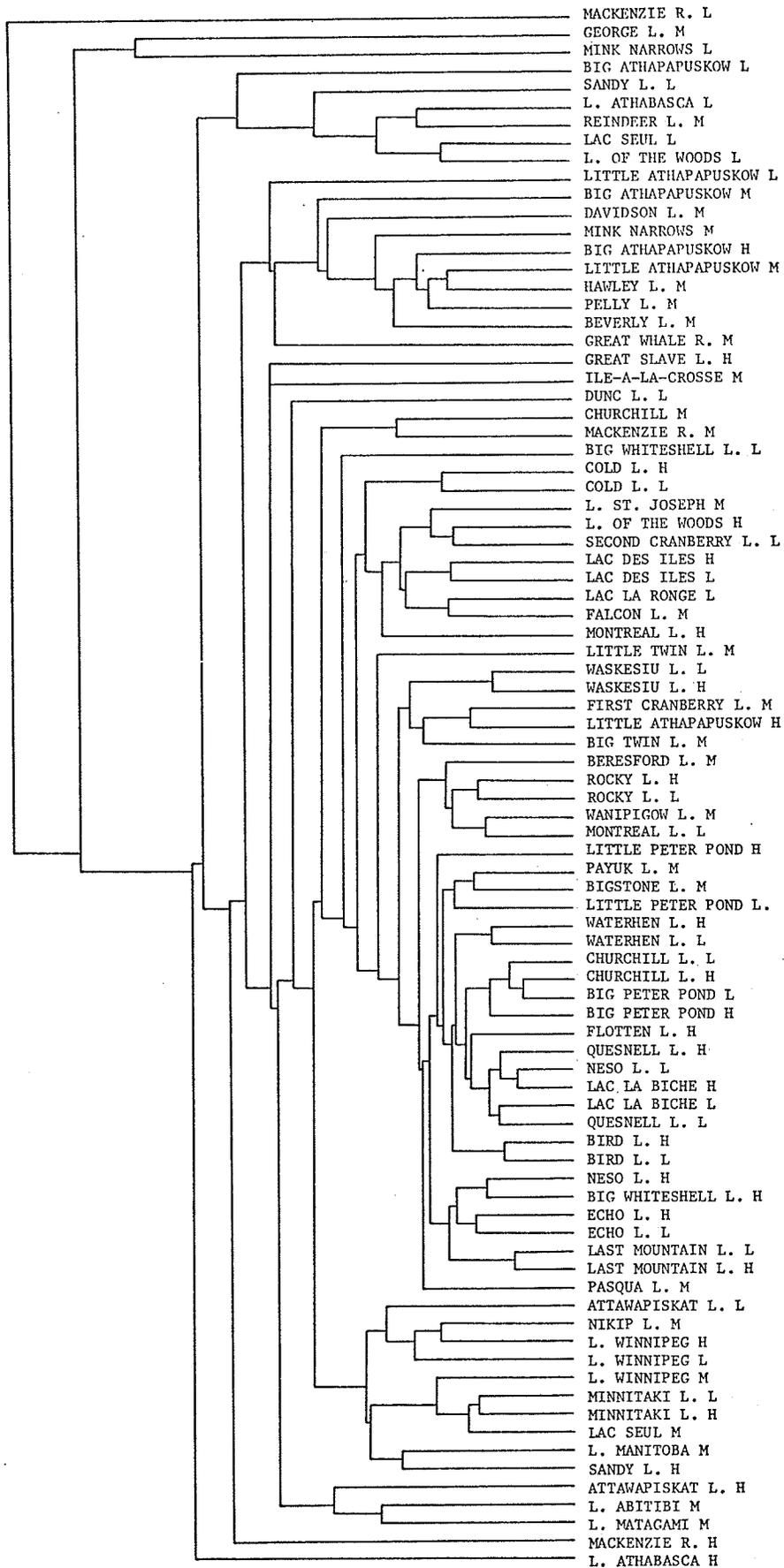


Fig. 6. Phenogram of the 86 forms constructed from a matrix of mean square distance by the average linkage unweighted group pair method. The "l", "m" or "h" after each locality refers to the designation of the form as lower, medium or higher in Table II.

2.5 2.0 1.5 1.0 0.5 0



- MACKENZIE R. L
- GEORGE L. M
- MINK NARROWS L
- BIG ATHAPAPUSKOW L
- SANDY L. L
- L. ATHABASCA L
- REINDEER L. M
- LAC SEUL L
- L. OF THE WOODS L
- LITTLE ATHAPAPUSKOW L
- BIG ATHAPAPUSKOW M
- DAVIDSON L. M
- MINK NARROWS M
- BIG ATHAPAPUSKOW H
- LITTLE ATHAPAPUSKOW M
- HAWLEY L. M
- PELLE L. M
- BEVERLY L. M
- GREAT WHALE R. M
- GREAT SLAVE L. H
- ILE-A-LA-CROSSE M
- DUNC L. L
- CHURCHILL M
- MACKENZIE R. M
- BIG WHITESHELL L. L
- COLD L. H
- COLD L. L
- L. ST. JOSEPH M
- L. OF THE WOODS H
- SECOND CRANBERRY L. L
- LAC DES ILES H
- LAC DES ILES L
- LAC LA RONGE L
- FALCON L. M
- MONTREAL L. H
- LITTLE TWIN L. M
- WASKESIU L. L
- WASKESIU L. H
- FIRST CRANBERRY L. M
- LITTLE ATHAPAPUSKOW H
- BIG TWIN L. M
- BERESFORD L. M
- ROCKY L. H
- ROCKY L. L
- WANIPIGOW L. M
- MONTREAL L. L
- LITTLE PETER POND H
- PAYUK L. M
- BIGSTONE L. M
- LITTLE PETER POND L.
- WATERHEN L. H
- WATERHEN L. L
- CHURCHILL L. L
- CHURCHILL L. H
- BIG PETER POND L
- BIG PETER POND H
- FLOTTEN L. H
- QUESNELL L. H
- NESO L. L
- LAC LA BICHE H
- LAC LA BICHE L
- QUESNELL L. L
- BIRD L. H
- BIRD L. L
- NESO L. H
- BIG WHITESHELL L. H
- ECHO L. H
- ECHO L. L
- LAST MOUNTAIN L. L
- LAST MOUNTAIN L. H
- PASQUA L. M
- ATTAWAPISKAT L. L
- NIKIP L. M
- L. WINNIPEG H
- L. WINNIPEG L
- L. WINNIPEG M
- MINNITAKI L. L
- MINNITAKI L. H
- LAC SEUL M
- L. MANITOBA M
- SANDY L. H
- ATTAWAPISKAT L. H
- L. ABITIBI M
- L. MATAGAMI M
- MACKENZIE R. H
- L. ATHABASCA H

2.5 2.0 1.5 1.0 0.5 0

MEAN SQUARE DISTANCE

cluster to which showed most resemblance in the matrix of mean square distances.

The most atypical form was the Mackenzie R. lower form, which joined the main cluster at a level of 2.56. The Mackenzie R. higher form was the fifth from last form to join the main cluster, at 1.58.

Six forms of the low group clustered together at 1.53 and they joined the main cluster at 1.70. The Little Athapapuskow lower form, a member of the low group, joined a small cluster of high group forms at 1.38. The eighth member of the low group, the George L. medium form, joined with the Mink Narrows lower form at 2.00, and both joined the main cluster at 2.26. Examination of the matrix of mean square distances showed that seven forms of the low group were most similar to other members of the low group; the exception was the Little Athapapuskow lower form, which was most similar to the Mink Narrows medium form. Also the Mink Narrows lower form was most similar to a member of the high group, the Great Whale R. medium form.

R-mode factor analysis had suggested that five forms of the high group (the higher forms from L. Athabasca, L. Attawapiskat and Sandy L., and the medium forms from L. Abitibi and L. Matagami) might constitute a separate group. From the results of the mean square distance, the L. Athabasca higher form was the most atypical member of the high

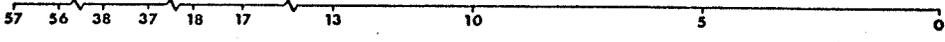
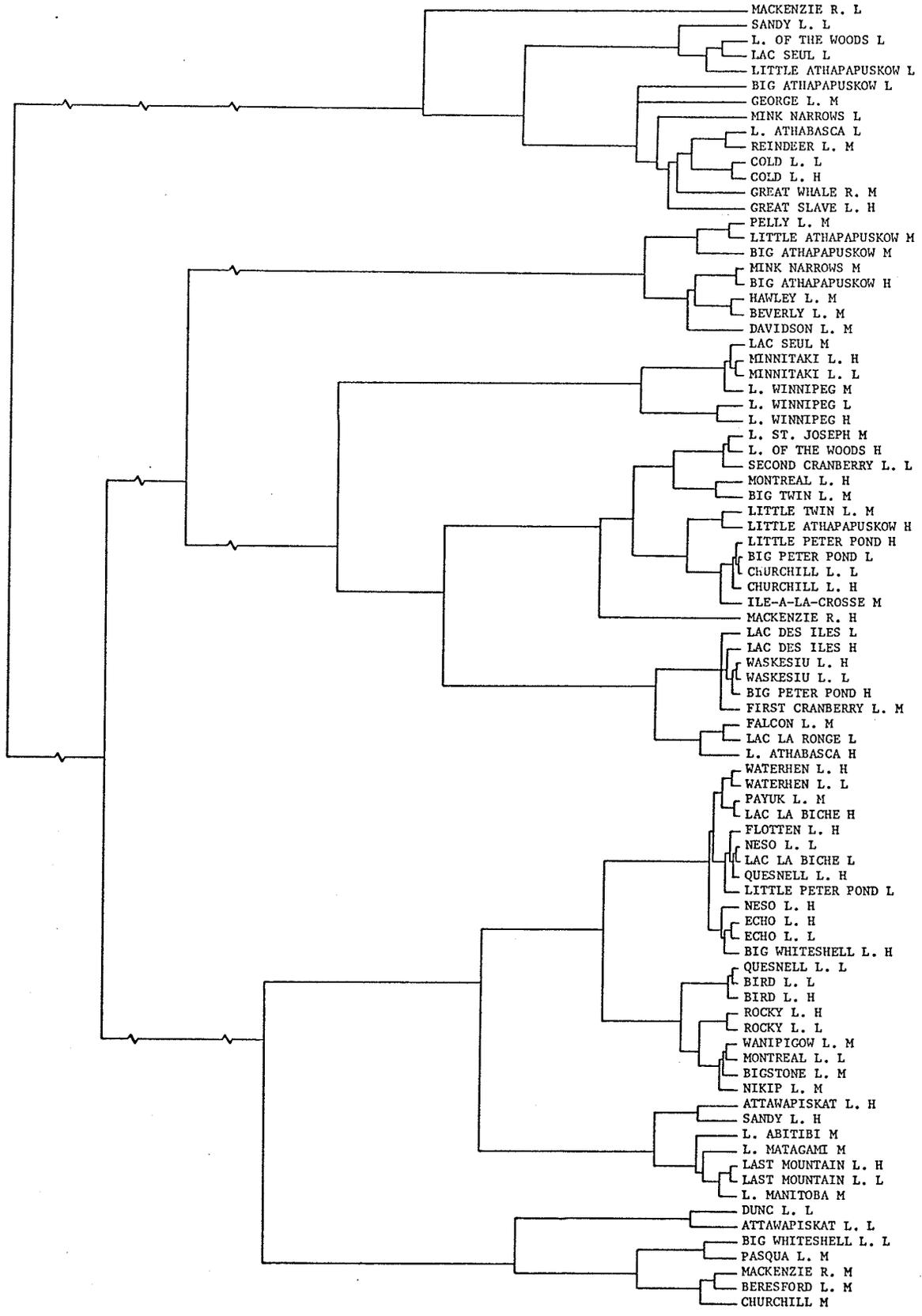
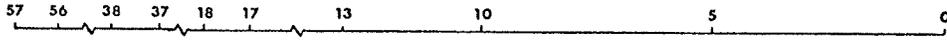
group, joining the main cluster at 1.75. The L. Attawapiskat higher form clustered with the medium forms from L. Abitibi and L. Matagami at 1.11, and these forms joined the main cluster at 1.36. The Sandy L. higher form joined a cluster at 0.80, and this cluster joined the main cluster at 1.20. The Dunc L. lower form clustered with the high group at 1.29. All forms of the high group and the Dunc L. lower form were most similar to members of the high group. It was concluded that the Dunc L. lower form and the five atypical high group forms, with the possible exception of the L. Athabasca higher form, belong in the high group.

In summary, the results from the mean square distance were in agreement with the results of R-mode factor analysis in the division of the forms into four groups, but raised questions as to the true affinity of the Little Athapapuskow and Mink Narrows lower forms and of the L. Athabasca higher form.

Information Analysis

Information is a physical property of data related to probability, with rare events having a higher information content than common events (Orloci 1968). A phenogram drawn from the results of information analysis of the 86 forms is shown in Fig. 7. The analysis showed the existence of three major clusters, which fused at information levels

Fig. 7. Phenogram of the 86 forms constructed from the results of information analysis. The "l," "m" or "h" after each locality refers to the designation of the form as lower, medium or higher in Table II.



INFORMATION

of 37.38 and 56.88. Although they were not distinct from these clusters, the last two forms to join with a cluster were the Mackenzie R. higher and lower forms; the former joined at 3.98 and the latter at 8.77.

The cluster that joined the other major clusters at 56.88 contained the eight forms composing the low group (including the Little Athapuskow lower form), the Mink Narrows lower form, four members of the high group (the Cold L. higher and lower forms, the Great Whale R. medium form and the Great Slave L. higher form), and the Mackenzie R. lower form.

The five members of the high group, whose factor scores had suggested they might form a separate group, did not cluster together. The higher forms from Attawapiskat L. and Sandy L. and the medium forms from L. Abitibi and L. Matagami clustered with the L. Manitoba medium form and the Last Mountain L. higher and lower forms as part of one of the two high group clusters. The L. Athabasca higher form was part of the other high group cluster. The levels at which the five forms joined their clusters, 1.20 or less, did not suggest that these forms were atypical. The Dunc L. lower form joined the high group cluster that contained the L. Abitibi medium form. Evidence for two distinct clusters of high group forms was absent from the results of mean square distance.

In summary, information analysis gave similar results to those of the preceding methods.

Q-mode Factor Analysis

One factor was extracted from the correlation matrix of the 86 forms. The factor loadings ranged from 0.48 to 0.84, and a histogram of these loadings is shown in Fig. 8.

The members of the low group had loadings ranging from 0.48 to 0.66, and the high group had a range of loadings between 0.58 and 0.84. Three forms of the low group (the lower forms from Big and Little Athapapuskow, and the George L. medium form) and the Mink Narrows lower form had loadings of less than 0.56, outside of the range of the high group, indicating that the Little Athapapuskow lower form is a member of the low group, and identifying the Mink Narrows lower form as a member of the low group. The other five members of the low group had loadings between 0.58 and 0.66, overlapping with nine forms of the high group.

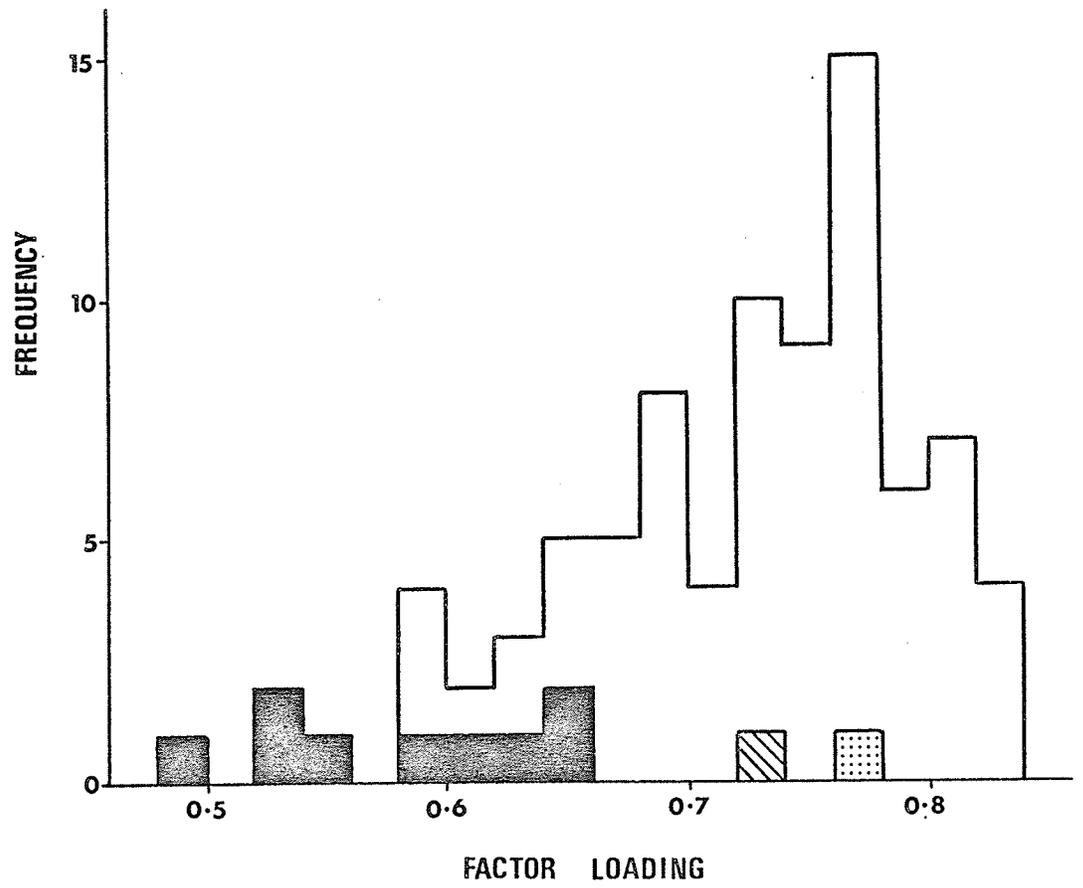
The Mackenzie R. higher and lower forms, with loadings of 0.77 and 0.73 respectively, on this basis, could not be distinguished from members of the high group.

R-mode Factor Analysis of Morphological and Environmental Variables

Correlation between morphological and 19 environ-

Fig. 8. Histogram of factor loadings from
Q-mode factor analysis for the 86 forms.

Key: low group , high group , Mackenzie
R. lower form , Mackenzie R. higher form .



mental variables was investigated by R-mode factor analysis. The lower forms from Dunc L. and Mink Narrows were excluded from the analysis as were the Beverly L., L. Matagami and Pelly L. medium forms, as the depths of those three lakes were not known, and the forms from Churchill, Great Whale R. and Mackenzie R., as these localities are not lakes. This left 76 forms to be considered in the analysis.

The main method of separating the high and low groups had been the scores of factor III based on the gillrakers (Table III). When factors were calculated for the morphological and the environmental variables (Table V), it was found that variation in the morphological variables was associated with environmental differences, except for the sixth factor which is largely a gillraker factor. Factor scores of this sixth factor separated the high group, with scores from 0.95 to 2.11, from the low group, with scores from -4.20 to -1.26, except for the Sandy L. lower form with a score of -0.45, but the Sandy L. lower form had not been separated from the high group by the factor scores of the gillraker factor in the original analysis. Factor scores of factor VI also showed that there was no distinct sub-group within the high group. It was concluded that the main basis of separating the low and high groups was not associated with the 19 environmental variables. Environmental variation within the low and high groups will be dealt with more fully below.

TABLE V

Rotated factor matrix of the morphological and environmental variables for the low and high groups. Factor loadings greater than 0.30 are underlined.

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Cum. % variance	25.36	40.43	54.12	62.02	67.42	72.21	<u>76.54</u>	79.83
% variance	25.36	15.07	13.69	7.90	5.40	4.79	4.33	3.29
<u>Morphological variable</u>								
Av. fork l.	.12	<u>.67</u>	.11	-.07	<u>.44</u>	.24	-.14	-.17
Max. fork l.	.09	<u>.75</u>	<u>.34</u>	.04	.27	.25	-.20	-.06
Body d.	.00	<u>.82</u>	-.21	.07	-.12	.23	.12	-.04
Pectoral l.	-.17	<u>.59</u>	<u>-.51</u>	.08	.08	.25	<u>.36</u>	-.10
Pelvic l.	-.12	<u>.63</u>	<u>-.49</u>	.09	.13	.26	<u>.38</u>	-.10
Head l.	<u>-.48</u>	.04	-.26	.07	<u>.52</u>	-.04	<u>.41</u>	.15
Eye diam.	<u>-.36</u>	.05	<u>-.63</u>	-.21	.02	-.16	-.10	-.11
Snout l.	<u>-.39</u>	<u>-.54</u>	.24	-.03	.29	-.23	.07	.15
Upper jaw l.	<u>-.44</u>	<u>-.48</u>	-.25	-.24	.21	-.22	-.09	.19
Mandible l.	<u>-.50</u>	<u>-.58</u>	-.23	-.19	.13	-.06	-.16	.05
Interorbital w.	.21	<u>.72</u>	.16	.22	-.22	.20	.05	.10

(cont'd)

TABLE V (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Premaxillae w.	-.20	<u>.62</u>	-.16	-.00	.06	.03	.01	-.02
Gillraker l.	-.14	-.02	-.19	-.17	-.26	<u>.73</u>	.10	-.10
Profile	<u>-.43</u>	.04	-.04	<u>-.30</u>	.08	.25	-.04	.03
Premaxilla ang.	.09	.22	-.00	-.23	-.02	-.24	-.11	<u>-.66</u>
Lateral line scales	<u>.49</u>	.09	<u>.52</u>	-.29	.22	.07	.23	.26
Upper rakers	.11	<u>.40</u>	.13	.03	.06	<u>.86</u>	-.01	.01
Lower rakers	.14	<u>.36</u>	.10	.05	.04	<u>.87</u>	.01	.05
Total rakers	.13	<u>.38</u>	.12	.05	.05	<u>.87</u>	.00	.04
<u>Environmental variable</u>								
Latitude	-.11	-.07	<u>.67</u>	<u>-.68</u>	-.06	.02	.15	-.04
Longitude	-.03	-.00	<u>.88</u>	-.11	-.09	.02	<u>.35</u>	-.07
Altitude	.20	.01	.26	<u>.33</u>	-.09	.07	<u>.73</u>	.06
January temp.	.21	.11	-.19	<u>.84</u>	-.06	.03	.25	-.04
July temp.	.16	.03	-.05	<u>.83</u>	.04	-.04	-.38	.17
Degree days	.20	.12	-.11	<u>.91</u>	-.10	.03	-.07	.06
Snow cover	-.02	-.18	-.03	<u>-.83</u>	-.01	.03	-.25	.21
Frost free days	.05	-.08	<u>-.40</u>	.23	-.02	-.00	<u>-.75</u>	.05
Precipitation	.05	.03	<u>-.89</u>	.20	.09	-.05	-.04	.12
Lake area	<u>-.95</u>	-.01	.03	-.17	-.06	-.07	.06	.04

(cont'd)

TABLE V (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Lake l.	<u>-.97</u>	-.02	.02	-.11	-.04	-.05	-.02	.03
Lake w.	<u>-.90</u>	.04	-.02	-.20	-.03	-.12	.09	.08
Shoreline l.	<u>-.97</u>	-.08	-.03	-.12	-.01	-.07	-.03	.05
Shoreline dev.	<u>-.71</u>	-.21	-.15	.03	.09	-.03	-.22	.06
Max. depth	<u>-.47</u>	<u>-.55</u>	<u>.38</u>	-.27	.19	-.15	.08	-.14
TDS	-.21	-.10	<u>.48</u>	.01	<u>-.69</u>	.01	.11	.15
TDS/Max. depth	<u>.32</u>	<u>.45</u>	-.06	.26	<u>-.61</u>	.15	-.01	.22
Drainage basin area	<u>-.88</u>	-.02	.05	.01	.06	.08	.13	<u>-.35</u>
Flushing index	-.02	-.02	.04	.28	.20	.26	.12	<u>-.68</u>

Summary - Although differing in details, the results of R-mode factor analysis, mean square distance, information analysis and Q-mode factor analysis of the same data suggested that the 86 forms of ciscoes composed four groups. The Mackenzie R. lower form and the Mackenzie R. higher form composed two separate groups; the lower forms from L. Athabasca, Big Athapapuskow, Lac Seul, Lake of the Woods, Little Athapapuskow, Mink Narrows and Sandy L., together with the medium forms from George L. and Reindeer L. composed the low group; the remaining 75 forms composed the high group. Two forms in this high group occurred sympatrically in 20 lakes, and three in L. Winnipeg. Differences in gillrakers, the main basis of differentiating between the low and high groups, was not associated with variation in any of the 19 environmental variables.

THE DIFFERENCES BETWEEN FORMS
WHEN THEY ARE SYMPATRIC

Materials and Methods

The same material was used as in the previous section. In the equating of forms of ciscoes, a form of the low and high group had been found sympatrically in seven localities (L. Athabasca, Big Athapapuskow, Lac Seul, L. of the Woods, Little Athapapuskow, Mink Narrows and Sandy L.). Three sympatric forms of the high group occurred in L. Winnipeg, and two sympatric forms of the high group occurred in 20 lakes (Attawapiskat, Big Athapapuskow, Big Peter Pond, Big Whiteshell, Bird, Churchill L., Cold, Echo, Lac des Iles, Lac la Biche, Last Mountain, Little Athapapuskow, Little Peter Pond, Minnitaki, Montreal, Neso, Quesnell, Rocky, Waskesiu, Waterhen). The three sympatric forms found in the Mackenzie R. belong to different groups; the Mackenzie R. lower and higher forms each formed a separate group, and the Mackenzie R. medium form was placed in the high group.

Methods of mathematical analysis were also similar to those used in previous sections, except where outlined below.

Variation in the Degree of Differences between Sympatric Forms

The degree of morphological differences between sym-

patric forms was examined by calculating mean square distances. This value was highest (3.19) between the Mackenzie R. higher and lower forms, the latter very distinctive form also differing by 2.30 from its third sympatric partner, the medium form (a member of the high group). The distance between the Mackenzie R. higher form and the sympatric medium form was 1.53. Where forms of the high group and of the low group occurred sympatrically, their distances varied from 0.89 (Lac Seul) to 1.97 (Big Athapapuskow). But when two forms of the high group occurred sympatrically, their differences were usually much less, with distances ranging from 0.28 (Last Mountain L.) to 1.16 (Montreal L.). In only five of the 22 cases of sympatric occurrence of forms of the high group were the mean square distances as great as in any of the cases of sympatric occurrence of forms of the low and high group.

How Environment Effects Differences between Sympatric Forms

The effect of the 19 environmental variables on the mean square distance between sympatric forms was investigated by R-mode factor analysis. This showed that the presence of a form of the low group and its distance from sympatric forms of the high group was associated most closely with increased lake depth; the correlation between lake depth

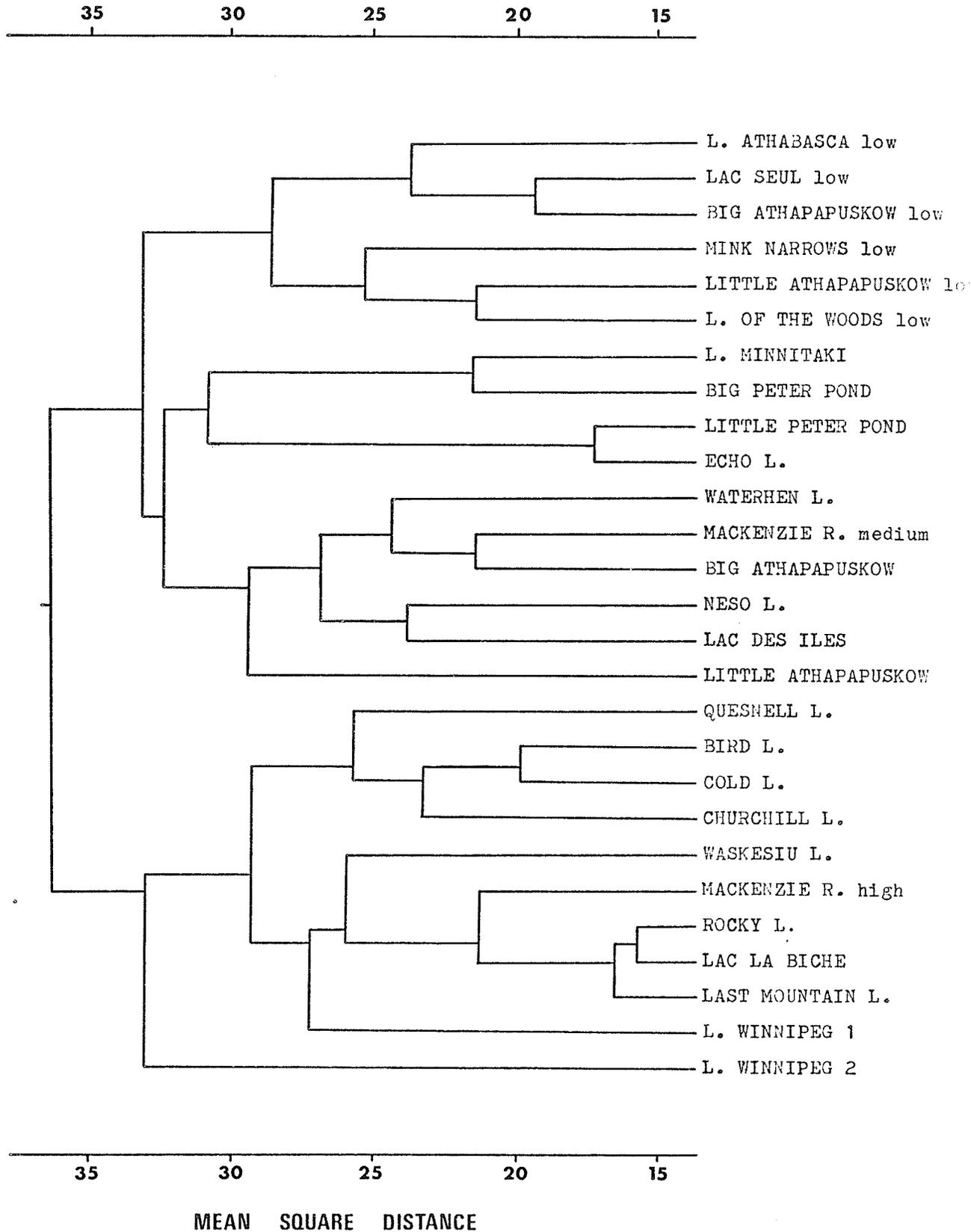
and distance between the sympatric forms of the low and high groups was 0.54, significant at $p < 0.01$ (critical value = 0.37). The factor accounting for distance between sympatric forms of the high group had its next highest loading on total dissolved solids; the two had a correlation of 0.32, significant at $p < 0.05$ (critical values, $p < 0.05 = 0.29$, $p < 0.01 = 0.37$).

Which Characters Differ between Groups when They Occur Sympatrically?

Mean square distances were calculated between the discriminant functions that had been found in the separation of sympatric forms of ciscoes (Table I) to see if the discriminant functions separating sympatric forms were arrangeable into groups corresponding to the four groups found in the previous section, and to see which morphological variables differ between the groups when they occur sympatrically. The phenogram (Fig. 9) showed that all discriminant functions that separated a form of the low group from a form of the high group clustered at 28.6. The functions separating sympatric forms of the high group and the Mackenzie R. forms gave two clusters. The first high group cluster joined the low group cluster at 33.2, and these two clusters joined the second high group cluster at 36.4.

The sums of the squared coefficients and the average

Fig. 9. Phenogram of the discriminant functions separating sympatric forms of ciscoes, constructed from a matrix of mean square distances by the average linkage unweighted group pair method. "Low" refers to discriminant functions separating sympatric forms of the low group from forms of the high group; "medium" refers to discriminant functions separating the Mackenzie R. lower form from the sympatric medium form, and "high" to the discriminant function separating the Mackenzie R. higher and lower forms.



of the coefficients were calculated for each of the three clusters, and the values are given in Table VI. These results showed that gillraker counts accounted for most variance in the low group cluster, whereas fork length accounted for most variance in the two high group clusters. The two high group clusters differed mainly in the sign of the coefficients. Mean square distances were calculated between the averaged coefficients of the three clusters. When the signs of the coefficients were included in the analysis, the low group cluster was more similar to the first high group cluster (11.3) than to the second high group cluster (12.5); the distance between the two high group clusters was 15.6. When the signs of the coefficients were excluded from the analysis the two high group clusters were most similar (2.7); the low group cluster was more similar to the first high group cluster (8.5) than to the second high group cluster (9.4).

Interactions between the Degree of Morphological Difference and the Environment in the High Group

Variation in the magnitude of the morphological differences between sympatric forms of the high group was investigated by R-mode factor analysis that included the environmental variables. Table VII shows the matrix of factor loadings. The first factor showed that an increased difference in gillraker counts was associated with increased

TABLE VI

Sum of squared coefficients and the average of coefficients for the three clusters of discriminant functions found in the separation of sympatric forms of ciscoes

Cluster:	Sum of squared coefficients			Average of coefficients		
	High		Low	High		Low
	One	Two		One	Two	
<u>Morphological variable</u>						
Fork l.	22.4	27.8	5.8	0.41	-0.46	0.08
Body d.	0.5	1.4	0.4	0.02	-0.03	0.03
Head l.	5.8	11.3	11.5	0.09	-0.12	-0.09
Eye diam.	4.2	0.3	1.9	0.06	0.02	-0.04
Snout l.	5.4	8.3	4.1	-0.08	0.18	-0.12
Interorbital w.	5.4	6.3	8.0	-0.17	0.10	0.22
Upper jaw l.	7.4	4.5	7.2	-0.10	0.09	-0.23
Mandible l.	4.6	4.5	2.7	-0.01	-0.11	0.01
Premaxillae w.	3.7	3.8	1.1	-0.08	0.01	-0.06
Gillraker l.	3.7	3.7	3.5	-0.02	-0.10	0.16
Pectoral l.	10.7	6.3	7.9	-0.12	0.17	0.08
Pelvic l.	11.8	10.0	5.4	-0.02	0.14	-0.01
Profile	8.1	8.1	1.8	0.02	0.12	0.02

(cont'd)

TABLE VI (cont'd)

Cluster:	Sum of squared coefficients			Average of coefficients		
	High		Low	High		Low
	One	Two		One	Two	
<u>Morphological variable</u>						
Premaxilla ang.	1.9	0.2	1.2	0.00	0.03	-0.06
Lateral line scales	1.6	0.8	0.8	-0.04	0.01	-0.05
Upper rakers	0.9	2.0	7.0	0.06	0.11	0.22
Lower rakers	2.1	0.7	29.8	0.05	0.04	0.52

TABLE VII

Rotated factor matrix from R-mode factor analysis of environmental variables and the magnitude of morphological differences between sympatric forms of the high group. Factor loadings greater than 0.30 are underlined.

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Cum. % variance	24.08	39.84	52.36	62.88	70.86	76.55	81.36	84.94
% variance	24.08	15.76	12.52	10.52	7.98	5.69	4.81	3.58
<u>Morphological variable</u>								
Av. fork l.	<u>.73</u>	.08	-.09	.22	<u>-.50</u>	-.05	-.18	-.00
Max. fork l.	<u>.66</u>	-.26	-.08	<u>.36</u>	-.17	.05	.07	<u>-.37</u>
Body d.	.11	-.03	.10	<u>.80</u>	.15	-.23	.18	-.29
Pectoral l.	<u>.85</u>	-.13	.01	-.07	.07	-.20	-.00	-.15
Pelvic l.	<u>.75</u>	.05	.25	.08	<u>.31</u>	.11	.10	.01
Head l.	<u>.35</u>	.03	-.23	<u>.73</u>	.19	-.08	.20	-.16
Eye diam.	<u>.43</u>	<u>.38</u>	<u>-.47</u>	-.07	<u>-.31</u>	.22	-.08	<u>-.34</u>
Snout l.	.11	-.05	.16	.09	-.19	.03	<u>-.73</u>	-.16
Upper jaw l.	.17	.21	-.25	.11	.11	-.18	<u>.53</u>	<u>-.53</u>

(cont'd)

TABLE VII (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
<u>Morphological variable</u>								
Mandible l.	-.02	.17	.03	.29	.05	-.01	<u>.40</u>	<u>-.78</u>
Interorbital w.	-.12	<u>.54</u>	.26	-.02	.17	-.08	<u>.45</u>	-.13
Premaxillae w.	-.26	<u>.65</u>	-.08	<u>.39</u>	.04	-.24	<u>.31</u>	-.02
Gillraker l.	<u>.34</u>	<u>.34</u>	<u>-.43</u>	<u>.33</u>	-.04	-.10	-.01	<u>-.38</u>
Profile	.01	.04	.03	.20	.01	<u>.32</u>	-.03	<u>-.85</u>
Premaxilla ang.	.10	.18	-.24	-.08	<u>-.39</u>	<u>-.53</u>	<u>.35</u>	<u>-.47</u>
Lateral line scales	<u>.43</u>	.20	-.22	<u>.34</u>	-.29	.19	<u>.48</u>	.05
Upper rakers	<u>.80</u>	-.03	-.15	-.14	-.28	.02	.01	-.07
Lower rakers	<u>.81</u>	.21	-.10	.20	<u>-.34</u>	-.08	.23	.13
Total rakers	<u>.80</u>	.15	-.15	.14	<u>-.37</u>	-.02	.18	.11
<u>Environmental variable</u>								
Latitude	.06	.04	<u>.74</u>	-.05	<u>-.63</u>	-.00	.13	.05
Longitude	-.20	-.01	<u>.96</u>	-.03	-.02	.04	.06	.08
Altitude	-.19	-.10	<u>.70</u>	-.06	.26	.25	.24	<u>.34</u>
January temp.	-.08	-.12	.06	-.10	<u>.80</u>	.28	-.01	.19
July temp.	-.12	-.20	<u>-.34</u>	.15	<u>.65</u>	-.21	<u>-.33</u>	<u>-.30</u>
Degree days	-.15	-.13	-.07	.15	<u>.92</u>	-.08	-.03	-.16
Snow cover	<u>.37</u>	-.06	-.24	.07	<u>-.83</u>	.02	.06	-.05

(cont'd)

TABLE VII (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
<u>Environmental variable</u>								
Frost free days	<u>.44</u>	-.10	<u>-.56</u>	.28	<u>.37</u>	-.13	-.16	<u>-.33</u>
Precipitation	.02	.03	<u>-.92</u>	-.09	-.11	.07	.10	.16
Lake area	.02	<u>.94</u>	.14	.04	-.21	.09	.03	-.06
Lake l.	.15	<u>.93</u>	-.01	.05	-.00	.02	-.06	-.12
Lake w.	-.12	<u>.91</u>	-.08	-.03	-.20	.04	.07	-.07
Shoreline l.	.21	<u>.94</u>	-.06	.06	-.15	.12	-.06	-.03
Shoreline development	<u>.51</u>	<u>.43</u>	<u>-.38</u>	.10	-.03	.18	-.28	.11
Max. depth	.11	<u>.33</u>	<u>.33</u>	-.06	-.03	<u>.81</u>	-.03	-.21
TDS	<u>.39</u>	<u>.44</u>	<u>.69</u>	.16	-.09	.01	-.14	-.10
TDS/Max. depth	.16	-.04	.20	.26	-.04	<u>-.88</u>	-.06	.08
Drainage basin area	-.01	<u>.77</u>	-.03	<u>-.55</u>	.15	.15	.10	.09
Flushing index	.04	-.16	-.20	<u>-.68</u>	<u>.51</u>	-.02	.17	.16

differences in fork length, paired fin lengths, eye diameter, head length, gillraker length and lateral line scale numbers, and all the increased differences were associated with a higher shoreline development, more dissolved solids, more frost free days and a longer lasting snow cover. Similarly the remaining seven factors in Table VII can be seen to show certain correlations between morphological characters and the environment, although the significance and underlying mechanism of these correlations is not clear.

Multiple regression was used to predict the magnitude of the morphological differences between sympatric members of the high group; lake area frost free days, degree days, total dissolved solids and maximum lake depth were used to predict the differences. In addition differences in maximum and average fork lengths were used to predict all differences except for maximum and average fork lengths. Multiple correlation coefficients ranged from 0.44 (snout length) to 0.82 (lower and total number of gillrakers), but the regression was only significant for average fork length, eye diameter, lower and total gillraker numbers. Details of the significant regressions are shown in Table VIII. Frost free days and degree days were of most use in predicting differences in average fork length, and differences in average fork length were of most use in predicting the differences in eye diameter, and in lower and total gillraker

TABLE VIII

Multiple regression of the magnitude of the morphological differences between sympatric forms of the high group. Only variables for which the regression was significant are given. Critical values: av. fork l., $F_{0.01} = 4.56$,

$t_{0.05} = 2.13$, $t_{0.01} = 2.95$; all other variables, $F_{0.05} = 2.84$,
 $F_{0.01} = 4.44$, $t_{0.05} = 2.16$, $t_{0.01} = 3.01$.

Variable	F-test	Multiple correlation coefficient	y intercept	Max. fork l. mm.	Av. fork l. mm.	Lake area mi. ²	Frost free days	Degree days	TDS ppm.	Max. depth m.
Av. fork l.	4.99**	0.79	4.70			0.006	2.454	-6.716	0.627	-0.230
						0.01	0.58	-0.69	0.41	-0.19
						0.06	3.23**	3.84**	2.04	0.98
Eye diam.	3.38*	0.80	-0.37	-0.041	0.169	0.050	0.636	-0.586	-0.152	0.129
				-0.17	0.53	0.32	0.47	-0.19	-0.31	0.33
				0.68	1.70	1.50	1.83	0.71	1.31	1.55
Lower rakers	3.75*	0.82	0.45	0.139	0.311	0.055	0.397	-1.208	0.121	-0.089
				0.25	0.44	0.16	0.13	-0.17	0.11	-0.10
				1.05	1.46	0.77	0.53	0.68	0.49	0.50

(cont'd)

TABLE VIII (cont'd)

Variable	F-test	Multiple correlation coefficient	y inter-cept	Max. fork l. mm.	Av. fork l. mm	Lake area mi. ²	Frost free days	Degree days	TDS ppm.	Max. depth m.
Total rakers	3.70*	0.82	0.68	0.116	0.353	0.027	0.857	-1.975	0.099	-0.000
				0.19	0.44	0.07	0.25	-0.25	0.08	-0.00
				0.77	1.45	0.32	1.00	0.97	0.35	0.00

b
standardised b
t-test

** significant at $p < 0.01$.

* significant at $p < 0.05$.

All other F and t values are not significant.

numbers.

Consistency of Differences between Sympatric Forms

The sign test was used to test the consistency of the sign of each variable between sympatric forms of the high group. If the sympatric forms were arranged on the basis of their relative gillraker counts, the only significant consistency in the 23 forms was that 74% of the forms with the higher gillraker count had a higher average fork length. If the sympatric forms were arranged by their relative average fork lengths, 74% of the larger forms had higher gillraker counts, 78% had more lateral line scales and 80% had longer pectoral fins; variation in the magnitude of these differences are associated with variation in some environmental variables (see above and factor I in Table VIII).

All seven forms of the low group had fewer gillrakers, a longer upper jaw and a longer snout than the sympatric forms of the high group; six forms of the low group had a longer head, shorter gillrakers and a larger premaxilla angle than in the high group.

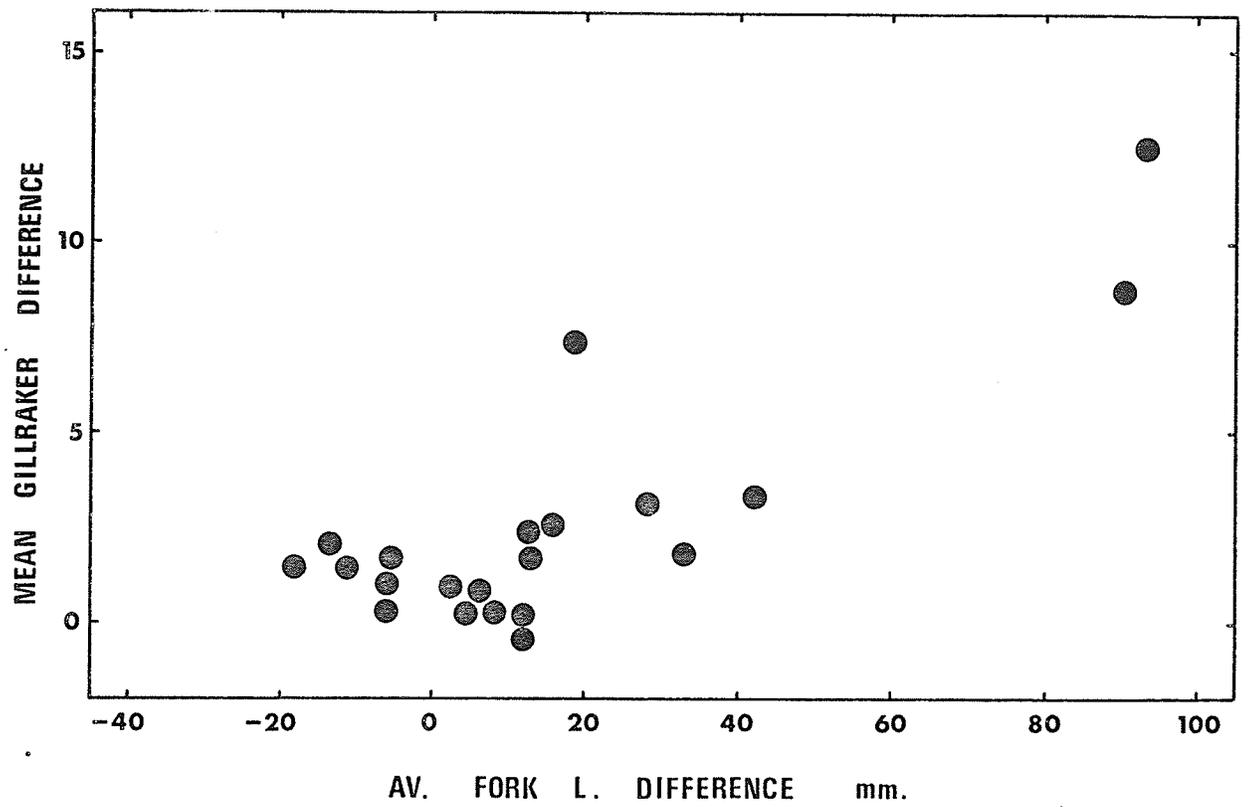
Gillraker Differences between Sympatric Forms

The interrelationships of differences in gillraker number and average fork length were investigated further

because gillraker numbers were most useful in separating sympatric forms of the low and high groups, and fork length was most useful in separating sympatric forms of the high group. If a member of the low group occurred sympatrically with more than one form of the high group, the differences between the low group and the forms of the high group were averaged. The difference between gillraker counts was plotted against the difference in fork lengths for sympatric members of the low and high group; there was no significant correlation between the two variables, $r = 0.03$ (critical value, $p < 0.05 = 0.75$). In contrast the correlation between the two variables for sympatric forms of the high group (Fig. 10) was significant, $r = 0.83$ (critical value, $p < 0.01 = 0.55$).

Summary - Study of the differences between sympatric forms of ciscoes confirmed the distinctive nature of the Mackenzie R. lower form, the Mackenzie R. higher form, the low group and the high group. There was more consistency in the differences between sympatric pairs of forms belonging one each to the low and to the high groups, than between sympatric pairs (or trios) of forms both belonging to the high group. When occurring sympatrically with high group forms, forms of the low group had fewer gillrakers and longer snouts and upper jaws than the high group forms, whereas differences

Fig. 10. Plot of the differences of gill-raker numbers against differences in fork length for sympatric forms of the high group.



between sympatric forms of the high group were related mainly to differences in fork length. Variation in the differences between sympatric forms of the high group were associated with variation in certain of the 19 environmental parameters and with size differences.

MORPHOLOGICAL VARIATION WITHIN THE HIGH GROUP AND THE LOW GROUP

Morphological variation within each group was investigated by R-mode factor analysis using the environmental variables for each group and the morphological data for each form. The same forms were excluded as were excluded in the section entitled "R-mode Factor Analysis of Morphological and Environmental Variables"; this left 68 high group forms and eight low group forms to be considered in the analyses.

Morphological Variation within the High Group

The factor loadings from the analysis of the high group are shown in Table IX. The first factor showed that decreased lake size was associated with decreased lake depth and dissolved solids, and these were associated with increased scale numbers, decreased profile, shorter jaws and head, and a smaller eye. Factor II showed the precipitation and frost free days increased and dissolved solids decreased to the south and east; this was associated with increased eye diameter and upper jaw length, and decreased scale numbers. Increased gillraker numbers were associated with a longer fork length (factor III). Fewer scales were associated with warmer temperatures to the south (factor

TABLE IX

Rotated factor matrix from R-mode analysis of morphological and environmental variables of the high group. Factor loadings greater than 0.30 are underlined.

	Factor							
	I	II	III	IV	V	VI	VII	VIII
Cum. % variance	23.97	39.46	51.04	60.92	67.97	73.24	77.29	80.57
% variance	23.97	15.49	11.58	9.88	7.05	5.27	4.05	3.28
<u>Morphological variable</u>								
Av. fork l.	.12	.05	<u>.64</u>	-.17	-.31	-.05	-.28	<u>-.38</u>
Max. fork l.	.10	-.10	<u>.56</u>	-.01	<u>-.37</u>	.11	-.16	<u>-.51</u>
Body d.	-.07	.07	.24	.07	<u>-.83</u>	-.11	-.12	-.07
Pectoral l.	-.24	.12	.23	.14	<u>-.68</u>	<u>-.54</u>	-.15	-.07
Pelvic l.	-.18	.13	.21	.14	<u>-.66</u>	<u>-.58</u>	-.17	.01
Head l.	<u>-.43</u>	-.02	.09	.10	.07	<u>-.78</u>	.05	-.03
Eye diam.	<u>-.39</u>	<u>.53</u>	-.23	-.20	-.20	-.17	-.04	.10
Snout l.	-.22	-.24	-.16	-.00	<u>.65</u>	-.09	.05	.17
Upper jaw l.	<u>-.32</u>	<u>.30</u>	-.12	-.21	<u>.42</u>	-.11	.13	<u>.54</u>
Mandible l.	-.44	.27	-.03	-.14	.46	-.00	.08	.47
Interorbital w.	.27	-.23	.06	.27	-.69	.28	.02	-.19

(cont'd)

TABLE IX (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
<u>Morphological variable</u>								
Premaxillae w.	-.01	.24	-.16	-.02	<u>-.65</u>	-.15	-.07	-.18
Gillraker l.	-.17	.13	.02	-.09	.14	.06	-.05	<u>.75</u>
Profile	<u>-.49</u>	.11	.13	-.29	<u>.34</u>	-.12	-.02	-.05
Premaxilla ang.	.05	-.01	.27	-.16	-.26	.26	<u>-.70</u>	.06
Lateral line scales	<u>.51</u>	<u>-.47</u>	.15	<u>-.36</u>	.13	-.15	.21	-.26
Upper rakers	.10	-.02	<u>.94</u>	.01	-.09	-.04	-.06	-.04
Lower rakers	.08	-.04	<u>.95</u>	.05	-.07	-.06	.02	.07
Total rakers	.09	-.03	<u>.97</u>	.04	-.08	-.05	-.01	.03
<u>Environmental variable</u>								
Latitude	-.09	<u>-.66</u>	.05	<u>-.63</u>	.20	.10	.03	-.17
Longitude	-.02	<u>-.88</u>	.04	.06	.15	.05	-.00	-.29
Altitude	.21	<u>-.67</u>	-.02	<u>.46</u>	-.08	-.27	.03	.17
January temp.	.15	-.04	-.03	<u>.86</u>	-.16	-.15	-.12	.10
July temp.	.07	.23	.09	<u>.82</u>	-.01	.05	.20	-.29
Degree days	.09	.06	.09	.93	-.15	.05	.06	-.05
Snow cover	.02	.18	.07	-.85	.14	.08	.25	.12

(cont'd)

TABLE IX (cont'd)

	Factor							
	I	II	III	IV	V	VI	VII	VIII
<u>Environmental variable</u>								
Frost free days	.01	<u>.75</u>	.14	.30	.03	<u>.31</u>	.16	-.13
Precipitation	.04	<u>.74</u>	-.14	.11	-.25	-.28	.05	<u>.37</u>
Lake area	<u>-.95</u>	-.11	-.08	-.12	.02	-.03	.04	.11
Lake l.	<u>-.97</u>	-.02	-.06	-.07	.04	-.02	.04	.07
Lake w.	<u>-.89</u>	-.07	-.17	-.18	-.02	-.11	.08	.06
Shoreline l.	<u>-.97</u>	.02	-.07	-.06	.08	-.05	.08	.11
Shoreline development	<u>-.68</u>	.30	-.03	.10	.19	-.08	.25	.12
Max. depth	<u>-.41</u>	-.28	-.17	-.28	<u>.67</u>	-.03	-.17	-.00
TDS	<u>-.38</u>	<u>-.62</u>	-.08	-.01	-.01	<u>.40</u>	.24	.07
TDS/Max. depth	.18	-.12	.12	.28	<u>-.70</u>	.29	<u>.34</u>	.05
Drainage basin area	<u>-.84</u>	-.09	-.06	.05	.07	-.18	<u>-.38</u>	.03
Flushing index	.07	.02	.02	.28	.09	-.25	<u>-.68</u>	-.10

III). Fewer scales were associated with warmer temperatures to the south (factor IV). Factor V showed that increased lake depth was associated with decreased body depth, fork length, paired fin lengths, and interorbital and premaxillae widths, and with increased snout length and jaw lengths. Increased dissolved solids and frost free days were associated with shorter paired fins and head (factor VI). A decreased flushing index was associated with a decreased premaxilla angle (factor VII). Increased precipitation was associated with increased gillraker and jaw lengths, and decreased fork length (factor VIII).

Factor scores were calculated from the matrix of factor loadings, and did not show any groupings of the forms that could not be accounted for by environmental influences. The factor scores suggested that the second factor might reflect the influence of the Precambrian shield: non-shield forms had scores from -1.75 to -0.16, and forms from the shield or the edge of the shield had scores from -0.18 to 1.85. The third factor (gillrakers and fork length) did not show any distinct grouping of the forms.

Multiple regression was used to predict values for the morphological variables of the same high group forms from values of the environmental variables. The regressions were significant for all variables except maximum fork length, gillraker length and premaxilla angle, with multiple corre-

lation coefficients ranging from 0.35 for maximum fork length to 0.84 for interorbital width. Details of the regressions are shown in Table X. Maximum lake depth was significant in the prediction of ten variables: maximum and average fork lengths, body depth, eye diameter, interorbital and premaxillae widths and paired fin lengths decreased with increased lake depth, and snout length and profile increased. Lake area was significant in the prediction of nine variables: body depth, head length, eye diameter, jaw lengths and paired fin lengths increased with increased lake area, whereas scale numbers decreased. Gill-raker numbers, scales and premaxilla angle increased and premaxillae width decreased with increased average fork length. Total dissolved solids was significant in the prediction of six variables: head length, eye diameter and paired fin lengths decreased, and interorbital width and scale numbers increased with increased dissolved solids. Eye diameter and mandible length increased with increased numbers of frost free days, whereas interorbital width and scale numbers decreased. Increased maximum fork length was associated with increased body depth, interorbital and premaxillae widths. Eye diameter decreased with increased numbers of degree days.

TABLE X

Multiple regression of the morphological variables for the high group.

Critical values: max. and av. fork l., $F_{0.05} = 2.37$, $t_{0.05} =$

2.00; all other variables, $F_{0.05} = 2.17$, $F_{0.01} = 2.95$,

$t_{0.05} = 2.00$, $t_{0.01} = 2.66$.

Variable	F-test	Multiple correlation coefficient	y intercept	Predictors							Max. depth m.
				Max. fork l. mm.	Av. fork l. mm.	Lake area ² mi.	Frost free days	Degree days	TDS ppm		
Max. fork l.	1.72	0.35	2.72	b	-0.010	-0.105	0.030	0.016	-0.092	-0.092	
				standardised b	-0.09	-0.08	0.02	0.04	-0.31	-0.31	
				t-test	0.67	0.60	0.12	0.27	2.04*	2.04*	
Av. fork l.	3.13*	0.45	3.34	b	0.006	-0.130	-0.326	-0.084	-0.132	-0.132	
				standardised b	0.06	-0.10	-0.18	-0.18	-0.44	-0.44	
				t-test	0.41	0.76	1.35	1.37	2.97*	2.97*	
Body d.	9.00**	0.72	1.58	b	0.252	-0.093	-0.105	0.002	-0.099	-0.099	
				standardised b	0.51	-0.19	-0.12	0.01	-0.68	-0.68	
				t-test	3.24**	1.17	1.10	0.09	5.48**	5.48**	

(cont'd)

TABLE X (cont'd)

Variable	F-test	Multiple correlation coefficient	y inter-cept	Predictors						
				Max. fork l. mm.	Av. fork l. mm.	Lake area mi. ²	Frost free days	Degree days	TDS ppm	Max. depth m.
Head l.	3.74**	0.55	1.71	0.006	-0.011	0.010	-0.051	0.075	-0.036	0.009
				0.03	-0.06	0.49	-0.20	0.22	-0.41	0.17
Eye diam.	7.87**	0.69	1.20	0.15	0.29	3.76**	1.68	1.68	3.13**	1.11
				-0.053	-0.009	0.017	0.146	-0.170	-0.038	-0.026
Snout l.	4.80**	0.60	1.09	-0.18	-0.03	0.55	0.38	-0.33	-0.28	-0.30
				1.11	0.17	4.84**	3.61**	2.87**	2.47*	2.31*
Interorbital w.	20.55**	0.84	0.81	-0.050	0.015	0.000	-0.051	0.062	-0.005	0.032
				-0.24	0.07	0.01	-0.19	0.17	-0.05	0.53
				1.34	0.39	0.08	1.61	1.35	0.39	3.70**
				0.214	-0.099	-0.006	-0.098	0.057	0.058	-0.068
				0.55	-0.26	-0.13	-0.19	0.08	0.32	-0.60
				4.47**	2.04	1.56	2.44*	0.97	3.81**	6.16**

(cont'd)

TABLE X (cont'd)

Variable	F-test	Multiple correlation coefficient	y inter-cept	Predictors							
				Max. fork l. mm.	Av. fork l. mm.	Lake area mi. ²	Frost free days	Degree days	TDS ppm	Max. depth m.	
Upper jaw l.	6.88**	0.67	1.36	-0.086	0.002	0.006	0.035	-0.031	-0.016	0.010	
				standardised b				-0.09	-0.18	0.17	
				t-test				0.75	1.51	1.31	
Mandible l.	8.02**	0.70	1.38	-0.017	-0.028	0.006	0.052	-0.043	-0.014	0.008	
				standardised b				-0.18	-0.22	0.19	
				t-test				1.54	1.96	1.48	
Premaxillae w.	2.85*	0.50	1.05	0.100	-0.088	0.005	-0.008	-0.056	-0.017	0.026	
				standardised b				-0.18	-0.20	-0.48	
				t-test				1.29	1.48	3.14*	
Gillraker l.	1.41	0.38	1.19	-0.040	-0.054	0.007	0.016	-0.049	-0.024	-0.003	
				standardised b				-0.09	-0.17	-0.03	
				t-test				0.62	1.18	0.18 ⁸⁰	

(cont'd)

TABLE X (cont'd)

Variable	F-test	Multiple correlation coefficient	y inter-cept	Predictors	Max. fork l. mm.	Av. fork l. mm.	Lake area mi. ²	Frost free days	Degree days	TDS ppm	Max. depth m.
Pectoral l.	6.70 ^{**}	0.66	1.51	b	0.023	0.036	0.017	-0.063	0.067	-0.033	-0.045
					standardised b	0.08	0.12	0.53	-0.16	0.13	-0.24
Pelvic l.	8.28 ^{**}	0.70	1.56	b	0.45	0.69	4.52 ^{**}	1.46	1.06	2.05 [*]	3.79 ^{**}
					t-test	0.014	0.056	0.019	-0.089	0.084	-0.052
Profile	5.14 ^{**}	0.61	1.83	b	0.04	0.17	0.51	-0.20	0.14	-0.34	-0.48
					t-test	0.26	1.00	4.61 ^{**}	1.94	1.25	3.06 ^{**}
Premaxilla ang.	1.84	0.42	1.30	b	-0.017	0.039	0.004	0.030	-0.024	-0.003	0.018
					t-test	-0.12	0.29	0.27	0.16	-0.10	-0.05
				b	0.67	1.55	2.17 [*]	1.43	0.79	0.42	3.21 ^{**}
					t-test	-0.002	0.158	-0.002	0.008	-0.012	-0.007
				b	-0.01	0.44	-0.04	0.02	-0.02	-0.04	0.12
					t-test	0.03	2.03 [*]	0.27	0.13	0.12	0.30

(cont'd)

TABLE X (cont'd)

Variable	F-test	Multiple correlation coefficient	y inter-cept	Predictors							
				Max. fork l. mm.	Av. fork l. mm.	Lake area mi. ²	Frost free days	Degree days	TDS ppm	Max. depth m.	
Lateral line	11.55**	0.76	1.92	b	-0.007	0.074	-0.015	-0.091	-0.070	0.030	0.010
				standardised b	-0.04	0.35	-0.65	-0.32	-0.19	0.30	0.16
Upper rakers	7.03**	0.67	0.61	t-test	0.25	2.29*	6.35**	3.42**	1.80	2.97**	1.40
				b	0.020	0.183	-0.002	0.023	0.057	0.009	0.010
Lower rakers	4.16**	0.57	0.89	standardised b	0.07	0.65	-0.09	0.06	0.11	0.07	0.12
				t-test	0.41	3.68**	0.77	0.58	0.94	0.62	0.89
Total rakers	5.32**	0.62	1.07	b	0.009	0.166	-0.002	0.038	0.051	0.019	0.004
				standardised b	0.03	0.56	-0.07	0.09	0.10	0.14	0.04
				t-test	0.15	2.88**	0.58	0.80	0.73	1.06	0.28
				b	0.012	0.173	-0.003	0.033	0.053	0.016	0.006
				standardised b	0.04	0.60	-0.08	0.08	0.10	0.12	0.07
				t-test	0.23	3.25**	0.67	0.75	0.83	0.96	0.49

** significant at p < 0.01.

* significant at p < 0.05.

All other F and t values are not significant.

Morphological Variation within the Low Group

Only eight forms were included in the low group analysis, so factor scores and regression equations were not calculated. Since the sample size was so small, less reliance should be placed upon the factor loadings (Table XI) and the interpretation of the factors than for the high group. The first factor is essentially the same as for the high group, but increased lake size was associated with increased fork length and not with profile or scale numbers. The second factor reflected climatic changes to the south and east, with shallower lakes occurring to the south and east; this was associated with increased head and paired fin lengths, decreased premaxilla angle and scale numbers. Higher July temperatures and increased dissolved solids were associated with fewer gillrakers, shorter paired fins, jaws and head lengths, narrower interorbital width, more scales and a more vertical premaxilla (factor III). Increased dissolved solids, shallower lakes and more frost free days were associated with an increased profile, longer gillrakers, increased interorbital width, premaxilla angle and body depth, and a shorter average fork length (factor IV). The fifth factor showed that increased shoreline development was associated with a deeper body, a smaller eye, narrower premaxillae, shorter snout and jaws, shorter average fork length, but increased maximum fork length. The sixth factor

TABLE XI
 Rotated factor matrix from R-mode analysis of
 morphological and environmental variables
 of the low group. Factor loadings
 greater than 0.30 are underlined.

	Factor						
	I	II	III	IV	V	VI	VII
Cum. % variance	34.97	59.97	74.58	84.89	92.33	96.95	99.99
% variance	34.97	22.00	17.61	10.31	7.44	4.62	3.04
<u>Morphological variable</u>							
Av. fork l.	<u>.83</u>	.22	-.18	<u>-.34</u>	<u>-.32</u>	.09	-.09
Max. fork l.	<u>.85</u>	.01	-.09	-.08	<u>.40</u>	<u>.31</u>	-.04
Body d.	.30	.04	-.30	<u>.40</u>	<u>.79</u>	.16	.11
Pectoral l.	.17	<u>.43</u>	<u>-.78</u>	.14	-.24	.26	.18
Pelvic l.	<u>.33</u>	<u>.53</u>	<u>-.68</u>	.24	-.20	.07	.22
Head l.	<u>.46</u>	<u>.56</u>	<u>-.43</u>	-.26	-.26	.09	<u>.37</u>
Eye diam.	<u>.47</u>	.10	-.03	-.00	<u>-.72</u>	<u>.50</u>	-.01
Snout l.	-.10	-.22	-.26	.13	<u>-.81</u>	<u>-.44</u>	.03
Upper jaw l.	-.23	-.27	<u>-.46</u>	.08	<u>-.78</u>	.22	.09
Mandible l.	<u>.39</u>	-.05	<u>-.56</u>	-.02	<u>-.69</u>	-.06	.25
Interorbital w.	.04	.00	<u>-.43</u>	<u>.65</u>	.15	.12	<u>-.59</u>

(cont'd)

TABLE XI (cont'd)

	Factor						
	I	II	III	IV	V	VI	VII
<u>Morphological variable</u>							
Premaxillae w.	<u>.79</u>	-.17	.08	.19	<u>-.54</u>	-.03	.11
Gillraker l.	<u>.54</u>	-.27	<u>-.39</u>	<u>.68</u>	.01	.04	.16
Profile	.24	-.04	.03	<u>.96</u>	-.09	-.09	-.05
Premaxilla ang.	.07	<u>-.42</u>	<u>.45</u>	<u>.46</u>	<u>-.33</u>	<u>-.49</u>	-.24
Lateral line scales	-.25	<u>-.60</u>	<u>.63</u>	-.02	.07	-.14	<u>-.39</u>
Upper rakers	.30	-.17	<u>-.92</u>	.15	.05	-.02	-.09
Lower rakers	.08	-.06	<u>-.97</u>	-.12	-.12	-.13	-.09
Total rakers	.17	-.11	<u>-.97</u>	-.01	-.06	-.09	-.09
<u>Environmental variable</u>							
Latitude	.15	<u>-.96</u>	.04	.08	-.01	-.24	.01
Longitude	.12	<u>-.79</u>	.22	-.14	.15	<u>-.51</u>	-.10
Altitude	-.00	<u>.45</u>	.16	-.11	.13	<u>.86</u>	-.08
January temp.	-.18	<u>.93</u>	.20	-.09	.20	.04	.07
July temp.	-.20	<u>.83</u>	<u>.35</u>	-.22	<u>.31</u>	-.07	-.03
Degree days	<u>-.32</u>	<u>.88</u>	.16	-.22	.15	.06	-.16
Snow cover	-.04	<u>-.90</u>	.10	<u>.31</u>	-.10	.21	.19
Frost free days	<u>-.36</u>	<u>.82</u>	.03	<u>.36</u>	-.02	.17	-.19

(cont'd)

TABLE XI (cont'd)

	Factor						
	I	II	III	IV	V	VII	VII
<u>Environmental variable</u>							
Precipitation	-.02	<u>.87</u>	-.10	.08	-.02	<u>.45</u>	.17
Lake area	<u>.89</u>	-.20	-.29	.24	-.13	-.05	-.07
Lake l.	<u>.92</u>	-.26	-.23	.13	-.02	-.01	.08
Lake w.	<u>.96</u>	.02	-.11	.10	.04	-.12	-.19
Shoreline l.	<u>.96</u>	-.18	-.14	.07	.10	.00	.01
Max. depth	<u>.36</u>	<u>-.81</u>	.22	<u>-.34</u>	.02	-.02	-.24
TDS	<u>-.68</u>	.09	<u>.30</u>	<u>.57</u>	.24	-.23	.00
TDS/Max. depth	<u>-.61</u>	<u>.55</u>	.03	<u>.53</u>	.12	-.11	.15
Drainage basin area	<u>.91</u>	-.23	-.25	.21	-.05	-.07	.04
Flushing index	<u>.88</u>	-.28	-.10	.16	.13	-.10	.30

showed that precipitation increased with altitude in the east, and that this was associated with increased eye diameter and maximum fork length, and a shorter snout and decreased premaxilla angle. The last factor showed an association between fewer scales, decreased interorbital width and increased fork length.

Summary - Much of the variation between forms of the high group and between forms of the low group can be attributed to differences in climate, lake morphometry and chemistry, and the average fork length of the form. Environmental variables can be used to predict the morphology of a form.

OSTEOLOGY

Materials and Methods

Selected skull bones from 63 ciscoes and one whitefish (Table XII) were examined. The ciscoes included representatives of most forms of the low group and any sympatric forms of the high group, representatives of the group that were separable by gillraker counts, representatives of the high group from throughout its range (including both tullibee and lake herring phenotypes), and representatives of the Mackenzie R. lower and higher forms. Skulls were prepared by placing them in 10% KOH for two or three days. The following cranial bones were examined: angular (articular), autopalatine, dentary, hypethmoid, maxilla, premaxilla, prevomer, quadrate, supraethmoid, supralingual plate and supramaxilla; nomenclature follows Harrington (1955). The following measurements (Fig. 2) were found to be of taxonomic value: dentary--maximum distance from the most anterior point to the anterior edge of the coronoid plate; maxilla--minimum vertical height at the junction of the anterior and posterior portions of the distal plate. Differences between the measurements for different groups were tested by analysis of covariance (ANCOVA) (Snedecor and Cochran 1967), using head length as the covariate.

TABLE XII

The localities and numbers of ciscoes and whitefish
used in the examination of skull bones.

Key: MRL - Mackenzie R. lower form,

MRH - Mackenzie R. higher form.

Locality	Form			Group				
	Lower	Medium	Higher	Low	High	MRL	MRH	Whitefish
L. Athabasca	2		1	2	1			
Big Atha- papuskow	2	2	2	2	4			
Churchill		2			2			
Cold L.	1		1		2			
Dunc L.	1		1		2			
Flotten L.	1		1		1			1
George L.		1		1				
Lac la Biche	2		1		3			
Lac la Ronge	1		1		2			
Lac Seul	8	8	1	8	9			
Lake of the Woods	1		1	1	1			
Little Atha- papuskow	1	2	2	1	4			
Lyons L.								1

(cont'd)

TABLE XII (cont'd)

Locality	Form			Group				
	Lower	Medium	Higher	Low	High	MRL	MRH	Whitefish
Mackenzie R.	2	1	2		1	2	2	
Mink Narrows	1	1	1	1	2			
Montreal L.	2		1		3			
L. St. Joseph		1			1			
Second Cran- berry L.	1		1		2			
West Hawk L.		2			2			

Results

The shapes of the angular, autopalatine, hypethmoid, premaxilla, prevomer, quadrate and supramaxilla were not found to be of any use in distinguishing between the four groups. but statistical differences may have been overlooked.

Individuals of the low and high groups showed considerable variation in the shapes of the dentary (Fig. 11), maxilla (Fig. 12), supraethmoid (Fig. 13) and supralingual plate, so that it was not possible to find a single character that separated all individuals of each group. Some generalisations can be made as to the differences between the bones of the two groups, but whereas the generalisations were of use in grouping individuals from one locality, they cannot be relied upon in grouping individuals from different localities. The maxilla of the low group tended to be less deep than in the high group; the supraethmoid had fewer posterior projections than in the high group, and those were often shorter; the supralingual plate of the high group was more spatulate. No consistent differences were found between sympatric forms of the high group, nor between the tullibee and lake herring phenotypes.

One statistical difference between the high and low groups was investigated. This was the maximum distance the

Fig. 11. Representative dentary bones of the four groups. Key: upper left - Mackenzie R. lower form; upper right - Mackenzie R. higher form; centre row - two representatives of low group; bottom row - two representatives of high group.

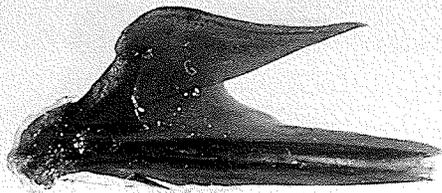
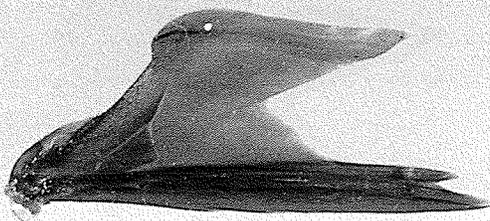
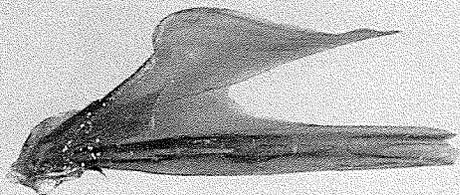
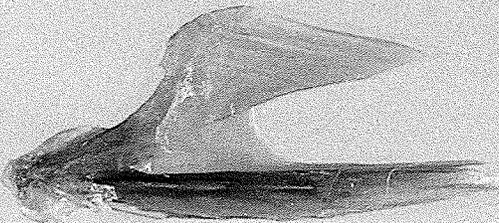
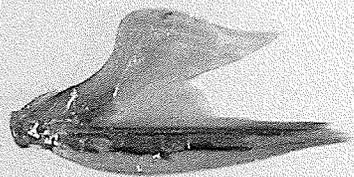
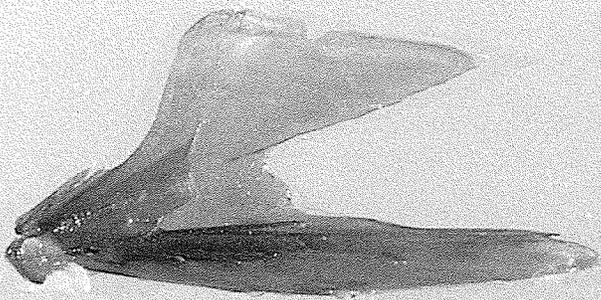


Fig. 12. Representative maxillae of the four groups. Key as in Fig. 11.

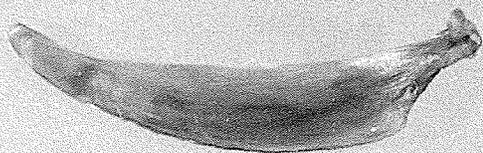
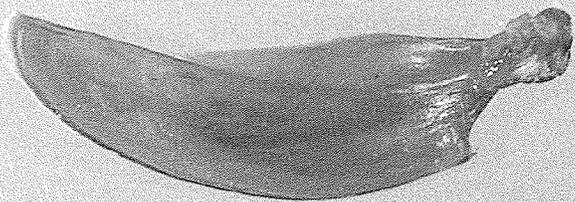


Fig. 13. Representative supraethmoid bones of the four groups. Key as in Fig. 11.

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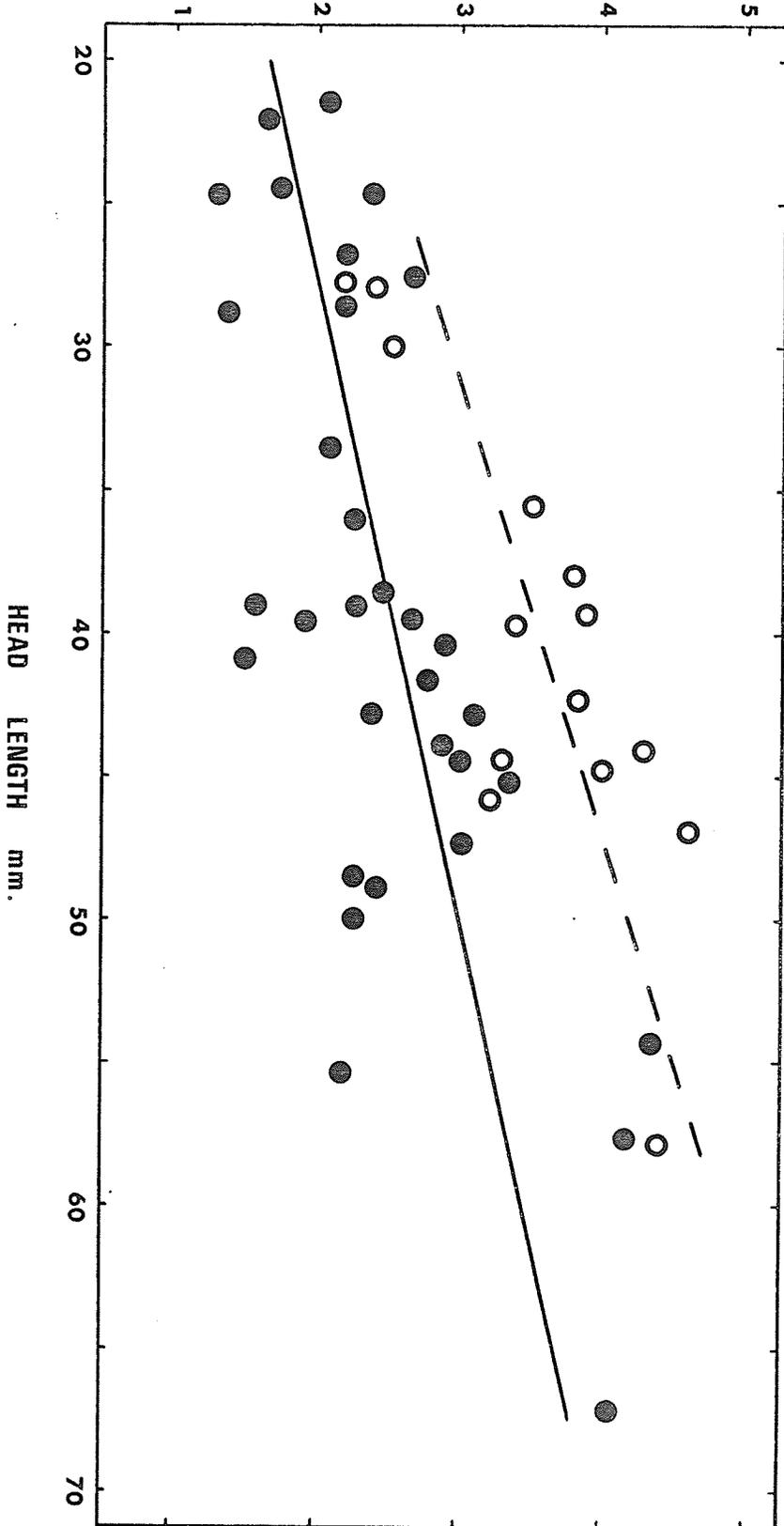


dentary projected in front of the coronoid plate minus the width of the maxilla (see Fig. 2). This index was higher in the low group, but varied with the size; the values were plotted against head length and showed some overlap between the two groups (Fig. 14). Regression lines for both groups were significant ($p < 0.01$); ANCOVA showed that although the slopes did not differ significantly ($F = 0.52$), the intercepts did ($F = 31.65$). Critical values are: for slopes, $p < 0.05$, $F = 4.07$; for intercepts, $p < 0.01$, $F = 7.25$. The variance of the two regression lines did not differ significantly ($F = 1.26$, critical value for $p < 0.05 = 2.95$).

Weak teeth were found on all individuals of the low and high groups (fork lengths of the specimens examined ranged from 95mm. to 295mm). Teeth were found on the supralingual plate, premaxillae, dentaries, autopalatines and occasionally on the vomer. The number of teeth varied considerably. The individuals of the low group had teeth on the supralingual plate, premaxillae, dentaries and often on the autopalatines, and these were usually larger and more numerous than the teeth on the corresponding bones of high group individuals; palatine teeth were rare in individuals of the high group. The two individuals of the Mackenzie R. lower form had teeth on the dentary, premaxillae and supralingual plate; the two individuals of the Mac-

Fig. 14. Regression of dentary projection
minus maxilla width against head length for
the low and high groups. Key: low group ○ ,
high group ● .

DENTARY PROJECTION — MAXILLA WIDTH mm.

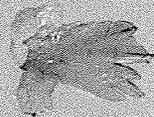
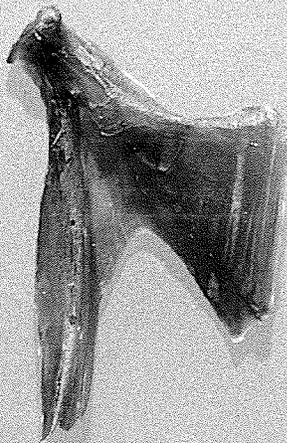


kenzie R. higher form had teeth on the dentary, supralingual plate and autopalatines.

The representatives of the Mackenzie R. lower and higher forms differed from each other and from the high and low groups. The dentary (Fig. 11) of the Mackenzie R. higher form had a pronounced convex ventral edge. The maxilla of the Mackenzie R. higher form had a ventral projection on the condyle, and the maxilla of the Mackenzie R. lower form had a convexity on the dorsal surface (Fig. 12). The supraethmoid of the Mackenzie R. lower form was squarer and had shorter posterior projections than in the other groups, whereas the supraethmoid of the Mackenzie R. high form had a more pronounced waist and an anterior projection (Fig. 13). The supralingual plates of the Mackenzie R. lower and higher forms differed in shape and arrangement of the teeth; the Mackenzie R. lower form resembled the low group, and the Mackenzie R. higher form resembled the high group.

The maxilla, supramaxilla and supralingual plate of the Flotten L. lower form (38 gillrakers) most closely resembled those of the Lyons L. whitefish (Fig. 15). However the Flotten L. lower form differed from the whitefish in lacking a concavity on the posterior tip of the coronoid plate, and in having a supraethmoid that lacked a distinct median ridge. The supraethmoid did not resemble a supraethmoid from a cisco. It was concluded that the Flotten L.

Fig. 15. The dentary, maxilla, supramaxilla and supraethmoid of the Flotten L. lower form and Lyons L. whitefish. Key: upper left - dentary; upper right - supraethmoid; lower left - maxilla; lower right - supramaxilla. For each pair of bones the Lyons L. whitefish is on the left, the Flotten L. lower form on the right.



lower form was a whitefish and not a cisco, although it may have been a hybrid between a cisco and a whitefish.

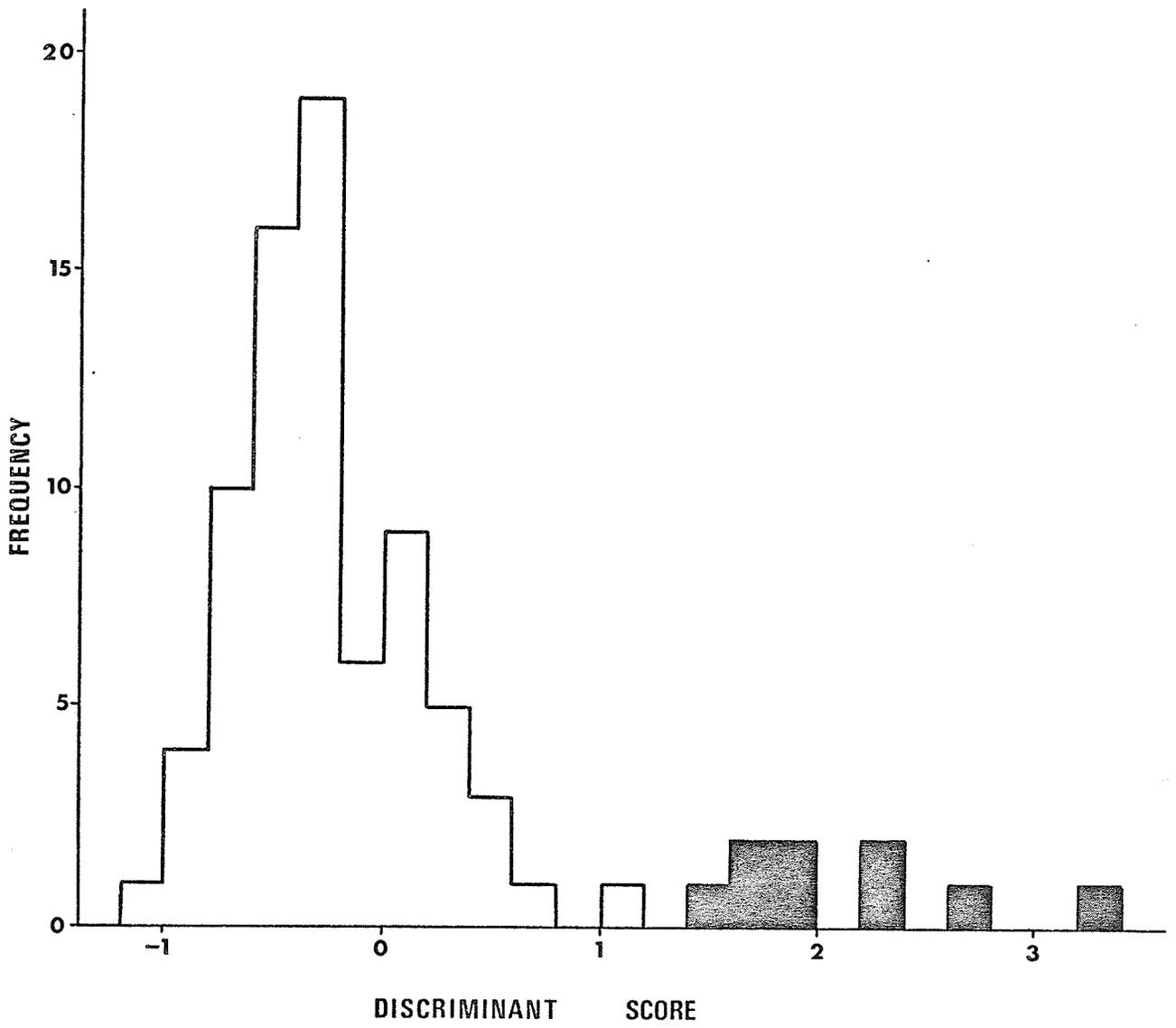
DISTINGUISHING THE GROUPS OF CISCOES
IN CENTRAL CANADA

Differences between the Groups of Ciscoes

Discriminant analysis was used to find the best method of separating the nine members of the low group (including the Mink Narrows lower form) from the 75 forms of the high group (including the Dunc L. lower form.) The differences between these two groups and the Mackenzie R. lower form and higher form were not investigated by discriminant analysis as each of the latter two groups were composed of only one form. The results of separating the Mackenzie R. lower and higher forms from each other and from the Mackenzie R. medium form, a form of the high group, were given in Table I.

The discriminant scores (Fig. 16) separated the forms of the low group from forms of the high group. The Great Whale R. medium form, a form of the high group, had a score of 1.13 and was closer to the nearest member of the low group (L. Athabasca lower form, 1.47) than to the nearest form of the high group (Cold L. higher form, 0.77). The differences between the groups was large, with a calculated chi-square value of 104.84. The discriminant coefficients of the 18 characters are given below in descending order of their use in separating the low and high group forms: pectoral length 0.64, lower raker numbers -0.46,

Fig. 16. Morphological differences,
(expressed as discriminant scores)
separating forms of the low group from forms
of the high group. Key: low group ■ ,
high group □ .



pelvic length -0.32, gillraker length -0.23, eye diameter -0.21, upper raker numbers -0.19, maximum fork length -0.19, interorbital width -0.14, upper jaw length 0.15, mandible length 0.13, premaxillae width -0.13, snout length 0.05, lateral line scale numbers -0.09, head length -0.08, profile 0.05, premaxilla angle 0.04, average fork length 0.04, body depth -0.04. Low group forms had higher scores than high group forms.

Table XIII shows the range, mean, standard deviation of each character for the four groups. The Mink Narrows and Dunc L. lower forms were excluded from their respective groups. The magnitude of differences between the four groups are shown by the F value from ANOVA.

The Mackenzie R. lower form differed from all other groups in eye diameter, interorbital width, mandible length, premaxillae width, premaxilla angle, profile and lateral line scale numbers; it differed from the low group in maximum fork length, from the low and high groups in average fork length, and from the high group and the Mackenzie R. higher form in head length. The Mackenzie R. higher form differed from all groups in head length and premaxilla angle. The low group differed from the other groups in snout length, upper jaw length and upper raker numbers. The low group also differed from the high group in maximum fork length, body depth, interorbital width, mandible

TABLE XIII

Differences in the variables of the four groups. 103
 There was only one sample for both the Mackenzie R.
 Lower and Mackenzie R. Higher forms.

Variable	Group	Range		Mean	Standard Deviation	F Value from Anova
		Lower	Upper			
Max. fork l.	Low	190.0	295.0	232.5	40.16	2.7
	High	159.0	485.0	289.9	69.84	
	Mackenzie R. Lower	381.0				
	Mackenzie R. Higher	347.0				
Av. fork l.	Low	98.8	220.0	172.6	38.69	3.8
	High	106.7	340.5	209.1	51.33	
	Mackenzie R. Lower	336.8				
	Mackenzie R. Higher	254.0				
Body d.	Low	35.5	44.8	40.2	3.30	5.3
	High	28.6	59.5	47.1	5.70	
	Mackenzie R. Lower	36.5				
	Mackenzie R. Higher	39.8				
Head l.	Low	43.3	50.4	46.9	2.34	6.6
	High	38.8	50.6	44.9	2.25	
	Mackenzie R. Lower	51.0				
	Mackenzie R. Higher	39.0				
Eye diam.	Low	9.5	11.5	10.8	0.64	2.4
	High	8.7	13.0	10.5	0.81	
	Mackenzie R. Lower	8.8				
	Mackenzie R. Higher	11.4				
Snout l.	Low	11.2	12.4	11.7	0.49	11.0
	High	9.1	12.6	10.6	0.55	
	Mackenzie R. Lower	10.0				
	Mackenzie R. Higher	10.0				
Interorbital w.	Low	8.2	9.6	8.8	0.53	11.9
	High	7.4	12.0	10.3	1.01	
	Mackenzie R. Lower	14.2				
	Mackenzie R. Higher	8.6				

(Cont'd.)

Variable	Group	Range		Mean	Standard Deviation	F Value from Anova
		Lower	Upper			
Upper Jaw l.	Low	16.0	18.9	17.1	0.89	17.5
	High	13.7	16.9	15.1	0.74	
	Mackenzie R. Lower	14.4				
	Mackenzie R. Higher	15.2				
Mandible l.	Low	20.3	22.3	21.4	0.63	12.4
	High	18.9	23.6	20.3	0.75	
	Mackenzie R. Lower	23.9				
	Mackenzie R. Higher	20.3				
Premaxillae w.	Low	7.2	9.1	8.4	0.70	10.4
	High	7.5	9.3	8.7	0.39	
	Mackenzie R. Lower	10.9				
	Mackenzie R. Higher	8.2				
Gillraker l.	Low	3.7	8.1	6.3	1.35	9.5
	High	5.9	9.1	7.7	0.66	
	Mackenzie R. Lower	7.7				
	Mackenzie R. Higher	6.9				
Pectoral l.	Low	26.7	36.3	31.1	2.99	1.3
	High	26.1	38.9	32.6	2.49	
	Mackenzie R. Lower	35.4				
	Mackenzie R. Higher	31.7				
Pelvic l.	Low	26.3	35.9	30.8	3.51	2.1
	High	25.3	37.8	33.0	2.74	
	Mackenzie R. Lower	36.0				
	Mackenzie R. Higher	34.9				
Profile	Low	71.7	93.0	85.3	6.30	16.3
	High	72.4	97.6	84.8	3.48	
	Mackenzie R. Lower	110.8				
	Mackenzie R. Higher	78.5				

(Cont'd.)

Variable	Group	Range		Mean	Standard Deviation	F Value from Anova
		Lower	Upper			
Premaxilla ang.	Low	40.9	61.3	49.0	6.47	10.6
	High	38.0	64.7	46.0	4.96	
	Mackenzie R. Lower	68.4				
	Mackenzie R. Higher	29.7				
Lateral line scales	Low	66.9	71.0	68.9	1.38	9.1
	High	61.7	80.9	71.1	3.93	
	Mackenzie R. Lower	89.0				
	Mackenzie R. Higher	76.7				
Upper rakers	Low	10.3	14.7	12.8	1.34	23.3
	High	14.9	21.6	17.1	1.37	
	Mackenzie R. Lower	16.4				
	Mackenzie R. Higher	16.2				
Lower rakers	Low	19.1	25.5	22.7	1.99	19.9
	High	25.9	41.3	30.2	2.72	
	Mackenzie R. Lower	26.0				
	Mackenzie R. Higher	28.2				
Total rakers	Low	29.4	40.2	35.5	3.25	21.9
	High	40.9	62.9	47.3	4.01	
	Mackenzie R. Lower	42.4				
	Mackenzie R. Higher	44.4				

length, gillraker length, pelvic fin length and lower raker numbers, and from the high group and the Mackenzie R. higher form in total raker numbers.

The Grouping of Previously Ungrouped Forms from Central Canada

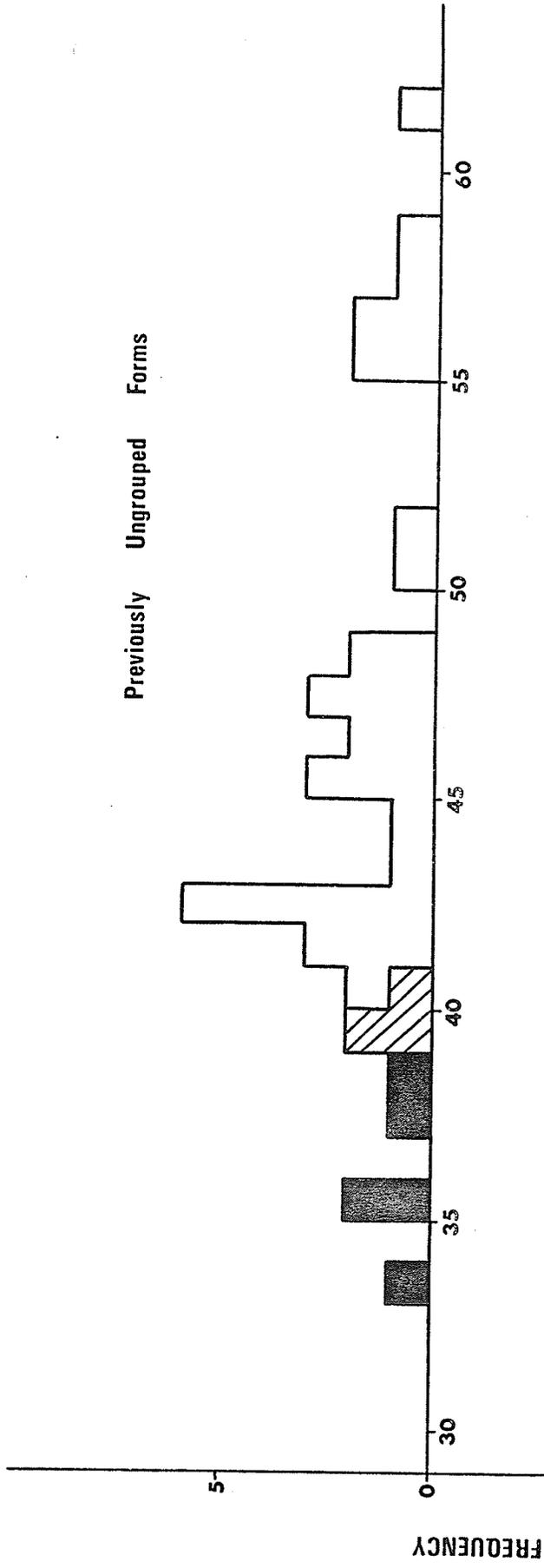
The ungrouped forms (Table II), many with only one or two individuals, were placed tentatively in either the low or high group; none of the ungrouped forms resembled the Mackenzie R. lower or higher forms.

The low group had mean total gillraker counts ranging from 29.4 to 40.2, the high group from 39.3 (Dunc L. lower form) to 62.9 (Table XIII and Fig. 17). The Big Trout L., Clearwater L., Deer L., Great Slave L. lower forms and the Tazin R. medium form had gillraker means of less than 39.3 and were placed provisionally in the low group. The Barrow L. lower form (39.5), the L. Winnipeg lower form from the Royal Ontario Museum (39.3) and the Wholdaia L. medium form (40) had gillraker means within the region of overlap (39.3-40.2) and were not grouped by gillraker means. The Baker L. medium form (40.5) and all other unidentified forms had gillraker means within the range of the high group with which they were grouped. The range and mean total number of gillrakers for each form were given in Table II.

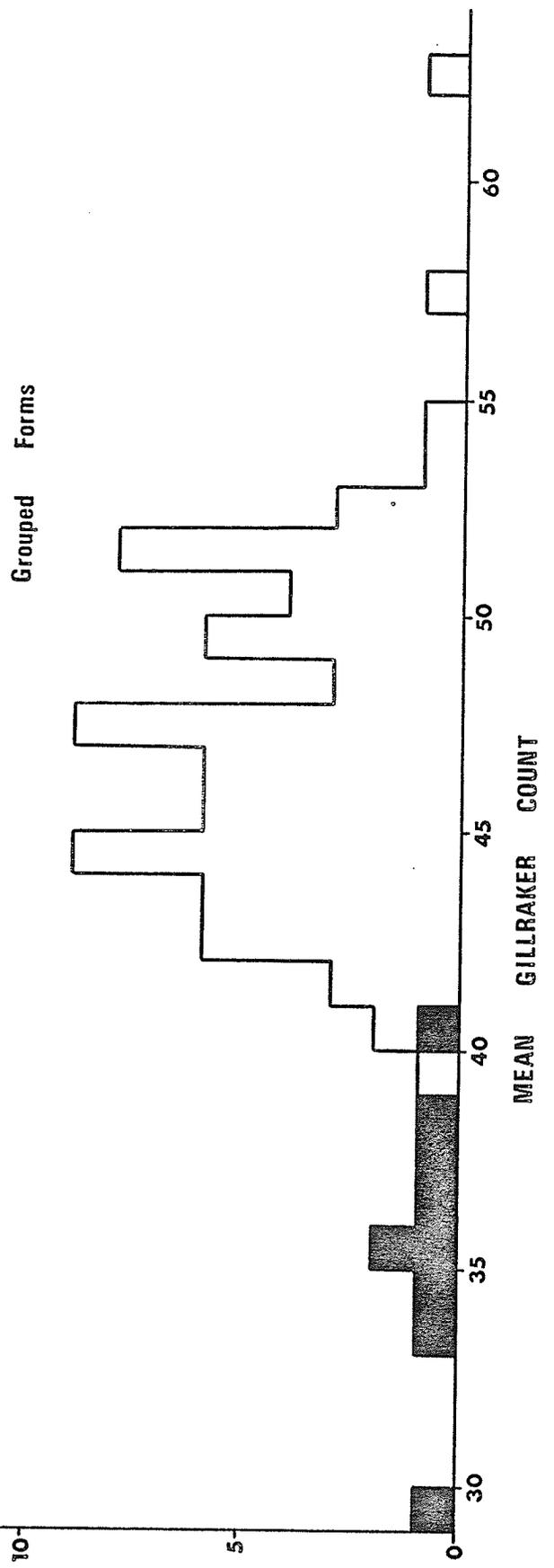
The index of snout length + upper jaw length +

Fig. 17. The use of mean gillraker counts to group previously ungrouped forms from central Canada. Key: low group  , high group  ; forms not grouped by mean gillraker counts  .

Previously Ungrouped Forms



Grouped Forms



mandible length - mean total gillrakers ranged from -17.1 to 7.7 for the high group, and from 12.3 to 20.6 for the low group. Values estimated for the Barrow L. and L. Winnipeg lower forms were 11.8 and 12.3 respectively, so these forms were placed in the low group. The Wholdaia L. medium form had shorter jaws and snout and was placed provisionally in the high group. The lower forms from Big Trout L., Clearwater L., Deer L. and Great Slave L. also had long jaws and snout and so fitted the low group in these characters also. The Tazin R. medium form and the forms placed tentatively in the high group had shorter jaws, so all these forms were placed in the high group.

Summary - The Mackenzie R. lower form is best separated from all other groups by its high lateral line scale count, profile, interorbital width and premaxilla angle, and also by its long head and small eye (Table XIII). The low group is best separated from the other groups by its fewer gillrakers; the range in total number of gillrakers for the low group is from 29.4 to 40.2 and only overlap with the Dunc L. lower form (39.3) of the high group, but the index of snout length + upper jaw length + mandible length plotted against the total number of gillrakers (Fig. 5) separated all the low group from all the high group. The Mackenzie R. higher form is best separated from all

other groups by its low premaxilla angle, and also by its short head, although two forms of the high group had shorter heads (Table XIII). Differences between sympatric forms of the high group were mainly in fork length.

It should be stressed that the above applies to the values obtained from regression or the mean values of the 19 morphological characters for each form.

Forms of the low group were found at 15 localities, and were found sympatrically with one form of the high group at nine localities and with two or more forms of the high group at four localities. High group forms were found at 78 localities with two sympatric forms of the high group at 24 localities and with three to five sympatric forms in L. Winnipeg. The Mackenzie R. lower and higher forms were found at only one locality, where they were sympatric with a form of the high group.

REVIEW OF THE TAXONOMIC HISTORY OF
NORTH AMERICAN CISCOES

The statements and nomenclature in this section represent a review of past and current beliefs prior to this study; their inclusion here is to indicate the prior state of knowledge and does not imply agreement by the author. The author's opinion as to the nomenclature of central Canadian ciscoes is presented in the section entitled "Nomenclature of Ciscoes in Central Canada."

Generic Nomenclature

Ciscoes have been separated from whitefish on the basis of having many long gillrakers, antrorse premaxillae, and maxillae ending beneath the pupil. Whitefish have been placed in the genus Coregonus, following Linnaeus (1758). North American ciscoes were first described under the generic name of Coregonus by Lesueur (1818), and then under Salmo by Richardson (1836). Between 1850 and 1911, most American workers followed Agassiz (1850) in placing ciscoes in the genus Argyrosomus, though some (e.g. Bean 1881; Jordan and Gilbert 1883) continued to use the generic name of Coregonus for the ciscoes. Gill pointed out to Jordan and Evermann (1911) that Argyrosomus was occupied by the sciaenid Argyrosomus aquila described by de la Pylaie

in 1835. Therefore they replaced Argyrosomus by Leucichthys, first used by Dybowski in 1874 for the coregonids with a terminal mouth (ciscoes). Jordan and Evermann (1911) also introduced the subgenera Thrissomimus, Cisco and Allosomus for the slender-bodied ciscoes (lake herrings), the deep-water ciscoes (chubs), and the deep-bodied ciscoes (tullibeas) respectively. Most American workers, like the Eurasians, now consider that the differences between ciscoes and whitefish are insufficient to warrant generic separation and both should be included in the genus Coregonus (Walters 1955). This is because L. autumnalis, the type species of Leucichthys, sometimes has retrorse premaxillae (Walters 1955), and some Eurasian whitefish have numerous long gillrakers (Berg 1948), and this condition also has evolved in Prosopium gemmiferum (Norden 1961). Some authors place ciscoes in a separate subgenus, Leucichthys, from the whitefish, and others (e.g. Scott and Smith 1962) still retain the separate genus, Leucichthys, for the ciscoes.

Current Taxonomic Differences between North American Ciscoes

Early workers did not recognise the great phenotypic plasticity of coregonids, and, in consequence, described new species on the basis of morphological differences that are now thought to be non-genetic. In

addition the early descriptions often were vague and based on a single specimen. The result has been the description of 39 species of ciscoes from N. America, of which 36 are endemic. These 36 ciscoes are listed in Table XIV, each with its type locality, the source of its original description, and its present taxonomic status. At the present time, only twelve species are considered to be valid (Bailey et al, 1970).

The following is a review of the current taxonomy of N. American ciscoes, based largely on Koelz's (1929, 1931) work on the ciscoes of the Great Lakes basin and northeastern U. S. A., and Dymond's (1943) work on ciscoes from northwestern Canada. The characters used most extensively in cisco taxonomy are gillraker counts, lateral line scale counts, profile, and jaw characteristics. Table XV shows the differences for these characters between the twelve currently recognised species, together with the geographical ranges of the species. Details of the species distribution can be found in Hubbs and Lagler (1964), McPhail and Lindsey (1970), and Paetz and Nelson (1970).

Geographical distribution separates the three arctic ciscoes, C. autumnalis, C. laurettae, and C. sardinella, from the other nine species, and also separates C. autumnalis from C. laurettae (McPhail 1966).

Gillraker counts usually separate C. johannae, C.

TABLE XIV.

The Nomenclature of Ciscos Endemic to North America.

Original Nomenclature	Described by	Type Locality	Present status: species and authority
<u>C. albus</u>	Lesueur (1818)	L. Erie	<u>C. artedii</u> , Koelz (1929)
<u>C. artedii</u>	Lesueur (1818)	L. Erie	Unchanged ¹
<u>S. harengus</u>	Richardson (1836)	L. Huron	<u>C. artedii</u> , Koelz (1929)
<u>S. lucidus</u>	Richardson (1836)	Great Bear L., NWT	<u>C. artedii</u> , Dymond (1943)
<u>S. tullibee</u>	Richardson (1836)	Pine Island L., Sask.	<u>C. artedii</u> , Koelz (1929)
<u>C. clupeiiformis</u>	De Kay (1842)	L. Ontario	<u>C. artedii</u> , Koelz (1929)
<u>A. hoyi</u>	Gill, in Hoy (1872)	L. Michigan	Unchanged ²
<u>A. nigripinnis</u>	Gill, in Hoy (1872)	L. Michigan	Unchanged ²
<u>A. sisco</u>	Jordan (1875)	L. Tippecanoe, Ind.	<u>C. artedii</u> , Koelz (1929)
<u>C. laurettae</u>	Bean (1881)	Pt. Barrow, Alaska	Unchanged ¹
<u>C. pusillus</u>	Bean (1888)	Kobuk R., Alaska	<u>C. sardinella</u> , Dymond (1943) ¹
<u>C. osmeriformis</u>	Smith (1894)	Seneca L., N.Y.	<u>C. artedii</u> , Koelz (1931)
<u>C. prognathus</u>	Smith (1894)	L. Michigan	<u>C. nigripinnis</u> , Koelz (1929) ²
<u>A. alascanus</u>	Scotfield (1899)	Pt. Hope, Alaska	<u>C. laurettae</u> , McPhail (1966) ¹
<u>A. eriensis</u>	Jordan & Evermann (1909)	L. Erie	<u>C. artedii</u> , Koelz (1929)
<u>A. huronius</u>	Jordan & Evermann (1909)	L. Huron	<u>C. artedii</u> , Koelz (1929)
<u>A. zenithicus</u>	Jordan & Evermann (1909)	L. Superior	Unchanged ²
<u>A. johannae</u>	Wagner (1910)	L. Michigan	Unchanged ²
<u>L. cyanopterus</u>	Jordan & Evermann (1911)	L. Superior	<u>C. nigripinnis</u> , Koelz (1929) ²
<u>L. manitoulinus</u>	Jordan & Evermann (1911)	L. Huron	<u>C. artedii</u> , Koelz (1929)
<u>L. ontariensis</u>	Jordan & Evermann (1911)	L. Ontario	<u>C. artedii</u> , Koelz (1929)

(Cont'd.)

TABLE XIV (Cont'd.)

Original Nomenclature	Described by	Type Locality	Present status: species and authority
<u>L. supernas</u>	Jordan & Evermann (1911)	L. Superior	<u>C. artedii</u> , Koelz (1929)
<u>L. birgei</u>	Wagner (1911)	Green L., Wisc.	<u>C. artedii</u> , Koelz (1931)
<u>L. macropterus</u>	Bean (1916)	L. Erie	<u>C. artedii</u> , Smith (1964)
<u>L. athabascae</u>	Harper & Nichols (1919)	L. Athabasca, Sask.	<u>C. zenithicus</u> , Dymond (1943)
<u>L. entomophagus</u>	Harper & Nichols (1919)	Tazin R., NWT	<u>C. zenithicus</u> , Dymond (1943)
<u>L. macrognathus</u>	Harper & Nichols (1919)	Great Slave L., NWT	<u>C. zenithicus</u> , Dymond (1943)
<u>L. gemmifer</u>	Snyder (1919)	Bear L., Utah	<u>P. gemmiferum</u>
<u>L. kiyi</u>	Koelz (1921)	L. Michigan	Unchanged
<u>L. alpenae</u>	Koelz (1924)	L. Michigan	Unchanged ²
<u>L. reighardi</u>	Koelz (1924)	L. Michigan	Unchanged ²
<u>L. nipigon</u>	Koelz (1925)	L. Nipigon	Unchanged
<u>L. hubbsi</u>	Koelz (1929a)	Ives L., Mich.	Not valid, Bailey et al. (1970)
<u>L. bartletti</u>	Koelz (1931)	Siskiwit L., Mich.	Not valid, Bailey et al. (1970)
<u>L. churchillensis</u>	Fowler (1948)	Churchill, Man.	Not valid, Bailey et al. (1970)
<u>L. nueltinensis</u>	Fowler (1948)	Nueltin L., NWT	Not valid, Bailey et al. (1970)

¹ see Table XIX² see Table XVIII

TABLE XV.

The current use of key taxonomic characters and geographical distribution in the separation of species of ciscoes, compiled from Koelz (1929), Hubbs and Lagler (1964) and McPhail and Lindsey (1970).

Valid Species	Gillrakers			Lateral Line Scales	Profile	Mandible	Range			
	lower	upper	total				Arctic	Canada (excluding Arctic and Great Lakes)	Great Lakes and L. Nipigon	U.S.A. (excluding Arctic and Great Lakes)
<u>alpenae</u>	11-17	20-30	33-46	68-96	elliptical	protruding			x	
<u>artedii</u>	14-18	28-35	41-51	67-89	elliptical	equal	x		x	x
<u>autumnalis</u>	15-17	26-31	41-48	82-110	elliptical	equal		x		
<u>hoiyi</u>	14-18	24-30	37-48	66-77	elliptical	protruding			x	
<u>johanna</u>	9-13	17-23	26-36	67-91	ovate	equal			x	x
<u>k. kiyi</u>	13-16	22-28	34-45	70-91	ovate	protruding			x	x
<u>k. orientalis</u>	15-17	27-29	41-48	71-91	ovate	protruding			x	x
<u>laurettae</u>	12-15	21-25	33-41	76-95	elliptical	equal		x		
<u>n. nigripimimis</u>	16-19	28-34	41-52	72-89	ovate	equal			x	x
<u>n. regalis</u>	16-19	28-32	44-54	66-81	ovate	equal		x	x	x
<u>n. cyanopterus</u>	14-16	24-28	36-48	73-91	ovate	equal			x	x
<u>n. prognathus</u>		39-42	39-42	77-88	ovate	equal			x	x
<u>nipigon</u>	19-24	35-43	54-66	68-82	elliptical	equal		x	x	x
<u>r. reighardi</u>	12-14	21-26	30-43	66-96	elliptical	included		x	x	x
<u>r. dymondi</u>	11-14	21-24	32-42	64-83	elliptical	included			x	x
<u>sardinella</u>	14-18	28-35	42-53	78-98	elliptical	equal		x		
<u>zenithicus</u>	12-17	22-28	35-44	69-90	elliptical	included		x		x

laurettae and C. reighardi, with less than 40, from C. artedii. C. autumnalis, C. nigripinnis and C. sardinella, which usually have between 40 and 50, and from C. nipigon, which usually has more than 53 gillrakers.

Generally C. hoyi, C. reighardi and C. zenithicus have fewest lateral line scales, and C. johannae and the arctic ciscoes have the most.

In the Great Lakes basin, the three most abyssal species, C. johannae, C. kiyi and C. nigripinnis, have an ovate profile (deeper forward than medially), whereas the other species are elliptical (deepest medially). Outside the Great Lakes basin, C. nigripinnis is often elliptical.

The mandible usually protrudes in C. alpenae, C. hoyi and C. kiyi, and usually is included in C. autumnalis, C. laurettae, C. reighardi and C. zenithicus. The premaxillae often approach the vertical in the latter four species. The jaws of the other species are usually equal.

The relative size of body parts has been used extensively, although growth is usually allometric, and morphometry varies with growth rate (Hile 1937). The shorter prepelvic distance of C. sardinella separates it from C. artedii. The following generalizations on the relative size of body parts of sympatric species may be made from Koelz's (1929) work in the Great Lakes, but the results do not always hold true for L. Nipigon:

Head: C. artedii the shortest; C. hoyi, C. johannae and C. kiyi the longest.

Snout: C. artedii and C. hoyi the shortest; C. alpenae, C. johannae, C. kiyi and C. zenithicus the longest.

Eye: C. alpenae and C. johannae the smallest; C. hoyi and C. kiyi the largest.

Upper jaw: C. artedii the shortest; C. hoyi and C. zenithicus the longest.

Paired fins: C. artedii and C. reighardi the shortest; C. hoyi and C. kiyi the longest.

Gillraker length: C. johannae and C. reighardi the shortest; C. artedii, C. hoyi and C. nigripinnis the longest.

Koelz (1929, 1931) described 24 subspecies of C. artedii, four of C. nigripinnis, and two of C. kiyi and of C. reighardi. He recognised subspecies on the basis of differences in gillraker and lateral line scale counts, and morphometry.

The Distribution and Current Taxonomy of Ciscoes from Central Canada

Sympatric forms of ciscoes are known from several localities in central Canada and have been referred to five species (Table XVI). Two or three forms occur at these localities, except L. Winnipeg, where five have been recorded (Bajkov 1932). Up to eight sympatric forms are known from the Great Lakes basin (Koelz 1929). Table

TABLE XVI.

The recorded Canadian occurrences of C. hoyi,
C. nigripinnis, C. nipigon and C. zenithicus
(including C. reighardi) outside of the Great
Lakes basin, and their sympatry with C. artedii.

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Lakes	<u>artedii</u>	<u>hoyi</u>	<u>nigripinnis</u>	<u>nipigon</u>	<u>zenithicus</u>	Sources
L. Abitibi				x		Dymond & Hart (1927)
L. Athabasca	x		x		x	Dymond & Pritchard (1930)
L. Athapuskow	x	x			x	Clarke (MS 1970)
L. Attawapiskat	x		x		x	Ryder et al. (1964)
Baby L.				x		R.O.M. ¹
Barrow L.	x				x	Paterson (1969)
Big Trout L.	x				x	Ryder et al. (1964)
Black Sturgeon L.				x		Bajkov (1932)
Burntwood L.	x		x			Dymond & Pritchard (1930)
Clearwater L.		x			x	Clarke (MS 1970)
Deer L.	x		x			Ryder et al. (1964)
Eagle L.			x			Dymond & Pritchard (1930)
Eva L.		x				Lindeborg (1941)
Fishing L.		x				R.O.M.
George L.		x				Gibson & Johnson (MS 1969)
Great Slave L.	x		x		x	Dymond (1943); Rawson (1947)
Heart L.	x		x			Dymond & Pritchard (1930)
Lac la Ronge			x		x	Rawson & Atton (MS 1953)
Lac Seul	x			x		Dymond & Pritchard (1930)
Lake of the Woods	x		x		x	Hinks (1957)

(Cont'd.)

Lakes	<u>artedii</u>	<u>hoyi</u>	<u>nigripinnis</u>	<u>nipigon</u>	<u>zenithicus</u>	Sources
Little Trout L.			x			Dymond & Pritchard (1930)
Long L.			x			Harkness & Hart (1927)
Manistikwan L.		x				Clarke (MS 1970)
L. Manitoba			x			Dymond & Pritchard (1930)
Matagami L.				x		R.O.M.
Olga L.				x		R.O.M.
Reindeer L.	x		x		x	Bajkov (1932); Dymond (1943)
Rocky L.		x				Clarke (MS 1970)
Sandy L.	x	x				R.O.M.
Tazin R.					x	Dymond (1943)
Trout L.	x				x	R.O.M.
Twelve Mile L.			x			R.O.M.
Wabigoon L.			x			Dymond & Pritchard (1930)
Waskesiu L.	x		x			Dymond & Pritchard (1930)
Waswanipi L.				x		N.M.C. ²
White Partridge L.	x				x	R.O.M.
L. Winnipeg	x	x	x	x	x	Bajkov (1932)

¹Royal Ontario Museum²National Museum of Canada

XVI is a collation of published records and museum labels of four species of ciscoes from all Canadian localities outside of the Great Lakes and St. Lawrence basin.

Two forms of C. artedii, the slender lake herring and the deep-bodied tullibee, are said to be widely distributed in central Canada. Richardson (1823) was the first to identify a cisco, C. artedii, from central Canada (the ciscoes he caught at the mouth of the Coppermine R. were probably C. sardinella). Later he concluded that these fish should belong to a new species, C. tullibee, whose type locality is Pine Island L. (now Cumberland L., Saskatchewan); also he described C. lucidus from Great Bear L. (Richardson 1836). Specimens of C. tullibee were redescribed by Dymond (1928). Koelz (1929) considered C. tullibee to be a subspecies of C. artedii. Most workers have followed this, though Dymond and Pritchard (1930) and Hinks (1957) preferred to consider C. tullibee to be a distinct species. Dymond (1943) suggested that the tullibee may be more closely related to C. nigripinnis than to C. artedii, but its relationship was not clear. Dymond (1943) considered that C. lucidus, described from Herschel Is. (Scofield 1899) and Hudson Bay (Bajkov 1932), as well as from Great Bear L., was conspecific with C. artedii. Scofield's (1899) report of C. lucidus probably referred to C. sardinella. Koelz (1931) described two other subspecies of C. artedii from

central Canada: C. a. magnus from Lesser Slave L., and C. a. winnipegosis from L. Winnipegosis and several lakes in northwestern Ontario and also from Michigan.

McPhail and Lindsey (1970) referred all the ciscoes of central Canada that have 40 to 50 gillrakers to the "C. artedii complex," recognising that sibling species may be involved. All populations referred to as C. artedii, C. lucidus and C. tullibee (above), or C. nigripinnis and C. hoyi (below) would belong to the "C. artedii complex"; C. nipigon and C. zenithicus would not.

C. nigripinnis is said to occur in several lakes in central Canada, often sympatrically with C. artedii (Table XVI). It differs from C. nigripinnis of the Great Lakes basin in being elliptical rather than ovate. In appearance it is very similar to C. tullibee, but it usually has a longer head and more pigmentation especially in the fins. C. nigripinnis was reported to occur sympatrically with C. artedii in Waskesiu L. (Dymond and Pritchard 1930), but Kooyman (MS 1970) considered both species to be members of one phenotypically variable species, which he referred to as the "C. artedii complex." Rawson (1947) recorded C. nigripinnis from L. Athabasca and Great Slave L. He suggested that the specimens from L. Athabasca may be variants of the tullibee, which also occurs in that lake. The specimens from Great Slave L. were slender, suggesting that

they may be variants of the lake herring that occurs there.

C. hoyi was first recorded from L. Winnipeg by Bajkov (1932). It has since been recorded from four other lakes in central Canada, and Clarke (MS 1970) tentatively identified ciscoes from four northwestern Manitoban lakes as this species (Table XVI).

C. nipigon is reported to occur sympatrically with C. artedii in Lac Seul and L. Winnipeg, and is the only cisco in five Ontario and Quebec lakes (Table XVI).

C. zenithicus has been recorded from twelve lakes in central Canada (Table XVI). The ciscoes, similar to C. zenithicus, from L. Athapapuskow and Clearwater L. were described under the name of C. reighardi (Clarke MS 1970).

Harper and Nichols (1919) collected 25 specimens of C. entomophagus from the Tazin R. Of these 24 were less than 87 mm. fork length. They also collected and named one specimen of C. athabascae from L. Athabasca, and one of C. macrognathus from Great Slave L. They recorded the gill-raker counts of the three type specimens as 33, 35 and 41 respectively. Dymond (1943) recorded their counts as 35, 35 and 37, and on this basis considered all three species to be synonyms of C. zenithicus. McPhail and Lindsey (1970) recorded the counts as 37, 40+ and 42. This, together with their published descriptions, suggests that C. athabascae and C. macrognathus should belong to the

"C. artedii complex," whereas C. entomophagus probably represents a distinct species (McPhail and Lindsey 1970), possibly C. zenithicus. Kendall (1924) states C. athabascae to be most like the tullibee.

Fowler (1948) described C. nueltinensis from Nueltin L. and C. churchillensis from Churchill, each on the basis of one specimen. They are not recognised as valid species (Bailey et al. 1970).

Many lakes contain unidentified populations of ciscoes, often as sympatric pairs or sympatrically with C. artedii. Unidentified populations of ciscoes occur in Dore L. (Johnson MS 1968), Greig L. (Lane MS 1967), and Beverly and Kathawachaga lakes (McPhail and Lindsey 1970). Dwarf ciscoes occur sympatrically with C. artedii in Great Bear L. (Kennedy 1949) and in Cedar L. (Schweitzer MS 1968).

Some Nomenclatural Confusion in Cisco Taxonomy

Confusion has arisen in the nomenclature of several ciscoes. Table XVII lists the species, and their synonyms, recognised in five major reviews of cisco taxonomy between 1866 and 1931.

Lesueur (1818) referred to C. albus as a whitefish, but Koelz (1929) pointed out that since Lesueur illustrated the deep-bodied L. Erie cisco and failed to point out the

TABLE XVII.

Some changes in the taxonomy of North American ciscoes (excluding the arctic ciscoes) between 1866 and 1931.

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Original Name	Authority				
	Gunther (1866)	Jordan & Gilbert (1883)	Jordan & Evermann (1896)	Jordan & Evermann (1911)	Koelz (1929, 1931)
<u>albus</u>	whitefish	whitefish	whitefish	whitefish	<u>artedii</u>
<u>artedii</u>	<u>clupeiformis</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>
<u>harengus</u>	<u>harengus</u>	<u>artedii</u>	<u>artedii</u>	<u>harengus</u>	<u>artedii</u>
<u>lucidus</u>	<u>lucidus</u>	<u>artedii</u>	<u>lucidus</u>	<u>lucidus</u>	-
<u>tullibee</u>	<u>tullibee</u>	<u>tullibee</u>	<u>tullibee</u>	<u>tullibee</u>	<u>artedii</u>
<u>clupeiformis</u>	<u>clupeiformis</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u> ³	<u>artedii</u>
<u>hoi</u> ¹		<u>hoi</u>	<u>hoi</u> ²	<u>hoi</u>	<u>hoi</u>
<u>nigripinnis</u> ¹		<u>nigripinnis</u>	<u>nigripinnis</u>	<u>nigripinnis</u>	<u>nigripinnis</u>
<u>sisco</u>			<u>artedii</u>	<u>sisco</u>	<u>artedii</u>
<u>osmeriformis</u>			<u>osmeriformis</u>	<u>osmeriformis</u>	<u>artedii</u>
<u>prognathus</u> ¹			<u>prognathus</u>	<u>prognathus</u>	<u>nigripinnis</u>
<u>eriensis</u>				<u>eriensis</u>	<u>artedii</u>
<u>huronius</u>				<u>sisco</u>	<u>artedii</u>
<u>zenithicus</u> ¹				<u>zenithicus</u>	<u>zenithicus</u>
<u>johannae</u> ¹				<u>johannae</u>	<u>johannae</u>
<u>cyanopterus</u> ¹				<u>cyanopterus</u>	<u>nigripinnis</u>
<u>manitoulinus</u>				<u>manitoulinus</u>	<u>artedii</u>
<u>ontariensis</u>				<u>ontariensis</u>	<u>artedii</u>
<u>supernas</u>				<u>supernas</u>	<u>artedii</u>
<u>birgei</u>					<u>artedii</u>
<u>macropterus</u>					<u>artedii</u>

(Cont'd.)

Original Name	Authority				
	Gunther (1866)	Jordan & Gilbert (1883)	Jordan & Evermann (1896)	Jordan & Everman (1911)	Koelz (1929, 1931)
<u>kiyi</u>					<u>kiyi</u>
<u>alpenae</u> ¹					<u>alpenae</u>
<u>reighardi</u> ¹					<u>reighardi</u>
<u>nipigon</u>					<u>nipigon</u>
<u>hubbsi</u>					<u>hubbsi</u>
<u>bartletti</u>					<u>bartletti</u>
Nos. of spp. recognised:	4	4	6	16	11

¹see Table XVIII

²but not of Bean (1882) = osmeriformis

³but not of Agassiz (1850) = harengus

obvious differences in the mouth of whitefish and C. artedii, Lesueur was describing a cisco. Jordan (1884) recognised C. albus to be a cisco, but until Koelz (1929) considered it to be a subspecies of C. artedii, all other workers considered it to be either a distinct species of whitefish or a synonym of the whitefish, C. clupeiformis (Table XVII).

De Kay (1842) described a cisco from L. Ontario and called it C. clupeiformis, the classically correct spelling of the specific name of the whitefish, C. clupeiformis, described by Mitchill (1818). However only Evermann and Smith (1896) confused C. clupeiformis with the whitefish, although Gunther (1866) reduced C. artedii, described by Lesueur in 1818, to synonymy with C. clupeiformis, presumably as C. clupeiformis had precedence. This was followed by Jordan (1875). C. clupeiformis is now considered to be a synonym of C. artedii (Koelz 1929).

Although C. macropterus, described by Bean (1916) from L. Erie had a gillraker count of 30, Koelz (1929) considered it to be a synonym of C. artedii. Following the discovery of C. alpenae in L. Erie, Scott and Smith (1962) considered that C. macropterus was a synonym of C. alpenae. Smith (1964) re-examined the type specimen of C. macropterus and found the gillraker count to be 47; he concluded that C. macropterus was a synonym of C. artedii.

Of the 24 subspecies of C. artedii that Koelz (1931) recognised, 13 were described originally as species. C. huronius was regarded by Jordan and Evermann (1911) to be a subspecies of C. sisco, but Koelz (1929) considered both to be subspecies of C. artedii (Table XVII).

Hoy (1872) gave an inadequate description of C. hoyi. Milner (1874) redescribed C. hoyi, but Koelz (1929) believed that Milner's material was a mixture of C. hoyi and C. zenithicus. Bean (1882) found C. hoyi in several New York lakes, but Jordan and Evermann (1896) identified these ciscoes as C. osmeriformis, now a subspecies of C. artedii (Koelz 1931). The description of C. hoyi by Evermann and Smith (1896) was a mixture of C. johannae and C. zenithicus (Koelz 1929). C. hoyi of Jordan and Evermann (1911) is C. zenithicus, whereas the true C. hoyi was described with C. alpenae as C. johannae (Koelz 1929). C. prognathus of Evermann and Smith (1896) refers to a mixture of several species, probably C. alpenae, C. hoyi, part of C. nigripinnis, and C. reighardi (Koelz 1929). Clemens (1922) identified C. prognathus from L. Erie, but Koelz (1929) believed it to be C. artedii. The confusion in nomenclature of C. hoyi, C. johannae, C. prognathus and C. zenithicus is shown in Table XVIII.

TABLE XVIII.

Koelz's opinion as to earlier confusion in the nomenclature of certain Great Lakes ciscoes.

Species of Koelz (1929)	Previous nomenclature		
	Milner (1874)	Evermann & Smith (1896)	Jordan & Evermann (1911)
<u>alpenae</u>		<u>prognathus</u>	<u>johannae</u>
<u>hoi</u>	<u>hoi</u>	<u>prognathus</u>	<u>johannae</u>
<u>johannae</u>		<u>hoi</u>	
n. <u>nigripinnis</u>		<u>nigripinnis</u>	<u>nigripinnis</u>
n. <u>cyanopterus</u>		<u>prognathus</u>	<u>cyanopterus</u>
n. <u>prognathus</u>		<u>prognathus</u>	<u>prognathus</u>
<u>reighardi</u>		<u>prognathus</u>	
<u>zenithicus</u>	<u>hoi</u>	<u>hoi</u>	<u>zenithicus</u> + <u>hoi</u>

The Arctic Ciscoes and Synonymy with Eurasian Ciscoes

Three species of ciscoes have been named from the arctic coast of N. America (Tables XIV and XIX), and four species originally named from Russia have become involved in their synonymy (Table XIX). Three species of arctic ciscoes are recognised now from N. America. These are C. autumnalis, C. laurettae which used to be a synonym of C. autumnalis, and C. sardinella (McPhail and Lindsey 1970). C. alascanus, and probably C. subautumnalis, used to be synonyms of C. laurettae (McPhail 1966), and C. pusillus of C. sardinella (Dymond 1943). There are two morphologically distinct and allopatric forms of C. sardinella, which McPhail and Lindsey (1970) therefore refer to as the "C. sardinella complex."

Two other Eurasian coregonids have been involved in the synonymy of the arctic ciscoes and C. artedii (Table XIX). Some Eurasian workers (Svardson 1957; Nikolsky and Reshetnikov 1970) consider C. artedii and C. sardinella to be conspecific with C. albula, but McPhail and Lindsey (1970) report that there are protein differences between C. artedii and C. sardinella.

TABLE XIX.

The Nomenclature of Arctic Ciscos and their proposed relationships to C. alba, C. oxyrhynchus and C. artedii.

Species	Original Description	Type Locality	Authority						
			Jordan & Evermann (1896)	Dymond (1943)	Walters (1955)	Svardson (1957)	McPhail (1966)	Nikolsky & Reshetnikov (1970)	
<u>alba</u>	Linnaeus (1758)	Europe		<u>alba</u>	<u>alba</u>	<u>alba</u>	<u>alba</u>	<u>alba</u>	<u>alba</u>
<u>oxyrhynchus</u>	Linnaeus (1758)	Europe				<u>oxyrhynchus</u>			
<u>autumnalis</u>	Pallas (1776)	Russia	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>
<u>artedii</u>	Lesueur (1818)	N. America	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>	<u>artedii</u>
<u>sardinella</u>	Valenciennes (1848)	Russia	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>
<u>laurettae</u>	Bean (1881)	N. America	<u>laurettae</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>oxyrhynchus</u>	<u>laurettae</u>	<u>autumnalis</u>
<u>merki</u>	Jordan & Gilbert (1883), not of Gunther (1866)	Russia	<u>pusillus</u>	<u>sardinella</u>					
<u>pusillus</u>	Bean (1888)	N. America	<u>pusillus</u>	<u>sardinella</u>	<u>sardinella</u>	<u>sardinella</u>	<u>alba</u>	<u>sardinella</u>	
<u>alascamus</u>	Scofield (1899)	N. America	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>	<u>autumnalis</u>		<u>laurettae</u>	<u>autumnalis</u>
<u>subautumnalis</u>	Kaganowsky, in Berg (1932)	Russia			<u>autumnalis</u>	<u>autumnalis</u>		<u>laurettae</u>	<u>autumnalis</u>

NOMENCLATURE OF CISCOES IN CENTRAL CANADA

This section is the author's opinion as to the correct nomenclature of the ciscoes of central Canada.

An additional 114 ciscoes from 16 localities in the St. Lawrence drainage basin and from one locality on the Yukon R. system (Fig. 1 and Appendix 1) were examined as well as the material from central Canada.

In this section some reference is made to the characteristics of individual ciscoes; this subject is discussed more fully in the section entitled "Identification of Individual Ciscoes".

Mackenzie R. Lower Form - Coregonus autumnalis (Pallas).

The original descriptions of C. laurettae (Bean 1881) and C. alascanus (Scofield 1899) are inadequate. The Mackenzie R. lower form is similar to the descriptions of C. laurettae (Bean 1881; Dymond 1943) and C. alascanus (Scofield 1899) in general appearance, the small eye, long mandible, almost vertical premaxillae and high scale count. Dymond (1943) considered that C. laurettae and C. alascanus were conspecific with C. autumnalis, originally described from Siberia by Pallas (1776). This view was supported by Walters (1955), but McPhail (1966) showed that C. laurettae was distinct from C. autumnalis in distribution and in having 25 or fewer gill-rakers on the lower limb of the first arch, whereas C. autumnalis

had 26 or more gillrakers. The total number of gillrakers on the first arch ranged from 33 to 40 for C. laurettae and from 41 to 48 for N. American C. autumnalis (McPhail and Lindsey 1970). McPhail (1966) concluded that C. laurettae was a distinct species from C. autumnalis, and that C. alascanus was a synonym of C. laurettae. The gillraker count of the Mackenzie R. lower form ranges from 40 to 44 (Table XX), and 26 or more gillrakers occur on the lower limb of the gill arch if the central gillraker is included in the count of the lower limb rather than in the count of the upper limb. The Mackenzie R. lower form occurs in the geographical range of C. autumnalis, not C. laurettae (McPhail 1966). It is concluded that the Mackenzie R. lower form probably belongs to the species C. autumnalis.

Mackenzie R. Higher Form - Coregonus sardinella Valenciennes.

The original description of C. pusillus (Bean 1888) is inadequate, but the descriptions of specimens in Dymond (1943) are similar to the Mackenzie R. higher form in appearance, morphometry and the short pre-pelvic distance. The Mackenzie R. higher form differs from the Mackenzie R. lower form in its larger eyes, smaller head, narrower interorbital width, fewer scales, more gillrakers, less vertical premaxillae and more pigmentation, similar to the differences between C. pusillus and C. autumnalis (Dymond 1943). Dymond (1943) and Walters (1955) recognised that C. pusillus was a synonym of the Asiatic

C. sardinella. The short prepelvic distance (McPhail and Lindsey 1970) is a common feature of the Mackenzie R. higher form, C. pusillus and C. sardinella, whereas all other ciscoes in N. America have a longer prepelvic distance. Specimens examined from Lac Laberge (Fig. 1 and Appendix 1) are similar to the Mackenzie R. higher form in having a short prepelvic distance. Both forms had been identified as C. sardinella at the Royal Ontario Museum. It is concluded that the Mackenzie R. higher form probably belongs to the species C. sardinella.

Low Group - Coregonus prognathus Smith.

The following original descriptions of species or specimens from type localities are similar to the low group: a) original description of C. johannae (Wagner 1910) fits low group in gillraker count and appearance; b) original descriptions of C. prognathus (Smith 1894), C. cyanopterus (Jordan and Evermann 1911), C. kiyi (Koelz 1921), C. alpenae and C. reighardi (Koelz 1924), and C. bartletti (Koelz 1931) intermediate between the low and high group in gillraker count, but general appearance, morphometry and gillraker counts of specimens from type localities (original descriptions, Koelz 1929, and specimens of C. cyanopterus and C. kiyi examined at R.O.M.) fit low group; c) original gillraker count of holotype of C. zenithicus (Jordan and Evermann 1909) is wrong, and corrected count (Koelz 1929) fits high group, but general appearance and morphometry (Jordan and Everman 1909; Koelz 1929)

fit low group.

In the Great Lakes and L. Nipigon, C. zenithicus from all localities except L. Superior, and all forms of C. alpenae, C. johanna, C. k. kiyi and C. reighardi have mean gillraker counts of less than 40.2 (Koelz 1929), similar to the low group in central Canada. C. zenithicus from L. Superior had 40.3 gillrakers, and C. prognathus and C. cyanopterus have 40.5 gillrakers (Koelz 1929) but in having long upper jaws (Koelz 1929) are similar to the low group.

The low group from central Canada had been named C. zenithicus, C. reighardi, C. artedii and C. hoyi (see Table XVI), but specimens from the type localities of the latter two species are most similar to the high group (see below). The holotype of C. zenithicus (Jordan and Evermann 1909) from L. Superior has 45 gillrakers (Koelz 1929), not 42 (Jordan and Evermann 1909). In this it is more similar to the high group, but in the long snout, long upper jaw, long included mandible, greater premaxilla angle and the pale colouration except for a dusky margin to the anal, caudal, dorsal and pectoral fins (Jordan and Evermann 1909; Koelz 1929) it resembles the low group. Examined specimens of C. zenithicus from the Great Lakes and L. Nipigon and those described by Koelz (1929) resemble the low group in their gillraker counts and morphometry. C. zenithicus and C. reighardi are very similar in all respects (Clarke MS 1970) and several forms of the low group are more similar to C. reighardi than to C. zenithicus in having fewer

gillrakers and slightly different morphometry. The low group from Big Athapapuskow most closely resembles C. johannae in its low gillraker count (Tables II and XV); Koelz (1929) distinguished C. johannae from C. zenithicus and C. reighardi by its ovate profile and fewer gillrakers, but both characters vary within or between populations (see above). C. alpenae differed from C. zenithicus and C. reighardi in its larger size, smaller body parts and a mandible that usually protruded (Koelz 1929), but the mandible protruded in only 50% of C. alpenae from L. Erie (Scott and Smith 1962); these differences may be associated with a large size since the Barrow L. low group is the largest form of the low group in central Canada and resembles C. alpenae in its morphometry. The original descriptions of C. bartletti (Koelz 1931) and C. kiyi (Koelz 1921) are more similar to the low group than to the high group. The description of C. bartletti (Koelz 1931) does not differ greatly from the low group in any respect, but C. kiyi (Koelz 1921, 1929; specimens examined at the R.O.M.) differs from the low group in having a larger eye, much longer paired fins and a mandible that usually protrudes.

Koelz (1929) considered C. prognathus from L. Ontario and C. cyanopterus from L. Superior to be sub-species of C. nigripinnis. They resembled typical C. n. nigripinnis in profile and general body shape, but differed from typical C. n. nigripinnis in having fewer gillrakers, longer head, snout and jaws, less body depth and less pigment especially in the fins

(Koelz 1929). In these characters they resemble C. zenithicus and C. reighardi more closely than they do C. n. nigripinnis. Also in having dusky edges to the anal, caudal, dorsal and pectoral fins (Koelz 1929), they resemble C. zenithicus and C. reighardi. Specimens of C. cyanopterus and C. zenithicus from L. Superior were examined at the R.O.M.; C. cyanopterus differs from C. zenithicus in its larger size, deeper body, ovate profile and shorter maxillae, similar to the differences between C. prognathus and C. reighardi in L. Ontario (Koelz 1929). The largest specimen of C. reighardi from L. Ontario that Koelz (1929) examined was intermediate between small C. reighardi and C. prognathus in having a more ovate profile, a deeper body and a smaller eye than small C. reighardi. Large C. zenithicus in L. Superior had a smaller head and eyes, a larger snout and longer fins than small C. zenithicus (Koelz 1929), and in this respect are similar to C. cyanopterus. It is suggested that C. cyanopterus and C. prognathus are not subspecies of C. nigripinnis, but that C. cyanopterus and C. zenithicus from L. Superior are conspecific, and that C. prognathus and C. reighardi from L. Ontario are conspecific.

Of the names applicable to the low group, C. prognathus (Smith 1894) has precedence over C. zenithicus (Jordan and Evermann 1909) and other possible names. Unfortunately, the condition of the holotype of C. prognathus is such that it is impossible to confirm that it is similar to the low group, and C. prognathus is extinct in its type locality of L. Ontario

(W. B. Scott, personal communication). However the original description of C. prognathus (Smith 1894) and its subsequent description (Koelz 1929) are sufficient to show the similarity of C. prognathus to the low group of central Canada. Therefore it is suggested that the name of the low group in central Canada should be C. prognathus. Alternative methods of arriving at the correct nomenclature for the low group are: i) to use the name C. zenithicus since this name commonly is used at present for members of the low group; ii) to examine, in order of their original descriptions, the holotypes of C. zenithicus (Jordan and Evermann 1909), C. johannae (Wagner 1910), C. cyanopterus (Jordan and Evermann 1911), C. kiyi (Koelz 1921), C. alpenae and C. reighardi (Koelz 1924), and C. bartletti (Koelz 1931) to find the earliest designated holotype which is in good enough condition to form the basis of the nomenclature of the low group. The author prefers the first suggestion, that C. prognathus should be used for the name of the low group in central Canada. Therefore C. zenithicus (Jordan and Evermann 1909), C. cyanopterus (Jordan and Evermann 1911) and C. reighardi (Koelz 1929) should be junior synonyms of C. prognathus (Smith 1894). Additional synonyms of C. prognathus from central Canada should be C. hoyi from George L. (Gibson and Johnson MS 1969) and from Sandy L. (R.O.M. identification), C. artedii from Deer L. (Ryder et al. 1964), and some C. artedii from Lac Seul and Sandy L. (R.O.M. identifications); it is suggested that C. prognathus should not include C. zenithicus from L. Attawapiskat (Ryder et al. 1964).

The status of C. alpenae (Koelz 1924), C. johannae (Wagner 1910), C. k. kiyi (Koelz 1921) and C. bartletti (Koelz 1931) is not clear, but they may be synonyms of C. prognathus.

High Group - Coregonus artedii Lesueur.

The following original descriptions of species or of specimens from type localities are similar to the high group:

a) original descriptions of C. artedii and C. albus (Lesueur 1818), C. tullibee, C. lucidus and C. harengus (Richardson 1836), C. clupeiformis (De Kay 1842), C. nigripinnis and C. hoyi (Gill, in Hoy 1872) and C. sisco (Jordan 1875) are inadequate, but specimens from their type localities (Koelz 1929, 1931; Dymond 1928, 1943; and specimens of C. artedii and C. hoyi examined at R.O.M.) fit high group in gillraker count, morphology and appearance; b) descriptions of holotypes of C. osmeriformis (Smith 1894), C. eriensis and C. huronius (Jordan and Evermann 1909), C. supernas and C. manitoulinus (Jordan and Evermann 1911), C. macropterus (Bean 1916, but original gillraker count wrong, see Smith 1964), C. athabascae (Harper and Nichols 1919, but original gillraker count wrong, see McPhail and Lindsey 1970), C. nipigon (Koelz 1925) and C. hubbsi (Koelz 1929a) fit high group in gillraker counts, morphometry and appearance; c) descriptions of holotypes of C. ontariensis (Jordan and Evermann 1911), C. birgei (Wagner 1911), C. macrognathus and C. entomophagus (Harper and Nichols 1919, but original gillraker counts wrong, see McPhail and Lindsey 1970)

and C. churchillensis and C. nueltinensis (Fowler 1948) are intermediate in gillraker counts, but their general appearance and morphometry, or gillraker counts of specimens from the type localities (Koelz 1929, 1931) fit high group.

In the Great Lakes and L. Nipigon, mean gillraker counts for all populations of C. artedii, C. hoyi, C. kiyi orientalis, C. n. nigripinnis, C. n. regalis and C. nipigon are greater than 40.9 (Koelz 1929) and hence are similar to the high group in central Canada. All other populations of ciscoes examined from the St. Lawrence drainage basin (Fig. 1 and Appendix 1) are similar to the high group in their mean gillraker count; all had been identified at the R.O.M. or N.M.C. as C. artedii except in Long L. (C. nigripinnis) and Baby L. (C. nipigon).

Forms of the high group in central Canada had been identified as C. artedii, C. hoyi, C. nigripinnis, C. nipigon and C. zenithicus (see Table XVI). Koelz (1929) distinguished C. hoyi from the other species by its protruding mandible, C. nigripinnis from the other species by its gillraker counts of 54 or more, and C. zenithicus is most similar to the low group. In central Canada these species in the high group form a continuous series with no distinctive features separating them; C. hoyi is the smallest with least gillrakers, then C. artedii, C. nigripinnis, and C. nipigon is the largest with most gillrakers. C. tullibee is intermediate between C. artedii and C. nigripinnis. Examination of C. lucidus from its type

locality, Great Bear L., show it is similar to the high group with no features that warrant its separation from the high group. Dymond (1943) concluded that C. tullibee and C. lucidus were synonyms of C. artedii. Of these names C. artedii (Lesueur 1818) has precedence, so it is suggested that C. lucidus and C. tullibee (Richardson 1836), C. nigripinnis and C. hoyi (Gill, in Hoy 1872) (except from George L. = C. prognathus), C. zenithicus from Attawapiskat L. (Ryder et al. 1964) (all other C. zenithicus = C. prognathus) and C. nipigon (Koelz 1929) are synonyms of C. artedii; some C. artedii from Lac Seul and Sandy L. (R.O.M. identifications), and all C. artedii from Deer L. (Ryder et al. 1964) are suggested to be synonyms of C. prognathus.

Dymond (1943) considered that C. athabascae, C. macrognathus and C. entomophagus were synonyms of C. zenithicus, but his recorded gillraker counts are wrong (McPhail and Lindsey 1970). The holotypes of these three species were examined at the N.M.C. C. athabascae and C. macrognathus are in fact more similar to the high group at their type locality than to the low group. The 17 gillrakers on the upper limb of the first gill arch of the holotype of C. athabascae (the lower limb is incomplete) identify it as a member of the high group, and the long pectoral fins of C. macrognathus (21.04% fork length) also identify it as a member of the high group; also the general appearance of the two holotypes resemble typical forms of the high group. The holotype of C. entomophagus from Tazin R. is

identified as a member of the high group by its interorbital width (6.57% form length); in general appearance it is most similar to the Mackenzie R. medium form, the only other riverine form examined and a member of the high group. On this basis it is suggested that C. athabascae, C. entomophagus and C. macrognathus are synonyms of C. artedii.

There are no distinguishing features between the original description of C. churchillensis (Fowler 1948) and the Churchill medium form which was included in the high group; the original description of C. churchillensis (Fowler 1948) enables it to be identified as a member of the high group by its head length (20.53% fork length) and inter-orbital width (7.08% fork length). Only the general appearance and colouration in the original description of C. nueltinensis (Fowler 1948) identify it as a form of the high group. C. churchillensis and C. nueltinensis are probably synonyms of C. artedii.

Summary - the Mackenzie R. low form is identified as C. autumnalis, the Mackenzie R. high form as C. sardinella, the high group as C. artedii, and the correct name of the low group is suggested to be C. prognathus. Suggested new synonyms of C. artedii in central Canada are C. hoyi (except from George L.), C. nigripinnis, C. nipigon, C. zenithicus from Attawapiskat L., C. athabascae, C. entomophagus, C. macrognathus, C. churchillensis and C. nueltinensis. Suggested new synonyms of C. prognathus are C. zenithicus (except from Attawapiskat L.), C. cyanopterus, C. reighardi, C. hoyi from George L., C. artedii from Deer L., and some C. artedii from Lac Seul and Sandy L.

MORPHOLOGICAL DIFFERENCES AND DISTRIBUTION
OF CISCOES IN CENTRAL CANADA

Operations involved in delimiting species are either divisive or agglomerative, and may be based on geographical, phenetic or reproductive information (Sokal and Crovello 1970). Since species are defined by reproductive isolation (Mayr 1963), reproductive information should be used in separating sympatric species and in grouping allopatric populations. Even under ideal conditions this would be very time consuming, so in practice the species definition is non-operational and decisions that should be based on reproductive information are based on phenetic information. Unfortunately, because of polymorphisms and phenotypic plasticity, phenetic similarity or dissimilarity need not reflect interbreeding or the lack of interbreeding. As practical taxonomy is based on phenetic, rather than reproductive, information, it is imperative that the range of variation in morphological characters of the group under study is known. However it is necessary to know the taxonomy of the group before full knowledge of phenotypic variation within a species can be known, and conversely full knowledge of phenotypic variation within a species must be known before species can be delimited correctly.

This circularity in taxonomy is usually not important

in practice, as most taxa have some characters that are recognisable as being constant within species but varying between species. In cisco taxonomy this circularity is very important because their phenotypic plasticity has hindered their taxonomy. No characters are known at present that are constant within species but vary between species, nor is the full range of variation of characters known. The problem in cisco taxonomy is to separate the environmental component of the phenotype from any taxonomic component. Factor analysis provides a method to identify some of the more obvious factors as modifiers of morphological characters, so this circularity will not be referred to in the following discussion.

The study of the taxonomy and phenotypic variation within a group depends upon the sampling of specimens. Ideally specimens from all localities should be studied, or from localities spread evenly throughout the area under study. Poor access limited the number of sampling sites in the north of central Canada and in northern Ontario, resulting in a disproportionate number of samples from the southern part of central Canada; confidence in the interpretation of some results should reflect the unbalanced sampling of ciscoes.

Intraspecific and Interspecific Differences in
the Morphology of Ciscos

Factors affecting the Value of Morphology in Cisco Taxonomy

Three factors reduce the value of most characters in coregonid taxonomy. Firstly, growth of body parts is rarely isometric, larger fish often having relatively smaller body parts (Hile 1937). Secondly, sexual dimorphism occurs (Hile 1937; Loch MS 1971). Thirdly, environmental differences result in extensive intraspecific variation (Hile 1937; Svardson 1950); transplantation experiments (Svardson 1950, 1952) showed that much intraspecific variation is a result of phenotypic plasticity rather than selection upon the genotype.

The size of body parts usually is compared by analysis of covariance (Martin 1949; Loch MS 1971) as this counteracts the effect of allometric growth, but heterogeneity of variance discovered in preliminary analyses rendered ANOCOVA unsuitable for this study. Instead each body part was regressed against either fork length or head length, and values were calculated from the regression equations for the size of the body parts at either 200mm. fork length or 45mm. head length; these values were used in subsequent analyses. As the accuracy of this technique is dependent upon the size range of each form, it is probable that some error occurred

because of an inadequate size range of certain forms, although forms in which the size range was obviously inadequate were excluded from the analyses. There was little correlation between size of body parts and fork length of the different forms of ciscoes and this was associated with environmental variation (Tables III, VI and X). Since the regression technique is not applicable to the identification of individuals, the relative size of body parts was used for this and in the key to the ciscoes. For these two purposes it is hoped that the size range of the specimens of C. artedii and C. prognathus (Table XX) was sufficient to counteract the effects of allometric growth, but no C. sardinella smaller than 175mm. fork length nor C. autumnalis smaller than 300mm. fork length were examined. This was reflected in the relative size of body parts of C. autumnalis, which was consistently the smallest; the relative size of body parts based only on large fish showed that C. autumnalis had the shortest mandible, whereas this species had the longest mandible when calculated by the regression technique (Table XIII).

Sexual dimorphism is known to occur in C. artedii (Hile 1937), with males having longer fins and heads, larger eyes and less deep bodies than the females. In C. clupearformis, males often have longer fins and more slender bodies than females (Hart 1931; Loch MS 1971); some characters showed sexual dimorphism in one lake but not in another (Loch MS 1971), while in other lakes there was no evidence for sexual dimorphism

(Kennedy 1943; Fenderson 1964). Discriminant analysis showed no significant or consistent differences between sexes of C. artedii in Big Peter Pond and Montreal L., or of C. prognathus in Lac Seul, so the effects of sexual dimorphism were ignored although they may have been significant at other localities. It is possible that the degree of sexual dimorphism is affected by the environment.

Koelz (1929, 1931) recognised the great intraspecific variation in cisco morphometry, but overemphasized the use of profile and of jaw characteristics (whether the lower jaw is included in, equal to or longer than the upper jaw) in separating and identifying species of ciscoes. In central Canada, ciscoes had been identified on the basis of their gillraker counts, profile, jaw characteristics and pigmentation without any adequate study on the variability of these characters in central Canada. In the Great Lakes, an ovate profile separated the three most abyssal species of ciscoes (C. johannae, C. kiyi and C. nigripinnis) from the other ciscoes (Koelz 1929), but some C. johannae and C. kiyi, and smaller C. nigripinnis were elliptical, and some larger C. artedii were ovate. The profile of C. artedii from central Canada is more ovate in shallow lakes (Table IX). Svardson (1949) showed by transplantation experiments that, at least in some cases, the profile of some coregonids may be phenotypically plastic. Populations of C. artedii in central Canada had been identified as C. nigripinnis by their ovate

profile, which has been shown to vary between lakes in a predictable way (Table X), and by the presence of dark pigment, especially in the fins. Like an ovate profile, pigmentation is usually more pronounced in shallow lakes, especially in shallow, turbid lakes. Koelz (1929) recognised that the jaw characteristics of C. zenithicus were variable and that deep water races of C. artedii and C. hoyi had longer mandibles. Variation in jaw characteristics occurs in L. Erie C. alpenae (Scott and Smith 1962) and within and between forms of C. artedii and C. prognathus in central Canada.

In central Canada, the phenotypes of populations previously identified as C. hoyi, C. artedii, C. nigripinnis and C. nipigon form a continuous series with no distinctive features separating them. Differences between the populations may be attributable to differences in lake morphometry, chemistry and climate (Table IX); water depth (Koelz 1929) and temperature (Vladykov 1934) can also affect morphometry. Likewise the phenotypes of populations previously identified as C. zenithicus and C. reighardi form a continuous series with no distinctive features separating them. Sympatric forms of C. artedii occur in 26 lakes, but differences between them are not consistent and are associated with size differences or environmental variation (Tables VII and VIII).

Morphometric differences result from variation in growth rate, with fast growing fish usually having relatively

smaller body parts and greater body width (Hile 1937). Growth rate is known to be affected by population density (Hile 1936) and the trophic conditions of a lake (Kozikowska 1961). The correlation between growth rate and coregonid morphometry was shown by transplantation experiments, which also showed that intraspecific variation in both was mainly phenotypic rather than genetic (Svardson 1950, 1952). The early development is more important than the subsequent growth rate in determining the relative size of body parts (Martin 1949); size at the four inflections in growth controls subsequent morphometry with a larger size at the eyed egg stage or ossification, and a smaller size at hatching or at maturity, all resulting in larger body parts. Little is known about how environmental conditions on the spawning grounds affect early development.

Besides affecting morphometry, the rate of early development is capable of modifying meristic characters within certain limits (Mottley 1937), with factors prolonging development associated with an increased number of somites and of most meristic parts (Hubbs 1926). Intraspecific variation in scale counts is mainly phenotypic as Svardson (1952) showed by transplantations that modified lateral line scale counts by up to eleven units. Variation in scale counts of C. artedii is associated with climatic differences (Table IX), but differences in scale counts of

sympatric forms of C. artedii are associated with size differences (Table VII). The high scale counts for C. autumnalis may result from the large size or the low temperatures, or it may be partly genetic. Size of fish bear the same relationship to the environment as do the number of segments (Vladykov 1934), so vertebral counts vary with the average body length of spawning females, egg size and time of spawning (see Lindsey and Ali 1971). The exact role of temperature in the modification of somite numbers is in question (Tatarko 1968).

Gillraker number is one of the least plastic characters used in coregonid taxonomy and is apparently controlled by a polygenic complex (Svardson 1952). During transplantations, gillraker numbers never changed by more than two units (Svardson 1952; Loch MS 1971), but aquarium reared C. clupeaformis (Koelz 1929) and Oncorhynchus nerka (McCart and Andersen 1967) had gillraker counts modified by up to four units. Although not very plastic, gillrakers are responsive to selection pressure (Svardson 1949) and both their number and length are correlated to diet (Svardson 1952; Kliever 1970). Also mean gillraker numbers are positively correlated to average body size in the Eurasian cisco C. albula (Himberg 1970) and in C. artedii (Tables IX and X). The range of mean gillraker counts in C. artedii and C. prognathus are 21.8 and 10.8 respectively, suggesting a genetic difference in gillraker number of some populations

of each species in response to size or trophic conditions. Gillraker counts of C. artedii form a continuous series, so it is artificial to consider that ciscoes with more than 54 gillrakers belong to a separate species, C. nipigon, especially since these populations have a large fork length, and several populations are known each with more than and less than 54 gillrakers (Table II). Size differences are correlated to the differences in gillraker counts of sympatric forms of C. artedii (Fig. 10), but, at least in some cases, the differences are probably genetic rather than phenotypic, as the differences may exceed two units. Gillraker counts in C. lavaretus form two genetic clines, with high counts decreasing and low counts increasing with increasing temperature (Himberg 1970). No cline was found in central Canadian ciscoes, but populations of C. artedii from the North West Territories and Hudson Bay generally had lower mean counts than had populations from elsewhere (Table II).

Interspecific Differences between Ciscoes in Central Canada

Study of intraspecific variation within C. artedii and C. prognathus shows that much of it is associated with environmental variation (Tables IX and X), and Svardson's (1950, 1952) work suggests that much intraspecific variation results from phenotypic plasticity rather than from genetic variation caused by selection. The exception

is variation in gillraker numbers, which is primarily genetic, but is correlated to differences in size and trophic conditions.

With only one sample of C. autumnalis and C. sardinella it was impossible to judge to what extent the differences between these species and between these species and C. artedii and C. prognathus were interspecific or associated with environmental variation. It is probable that part of the differences in scale counts and morphometry result from phenotypic plasticity, but the overall morphological dissimilarity of C. autumnalis and C. sardinella and the other ciscoes (Fig. 3, Table XIII) as well as distinct differences in their osteology (Figs. 11 to 13), warrant their separation as distinct species. Also protein differences have been reported between C. sardinella and C. artedii, but C. sardinella may be a complex of species (McPhail and Lindsey 1970).

Factor analysis enabled separation of interspecific variation between C. artedii and C. prognathus from variation associated with environmental differences. The separation of populations of C. artedii from populations of C. prognathus was essentially multivariate (Figs. 4 to 8), and the major difference between the two species, their mean gillraker counts, was not

associated with any environmental variable (Table V). The gillraker factor (Tables III and V) separated all populations of C. artedii from all populations of C. prognathus, except for Sandy L. C. prognathus. This raised doubts as to the true affinity of Sandy L. C. prognathus, but in all measures of overall similarity (Figs. 6 to 8) it was grouped with the other C. prognathus, and its actual mean gillraker count was not in the range of mean counts for C. artedii. Unlike the differences between sympatric forms of C. artedii, the differences between sympatric C. prognathus and C. artedii were consistent; C. prognathus always had fewer gillrakers (Table XXI), longer snouts and jaws than sympatric C. artedii. In part, these differences may be associated with the occurrence of C. prognathus in deep water (Table V). Inter-lake variation in the morphology of C. artedii and C. prognathus meant that there was no one character or combination of characters that separated all individuals of C. artedii from all individuals of C. prognathus. Despite this and the large size of the C. autumnalis examined, a partial key (see next section) was made to the ciscoes of central Canada, but it is questionable if a key in the traditional sense is of much use in coregonid taxonomy, as a multi-variate approach is better in theory and in practice, whereas a simple key is likely to lure the unwary into

unjustified identifications.

Besides differences in morphometry, meristics and gillrakers, interspecific differences were found in the skull bones of the four species. In Eurasia, Gasowska (1960, 1970) and Shaposhnikova (1970) concluded that the dentition, jaw bones and ethmoid region are of taxonomic importance. It was found that the shape of the supraethmoid, dentary and maxilla (Figs. 11 to 13) separate C. sardinella from the other three species, and the shape of the supraethmoid and dentary separate C. autumnalis from C. artedii and C. prognathus. These bones, especially the supraethmoid, are too variable to separate all individuals of C. prognathus from C. artedii, but usually could separate sympatric individuals of the two species. Sympatric forms of C. artedii were usually more similar to each other in their osteology than to any other possible grouping of forms of C. artedii. The dentition of the supralingual plate differed between the four species, and the dentition of C. prognathus was usually better developed than in C. artedii.

Norden (1961) reported that all young ciscoes (up to 80mm.) have teeth on the dentary, premaxillae and autopalatines, with the palatine teeth retained in adult C. sardinella, and weak premaxillary teeth occasionally retained in adult C. artedii. Dentary teeth were found on adults of all four species, and premaxillary teeth on adults of all species

except the two C. sardinella. Palatine teeth were found on both C. sardinella, often on C. prognathus and occasionally on C. artedii; vomerine teeth were found on a few C. prognathus and C. artedii.

Identification and Distribution of Ciscoes
in Central Canada

Identification of Individual Ciscoes

An attempt was made to separate all individuals of the four species from central Canada, using morphological characters, with body parts of each individual expressed as per cent fork length. The range of values for each character of the individuals of the four species are shown in Table XX. Various other ratios were used, but they were of little additional help.

It was possible to separate all individuals of C. autumnalis, C. sardinella and C. prognathus from each other, but it was impossible to separate all individuals of C. artedii from all individuals of the other three species. It should be remembered that individuals of the C. autumnalis and C. sardinella came from one locality, whereas C. artedii and C. prognathus were examined from several localities.

C. autumnalis individuals were separated from C. sardinella individuals in having an eye diameter of less than 4.0% fork length, a pelvic length of less than 14.8% fork length and 83 or more lateral line scales. Eye diameter and number of lateral line scales also distinguished C. autumnalis individuals from C. prognathus individuals, as did an upper jaw length of less than 6.75% fork length and a

TABLE XX

The range of individual characters and selected other characters for separating the four species. Individual body proportions are expressed as % fork length.

Character	<u>C. autumnalis</u>		<u>C. sardinella</u>		<u>C. prognathus</u>		<u>C. artedii</u>	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper
<u>Individual values</u>								
Fork l. - mm.	300	381	175	347	89	447	78	485
Body d.	17.44	20.37	17.94	27.09	13.23	28.36	12.55	33.74
Head l.	16.93	21.40	16.84	21.20	20.82	27.28	18.36	30.14
Eye diam.	2.89	3.93	4.47	5.09	4.12	7.49	3.38	7.31
Snout l.	4.25	4.99	3.69	4.63	4.08	7.46	3.88	6.92
Interorbital w.	4.46	5.45	2.95	4.54	3.30	5.91	3.18	7.21
Upper jaw l.	5.75	6.50	5.67	7.09	6.94	10.05	4.22	10.00
Mandible l.	7.48	9.27	6.74	9.24	9.46	13.50	7.59	13.31
Premaxillae w.	3.15	4.03	2.96	3.83	3.38	5.58	2.35	5.98
Gillraker l.	2.36	3.45	2.28	3.35	1.91	5.00	2.06	5.90
Pectoral l.	12.68	15.10	14.68	17.89	12.13	19.40	12.15	21.33
Pelvic l.	12.04	14.77	14.85	18.19	12.11	19.08	10.96	23.09
Profile	36.29	43.67	35.18	40.36	31.20	59.42	31.02	54.81
Premaxilla ang.	51	95	10	68	25	74	10	83
Lateral line scales	83	98	72	82	60	78	55	89
Upper rakers	15	18	15	18	8	16	12	24
Lower rakers	25	27	25	30	16	28	23	43
Total rakers	40	44	41	47	24	43	36	67
<u>Form values</u>								
Upper jaw l.	14.4		15.2		16.0	18.9	13.7	16.9
Total rakers	42.4		44.4		29.4	40.2	40.9	62.9
Index	4.9		1.1		12.3	20.6	-17.1	7.7
<u>Known Sympatry</u>	with <u>C. artedii</u> and <u>C. sardinella</u>		with <u>C. artedii</u> and <u>C. autumnalis</u>		with <u>C. artedii</u>		with <u>C. prognathus</u> , <u>C. autumnalis</u> and <u>C. sardinella</u>	

mandible length of less than 9.35% fork length. A mandible length of less than 9.35% fork length also distinguished C. sardinella individuals from C. prognathus individuals. The key in McPhail and Lindsey (1970) separated all individuals of C. autumnalis, C. sardinella and C. artedii. C. artedii individuals were separated from C. autumnalis individuals by the presence of pigment on the pelvic fins, and from C. sardinella individuals by a longer prepelvic distance. C. artedii individuals from the Mackenzie R. (Mackenzie R. medium form) were separable from Mackenzie R. C. autumnalis and C. sardinella individuals; the C. artedii individuals were distinguished from C. autumnalis individuals by an eye diameter of greater than 4.0% fork length, and from C. sardinella individuals by an interorbital width greater than 4.7% fork length.

Some individuals of C. prognathus and C. artedii were separable by their gillraker counts; 50% of C. prognathus individuals had total gillraker counts of 35 or less, and 77% of C. artedii individuals had total gillraker counts of 44 or more. After ten more characters (upper rakers, lower rakers, upper jaw length, gillraker length, mandible length, pelvic length, pectoral length, snout length, eye diameter and head length) were used, 69% of C. prognathus individuals and 85% of C. artedii individuals were grouped correctly. C. artedii occurred sympatrically with C. prognathus in 13

lakes, and the total number of gillrakers distinguished all individuals of the two species at eleven localities (Table XXI). In Lake of the Woods, one individual of each species was found with 41 gillrakers; individuals could be grouped correctly by the number of gillrakers on the lower limb, C. prognathus individuals had from 18 to 26, and C. artedii individuals had from 27 to 31. Discriminant coefficients for all localities were given in Table I. There was no simple way to separate all individuals of C. artedii and C. prognathus from L. Winnipeg.

Populations of C. artedii and C. prognathus were separable by their mean total gillraker counts, with C. prognathus having means from 29.4 to 40.2 and C. artedii from 40.9 to 62.7 (Table XX). Several forms, composed of only one or two individuals, had been grouped by their mean gillraker counts, although the individuals were not placed with either species by their individual characters. This raised doubts as to the correct grouping of the Great Slave L. lower form and of the Baker L., Cape Jones, Fishing L., James Bay, Osnaburgh L., Richmond Gulf, Tazin R. and Wholdaia L. medium forms. The overall similarity of these forms suggested that they were correctly grouped by their gillraker count except for the Tazin R. medium form, which is a form of C. artedii.

External Appearance, Diagnostic Characters and Distribution of the Ciscoes of Central Canada

C. autumnalis: the Mackenzie R. low form. Body elongate

TABLE XXI

The Use of Gillraker Counts in Distinguishing
between Sympatric Forms of C. prognathus and C. artedii.

Locality	<u>C. prognathus</u>		<u>C. artedii</u>	
	<u>n</u>	Range	<u>n</u>	Range
L. Athabasca	18	34 43	26	49 57
Barrow L.	15	37 41	21	44 51
Big Athapapuskow	16	24 36	43	38 49
Big Trout L.	1	35	2	40 45
Clearwater L.	2	33	28	38 49
Deer L.	2	35	2	50 52
Great Slave L.	1	38	5	42 49
Lac Seul	39	31 37	24	41 57
Lake of the Woods	18	30 41	16	41 51
Little Athapapuskow	14	32 37	32	40 54
Mink Narrows	8	34 40	21	43 58
Sandy L.	7	37 43	3	51 54
L. Winnipeg	5	37 43	37	38 61

and slightly compressed, premaxillae usually at an angle to the snout, tips of upper and lower jaws usually equal when mouth is closed, eyes small. Pigmentation weak, especially on fins. For range of morphological characters see McPhail and Lindsey (1970) and Table XX, for population value see Table XIII. Distinguished from C. sardinella, C. artedii and C. prognathus by immaculate pelvic fins, from C. laurettae by 26 or more gillrakers on the lower limb of the first gillarch; occurs sympatrically with C. sardinella, C. artedii and C. laurettae. Distinguished from sympatric C. sardinella and C. artedii by eye diameter less than 4.0% fork length.

Distribution: northern Europe, Siberia, western arctic N. America, except for Bering Sea area where it is replaced by C. laurettae. In central Canada it occurs in Mackenzie R. up to Fort Simpson and along arctic coast west of Bathurst Inlet. For distribution map see McPhail and Lindsey (1970) and Hatfield et al. (1972).

C. sardinella: the Mackenzie R. high form. Body elongate and somewhat compressed, premaxillae usually form straight line with snout, tip of lower jaw usually projects beyond tip of upper jaw when mouth is closed, eyes large. Dark pigment present on upper surfaces and fins. For range of morphological characters see McPhail and Lindsey (1970) and Table XX, for population value see Table XIII. Distinguished

from C. artedii, C. autumnalis and C. prognathus by short prepelvic distance. Occurs sympatrically with C. autumnalis; also distinguished from Mackenzie R. C. autumnalis by eye diameter greater than 4.0% fork length, and from Mackenzie R. C. artedii by interorbital width less than 4.7% fork length.

Distribution: Arctic Ocean and river mouths of Siberia and western N. America, and extensively throughout Yukon R. system. In central Canada occurs in Mackenzie delta region, and on arctic coast west of Bathurst Inlet. For distribution map see McPhail and Lindsey (1970) and Hatfield et al. (1972).

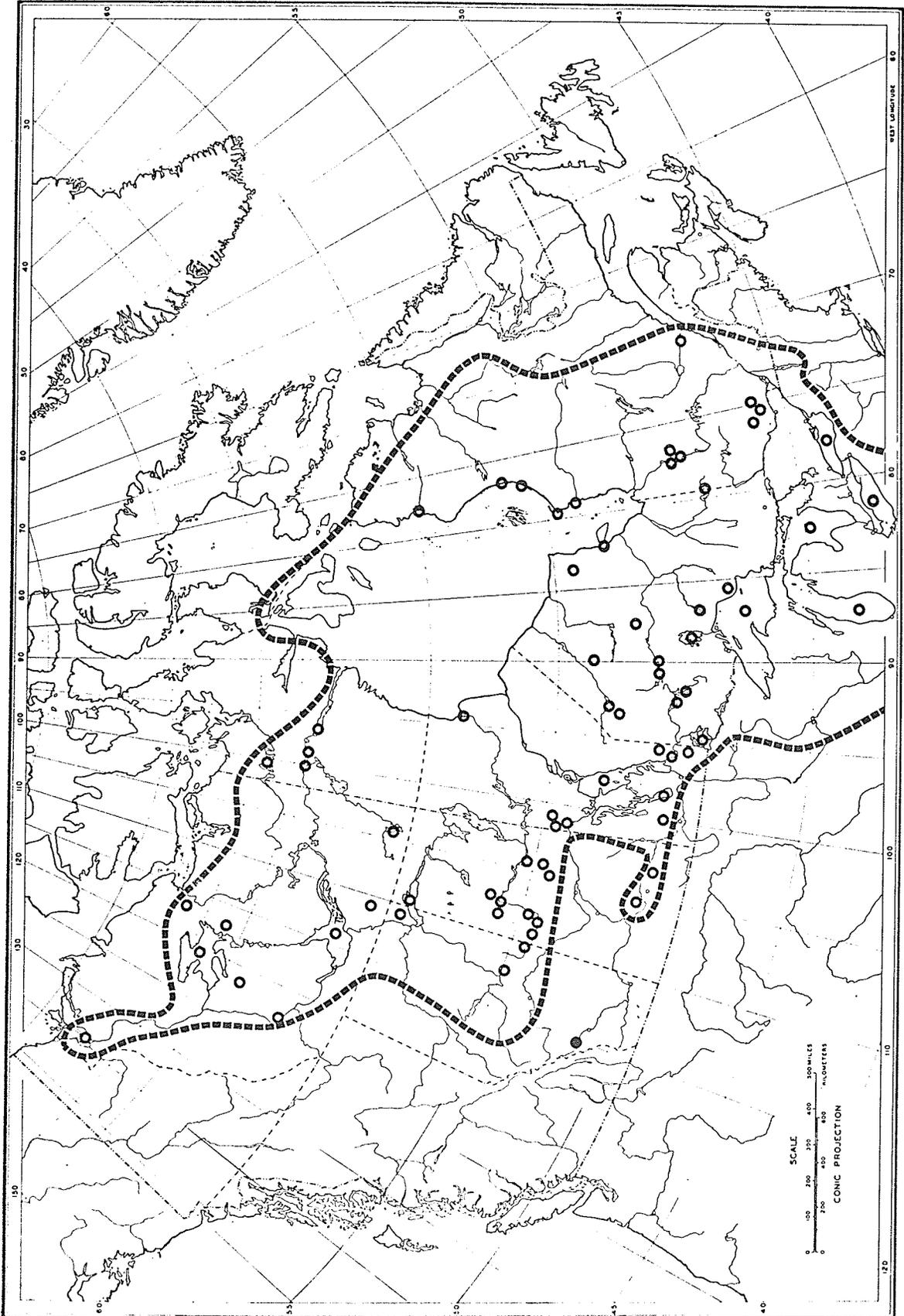
C. artedii: the high group. External appearance variable, ranging from small slender forms to large deep-bodied forms; often different forms of C. artedii occur sympatrically. Body usually compressed, premaxillae usually form straight line with snout but may be at an angle, tip of lower jaw equal to or projecting beyond tip of upper jaw when mouth is closed. Pigmentation variable but dark pigment present on upper surfaces and usually present on fins; fins often tipped black. For range of values of morphological characters see Table XX, and for range of population values see Table XIII. Distinguished from C. sardinella by long prepelvic distance and from C. autumnalis by pigmented fins. Occurs sympatrically with C. autumnalis and C. prognathus; in Mackenzie R. distinguished from C. autumnalis by eye diameter greater than

4.0% fork length, and from C. sardinella by interorbital width greater than 4.7% fork length; usually distinguished from sympatric C. prognathus by more gillrakers (Table XXI), shorter upper jaws and shorter snout.

Distribution: endemic to N. America, present in upper Mississippi, Great Lakes basin and central Canada. In central Canada is absent from western tributaries of Mackenzie R., upper Peace R., southern Alberta (except for introduced populations in Minnewanka and Spray lakes), southern Saskatchewan except Qu'Appelle valley, and southwestern Manitoba. The N. American range and arctic records of C. artedii are shown in McPhail and Lindsey (1970), Mackenzie R. records in Hatfield et al. (1972) and Alberta records in Paetz and Nelson (1970). Fig. 18 shows the Canadian range and selected records of C. artedii.

C. prognathus: the low group. External appearance variable. Body usually compressed or slightly compressed, premaxillae usually at an angle to the snout, tip of lower jaw included in, equal to or projecting beyond tip of upper jaw when mouth is closed. Pigmentation variable, often weak, fins pale with a dusky margin (especially on caudal), sometimes darker. For range of values for morphological characters see Table XX, and for range of population values see Table XIII. Distinguished from C. sardinella by long prepelvic distance, and from C. autumnalis by pigment on pelvic fins. Occurs sympatrically

Fig. 18. Distribution of C. artedii in
Canada. Localities from which
specimens were examined ○ , introduced
populations ● . Reported natural range
of C. artedii indicated by black and white
line (from McPhail and Lindsey 1970).



with C. artedii; usually distinguished from sympatric C. artedii by fewer gillrakers (Table XXI), longer upper jaws and longer snout.

Distribution: endemic to N. America. Occurs in Great Lakes and L. Nipigon, and reported from Trout L. and White Partridge L. in the St. Lawrence drainage (Fig. 23). Occurs in L. of the Woods, Lac Seul, Sandy L., Big Trout L., Deer L., George L., L. Winnipeg, Clearwater L., Big and Little Athapapuskow, Mink Narrows, Reindeer L., L. Athabasca, Barrow L., and Great Slave L., and reported from Lac la Ronge in central Canada (Fig. 19).

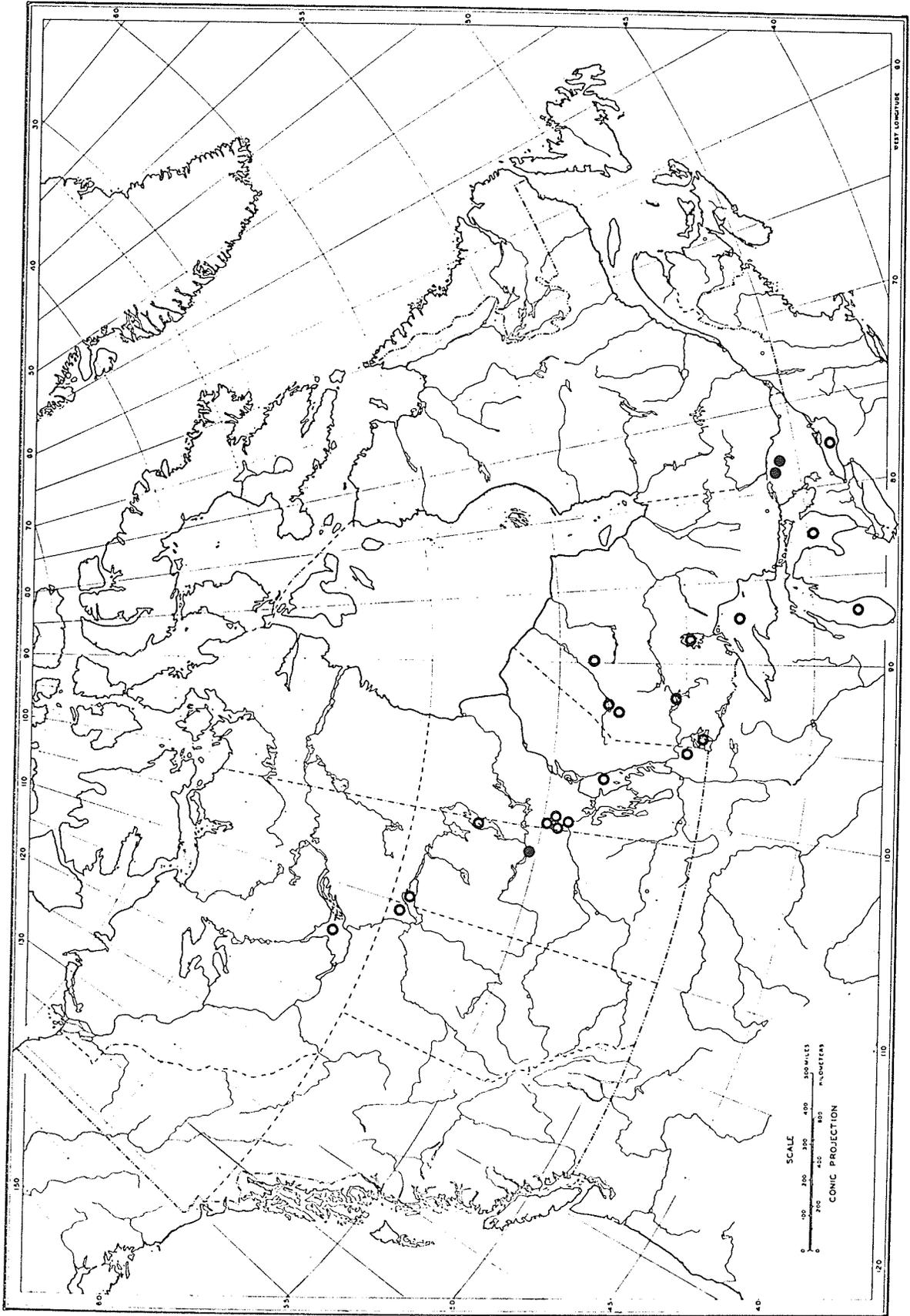
A Guide to the Separation of the Ciscoes from Central Canada

It was not possible to separate all individuals of C. prognathus from C. artedii using the guide below, although it was possible to separate all populations of these species (Fig. 5).

- | | |
|---|--|
| 1 | Eye diameter less than 4.0% fork length.....2 |
| | Eye diameter greater than 4.0% fork length.....3 |
| 2 | Tip of lower jaw does not project beyond upper jaw when mouth closed, pelvic fins immaculate.... <u>C. autumnalis</u> |
| | Tip of lower jaw projects slightly beyond tip of upper jaw when mouth is closed; pelvic fins never immaculate..... <u>C. artedii</u> |

Fig. 19. Distribution of C. prognathus.

Localities from which specimens
were examined ○ , reported localities ● .



- 3 Pelvic fins inserted forward, the distance from the snout to front of pelvic base equals distance from front of pelvic base to a point on the caudal peduncle ahead of the caudal flexure..... C. sardinella
- Pelvic fins inserted back, the distance from the snout to the front of pelvic base equals distance from front of pelvic base to a point on the caudal peduncle posterior to the caudal flexure.....4
- 4 Gillrakers 35 or less on first gillarch... C. prognathus
 Gillrakers 44 or more on first gillarch... C. artedii
 36-43 gillrakers on first gillarch.....5
- 5 Mean gillraker count of population known.....6
 Mean gillraker count of population not known.....7
- 6 Mean gillraker count of population less than 40.5..... C. prognathus
 Mean gillraker count of population greater than 40.5..... C. artedii
- 7 Either C. prognathus or C. artedii. Consult Table XX for differences between individuals, or Table XXI for differences in gillraker counts of sympatric forms from certain localities.

It should be remembered that this is essentially a

guide to the specimens examined by the author, and that the range of values in other specimens may be greater than that reported above, due to allometric growth or phenotypic plasticity.

EVOLUTION OF NORTH AMERICAN CISCOES

There has been much controversy whether the occurrence of sympatric sibling species of coregonids has been the result of allopatric differentiation followed by multiple invasions (Svardson 1970), or of fewer invasions followed by microgeographic (Behnke 1972) or by sympatric differentiation (Steinmann 1951). If differentiation had been allopatric, clustering of equivalent populations from different localities should result in monophyletic groups, but if sympatric differentiation occurred at each locality, any attempt to cluster equivalent populations from different localities would result in some polyphyletic groups. If on the other hand differentiation had been microgeographic there would be monophyletic groups in a single area, and clustering the morphologically equivalent populations from different areas would result in polyphyletic groups. As knowledge of the history of each population is lacking, the choice between allopatric, microgeographic and sympatric differentiation has to be based on morphological and zoogeographic information.

The morphological similarities of all populations of C. prognathus and of all populations of C. artedii (Figs. 6 and 7) can be interpreted as evidence for the monophyletic origin of each species, as can the consistent morphological differences between sympatric populations of the two species,

and the lack of correlation between the gillrakers and any environmental variable (Table V). An alternative explanation is that one species is polyphyletic with C. prognathus being derived from separate C. artedii populations or vice versa, and that the morphological similarity of populations of one species results from their existence in similar environments.

The distribution of all four cisco species in central Canada is explicable by the presence of each species in one refugium at the end of the Wisconsin glaciation. The present range of C. sardinella and C. autumnalis includes the Bering refugium, and it is believed that both species survived the glaciation in this refugium and have spread subsequently along the Arctic coast (McPhail and Lindsey 1970). The present distribution of C. artedii includes just one refugium, the Mississippi refugium, and it is believed that it survived the glaciation in this refugium and subsequently dispersed through a series of proglacial lakes (McPhail and Lindsey 1970). The present range of C. prognathus (Fig. 19) includes no refugia, but its distribution pattern is explicable by dispersal from just the Mississippi refugium. Since each species was present in just one refugium during the Wisconsin glaciation, it is suggested that only one basic stock of each species has invaded central Canada. The only possible exception to this is C. sardinella whose populations in the Yukon R. basin are morphologically distinct from those along the Arctic coast (McPhail and Lindsey 1970). Even if

C. sardinella populations along the Arctic coast were separate from those in the Yukon R. basin, there is as yet no evidence to believe that the Yukon R. form has crossed into central Canada.

C. artedii is much more widespread in central Canada than is C. prognathus, but it is possible on the evidence presented so far that the C. prognathus phenotype could have been derived from the C. artedii phenotype as a result of environmental pressures.

The morphological and zoogeographic evidence is consistent with the belief that extant populations of C. sardinella, C. autumnalis, C. artedii and C. prognathus are derived from single stocks of each of the four species at the end of the Wisconsin glaciation. Behnke (1972) believed that the species were distinct before the Wisconsin glaciation, whereas Hile (1937) and Booke (1968) believed that differentiation occurred in the refugia or in postglacial times.

Although it has been suggested that C. artedii is a monophyletic species, this does not account for the occurrence of two sympatric forms of C. artedii in 24 central Canadian lakes, and four forms in L. Winnipeg; in addition to the populations examined, sympatric forms of allied ciscoes are known from at least six other lakes (Table XVI). The differences between the sympatric forms are not consistent,

and are associated with differences in size and in the environment (Tables VII and VIII). The sympatric forms were not separable into different groups by any multivariate techniques (Figs. 6 and 7). Since C. artedii was present in only one refugium during the last glaciation, it is considered unlikely that two distinct stocks of C. artedii existed at the end of the glaciation as there is no morphological equivalence or explicable distribution pattern of the sympatric forms. Differentiation of sympatric forms of C. artedii may have been sympatric, microgeographic, or macrogeographic during the retreat of the ice.

If macrogeographic differentiation occurred between stocks of C. artedii during the retreat of the ice, most likely it would be between stocks in the L. Agassiz basin and in the L. Barlow-Ojibway basin. The reason to believe this is that all populations examined from the L. Barlow-Ojibway basin (L. Abitibi, L. Matagami, L. Olga, L. Waswanipi) had high gillraker counts, from 55 to 67 gillrakers, and many lakes in the L. Agassiz basin had sympatric forms, one having high gillraker counts (Lac Seul, L. Winnipeg, Second Cranberry L., Mink Narrows, Lac la Ronge).

L. Barlow-Ojibway was formed about 10,000 BP (Prest 1970), and was probably colonised by C. artedii from the Great Lakes. L. Agassiz and L. Barlow-Ojibway became confluent about 9,300 BP, but the Aguta ice readvance severed this

connection until further retreat of the ice re-established it about 8,600 BP; by 8,400 BP both lakes drained separately into Hudson Bay (Prest 1970). The time of isolation for the two stocks was short, and even then they still were connected indirectly via the Great Lakes, but the differentiation of a high gillrakered stock in L. Barlow-Ojibway could account for the occurrence of high gillrakered C. artedii in L. Attawapiskat and the L. Agassiz basin. A fact not fitting this hypothesis is the occurrence of high gillrakered populations in areas remote from the L. Agassiz basin (Waterhen L., L. Athabasca), which were apparently isolated from L. Agassiz before L. Agassiz was confluent with L. Barlow-Ojibway. Also, high gillrakered ciscoes are absent from the Great Lakes, southern Ontario and Quebec despite being able to colonise these areas from L. Barlow-Ojibway.

The correlation of mean gillraker count with size, and of size with environmental conditions (Table IX), and the distribution of the high gillraker counts suggests that the high gillraker counts result from local selection rather than from one distinct genetic stock originated in L. Barlow-Ojibway. This is supported further by the overall similarity of the L. Barlow-Ojibway populations with the other populations of C. artedii (Figs. 6 and 7), and the lack of low counts in the L. Barlow-Ojibway basin. The differentiation of two stocks may have been partially responsible for the occurrence

of sympatric forms of C. artedii in some areas of central Canada, but that other factors are involved is suggested by the occurrence of four sympatric forms of C. artedii in L. Winnipeg, and by the distribution of high gillrakered populations.

Behnke (1972) considered that, in some cases, sympatric species of coregonids result from recent allopatric differentiation caused by minor readvances of the ice margin during deglaciation, or by fluctuations in water levels. This latter mechanism is similar to that proposed by Fryer (1959) for speciation in East African cichlids. If this happened for C. artedii, the sympatric forms in a local area should be arrangeable into different clusters. Sympatric forms of C. artedii from five lakes in the Cranberry Portage area of northwestern Manitoba were not equivalent to each other in their overall morphology (Figs. 6 and 7) or gillraker counts (Table II). For instance in Mink Narrows and Little Athapapuskow the two sympatric forms have counts that can be equated, but in Big Athapapuskow the counts of both forms are closer to the lower counts in the other two lakes; at present the three lakes are interconnected by navigable channels. This does not rule out the possibility of the two forms resulting from microgeographic isolation, with the low counts of both forms in Big Athapapuskow resulting from introgression (Svardson 1970) or selection. It is also

possible that microgeographic isolation played a role in the differentiation of four forms of C. artedii in L. Winnipeg by water level fluctuations, minor ice readvances, the great distances involved or by homing to different spawning grounds. There were significant morphological differences between the C. artedii from the north and south ends of Montreal L. Such mechanisms may account for the multiplicity of coregonids in the Great Lakes basin.

Differentiation within a lake by homing to different spawning grounds is one mechanism suggested for sympatric speciation (Smith 1966). This may be a factor in the differentiation of three or more forms of C. migratorius in L. Baikal as it is possible to distinguish as many forms, differing in their ecology, gillrakers and morphology, as there are spawning rivers (Smirnov 1969). During their migration, C. artedii in L. Nipissing form distinct groupings (Fry 1937), which are interpretable as elementary populations. Lebedev (1969) believed that the formation of elementary populations could lead to sympatric speciation. Sympatric speciation was used to explain the origin of sympatric coregonids in Russia (Berg 1948) and in the Alps (Steinmann 1951). That sympatric forms of C. artedii in nine central Canadian lakes were more similar to each other than to any other form of cisco (Fig. 6), and that there is no firm evidence for the equivalence between members of pairs sympatric of C. artedii

even within a restricted area, are suggestive of sympatric differentiation, but does not rule out the possibility of microgeographic differentiation. Sympatric forms of C. artedii appear to be reproductively isolated in some lakes (Kooyman MS 1970), but not in others (Clarke MS 1970), suggesting that sympatric forms of C. artedii may behave as good species in some localities, but in other lakes may behave more as elementary populations.

The available evidence suggests that sympatric forms of C. artedii arose since the end of the Wisconsin glaciation by microgeographic and/or sympatric differentiation. The lack of equivalence between sympatric forms from different lakes and the lack of an explicable distribution pattern does not suggest macrogeographic differentiation or the presence of two distinct stocks at the end of the glaciation. Differentiation of stocks in glacial L. Agassiz and L. Barlow-Ojibway may explain partially the occurrence of sympatric forms of C. artedii in the L. Agassiz basin. There is no evidence to suggest whether the original differentiation of the four species was macrogeographic, microgeographic or sympatric, but their morphology and distribution suggest that each species was distinct at the end of the Wisconsin glaciation, and occurred in only one refugium. Each species is considered to be monophyletic.

Evolution in other Coregonids

Analysis of the morphology and zoogeography of N. American ciscoes failed to answer conclusively whether their differentiation was allopatric, microgeographic or sympatric. Other studies on coregonids may suggest whether allopatric, microgeographic or sympatric differentiation has played the major role in their differentiation, or whether all three are equally important.

Svardson (1957) believed that five species of coregonids invaded Scandinavia at the end of the last glaciation, as the maximum number of sympatric populations in Scandinavia is five, and that all populations of Eurasian coregonids are derived from the same five species. Besides his taxonomy being erroneous in the affinities of Scandinavian coregonids to the coregonids from elsewhere (Behnke 1970; Svardson 1970), his theory fails to deal with three points. These points are that seven sympatric forms of coregonids occur in L. Ladoga and L. Onega (Berg 1948), that two of his species hybridised extensively with a third species when the third species was introduced (Svardson 1949), and that an introduced population of one species remained reproductively isolated from the indigenous population of the same species (Svardson 1970). He explained the last two points by introgression dependent upon the local environment; to him (Svardson 1970), introgression included the incorporation of

genes of one species into the genotype of another species by extensive interbreeding, leading to the possible differentiation of isolated populations of the same species. This concept of introgression therefore implies that reproductive isolation can break down between species under certain circumstances, or can occur between populations of one species.

Whereas Svardson (1957) believed that the sympatric coregonids in Eurasia had differentiated allopatrically, Steinmann (1951) and Berg (1948) considered that the multiplicity of sympatric forms in the Alps and in Russia resulted from sympatric differentiation, and that the resultant taxonomic categories based on the equivalence of forms at different localities were polyphyletic. Kosswig (1963) also believed that the Scandinavian coregonids arose sympatrically at each locality, but that the sympatric differentiation was aided by the genetic heterogeneity of the original colonisers, which had been increased by hybridisation of different forms in a proglacial lake. Himberg (1970) believed that hybridisation played a role in the origin of Scandinavian whitefish in that C. muksun and C. pidschian hybridised to produce C. lavaretus, and these are the only whitefish in Scandinavia; this fails to account for the occurrence of more than three sympatric forms of whitefish in some lakes.

McCart (1970) believed that allopatric differentiation followed by hybridisation could account for the two or three sympatric forms of P. coulteri in the Bristol Bay drainages of Alaska. During the last glaciation, two forms of P. coulteri became differentiated in the Yukon-Bering refugium and in the Columbia refugium. Forms from each refugium subsequently invaded Naknek, Aleknagik and Chignik lakes, and in Chignik L. the two forms have hybridised to produce a third form. However the morphology of two recently described populations of P. coulteri from Elliot L. and Waterton L. suggests that the systematics and zoogeography of P. coulteri are more complex (Lindsey and Franzin 1972).

Both Behnke (1972) and Miller (1965) believe that the endemic Prosopium in Bear L. have evolved by microgeographic isolation caused by fluctuations in the water level of L. Bonneville.

Lindsey (1963) originally believed that the two sympatric forms of whitefish in Squanga L. represented two species, C. pidschian and C. clupeaformis, that had invaded Squanga L. from Siberia and the Mississippi refugium respectively. Recent studies of gene frequencies of N. American whitefish show that all whitefish in the Yukon basin are more similar to each other than to whitefish from elsewhere in N. America, and that there was no obvious equivalence between sympatric forms in Squanga L., Opeongo L. or in several lakes

in Maine in their biology, gene frequencies or gillraker counts (Lindsey et al. 1970). Nor was there any equivalence between the sympatric forms from different lakes in Maine (Fenderson 1964). Behnke (1972) and Lindsey et al. (1970) favour microgeographic isolation to account for the differentiation of the sympatric forms, but there is nothing in the data to rule out the possibility of sympatric differentiation (Lindsey et al. 1970). Endemic ciscoes are absent from all lakes in N. America where sympatric forms of whitefish occur. The absence of ciscoes may have enabled sympatric differentiation in whitefish to fill an unoccupied niche, or may have allowed different stocks of whitefish to invade and coexist in different niches. The two forms in Squanga L. were separated by their gillraker counts, feeding ecology and distribution, and reproductive behaviour (Lindsey 1963). Despite apparent differences in their reproductive behaviour, a study of their glycerol-3-phosphate dehydrogenase alleles (W. G. Franzin, personal communication) showed that separately the frequency of alleles in either form does not satisfy the Hardy-Weinberg equilibrium, whereas the frequency in the combined populations does. Taking into account the apparent differences in reproductive behaviour, the gene frequencies suggest that the two forms are becoming differentiated within Squanga L., but it is possible that the two forms are introgressing with selective pressure maintaining

differences in the gillrakers and ecology, or that they are two morphs of one population. Squanga L. whitefish certainly are worth further study.

There is no consensus of opinion among workers on coregonids as to the mechanisms to account for the diverse array of sympatric coregonids in some localities. Allopatric, microgeographic and sympatric differentiation have their advocates, and some believe that any of the above processes was aided by genetic heterogeneity of the invading stock resulting from previous introgression of different forms. It is possible that all processes have been involved in the differentiation of coregonids.

Evolutionary Theory and Taxonomic Practice

Mayr (1963) believed that gene flow between populations of a species has a cohesive effect, and that the lack of gene flow would enable differentiation of populations if they were under different selective regimes. Ehrlich and Raven (1969) concluded that the selective regime was more important than reproductive isolation in the differentiation of populations, and that reproductive isolation may result from differentiation rather than be a cause of it. Their reasons for this belief is that gene flow between adjacent populations usually is more restricted than was thought previously, that populations isolated for a long time often show little differentiation despite the lack of gene flow, and that

interbreeding does not necessarily stop differentiation (Ehrlich and Raven 1969). They point out that the local population is the unit of evolution, as is illustrated well by the genus Coregonus. Sympatric and allopatric populations of Coregonus often have gillraker counts differing by more than two units (Table IX), presumably a genetic difference (Svardson 1952), and differ in the gene frequencies of certain proteins (Lindsey et al. 1970). Genetic differences accumulated in allopatric or sympatric populations may result in reproductive isolation, and this and different selective regimes explain why sympatric populations may or may not be reproductively isolated. Apparently the sympatric whitefish in Squanga L. do not interbreed (Lindsey 1963), nor do C. artedii and C. prognathus in Big Athapapuskow (Clarke MS 1970), nor the sympatric forms of C. artedii in Waskesiu L. (Kooyman MS 1970), whereas the sympatric forms of C. artedii in Big Athapapuskow do interbreed (Clarke MS 1970). The greater importance of the selective regime can also explain why isolation between two species broke down when a third species was introduced (Svardson 1949), and why two populations of some species may become reproductively isolated (Svardson 1970). Selection for the utilisation of different spawning beds or time of spawning would help maintain existing differences and create new differences between sympatric forms; conversely selection for similar

requirements may enable introgression to occur. If differentiation is caused by different selective regimes, the models of allopatric, microgeographic and sympatric differentiation are essentially similar, differing only in the degree in which gene flow may affect the process of differentiation.

If, as appears the case, the selective regime, not reproductive isolation, is the major factor in determining whether differentiation or introgression occurs, the species concept based on reproductive isolation (Mayr 1963) should be abandoned. The species concept is neither necessary for practical taxonomy nor for evolutionary theory, so species should become just another taxonomic category, based on phenetic resemblance, to indicate the relationships of populations (Sokal and Crovello 1970). Simpson (1961) believed that all taxonomic categories should be monophyletic to indicate a common genetic lineage, and Behnke (1972) suggested that species status should be given to each distinct genetic lineage of coregonids that invaded northern N. America at the end of the Wisconsin glaciation. Evidence has been presented to show that C. autumnalis, C. sardinella, C. artedii and C. prognathus are morphologically distinct and that extant populations of each species are derived from one ancestral population at the end of the Wisconsin glaciation, and so meet the criteria for species status.

These criteria were not met by the sympatric forms of C. artedii, which are probably of postglacial origin and are probably polyphyletic. Where two or more forms occur sympatrically in N. America, it has been customary to give each form full species status, but this has not been the case in Asia, where several taxa of C. lavaretus occur sympatrically in many lakes (Berg 1948), and three or more taxa of C. migratorius occur in L. Baikal (Smirnov 1969). As there is no greater difference between sympatric populations of C. artedii than between allopatric populations, and as reproductive isolation is no longer an acceptable criterion for distinguishing species, there is no reason why species status should be given to each sympatric form, any more than species status should be given to each allopatric population. That sympatric forms are reproductively isolated at some localities and not at others is a result of differences in the environment and the process of differentiation at different localities.

Genetic differences exist between sympatric and allopatric populations of C. artedii, but within the present system of nomenclature there is no method to show the similarities and differences of so diffuse an array of forms within a species. The use of polytopic subspecies (Mayr 1969) would enable forms of C. artedii to be classified within the present nomenclatural system, but this would show

apparent relationships rather than the real relationships. As it does not indicate the genetic lineages, the use of polytopic subspecies is unacceptable. I agree with Behnke (1972) that a shorthand system should be developed for classifying genetically different populations of a species, a system that indicates their true relationships.

TAXONOMIC SPECULATION

The nine species of ciscoes in the Great Lakes and L. Nipigon (Koelz 1929) can be arranged into four groups on the basis of their phenetic similarity (Clarke MS 1970). In the Great Lakes, C. zenithicus is most similar to C. reighardi and vice versa; C. hoyi to C. kiyi and vice versa; C. artedii to C. n. nigripinnis and vice versa, and C. nipigon to C. n. nigripinnis. C. johannae resembled C. alpenae most closely but C. alpenae was most similar to C. kiyi; C. alpenae in L. Erie (Scott and Smith 1962) is intermediate in several characters between typical C. alpenae and C. johannae, suggesting that these two species form another group. The species in each of the groups differ from each other only slightly in morphometry and in gillrakers (except C. nipigon), but were separated from each other by profile or jaw characteristics, characters that vary within and between lakes and are not considered to be useful taxonomic characters. In the Great Lakes basin and in central Canada the phenotypes of C. prognathus, C. reighardi, C. zenithicus and C. cyanopterus intergrade, as do the phenotypes of C. hoyi, C. artedii, C. nigripinnis and C. nipigon, but C. hoyi in the Great Lakes may be distinct from C. hoyi in central Canada. It is possible that C. johannae and C. alpenae are conspecific with C. prognathus (including C. reighardi, C. zenithicus and

C. cyanopterus) as some populations in central Canada have characteristics in common with C. johannae or C. alpenae. If C. alpenae and C. johannae are conspecific with C. prognathus, then C. prognathus occurs in L. Erie; in fact Clemens (1922) reported the occurrence of C. prognathus in L. Erie, but Koelz (1929) believed this referred to C. artedii. C. hoyi and C. kiyi in the Great Lakes may be a distinct species group, or they may be conspecific with C. artedii (including C. n. nigripinnis and C. nipigon) for the L. Ontario forms of C. hoyi and C. kiyi are intermediate between typical C. artedii and typical C. hoyi and C. kiyi. It is considered that C. bartletti is a form of C. prognathus, and C. hubbsi of C. artedii. The above grouping of the Great Lakes ciscoes into two or three species must be classified as tentative speculation.

Svardson (1957) and Nikolsky and Reshetnikov (1970) concluded that Eurasian C. albula and C. sardinella were conspecific, and were conspecific with N. American C. artedii and C. sardinella, and that Eurasian and N. American C. autumnalis were conspecific. The shape of the maxillae in Fig. 16 and in Gasowska (1960), and of the supraethmoid bones in Fig. 17 and in Shaposhnikova (1970) support the theory that Eurasian and N. American C. autumnalis are conspecific, as are Eurasian and N. American C. sardinella. It has been concluded that C. artedii is distinct from C. sardinella, but

there is no further evidence as to the relationship of C. albula with either C. sardinella or C. artedii.

North American ciscoes can be distinguished from C. clupeaformis by the shape of the dentary, maxilla, supraethmoid. (Figs. 11 to 13, 15), supralingual plate and supra-maxilla. The Flotten L. whitefish was intermediate between typical C. clupeaformis and the ciscoes in the shape of the supraethmoid and dentary, but was similar to C. clupeaformis in other respects (Fig. 15). The Flotten L. whitefish may be a cisco-whitefish hybrid. Gasowska (1960) grouped C. clupeaformis with C. pidschian on the basis of the shape of the maxilla and supramaxilla. These two species are similar in the shape of the supraethmoid as well, but differ in the shape of the dentary (Fig. 15, and Gasowska 1970). The dentary of C. pidschian has no concavity at the posterior tip of the coronoid plate (Gasowska 1970), but this feature is present in some N. American C. clupeaformis as illustrated in Fig. 15 and in Cavender (1970). This character separates C. clupeaformis from C. pidschian and from the high gillrakered (38 gillrakers) whitefish in Flotten L., presuming that the latter is not a cisco-whitefish hybrid. Perhaps this character and the shape of the supraethmoid are worthy of further study in an attempt to elucidate the taxonomy of N. American whitefish and their relationship to Eurasian whitefish.

CONCLUSIONS

Four species of ciscoes, C. autumnalis, C. sardinella, C. artedii and C. prognathus, occur in central Canada. All 19 characters studied showed interspecific differences, but gillraker counts, upper jaw length, mandible length, snout length, eye diameter and interorbital width were of most use in separating the species. Intraspecific variation in the morphology of C. artedii and C. prognathus was associated with size differences and environmental variation. It was concluded that each species is monophyletic and survived the Wisconsin glaciation in only one refugium. Sympatric forms of C. artedii arose postglacially by either micro-geographic or sympatric differentiation; probably they behave as elementary populations, which do not interbreed at some localities but do interbreed at others. Intraspecific variation in coregonids suggests that the selective regime is more important than reproductive isolation in the differentiation of coregonids.

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A P P E N D I C E S

APPENDIX I

Sampling Localities, and the Numbers of
Ciscoes Examined from Each

Place Name and Number in Fig.1	Drainage	Lat. N	Long. W	Nos. Fish Examined		
				UM ¹	ROM ²	NMC ³
<u>Localities in central Canada</u>						
Aberdeen R., NWT (11)	Thelon	64°30'	100°00'		2	
L. Abitibi, Que. (73)	Abitibi	48 40	79 31		5	
L. Athabasca, Sask. (16)	Mackenzie	59 07	110 00	42	2	1
Attawapiskat L., Ont. (70)	Attawapiskat	52 18	87 54		12	
Baker L., NWT (12)	Thelon	64 00	96 00		2	
Barrow L., Alta. (15)	Mackenzie	59 17	111 14		6	
Beresford L., Man. (57)	Manigotogan	50 52	95 14	18		
Beverly L., NWT (10)	Thelon	64 36	100 30		5	
Big Athapapuskow L., Man. (40)	Saskatchewan	54 33	101 40	59		
Big Peter Pond, Sask. (17)	Churchill	56 00	108 50	70		
Bigstone L., Sask. (28)	Churchill	55 04	105 24	20		
Big Trout L., Ont. (69)	Severn	53 45	90 00		3	
Big Twin L., Man. (35)	Saskatchewan	54 40	101 27	14		
Big Whiteshell L., Man. (51)	Winnipeg	50 05	95 21	16		
Bird (Oiseau) L., Man. (59)	Bird	50 29	95 20	33		
Cape Jones, Que. (78)	-	54 30	79 45		1	
Churchill, Man. (32)	-	58 47	94 12	19	5	
Churchill L., Sask. (18)	Churchill	55 55	108 20	49		
Clearwater L., Man. (44)	Saskatchewan	54 05	101 00	30		
Cold L., Alta. (22)	Churchill	54 33	110 05	64		

(Cont'd.)

APPENDIX 1 (Continued)

Place Name and Number in Fig.1	Drainage	Lat. N	Long. W	Nos. Fish Examined		
				UM ¹	ROM ²	NMC ³
Davidson L., Man. (60)	Bird	50°27'	95°09'	3		
Deer L., Ont. (63)	Severn	52 38	94 25			4
Dismal L., NWT (3)	Coppermine	67 26	117 07			4
Echo L., Sask. (48)	Red	51 42	103 53	30		
Falcon L., Man. (53)	Winnipeg	49 42	95 15	14		
First Cranberry L., Man. (41)	Nelson	54 35	101 18	15		
Fishing L., Man. (49)	Red	50 44	100 42			1
Flotten L., Sask. (24)	Churchill	54 38	108 30	17		
Fort George, Que. (77)	-	53 50	79 00			3
Fort Simpson, NWT (7)	Mackenzie	61 52	121 23	13		
George L., Man. (52)	Winnipeg	50 15	95 30	5		
Great Bear L., NWT (4)	Mackenzie	66 00	120 00			5
Great Slave L., NWT (8)	Mackenzie	61 23	115 38			5 1
Great Whale R., Que. (79)	-	55 17	77 45			4
Greig L., Sask. (25)	Churchill	54 27	108 43	2		
Hawley L., Ont. (71)	Sutton	54 30	84 39			5
Ile-a-la-Crosse, Sask. (20)	Churchill	55 40	107 45	4		
James Bay, Ont. (72)	-	52 14	81 36			1
Kapsawi R., NWT (unknown)	Location unknown					1
Keller L., NWT (6)	Mackenzie	64 00	121 30			2
Lac des Iles, Sask. (23)	Churchill	54 26	109 26	21		
Lac la Biche, Alta. (21)	Athabasca	54 45	112 05	40		
Lac la Ronge, Sask. (29)	Churchill	55 08	105 00	6		
Lac Seul, Ont. (65)	Winnipeg	50 29	92 16	62	6	

(Cont'd.)

APPENDIX 1 (Continued)

Place Name and Number in Fig.1	Drainage	Lat. N	Long. W	Nos. Fish Examined		
				UM ¹	ROM ²	NMC ³
Lake of the Woods, Ont. (61)	Winnipeg	49°15'	94° 45'	34		2
Last Mountain L., Sask. (46)	Red	51 05	105 10	56		
Little Athapapuskow L., Man. (38)	Saskatchewan	54 40	101 40	46		
Little Peter Pond, Sask. (19)	Churchill	56 45	108 35	18		
Little Twin L., Man. (36)	Saskatchewan	54 39	101 27	11		
Mackenzie Delta, NWT (2)	Mackenzie	68 12	135 00	5	10	
Manistikwan (Big Island) L., Man. (33)	Saskatchewan	54 45	101 45	24		
L. Manitoba, Man. (50)	Dauphin	51 00	98 45	20		
L. Matagami, Que. (74)	Nottaway	49 53	77 30		3	
Mink Narrows, Man. (39)	Saskatchewan	54 36	101 37	29		
Minnitaki L., Ont. (66)	Winnipeg	49 58	92 00	40		
Montreal L., Sask. (31)	Churchill	54 20	105 40	74		
Neso L., Man. (34)	Saskatchewan	54 40	101 33	29		
Nikip L., Ont. (64)	Severn	52 53	91 53		4	
L. Olga, Que. (76)	Nottaway	49 47	77 15		1	
Osnaburgh L., Ont. (68)	Albany	51 12	90 09	1		
Pasqua L., Sask. (47)	Red	51 47	103 58	28		
Payuk L., Man. (37)	Saskatchewan	54 38	101 32	35		
Pelly (or Garry) L., NWT (9)	Back	65 59	101 12		4	
Pine Falls, Man. (58)	Winnipeg	50 35	96 15	7		
Povungnituk, Que. (81)	-	60 02	77 10			1
Quesnell (Caribou) L., Man. (56)	Manigotogan	50 55	95 39	27		
Reindeer L., Sask. (27)	Churchill	57 15	102 40		5	

(Cont'd.)

APPENDIX 1 (Continued)

Place Name and Number in Fig.1	Drainage	Lat. N	Long. W	Nos Fish Examined		
				UM ¹	ROM ²	NMC ³
Richmond Gulf, Que. (80)	-	56°15'	76°17'		1	
Rocky L., Man. (43)	Saskatchewan	54 09	101 30	34		
L. St. Joseph, Ont. (67)	Albany	51 05	90 35	16		
Sandy L., Ont. (62)	Severn	53 02	93 00		10	
Second Cranberry L., Man. (42)	Nelson	54 38	101 11	16		
Spark Plug L., NWT (5)	Mackenzie	66 07	117 52			1
Tazin R., NWT (13)	Mackenzie	60 35	110 23			1
Wanipigow L., Man. (55)	Wanipigow	51 07	96 00	15		
Waskesiu L., Sask. (30)	Churchill	53 57	106 15	49		
Waswanipi L., Que. (75)	Nottaway	49 34	76 29			1
Waterhen L., Sask. (26)	Churchill	54 28	108 25	27		
West Hawk L., Man. (54)	Winnipeg	49 46	95 11	13		
Wholdaia L., NWT (14)	Thelon	60 43	104 10		1	
L. Winnipeg, Man. (45)	Nelson	52 00	97 00	35	7	
<u>Extralimital Localities</u>						
Baby L., Ont. (88)	St. Lawrence	45 16	79 47			2
Dunc L., Ont. (84)	St. Lawrence	48 43	85 42	4		
L. Erie (89)	St. Lawrence	42 00	81 00		10	
L. Huron (87)	St. Lawrence	45 00	82 30		21	
Lac du Loups, Que. (91)	St. Lawrence	45 41	76 12			3
Lac Heney, Que. (92)	St. Lawrence	46 02	75 55			4
Lac Laberge, YT (1)	Yukon	65 11	135 12		2	

(Cont'd.)

APPENDIX 1 (Continued)

Place Name and Number in Fig.1	Drainage	Lat. N	Long. W	Nos. Fish Examined		
				UM ¹	ROM ²	NMC ³
Little Whitefish L., Que. (96)	St.Lawrence	45°42'	74°53'			4
Long L., Ont. (83)	St.Lawrence	49 30	86 50		4	
Meach L., Que. (95)	St.Lawrence	45 32	75 54		2	
L. Michigan (86)	St.Lawrence	44 00	87 00		10	
L. Nipigon, Ont. (82)	St.Lawrence	49 50	88 30		13	
L. Ontario (90)	St.Lawrence	43 45	78 00		16	
Saguenay Fjord, Que. (97)	St.Lawrence	48 26	70 52			3
L. Simon, Que. (93)	St.Lawrence	45 58	75 05			1
L. Superior (85)	St.Lawrence	47 40	88 00		14	
Wilson's L., Que. (94)	St.Lawrence	45 38	76 12			1

¹fish in collections at the University of Manitoba.

²fish examined at the Royal Ontario Museum.

³fish examined at the National Museum of Canada.

APPENDIX 2

The Choice of Numerical Taxonomic Method

Sokal and Sneath (1963) defined numeral taxonomy as "... the numerical evaluation of the affinity or similarity between taxonomic units and the ordering of these units into taxa on the basis of their affinities". The first step in numerical taxonomy is to calculate a matrix showing the similarities of the units. For this all characters should be of equal weight, and as many characters as possible should be used, but the characters should not be redundant or correlated with each other (Sokal and Sneath 1963).

Much work has been done using various methods of numerical taxonomy, but no one method has emerged as being best in all situations. The choice of method should reflect the type of data being analysed and the computational facilities available. The data, basically metric, consisted of counts and measurements made on a series of ciscoes.

The Choice of Similarity Coefficient

The choice of similarity coefficient depends partially on whether the data to be analysed are metric or non-metric. Association coefficients are used with non-metric data (Williams and Dale 1965), but metric data can be coded, with subsequent loss of information, so as to be useable with association coefficients. Information statistics, correlation and distance coefficients can be used with both types of data,

though information statistics primarily have been used with non-metric data. The correlation coefficient has been used most widely in numerical taxonomy, but it can result in fortuitously high similarities between samples (Eades 1965). Distance statistics have a better theoretical basis than correlation coefficients for calculating similarities, but all distance coefficients are affected by size, including the shape coefficient (Boyce 1964). If the effect of size is negated, the simplest and best distance coefficient is the mean square distance coefficient.

Calculation of Mean Square Distances

The effect of size in the data was negated by the following method. The data were transformed to \log_{10} and then regression lines were calculated for each measurement (\underline{y}_j) against fork length (\underline{x}). The deviations (\underline{e}_{ij}) of each cisco's measurements from the regression lines were calculated.

$$\underline{e}_{ij} = \underline{y}_{ij} - (\underline{a}_j + \underline{b}_j \underline{x}_i)$$

The \underline{e}_{ij} s are appropriate for use in the calculation of distance statistics if: i) different forms of ciscoes have a similar size distribution; ii) the regression lines of different groups are parallel. If size distributions do not overlap, the different forms will cluster together; if regression lines are not parallel, large fish of one form may cluster with small

fish of another form.

The e_{ij} s and the counts were standardised with a mean of 0.0, and a standard deviation of 1.0, to make the variables of equal weight. Mean square distances were then calculated for all possible pairs of ciscoes. The mean square distance was used in its square root form.

$$\underline{\text{msd}}_{i1} = \left(\frac{1}{k} \sum_{j=1}^k \underline{d}_j^2 \right)^{\frac{1}{2}}$$

where $\underline{d}_j^2 = (\underline{e}_{ij} - \underline{e}_{1j})^2$

Analysis of the Similarity Matrix

Factor analysis and cluster analysis have been used to analyse similarity matrices (Sokal and Sneath 1963), and both methods were used in preliminary investigations to see if either was suitable.

Factor analysis (Appendix 3) is applicable to the analysis of a matrix of distance coefficients only if the distances are replaced by proximities (a constant minus the distance), calculated by subtracting each coefficient from a constant (Boyce 1964). The distance matrices from several lakes were analysed in this way. In each case the number of factors extracted was equal to the number of ciscoes included in the analysis. Each cisco was associated with one factor, and in consequence this method was of no use in grouping the ciscoes.

There are several methods of cluster analysis (Sokal and Sneath 1963). Sneath (1969) concluded that methods of average linkage were best, then complete linkage, and single linkage was the worst. The latter method results in straggly clusters, the others in compact clusters. The matrix of distance coefficients of 16 ciscoes (a subsample from Lac Seul) was analysed by single linkage and the average unweighted group pair method. Both methods produced approximately similar phenograms. Eventually a computer programme was written for the average linkage unweighted group pair method.

Without computer programmes, cluster analysis is laborious and time consuming, so a simpler type of analysis was used in most of the work. By examining the matrix of distance coefficients, each cisco was grouped with the ciscoes with which it was most similar. For example, if ciscoes A and B were both most similar to C, and D was most similar to A, then the four ciscoes would be placed in a single group. The members of each group were examined to see if they were more similar to ciscoes of their own group or to ciscoes of another group. If the latter was the case, two or more groups might be merged or ciscoes moved from one group to another. Extremely atypical ciscoes were found by inspecting the sum of distances (\underline{sd}_i) for each fish, as they would have a high sum of distances,

$$\underline{sd}_i = \sum_{l=1}^n \underline{msd}_{il}$$

and each one might constitute a separate group.

APPENDIX 3

Factor Analysis

Factor analysis is an analytical, rather than hypothesis testing, branch of multivariate statistics that attempts to describe the complex relations of many variables in terms of the simpler relations of fewer hypothetical variables, the factors. The factors represent influences underlying the original variables. Underlying influences are investigated by R-mode analysis, in which factors are extracted from the correlation matrix of the variables.

A subsidiary aim of factor analysis is to develop a classificatory scheme. This may be achieved by Q-mode analysis, in which factors are extracted from the correlation matrix of the samples, or by the calculation of factor scores following R-mode analysis.

Good accounts of factor analysis are given by Cattell (1965a; 1965b) and Spencer (MS 1966).

The model underlying factor analysis is:

$$\underline{v}_j = \sum_{i=1}^k \underline{a}_{ij} F_i + \underline{a}_{ju} F_u + \underline{a}_{je} F_e$$

The \underline{a}_{ij} s are the factor loadings, and represent both the correlation of the factors and the variables (\underline{v}_j), and the weights to be given the factors in a regression to estimate the variables. The \underline{F}_i s are the common factors of which there

are two types (Wallace and Bader 1967); general factors having high loadings on all the variables, and group factors having high loadings on more than one variable, but not on all. F_u is a unique factor associated with each variable, and F_e is an error factor.

There are two types of factor analysis depending on the values present in the principal diagonal of the correlation matrix. Closed or principal components analysis has 1.0 in the principal diagonal. If this is the case, analysis will extract only common factors, but in accounting for all the variance the common factors will be distorted by the unique and error factors. It is unrealistic to believe that variables are perfectly correlated with themselves (Cattell 1965a) so the principal diagonal should not contain values of 1.0. Open or factor analysis places communalities (h_j^2) in the diagonal. The communality is the amount of variance of a variable accounted for by the common factors. When the common factors are extracted from the correlation matrix,

$$\sigma_j^2 = h_j^2 + \sigma_{uj}^2 + \sigma_{ej}^2$$

$$h_j^2 = \sum_{i=1}^k \sigma_{ij}^2$$

there is a residual left that is accounted for by unique and error factors. By setting communalities in the principal diagonal, the common factors are not distorted by the unique

and error factors. The communalities and the number of factors extracted from a matrix are interdependent and it is usual to decide upon the number of factors to be extracted from a matrix by mathematical concepts, statistical evaluation or by the factor structure criterion (Cattell 1965a).

The assumptions for factor analysis are:

- i) Individual factors and variables are linearly related.
- ii) There is no interaction effect between variables.
- iii) Factors act additively in respect to a variable.
- iv) There are no assumptions as to the distribution of the samples on the variables.

If these assumptions are violated, factor analysis gives an approximate solution (Cattell 1965b).

Calculations

The open factor analysis model was used.

- i) In the principal factor method, factors are extracted from the correlation matrix (\underline{R}) by analysing it for its latent roots (\underline{L} , the diagonal matrix of eigenvalues), and the associated vectors (\underline{V}) to give the principal factor matrix (\underline{A}). The square roots of the successive latent roots give

$$\begin{aligned}\underline{R} &= \underline{AA}' \\ \underline{R} &= \underline{VLV}' \\ \underline{AA}' &= \underline{VL}^{\frac{1}{2}} \underline{L}^{\frac{1}{2}} \underline{V}' \\ \underline{A} &= \underline{VL}^{\frac{1}{2}}\end{aligned}$$

the relative size of the successive extracted factors. The centroid method is a labour saving approximation to the principal factor method. The principal factor method was used.

ii) The principal factor matrix usually does not permit simple explanation (Cattell 1965a) and has to be rotated to produce an interpretable simple structure solution (Thurstone 1947). There are many possible methods of rotation, of which only varimax was available at the University of Manitoba Computer Centre. Varimax rotation gives as many high and low loadings and as few intermediate loadings as possible. Rotation occurs to maximise

$$\sum \underline{a}_i^4, \text{ while } \sum \underline{a}_i^2 \text{ is kept constant; this maximises the}$$

scatter among the loadings and tends to prevent a variable having high loadings on more than one factor.

This rotation produces orthogonal (uncorrelated) factors. It is improbable that the underlying causes are uncorrelated (Spencer MS 1966). Oblique rotations produce correlated factors that themselves can be factored to give an hierarchy of primary, secondary factors etc. Oblique rotation also separates the correlation of factors and variables from the loadings of the factors on the variables, which are fused in orthogonal rotations (Cattell 1965b).

iii) Factor scores measure the influence of the factors upon

the samples, and were calculated to have a mean of zero and a variance near unity (Spencer MS 1966). The factor matrix (F) is calculated from the factor loading matrix (A) and the standardised data matrix (Z).

$$\underline{F} = (\underline{AA}')^{-1} \underline{A}' \underline{Z}$$

APPENDIX 4

Discriminant Analysis

Discriminant analysis tests the differences between g predetermined groups, and creates m new variables, the discriminant functions, that best separate the groups. The number of discriminant functions in an analysis is the lesser of k (the number of original variables) and $g-1$. Accounts of discriminant analysis can be found in Cooley and Lohnes (1962), Seal (1964) and Green (1971).

The model for discriminant analysis is:

$$f_j = v_{1j}x_1 + v_{2j}x_2 + v_{3j}x_3 \dots\dots v_{kj}x_k$$

The x_1 are the original variables, and the v_{1j} are the discriminant coefficients.

The assumptions for discriminant analysis are:

- (i) The samples are from a multivariate normal population.
- (ii) The variance-covariance matrices, W_i , of the g groups are homogeneous. If the matrices are heterogeneous, the tests on the significance of separation are affected, but the discriminant functions are still of value in separating the groups.
- (iii) The discriminant functions are linear and additive in respect to the original variables.
- (iv) The g groups are defined a priori.

In addition each group should contain an equal

number of samples, and this number should be of the order $10k$ or greater.

Calculations

The calculations follow Seal (1964)

- i) For each group calculate the variance-covariance matrix.
- ii) Calculate the dispersion matrix (\underline{W}), which is analogous to the error sum of squares in analysis of variance.

$$\underline{W} = \sum_{i=1}^g \underline{W}_i$$

- iii) Calculate the matrix of total deviation (\underline{T}). This matrix is similar to the \underline{W}_i , except that the samples from each group are pooled.

- iv) Calculate the among populations deviation (\underline{A}), analogous to the treatment sum of squares in ANOVA.

$$\underline{A} = \underline{T} - \underline{W}$$

- v) Invert \underline{W} and postmultiply by \underline{A} . The resultant matrix ($\underline{W}^{-1}\underline{A}$) represents the proportion of variance among groups to within groups.
- vi) Analyse $\underline{W}^{-1}\underline{A}$ for its latent roots ($\underline{\lambda}_j$) and associated vectors (\underline{V}_j).

$$\left| \underline{W}^{-1}\underline{A} - \underline{\lambda}^2 \right| = 0$$

$$\left| \underline{\lambda}_j \underline{I} - \underline{W}^{-1}\underline{A} \right| \underline{V}_j = 0$$

The vectors are the discriminant functions, and the proportion of the variance accounted for by the \underline{j} th. function is

$$\frac{\lambda_{\underline{j}}}{\sum_{\underline{j}=1}^{\underline{m}} \lambda_{\underline{j}}}$$

vii) Test the significance of separation on each discriminant function by seeing if all the roots after the \underline{p} th. can be given zero values. Calculate chi-square with $(\underline{k}-\underline{p})(\underline{g}-\underline{p}-1)$ degrees of freedom.

$$\chi^2 = \left[(\underline{N}-1) - \frac{(\underline{k} + \underline{g})}{2} \right] \log_e \frac{\prod_{\underline{j}=\underline{p}+1}^{\underline{m}} (1 + \lambda_{\underline{j}}^2)}{1}$$

viii) Standardise and normalise the coefficients of each discriminant function. The coefficients then represent the relative contribution of each character in the discrimination of the groups.

ix) Calculate discriminant scores of each \underline{i} sample from the normalised, but not standardised, discriminant functions.

The discriminant scores

$$d_{\underline{ij}} = \sum_{\underline{l}=1}^{\underline{k}} v_{\underline{l}\underline{j}} (x_{\underline{il}} - \bar{x}_{\underline{l}})$$

are of use in classifying samples whose group affinities are unknown.

APPENDIX 5

Information Analysis

Information is a physical property of data related to probability, with rare events having a higher information content than common events (Orloci 1968). Whereas most multivariate techniques have rigid assumptions that should be met by the data to be analysed, information analysis does not require any assumptions to be made (Orloci 1969), making information analysis more suitable for certain analyses of biological data than the traditional multivariate techniques.

There are several information statistics that are suitable for taxonomic work. These include total information, joint information and mutual information (Orloci 1969). The mutual information statistic, also known as the error or independence component, was used in the work on cisco taxonomy.

Calculations

The calculations follow Orloci (1968). The quantity x_{ij} is the value of the j th variable of the i th individual, and X_i , X_j and N are the row, column and grand totals respectively of the data matrix. The mutual information is defined by

$$\begin{aligned}
 2\underline{I} &= 2 \sum_{\underline{i}=1}^{\underline{n}} \sum_{\underline{j}=1}^{\underline{k}} \frac{x_{\underline{i}\underline{j}}}{\underline{N}x_{\underline{i}\underline{j}}/X_{\underline{i}}X_{\underline{j}}} \ln \left(\frac{N x_{\underline{i}\underline{j}}}{X_{\underline{i}} X_{\underline{j}}} \right) \\
 &= 2 \left(\sum_{\underline{i}=1}^{\underline{n}} \sum_{\underline{j}=1}^{\underline{k}} \frac{x_{\underline{i}\underline{j}}}{\underline{N}x_{\underline{i}\underline{j}}/X_{\underline{i}}X_{\underline{j}}} \ln x_{\underline{i}\underline{j}} + \underline{N} \ln \underline{N} - \sum_{\underline{i}=1}^{\underline{n}} \frac{X_{\underline{i}}}{\underline{N}} \ln X_{\underline{i}} - \sum_{\underline{j}=1}^{\underline{k}} \frac{X_{\underline{j}}}{\underline{N}} \ln X_{\underline{j}} \right)
 \end{aligned}$$

If two individuals are identical, $2\underline{I} = 0$, and the value of $2\underline{I}$ increases with decreasing similarity between individuals.

Classification

Two forms of classification are possible: non-hierarchical sorting of individuals into previously defined classes, as in discriminant analysis; clustering individuals to form an hierarchy (Orloci 1969).

Cluster analysis was used to create an hierarchy among the forms of ciscoes. The hierarchy was formed by fusing the two individuals or clusters that produced the smallest increase in information, and this was repeated until all forms were joined in one cluster (Williams et al. 1966).